The Biological Diversity, Recovery from Disturbance and Rehabilitation of Mangroves in Darwin Harbour, Northern Territory

Kristin Metcalfe
BSc, MTEM

Faculty of Education, Health & Science
Charles Darwin University

Thesis submitted for the degree
of Doctor of Philosophy

28th February 2007

I declare that this work, now submitted as a thesis for the degree of Doctor of Philosophy of the Charles Darwin University, is the result of my own investigations, and all references to ideas and work of other researchers have been specifically acknowledged. I certify that the work embodied in this thesis has not been accepted in substance for any degree, and is not currently submitted in candidature for any other degree

Kristin Metcalfe
28th February 2007

ACKNOWLEDGMENTS

It has been a great privilege to return to full-time study to pursue a research project of my own design that explored several particularly fascinating 'black spots' in our knowledge of mangrove ecology. This opportunity was possible only with the support of an Australian Postgraduate Award Scholarship and assistance from several sponsors. The work was funded by a grant from the Parks and Wildlife Commission of the Northern Territory who also purchased some field equipment. In the latter stages of the project ConocoPhillips Pty Ltd provided a stipend for the use of intellectual property arising from this research. I was also the recipient of a $1,000 Research Grant from the Australian University Women's Association and a grant of $500 from the Centre for Tropical Wetlands Management.

A great many people have contributed to this work during the last eight years. Firstly, I am indebted to my supervisor Dr Keith McGuinness for his expert advice on experimental design and statistical analysis, as this knowledge forms the mainstay of the research. Keith's editorial skills, research experience and knowledge of mangrove ecology has substantially improved every chapter. I am also very grateful for his guidance, patience and sense of humour at all stages of the project.

Scientists including Drs David Lawson, Mick Guinea, Peter Saenger, John Woinarski, Owen Price, and Chandra Salgado-Kent provided advice on field methodology and preliminary results. I also gratefully acknowledge Kym Brennan for his valuable comments on every chapter and for tutoring me in the database skills required to process and interpret the many data sets analysed for this thesis.

A number of people generously volunteered to help me with fieldwork, often in humid, hot, and muddy conditions. I am extremely grateful for the assistance of Patrick Gray, Graham Clarke, Paul Lloyd, James Metcalfe, Martin Armstrong, Dean McAdam, Paul McHugh, Simon Minissale, Donna Lewis, Jelle Ferwerda and Rob Taylor. I am especially thankful to those crazy people who accompanied me in the mangroves at night, to survey bats. On two occasions, a team from the Australian Trust for Conservation Volunteers assisted with major fieldwork tasks; their help in constructing propagule pergolas and measuring endless numbers of seedlings was much appreciated.

The *Anabat* detector was provided by Damian Milne who also analysed the bat recordings and identified the bat species, while Martin Armstrong assisted with rodent identification.

Taxonomic classification of the diverse and poorly known crustacean fauna was possible only with the assistance of Dr Russell Hanley and Peter Davie (Queensland Museum). Other invertebrate species were identified by Northern Territory Museum curators including Drs Chris Glasby (polychaetes), Richard Willan (molluscs) and Helen Larson (fish). Ants were identified by Dr Alan Andersen (CSIRO). These specialists also kindly reviewed the relevant sections of the two invertebrate chapters. Dr Dianne Jones (WA Museum) identified several barnacle species, Dr Tim O'Hara (Victorian Museum) examined the brittle stars and Dr Dennis Gordon (NIWA, New Zealand) described a new genus of bryozoan sampled during these surveys. I enjoyed working with co-authors Chris Glasby and Dennis Gordon and greatly appreciate their contribution to the attached manuscripts.

Finally, I am immeasurably grateful for the wonderful support of my family during the entirety of this project. The love and unfailing encouragement of my parents Nina and Jim Bardsley, partner Kym Brennan, son James, sisters Belinda, Jenny, and former husband David were integral to this achievement. I so appreciate Kym's extraordinary patience, humour and strength—and especially his knack of gently delivering the 'quiet truth' during those critical times when I was swamped by it all. Little reminders (e.g. "well, there's always some small glitch..") plus a delicious, healthy dinner can be very reassuring for PhD students. I also thank my dear neglected friends, and many colleagues, who have generously listened, provided inspiration and encouragement during this intense scientific journey. Thank you Julie Crawford, Nicola Prichard, Kate Grenfell, Matt Bolam, Gavin Perry, Margie Landrigan, Richard Willan, Chris Glasby, Paul Lloyd, Peter Gill, Eugènie Regan, Tim Roberts, Big Dave, Colin and Niko, Alan Andersen, Maryanne McKaige and Julie Martin.

I would like to dedicate this work to my parents, Nina and Jim who have always supported my scientific interests and love of nature, beginning with the gift of that little microscope. I would also like to acknowledge two scientists, Professors Harry Recher and Colin Woodroffe, whose passionate enthusiasm for mangroves was inspirational, and infectious.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABSTRACT

Surveys were done of the diversity, distribution and abundance of vertebrate and invertebrate fauna in mangroves in Darwin Harbour. The four main mangrove assemblages—the hinterland margin, tidal flat, tidal creek and seaward—were studied at three sites and, where possible, surveys reported annual and seasonal variation. Four disturbed sites were also surveyed to investigate the effects of anthropogenic disturbance. Vertebrate surveys involved trapping (mammals), ultrasonic detection (bats) and audio-visual detection (birds). Invertebrates, and small resident fish, were sampled by quadrat and epifuanal searches, pitfall traps and anoxic mats in a composite methodology developed for this project.

Field studies were also done to investigate factors which may delay forest recovery. A two-year experiment in cyclone-damaged and bulldozed forests tested for effects of shade, predation and damage from floating debris on seedling survival and growth. Multi-species plantings at three degraded sites tested different rehabilitation techniques. Seedlings were either transplanted, nursery-grown or directly implanted as propagules.

Mammal diversity was low (13 species), and two herbivorous resident species comprised most captures, but arboreal mammal densities were remarkably high in the low-intertidal. The rich, predominantly insectivorous, avifauna (70 species) included nine mangrove specialists but four species comprised half of all records. Most birds occurred amongst dense tree cover of the two seaward assemblages. Mangrove bats (11 species) were mostly small insectivorous microbats most prolific at the landward fringe but large flocks of flying foxes periodically foraged in the seaward assemblage.

The invertebrate fauna was very diverse and dominated by crustaceans (31%), molluscs (31%) and worms (16%). Crustaceans were the most abundant, and molluscs the most diverse, faunal groups. Overall diversity and abundance of invertebrates increased to seaward and marked declines in the worm fauna occurred during the wet season.

Of the grand total of 254 invertebrate taxa, 163 were recorded at undisturbed sites and 171 in disturbed. There were, in general, no significant differences in diversity or abundance between disturbed and undisturbed forests. Multivariate analyses, however, clearly demonstrated differences in species composition between the two types of forest.

For instance, wading birds suited to foraging in waterbodies and clearings, were more common in some disturbed habitats. Polychaete worms appeared to be the most responsive indicators of environmental change, while gastropods and grapsid crabs in upper-intertidal areas were potentially most vulnerable to urbanisation.

The factors delaying the recovery of damaged forests were complex and varied with shoreline position. To seaward, recovery of cyclone-damaged *R. stylosa* was hindered by herbivorous turtles whilst to landward, poor dispersal and lack of recruitment refuges prolonged recovery. Field methods developed to facilitate natural recruitment showed promise for fast-tracking recovery of degraded ecosystems.

CHAPTER 1. GENERAL INTRODUCTION

1. GENERAL INTRODUCTION

1.1. Introduction

"Mangrove" is an ecological term that refers to the taxonomically diverse collection of about 70 plant species that grow along sheltered tropical and subtropical coasts in intertidal environments (Ellison, 1995; Blasco et al., 1996). The term may be used narrowly to refer only to trees and shrubs, but mangrove[1] may sometimes be used broadly to include a variety of other co-existing life forms, ranging from ferns, to climbers and palms (Wightman, 1989). Mangroves trees are characterised by a number of interesting anatomical, morphological and reproductive adaptations (Saenger, 1992) including aerial and above-ground roots (pneumatophores), salt glands, bouyant seeds, and vivipary (where seeds germinate while attached to the parent tree). These and other distinctive features enable them to thrive in dynamic coastal environments subject to periodic tidal flooding, in substrates that may be waterlogged, anoxic, saline and unconsolidated.

Presumably as a consequence of the extreme physiological challenges of mangrove habitats, regional floristic diversity is often low, varying from around 13 species in the Atlantic East Pacific to around 58 species in the Indo-West Pacific region (Duke et al., 1998). Australia has 41 mangrove species, mostly in northern Australia, which account for 57% of the world total (Duke, 2006). Mangroves occur in 112 countries and global coverage has been estimated at over 179,000 km^2 (Duke, 2006). After Indonesia and Brasil, Australian has the third largest area of mangroves in the world (11,500 km^2) representing 6.4% of the global mangrove resource.

Although floristically poor compared with other high biomass tropical forests such as rainforests (Ricklefs and Latham, 1993), mangroves rank among the world's most productive ecosystems (Boto et al., 1984; Leach and Burgin, 1985; Clough, 1992; Kaly and Jones, 1998; Metcalfe, 1999), producing organic carbon well in excess of the

[1] The term "mangrove" refers to both the individual plants and the forest community. "Mangal" is also used occasionally to refer to the forest community.

ecosystem requirements (Kathiresan and Bingham, 2001). They also have significant social and economic values, and have been exploited for many purposes, particularly as sources of forestry and fisheries products (Lee, 1999). Mangroves have been harvested by subsistence farmers for fuel, thatch, poles, timber and occasionally for food or medicine for many centuries (Kunstadter et al., 1985). In Australia, mangrove forests have been used as a resource by Aboriginals for thousands of years and are still important habitats for coastal indigenous communities (Davis, 1985; Wightman, 1989). Substantial managed forestry operations provide a source of commercial timber, charcoal and pulpwood, and until quite recently, the bark was widely used for tanning (Blasco et al., 1996). Heavy exploitation has however, left many mangrove habitats in severely degraded condition (Kathiresan and Bingham, 2001)

Despite their importance as a crucial resource for many tropical cultures, mangrove environments in western countries have traditionally been maligned as pestilent useless wastelands. To many, mangroves are still viewed only as insect-ridden, impenetrable swamps with strange looking trees and evil smelling, shoe-swallowing mud. Although true in some respects, these habitats are much more than this and have many other important ecological features and values. In addition to providing a range of products, they stabilise shorelines, provide protection from storms, cyclones and tsunamis, filter sediment and trap pollutants (Saenger and Siddiqui, 1993; Othman, 1994; Roberston and Phillips, 1995; Mazda et al., 1997; Gautier et al., 2001). As high biomass forests they produce copious amounts of organic material that, when broken down into detritus, or re-cycled by crabs into micro-particulates, feeds into complex coastal food webs (Lugo and Snedaker, 1974; Hutchings and Recher, 1982; Lee, 1998). Furthermore, many fish and crustacean species of subsistence and commercial importance utilise mangroves at some stage of their life cycle (Laegsdsgaard and Johnston, 1995; Vance et al., 1996; Martin, 2004).

The ecological significance of mangroves has been recognised only relatively recently however (Hutchings and Saenger, 1987; Bunt, 1992) and, although much ecological work has been undertaken during the last two decades, many of the often-acclaimed functions and roles of mangroves are still poorly understood. Few studies, for example, have attempted to quantify the links between mangroves and nearshore habitats (Lee, 1999), investigated their celebrated role as nursery sites (but see Laegsdsgaard and

Johnston, 1995; Martin, 2004), or specifically documented their rich faunal diversity—we still lack basic knowledge of many species, communities and processes.

Furthermore, environmental scientists are often faced by a paucity of information on key questions. As Lee (1999) observed "Despite decades of increased research effort, answers to many fundamental questions concerning practical management issues of tropical mangals are still largely unavailable." Data on the distribution, diversity and abundance of the total mangrove biota represents crucial baseline information, necessary for meaningful impact assessment, effective coastal planning and proper management. Indeed, a large part of the incentive to undertake this project draws from the necessity to respond adequately to real-world challenges in environmental assessment and monitoring of mangroves.

This project has three inter-related research themes, each of which attempts to address an important gap in our knowledge about these habitats. 1) spatial and temporal patterns in biological diversity, 2) the effects of disturbance on mangrove fauna, and 3) factors affecting the recovery and rehabilitation of disturbed forests (Figure 1-1).

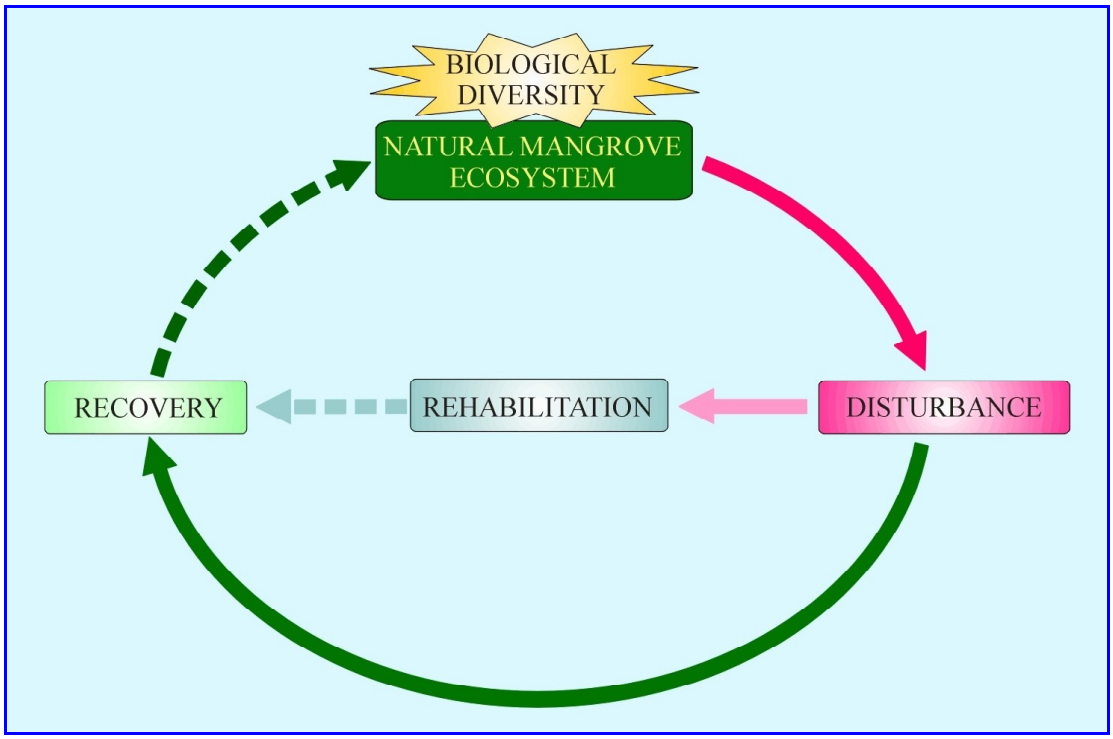


Figure 1-1: Diagrammatic overview of the main research themes and their inter-relationships

This thesis aims to provide inventory, baseline and ecological data on the biological diversity of natural ecosystems by study of the vertebrate and invertebrate fauna of

undisturbed mangroves in Darwin Harbour (yellow star, Fig. 1-1). It investigates the impacts of anthropogenic disturbance by comparison of the biota of undisturbed ecosystems with that affected by urban and industrial encroachment (dark pink arrow, Fig. 1-1). Previous severe disturbance in mangrove habitats in Darwin Harbour has resulted in recovery periods at decadal scales. Experimental studies were conducted within these disturbed (cyclone damaged and bulldozed) mangroves to investigate the factors contributing to substantial delays in their recovery (long green arrow, Fig. 1-1). The potential to short-cut prolonged recovery times was investigated in a range of different rehabilitation trials in degraded mangroves (pale pink and blue arrows, Fig. 1-1). Ultimately, the purpose of rehabilitation is to shorten recovery trajectories and the rapid reinstatement of pre-disturbance levels of biological diversity and ecosystem function (broken green arrow, Fig. 1-1).

1.2. Biological diversity of mangrove ecosystems

Occurring at the land-sea interface, mangrove communities support a broad range of marine and terrestrial organisms (Clough, 1982). Globally, mangroves are habitat for a diverse array of birds, reptiles (including crocodiles, lizards, snakes and turtles), mammals (including monkeys, deer, racoons, otters, dolphins, bats and tigers), numerous fish, crustaceans, molluscs, polychaetes and other worm taxa, spiders, ants and myriad other insects (Milward, 1982; Kathiresan and Bingham, 2001; Lacerda, 2001). Indeed, in terms of global biodiversity, mangroves are often listed, along with other wetlands and tropical forests, as being centres of biological diversity (Anon, 1994, 1996; Gopal and Junk, 2000).

Mangroves are, however, highly dynamic systems, and biological diversity may show marked spatial and temporal variation (Duke et al., 1998; Farnsworth, 1998). Faunal populations may change on a tidal, daily, spring-neap, lunar, seasonal or annual basis. Many vertebrate species have broader distributions through other habitats and only utilise mangroves intermittently (Hogarth, 1999). Large flocks of flying foxes for example, periodically visit mangrove environments to roost, or in response the availability of nectar (Palmer and Woinarski, 1999; Palmer et al., 2000). The majority of fish can only forage in mangroves during high tides, and many only utilise mangrove environments during their juvenile phases (Robertson and Duke, 1987; Laegdsgaard

and Johnston, 2001; Martin, 2004). Moreover, the predominantly marine invertebrate fauna is presumably regulated by daily and monthly variation in tidal cycles, and is also affected by climate, including (in Northern Australia) the effects of seasonal aridity and monsoons.

Biological diversity is also influenced by spatial variation at a number of scales: from global to regional, from place to place, and among tidal elevations (Duke et al., 1998; Farnsworth, 1998). Mangrove forests are not usually homogeneous forests, typically comprising a number of discrete floristic assemblages (see Chapter 2). Floristic assemblages are influenced by a complex range of physico-chemical and biotic factors, but often tend to occur along tidally maintained gradients in environmental factors which frequently match topographic contours (Duke et al., 1998). Any comprehensive assessment of mangrove biological diversity must account for such patterns. However, although it is well known that faunal assemblages in high intertidal habitats differ from those in the low intertidal (Berry, 1963; Macnae, 1967, 1968b; Sasekumar, 1974), few studies have comprehensively documented and quantified all (or as much as possible) of the fauna occurring within these different floristic assemblages.

Invertebrates are by far the most diverse and abundant component of mangrove faunal diversity, comprising animals from a broad range of phyla and a vast array of life forms. However, the taxonomy of many invertebrate groups is poorly known, and in many regions, including Northern Australia, they have been poorly collected and little studied. Indeed, with the exception of a few groups—such as crabs and molluscs—our knowledge of biological diversity (i.e. the complement of vertebrate and invertebrate animal species in an area) in mangrove habitats is still quite limited, despite decades of research. In this thesis, [species] diversity has been used to mean [species] richness, or the raw number of species.

Crabs, especially from the families Ocypodidae and Grapsidae, dominate most mangals worldwide, in terms of abundance and biomass (Golley et al., 1962). In the Indo-West Pacific region, crabs are known to play a pivotal ecological role in the functioning and productivity of mangrove ecosystems (Smith III et al., 1991; Davie, 1994; McGuinness, 1997; Lee, 1998, 1999). Not surprisingly, crabs have received considerable attention and are relatively well studied. Similarly, molluscs are also prominent in mangrove communities in many regions and have been the focus of several comprehensive

ecological studies (e.g. Vermeij, 1973; Wells and Slack-Smith, 1981; Wells, 1984; Reid, 1985; Wells, 1986; Barnes, 2003).

The information available on the invertebrate fauna of mangroves in northern Australia closely reflects the global patterns outlined above (and is reviewed in Chapter 5). The majority of Darwin Harbour research has focussed on crabs (Von Hagen and Jones, 1989; Audas, 1992; McGuinness, 1993; Nobbs, 1999; Nobbs and McGuinness, 1999, 2003; Salgado Kent, 2004; Salgado Kent and McGuinness, 2006) and to a lesser extent the molluscs (Gilham, 1980; Reid, 1985; McGuinness, 1994; Crowe, 1997; Crowe and McMahon, 1997). The insect fauna of mangroves in Darwin Harbour has been studied (Clay and Andersen, 1996; Nielsen, 1997a, 1997b; Shivas, 1999; Nielsen, 2000; Coupland, 2002) but other mangrove invertebrate groups—including crab families other than the Grapsidae and Ocypodidae, myriad crustaceans and worms—are poorly known. Most information concerning these invertebrates across Northern Australia derives from sporadic collection (Hanley, 1987).

Due to inherent logistical difficulties, mangrove vertebrates are also under-studied. Mammals and bats are largely unstudied and surveys of birds rarely extend into the dense forests (and deep mud) of lower intertidal zones (e.g. Woinarski et al., 1988; Noske, 1996; Woinarski et al., 2001; Noske, 2003). Despite the availability of rich nectar supplies in seaward *Sonneratia alba* forests throughout the year (Wightman, 1989; Metcalfe, 1999; Coupland, 2002), to my knowledge, no bird surveys have been conducted in this assemblage. Overall, baseline inventories of the fauna in mangroves are still very incomplete and much of that which we do know is poorly understood in terms of spatial and temporal variations in distribution and abundance. In a recent review of research on mangrove environments in Darwin Harbour, McGuinness (2002a) noted that despite substantial progress, there remain significant gaps in our knowledge of the ecology of these systems.

Darwin Harbour is currently listed in the Directory of Important Wetlands in Australia (ANCA, 1997), being noted as one of the richest mangrove systems in Australia. This is primarily on the basis of its floristic diversity and extent (Wightman, 1989). However, in the context of modern standards, this largely floristic knowledge-base is not adequate for addressing the conservation and monitoring issues emerging from continued urban and industrial expansion in and around Darwin Harbour. These demand a more

comprehensive and sophisticated knowledge of the fauna, in particular the invertebrate fauna, not just for the satisfaction of knowing what is there, but to be able to establish ecological bench marks against which detrimental change can be detected and appropriate management strategies formulated.

A major component of this study was therefore to conduct comprehensive fauna surveys within the mangrove forests of Darwin Harbour. Throughout this thesis "biological diversity" refers only to vertebrate and invertebrate organisms visible to the naked eye (i.e. excluding meiofauna and microfauna). Furthermore, as described in later chapters, it was not feasible to study all faunal groups so marine mammals, reptiles, spiders and most insects were excluded. For the taxa studied here, there has been just one previous survey that documented the vertebrate and invertebrate fauna in the mangroves of the Northern Territory (Hegerl et al., 1982), and none that have considered these in the context of abundance, and spatial and temporal variation. The existing literature and information on each of the faunal groups studied in this project is reviewed in the relevant chapters of this thesis.

1.3. Disturbance and mangrove environments

Natural disturbance

Like all natural environments, mangroves are vulnerable to damage arising from intermittent natural threats including storms, lightning, cyclones, geomorphic change, floods, hail and frost (Smith III et al., 1994; Allen et al., 2001; Diop, 2003). Considerable scientific attention has focussed on impacts associated with natural events such as hurricanes and cyclones (Craighead and Gilbert, 1962; Bardsley, 1985; Burke, 1992; Roth, 1992; Swiadek, 1997; Sherman et al., 2001; Hensel and Proffitt, 2003), changes in sea-level (Woodroffe et al., 1985; Woodroffe et al., 1993; Blasco et al., 1996) and, recently there has been interest in the effects of tsunamis (Preuss, 2005). Mangrove forests in northern Australia frequently experience tropical cyclones when they cross the coastline (Bardsley, 1985; McGuinness, 1992) and may incur major structural damage from defoliation, crown damage, windsway, trunk breakage and windthrow (Stocker, 1976; Bardsley, 1985). Mangroves are also affected by sediment movement, including erosion, sedimentation, "sand-blasting" and chenier formation associated with cyclonic winds,

waves and surge (Craighead and Gilbert, 1962; Smith III et al., 1994). Although the highly variable nature of cyclone disturbance to mangroves is well known (Craighead and Gilbert, 1962; Lugo and Snedaker, 1974; Sherman et al., 2001; Piou et al., 2006), several patterns in the impact of severe cyclones are evident. Most authors report that the tallest forests suffer the highest mortality (Roth, 1992; Smith III et al., 1994), mixed species forests appear more resistant than monospecific stands and delayed mortality is common (Bardsley, 1985; Sherman et al., 2001; Piou et al., 2006). Furthermore, species in the Rhizophoraceae family, which lack the ability to coppice and regenerate with epicormic shoots, are extremely vulnerable to defoliation (Gill and Tomlinson, 1971; Snedaker et al., 1992). Indeed, the two forest types in Darwin Harbour that suffered high mortality after cyclone Tracey were tall *Rhizophora stylosa* forests on the seaward margin and tall *Ceriops australis* at the landward fringe (McGuinness, 1992; EcoSystems, 1993; Ferwerda, 2000; Metcalfe, unpublished report). Both forest types have not fully recovered after three decades (pers. obs.) and are the subject of investigations on forest recovery conducted for this thesis.

Overall, due to their position at the land-sea interface, it appears that mangroves are vulnerable to, and act as a buffer against, a range of different types of disturbance originating from both realms. In this position, mangroves frequently bear the full brunt of tropical storms, cyclones and hurricanes and "appear less resistant but more resilient than other tropical forests" to such damage (Piou et al., 2006). In the changeable and dynamic context of many intertidal environments, however, severe disturbances may have unpredictable secondary impacts—including, for example, soil erosion, soil acidification and substrate collapse—which can occasionally result in forest death or loss of habitat (Kogo et al., 1987; Duke et al., 1997; Rubin et al., 1999; Allen et al., 2001). Natural disturbances clearly play a major role in structuring mangrove forests, which undergo frequent phases of destruction and recolonisation.

Anthropogenic disturbance

Globally, the range of disturbance associated with human activities, has been more significant than natural disturbance. Anthropogenic disturbance includes deforestation, clearing for aquaculture and other land uses, oil spills and pollution, fragmentation associated with industrial development and urbanisation, selective clearing for roads

and easements, timber harvesting and grazing (Ellison and Farnsworth, 1996; Primavera, 1998; Holguin et al., 2005). Indeed, anthropogenic disturbance to mangrove ecosystems varies enormously in character, severity and extent (McGuinness, 1992; Skilleter, 2000).

Ellison and Farnsworth (1996) classified anthropogenic disturbances into four types: listed in the order of increasing spatial and temporal scale these are extraction, pollution, reclamation and changing climate. Damage from climate change acts at a global scale, but disturbance to mangroves is more often studied at the regional level (Duke et al., 1997; Cahoon and Hensel, 2003; Alongi et al., 2005), or at a local scale involving estuaries or individual forests (Burke, 1992; Ellison and Farnsworth, 1993; Benfield et al., 2005). A number of recent studies have even focussed on disturbance at the level of individual canopy gaps (Ewel et al., 1988; Allen et al., 2001; Duke, 2001; Pinzón et al., 2003; Clarke, 2004). Temporal variation is also important in relation to the response of natural communities to disturbance. A "pulse" disturbance acts briefly over a short period whereas "press" disturbances act over a prolonged period of time, leading to very different effects (Skilleter, 2000). For research and management purposes, McGuinness (1988; 1992) classified some of the physical and temporal factors affecting natural communities into three broad categories: stresses, disturbances and catastrophes.

Anthropogenic disturbance is often catastrophic, involving the complete and permanent destruction of the habitat for conversion to other land uses, particularly for construction of urban centres and for shrimp pond construction (Primavera, 1995). Clearing and infilling for coastal development has led to alarming losses: more than 50% of the global mangrove area having been destroyed in the last 20 years (Holguin et al., 2005). Consequently mangroves are now one of the world's most threatened tropical environments, particularly since 2.1% of the total area continues to be lost each year (Valiela et al., 2001). This dramatic loss of mangrove through many parts of the world and the vulnerability of the habitat to environmental change is well documented (Saenger et al., 1983; Valiela et al., 2001; Diop, 2003). Recent studies report the negative impacts of widespread habitat loss on biodiversity and coastal productivity (Beardmore et al., 1997; Kaly and Jones, 1998; Roberts et al., 2001), often with devastating effects on coastal fisheries (Jernelov and Linden, 1983; Ellison and Farnsworth, 1996).

Furthermore, predicted rises in sea level from human-induced global climate change may have major implications for mangrove environments world-wide (Ong, 1995; Woodroffe, 1995; Ellison and Farnsworth, 1996; Skilleter, 2000).

As a consequence of such sustained destruction, studies allowing a clear evaluation of the changes in biological diversity caused by habitat loss, and particularly habitat fragmentation, are urgently needed to guide future management and conservation of mangroves (Cosson et al., 1999). In this context, studies of the biota as a whole are particularly useful, as changes in mangal community structure can exert effects on functioning (Farnsworth, 1998; Field et al., 1998) which may de-stabilise natural communities and lead to ecosystem dysfunction (Wilson, 1988; Naeem et al., 1994; Naeem et al., 1999)

Apart from the obvious and irreversible loss of mangroves through catastrophic "reclamation", numerous indirect impacts can result from less obvious stresses and disturbances associated with urbanisation. These include pollution (Lee, 1998) and reductions in freshwater inflow and modification of tidal regimes (Bird and Barson, 1982). Human settlements, industry and aquaculture have traditionally been concentrated around estuaries and mangroves have frequently been the repository for sewage, and often exposed high levels of organic pollution (Harbison, 1981; Clough et al., 1983; Clark et al., 1996; Hall and Frid, 1997). In estuaries characterised by sheltered embayments and coastlines with low wave action, mangroves are particularly vulnerable to chemical pollution, especially oil spills (Lewis, 1983; Getter et al., 1985; Burns et al., 1993; Grant et al., 1993; Duke et al., 1997). Increasingly, assemblages of intertidal plants and animals are being exposed to escalating concentrations of heavy metals (Harbison, 1981; Clough et al., 1983; Clark et al., 1996; Stark, 1998), siltation (Ellison, 1998; Newell et al., 1998; Morissey et al., 2003) and the introduction of exotic species (Cohen and Carlton, 1998). Major urban developments may thus deliver a complex cocktail of damaging—and potentially interacting—substances to estuarine habitats (Lindegarth and Hoskin, 2001). Furthermore, if negative impacts do occur, unless catastrophic, they may be largely unnoticed, partly because established biological indicators of ecosystem health are rare (Macintosh et al., 2002; Holguin et al., 2005).

The stresses imposed on mangrove ecosystems increase with burgeoning human population (Kunstadter et al., 1985; Valiela et al., 2001), and a number of studies

conducted on the densely populated eastern seaboard of Australia report degradation of mangrove habitats from pollution (Harbison, 1981; Mackey and Hodgkinson, 1995; Clark et al., 1996; Stark, 1998). Moreover, in this region, population growth has contributed to rapid and extensive mangrove destruction through demand for residential canal estates and boating marinas. Many estuaries that contained extensive areas of mangrove and saltmarsh as recently as 1950 now have little or no mangal left (Morton, 1989). By contrast, other areas have experienced a spread in mangrove area, often in association with changes in catchment land use leading to increased inputs of sediments (Saintilan and Williams, 1999; Morissey et al., 2003).

Northern Australia is fortunate in lacking the extreme pressure of environmental degradation and habitat loss facing coastal wetlands elsewhere. Over 70% of the Northern Territory coastline remains Aboriginal Land (Duke, 2006) and population levels are sufficiently low that pollution from urban centres is not yet an important issue. Indeed, the mangroves of this coastline are the least impacted in Australia and possibly the world (Duke, 2006). The major threat to mangrove habitats in the Darwin region is from clearing for coastal development (Duke, 2006). The city of Darwin is expanding rapidly, however, and there is a concomitant need for baseline data that provides the necessary platform for environmental impact assessment and monitoring projects. Such data is also necessary for informed land use planning, conservation and management of the mangrove resource as a whole. Clearly, understanding how communities are affected by disturbances is important for their conservation and management (McGuinness, 1992).

Disturbingly, however, the long-term impacts of most anthropogenic disturbance on mangrove ecology, including the ramifications of discharging various pollutants and sediments into these habitats, is poorly known (Lee, 1999). Although the effects of oil spills are well documented (Lewis, 1983; Getter et al., 1985; Samiullah, 1985; McGuinness, 1990; Burns et al., 1993; Clarke and Ward, 1994; Proffitt et al., 1995; Duke et al., 1997; Faraco and Lana, 2003), specific knowledge of the impacts of other diverse human activities on mangroves, remains surprisingly inadequate (McGuinness, 1992; Skilleter, 1996). The findings of a recent study, however, indicated that even relatively small scale changes in the structure of mangrove forests can result in significant effects on invertebrate faunal diversity and abundance (Skilleter and Warren, 2000).

Furthermore, as mangroves have important trophic links to near shore environments, the ramifications of disturbance for these relationships should also be investigated. As Lee (1999) observed "The need to understand disturbed mangals is probably as strong as for natural ones".

A major component of this study was therefore to investigate the effects of anthropogenic disturbance on mangrove fauna through comprehensive biological surveys conducted for Part 1 of this thesis. In particular, the impacts of urban, industrial and primary industry on the faunal communities of adjacent mangroves was studied. Furthermore, in Part 2, aspects of the long-term impacts of severe natural and anthropogenic disturbance on mangrove forests were investigated.

1.4. Recovery from disturbance

~1.4.1. Natural regeneration of mangrove forests

The factors involved in the natural regeneration of mangrove forests are not straightforward: many different biotic and edaphic variables can affect forest regeneration, and these will vary with the nature and frequency of disturbance, its severity and extent (Sherman et al., 2000). Prior to seedling establishment, important factors affecting forest recovery include propagule dispersal, the ability to establish, and predation. After establishment, factors such as competition, physiological stress and predation/herbivory may play a major role in determining seedling survival (McKee, 1995; McGuinness, 1997).

Given their susceptibility to frequent disturbance, one might expect mangroves to be well adapted to intermittent physical damage. Surprisingly, however, a number of studies and observations have shown that disturbed mangroves can take a long time to recover (Blanchard and Prado, 1995; Kaly and Jones, 1998), particularly in comparison with recovery times for most other tropical forests. In fact it may take several decades for successful revegetation to occur after complete deforestation (McGuinness, 1992; Ellison and Farnsworth, 1996; Imbert et al., 2000). Furthermore, some of the adaptations which enable mangroves to dominate dynamic tidal shores, including water-bouyant propagules for example, appear to hinder recruitment in some instances.

The reasons underlying delayed forest recovery have intrigued a number of authors (e.g. Smith III et al., 1994), and appear to be complex, varying with location, and the type and degree of damage. Recovery times will depend on the severity of the initial disturbance but may also be complicated and delayed by continuing disturbances (Chapman and Underwood, 1997; Kaly and Jones, 1998) or poor ability to regenerate (Blanchard and Prado, 1995; McGuinness, 1997a). A minimum of twenty years is generally required for mangrove habitats to recover from a major oil spill (Burns et al., 1993), and it may take several decades for mangal to recover from severe cyclone damage (Bardsley, 1985; Roth, 1992; Smith III et al., 1994; Hensel and Proffitt, 2003). Moreover, given the long time required for forests to regenerate after severe cyclone disturbance, studies on the long-term effects of such natural disturbances are rare (Ferwerda, 2000; Piou et al., 2006).

Soil erosion, acidification (McKee, 1993; McKee and Faulkner, 2000), erosion of sediments due to loss of tree cover (Duke et al., 1997; Cahoon and Hensel, 2003; Hensel and Proffitt, 2003; Duke, 2006), shortage of propagules (Elster et al., 1999), insect attack (Duke, 2006) weed invasion (Rubin et al., 1999) and other biotic factors (Ward et al., 1986; Smith III, 1987c; Smith III, 1988; Dahdouh-Guebas et al., 1998), have been linked with inhibited forest recovery. Presumably the interplay of several such factors can lead to the complete recruitment failures reported by several authors (Macnae, 1968a; Blanchard and Prado, 1995; McKee, 1995). In general, however, the processes delaying the recovery of mangrove forests after deforestation, are poorly understood. Although this is an aspect of mangrove ecology that commands more attention, few studies have investigated specific environmental factors that might affect the establishment, growth and survival of particular species (but see Ellison and Farnsworth, 1993; McKee, 1995; McGuinness, 1997).

Overall however, little is known about the response of mangrove communities in this region to disturbance (Wightman, 1989) and our knowledge of recovery processes in mangrove habitats both here and elsewhere, is still emerging (McGuinness, 1992; Blanchard and Prado, 1995; McGuinness, 1997a; Imbert et al., 2000; McGuinness, 2002a). In this thesis the influence of selected biotic and abiotic factors (shade, light, predation and damage from floating debris, soil salinity and compaction) on mangrove recovery, in bulldozed and cyclone damaged sites, was explored through experimental plantings.

~1.4.2. Rehabilitation of mangroves

Fragmentation, degradation and loss of habitat pose major threats to the biological diversity and productivity of terrestrial and vegetated marine ecosystems (Kaly and Jones, 1998; Cosson et al., 1999; Ritchie and Olff, 1999). These threats become of critical importance in mangrove environments, however, due to the potential loss of vital ecological function and biodiversity, especially given that mangrove forests have relatively poor recruitment ability (McKee, 1995; McGuinness, 1997a). As Kaly and Jones (1998) surmise, these habitats "rank among the most productive of marine systems and are perhaps the most susceptible to decimation". Indeed, with the massive global loss of mangrove habitat over the last few decades it is evident that their future conservation rests not just on protecting undisturbed patches but on restoring degraded systems (Chapman and Underwood, 1997; Field, 1998b; Ellison, 2000b; Lewis, 2005). Worldwide, there is an increasing role for mangrove restoration or rehabilitation as the area of harvested and degraded forests (which have been altered to the extent that they have lost the ability to self-regenerate) rapidly expands (Lewis and Streever, 2000). Widespread anthropogenic disturbance and deforestation have increased the importance of developing sound ecological techniques for restoration and rehabilitation (Field, 1996; Das et al., 1997; Edwards, 1998; Kaly and Jones, 1998; Ellison, 2000a; Lewis, 2005). Indeed, developing the knowledge and the skills necessary to restore self-sustaining systems—in which faunal diversity, productivity and functional links are roughly equivalent to natural habitats—may represent one of the most important and challenging areas of mangrove ecological research today.

Largely due to socio-economic differences, the objectives and goals of mangrove rehabilitation projects vary from place to place. Relatively simple reafforestation programs are widespread in subsistence cultures where the primary motive is to ensure a sustainable supply of natural resources. Mangrove forests have been managed by harvesting and replanting in this way for a very long time in Malaysia and the Sundarbans of Bangladesh (Kaly and Jones, 1998; Kairo et al., 2001). By contrast, rehabilitation and restoration are more often the goals of recent programs in developed nations. Growing awareness of their ecological value—as well as compliance with legislative requirements—has prompted the recent interest in restoration and has spawned an abundance of studies on the revegetation and rehabilitation of tidal forests

(e.g. Field, 1996; Edwards, 1998; Field, 1998a, 1998b; Field, 1999; Lewis et al., 1999; Holl and Howarth, 2000; Lewis and Streever, 2000; Walters, 2000; Ellison, 2000a, 2000b; Lewis, 2005). Nevertheless, even amongst healthy, intact mangrove forest, natural recruitment mechanisms may be substantially delayed by localised disturbance (for example by linear clearing for easements, tracks or pipelines). Clearly, there is scope for rehabilitation projects at a number of different scales and with a range of different goals.

Until recently, the primary response to rehabilitation has been simply to commence replanting of mangroves. However, this approach has been questioned on the basis of variable levels of success, high costs, and better awareness of the key processes underlying successful natural recruitment and recovery (Lewis, 1990; Lewis and Streever, 2000; Saenger and Rossetto, 2002). New approaches to restoration tend to work with natural recruitment, using naturally occurring propagules as the primary source for regeneration (Field, 1998a, 1998b) and are generally underpinned by the goal of re-establishing fully functioning ecosystems (Lewis, 1990; Ellison, 2000b). Although the basic techniques for propagating, culturing and planting mangroves are well documented, high failure rates for many previous rehabilitation projects emphasises the need to undertake pilot studies (Lewis, 1990, 2005). Furthermore, emerging understanding of natural recovery processes (e.g. the vital role of mature seed trees and recruitment refuges to initiate seedling establishment) portends a continuing role for artificial plantings.

Despite a number of overseas studies, and several highly successful projects in eastern Australia (Saenger, 1996, 2002) no comprehensive mangrove rehabilitation studies have previously been done in the Northern Territory. Areas of Darwin Harbour mangroves are still bare after being damaged by Cyclone Tracey in 1974 and others have lost mangrove cover as a result of vegetation clearing associated with coastal developments. These disturbed habitats presented ideal opportunities for research on rehabilitation and forest recovery. A pilot program involving both artificial and natural rehabilitation techniques was thus conducted as part of this study, to investigate the feasibility and effectiveness of these approaches.

1.5. Aims and objectives of this study

The primary aims of the research were to:

Aim 1: Document the distribution, diversity and abundance of the fauna of mangrove habitats in Darwin Harbour.

Specific objectives were:

- To develop a composite field methodology for rapid quantitative assessment of mangrove invertebrate fauna, including epifauna, infauna and benthic organisms to be tested in a pilot study and applied in this survey
- To document the distribution, diversity and abundance of vertebrate and macro-invertebrate fauna within the four major mangrove assemblages at three sites in Darwin Harbour, and to test for spatial and temporal (annual and seasonal) patterns in faunal diversity and abundance.

Aim 2: Examine the effects of anthropogenic disturbance on the fauna

Specific objectives were:

- To assess the impact of anthropogenic disturbance on vertebrate and invertebrate fauna by comparison of patterns in faunal distribution, diversity and abundance at undisturbed sites with that found in four moderately disturbed sites, located in mangroves adjacent to urban and industrial developments

Aim 3: Investigate the factors affecting the natural regeneration of disturbed mangrove forests and examine how rehabilitation may be facilitated

Specific objectives were:

- To investigate the biotic and abiotic factors affecting the recovery and regeneration of mangroves deforested by natural (cyclone damage) and anthropogenic (bulldozer) disturbance. Test the role of predation, light intensity, mechanical damage by floating debris, soil salinity and compaction on seedling growth and survival over two years.
- To investigate the size and nature of herbivores severely limiting seedling survival in cyclone-damaged *Rhizophora stylosa* forests, in an experiment using exclosures to selectively test for grazing by sea turtles.
- To test different *artificial* rehabilitation techniques in field experiments at three degraded sites by planting or transplanting seedlings, and by directly implanting propagules of four different mangrove species and monitoring their survival and growth for two years.
- To investigate the success of a rehabilitation technique designed to facilitate *natural* seedling recruitment by conducting field experiments comparing treatment and control plots installed in three assemblages, at three disturbed sites.

1.6. Structure of thesis

As outlined above, this project has three main research themes: survey of mangrove biological diversity; investigation of the response of faunal assemblages to disturbance and study of the factors governing recovery and rehabilitation of the forest (Figure 1-1). To present the findings of this research in an orderly fashion, the information has been presented in two sections and divided into nine chapters. Part 1 deals mainly with fauna—collectively termed biological diversity—and the impacts of disturbance on faunal assemblages. Part 2 concerns the flora of mangroves and research on the processes affecting the recovery of disturbed mangrove forests and their rehabilitation.

In Chapter 2, I outline the physical framework and the mangrove communities of the study area in Darwin Harbour. This provides the context for descriptions of each study site and the general methodology used for biological surveys.

In Chapters 3 and 4, I present the results of surveys of vertebrate fauna in undisturbed mangroves (Ch. 3) and in mangroves affected by anthropogenic developments (Ch. 4). I analyse patterns of spatial and temporal variation in the diversity and abundance of mammals, birds and bats. Patterns in bird foraging ecology are also described.

In Chapters 5 and 6, I describe a systematic survey of the diversity, distribution and abundance of invertebrate fauna in undisturbed (Ch. 5) and disturbed (Ch. 6) mangroves, commencing with the results of a pilot and a confirmation study. Two manuscripts arising from the work in these chapters are bound in the thesis as Appendices C and D.

Chapters 7 and 8 comprise Part 2 of the thesis and deal chiefly with flora. I investigate several inter-related areas of mangrove forest disturbance ecology and report the results of four plant growth studies. In Chapter 7, I examine the factors affecting the recovery of forests damaged by natural and by anthropogenic causes. In Chapter 8, the results of three rehabilitation experiments are analysed and considered.

In the final chapter of this thesis, Chapter 9, I summarise the major findings of the preceding five chapters and examine interrelationships between the three main areas of research. Several plant-animal relationships highlighted by this study are discussed and I conclude with a brief summary and several recommendations for further research.

CHAPTER 2. STUDY AREA AND GENERAL METHODOLOGY

CHAPTER 2. STUDY AREA AND GENERAL METHODOLOGY

2.1. Regional setting

Mangrove forests cover over 10,000 km^2 of the Australian coastline (Galloway, 1982). The majority occur in the tropics and increasingly these represent some of the largest, relatively undisturbed, mangroves in the world (Saenger et al., 1983; Hutchings and Saenger, 1987; Duke, 2006). The coast of the Northern Territory alone includes approximately 4,120 km^2 of mangrove environment (Wightman, 1989). Until recently, Australian mangroves had largely escaped the influence of intense population and economic pressures that have led to the exploitation and conversion of large areas of mangrove habitat elsewhere. The situation in Australia has rapidly changed however, with a decrease in total mangrove area from 11,617 km^2 in 1983 to 10,000 km^2 in 1990: a loss of 14% over 7 years (Valiela et al., 2001).

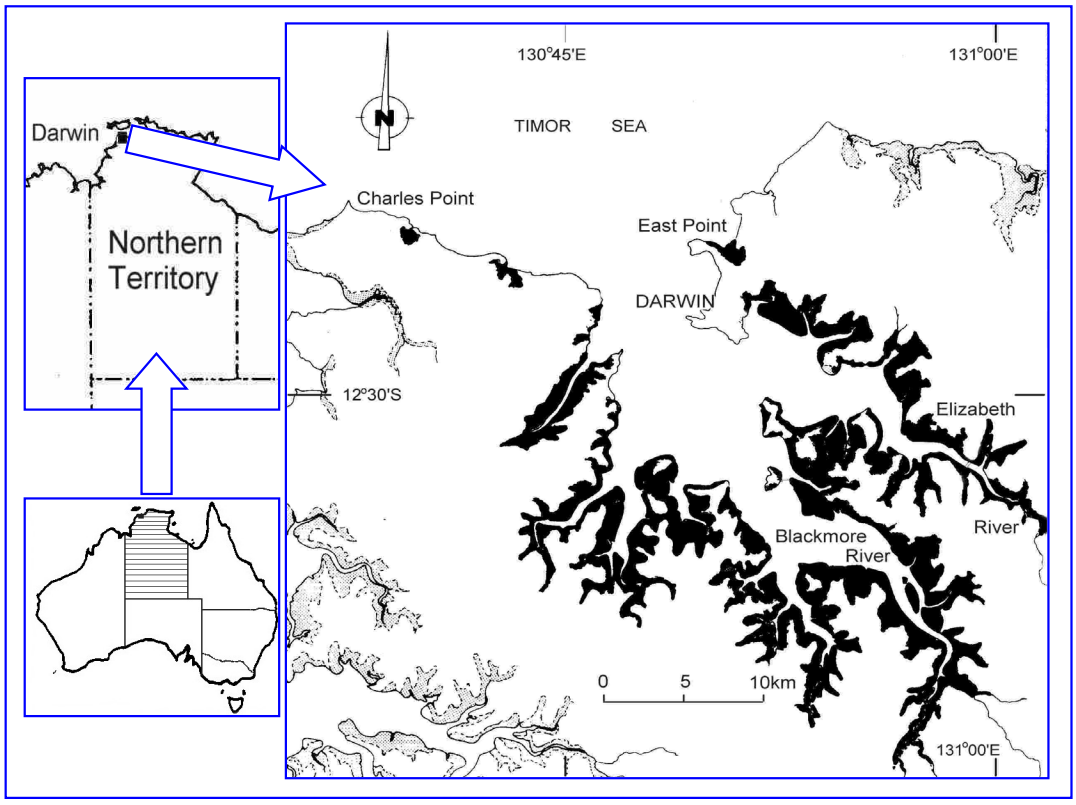


Figure 2-1: Map showing location of Darwin in the Northern Territory, Australia (left) and the distribution of mangroves (shaded in black within Darwin Harbour (right). Adapted from Larson (1988).

This research was undertaken in Darwin Harbour, situated on the north-western coastline of the Northern Territory between latitudes 12°20' and 12°40' S and longitudes 130°45' and 131°05'E. Darwin Harbour is bounded to the west and east by Charles Point and East Point respectively and contains approximately 20,400 hectares of healthy and relatively intact mangrove and saltflat habitat (Figure 2-1). The city of Darwin, situated on the north-eastern shores of the harbour, provides excellent opportunities for scientific research on mangrove habitats, being surrounded by this impressive natural resource. The recent, rapid growth of industry and infrastructure associated with the city of Darwin has, however, led to clearing of large tracts of mangroves. Such developments will place increasing pressure on the remaining mangrove resources, heightening the current need for baseline data from these communities for monitoring, management and conservation purposes.

Darwin Harbour has one of largest expanses of mangroves in the Northern Territory (Wightman, 1989). Acknowledged as an important natural resource on both the regional and global scales, the mangroves of Darwin Harbour constitute approximately 0.1% of the world's remaining mangrove area (Brocklehurst and Edmeades, 1996)

Climate

Darwin Harbour has a monsoonal climate with uniformly high temperatures and solar radiation. The mean maximum temperatures are between 30-34°C and mean minimum between 19-27°C. The mean annual rainfall for Darwin is 1,659 mm, with distinct alternation of wet and dry seasons (Bureau of Meteorology, 2006). The warmest temperatures, and 90% of the annual rainfall, occur during the wet season from November to April when moist winds blow from the north-west. The dry season, from May to October, has cooler temperatures, dry south-easterly winds and is virtually free of rain. Overall, annual evaporation exceeds rainfall by approximately 800mm and the period of mid-year aridity is a dominant feature of the regional climate (Taylor and Tulloch, 1985). Cyclones may occur during the wet season and these, and associated storm surges, can be highly destructive to mangrove communities (Bardsley, 1985; Wightman, 1989).

Geomorphology

Darwin Harbour was formed by the post-glacial marine flooding of a dissected terrestrial plateau and is thus known as a ria coast (Semeniuk, 1985). It comprises a large indented embayment with three main arms—East, Middle and West Arms—and has a total area of over 400 km^2. Two major rivers, the Elizabeth and Darwin Rivers, drain into the harbour and these, and their tributaries, have largely determined the structure of the embayment (Semeniuk, 1985). East Arm arose from the post glacial flooding of the Elizabeth River while similar marine flooding of the Darwin and Blackmore Rivers formed Middle Arm. Subsequent fluvial discharges have deposited the sediments upon which the current mangrove systems have established (Semeniuk, 1985). Thus the geomorphological setting, at the regional scale, is the combined result of past and present geomorphic processes.

At the community level, Darwin Harbour has developed as a result of the interplay between the terrestrial landforms, marine erosion and tidal flat deposition (Semeniuk, 1985). The resulting network of embayments, tidal channels, spits and islands has created the physical framework for the extensive system of mangrove-vegetated tidal flats observed in Darwin Harbour today. Thom (1982) noted that for any specific area, the history of the land surface combined with contemporary geomorphic and pedogenic processes together determine the pattern of mangrove growth, often in the form of discrete assemblages. Based on an extensive survey, Brocklehurst and Edmeades (1996) defined ten mangrove assemblages and two non-mangrove associates (beach and saltpan) within Darwin Harbour, four of which are examined in this research project.

On a finer scale, diverse and dynamic factors including sedimentation, geochemistry, microtopography, tides and hydrology contribute to the formation of local environmental gradients in soil moisture, salinity etc. These gradients, combined with climatic and biotic factors, play an important role in shaping the structure and composition of the distinct mangrove communities occurring in Darwin Harbour.

Hydrology

The intricate series of drowned valleys that comprise Darwin Harbour provide a very protected environment for mangroves (Galloway, 1982). The wave climate is very mild and long period swell does not often enter the harbour. Waves in Darwin Harbour are

generally less than 0.5 m in height with periods from 2 to 5 seconds (Byrne, 1988). Most waves are generated locally within the harbour or just offshore in Beagle Gulf. However, during cyclones, it is estimated that waves between 3 and 3.5 m in height could occur (Byrne, 1988).

Darwin Harbour has a macrotidal environment with a tidal range of about 7.8m. There are two high and low tides daily (semi-diurnal inequality) and the maximum daily tidal amplitude varies from approximately 5 to 8 m during spring tides, to around 2 to 4 m during neap tides. During spring tidal cycles currents of up to 2 m s^{-1} can occur in the main estuarine channels (Byrne, 1988) and these also influence development within mangrove habitats. Studies of topographic elevation within mangroves in Darwin Harbour, suggest an equilibrium between the gradients across tidal flats and the flows of tidal waters over them (Woodroffe, 1985). Tidal scouring contributes to the maintenance of a characteristic relationship between surface topography and frequency of tidal inundation which may be plotted as a hypsometric curve for a particular creek system or embayment (Woodroffe, 1985). Recent anthropogenic developments involving extensive reclamation in the mid- and upper intertidal zones of Darwin Harbour may have the potential to alter this equilibrium situation.

Overall, the macrotidal hydrodynamics of the harbour has contributed to the generation of a system of frequently flushed tidal channels with steep banks at low elevations. In contrast, above the level of mean high water neap tides—where tidal currents are minimal and flushing infrequent—extensive tidal flats with very flat terrain have developed.

Mangrove communities of Darwin Harbour

The mangrove communities of Darwin Harbour are some of the most floristically diverse in the Northern Territory, containing over 30 species of mangroves. Based on floristic diversity and extent, the mangroves of Darwin Harbour are placed as one of the three most significant mangrove resources in the Northern Territory (Wightman, 1989). Arnhem Bay and the South Alligator River containing 39 and 38 mangrove species respectively, are the other two. In Australia, such floristic diversity is only exceeded in north-eastern Queensland (Wells, 1983; Duke, 2006).

The structural features of mangrove communities in Darwin Harbour, are similar to those in many other parts of the world, showing pronounced shoreline zonation—with species arranged in nearly monospecific bands, often parallel to the coast (Saenger, 2002). Each mangrove zone or assemblage tends to develop at a particular topographic elevation (or regime of tidal inundation) but the pattern of zonation may alter with local geomorphic variation and disturbance—such that assemblages may resemble patches or strips, rather than extensive bands. The pattern of zonation generally evident in Darwin Harbour is shown in Figure 2-2. This community organisation is clearly visible from aerial photographs and on the ground, transitions from one assemblage to another may be abrupt (ie. within a space of 2 to 3 m).

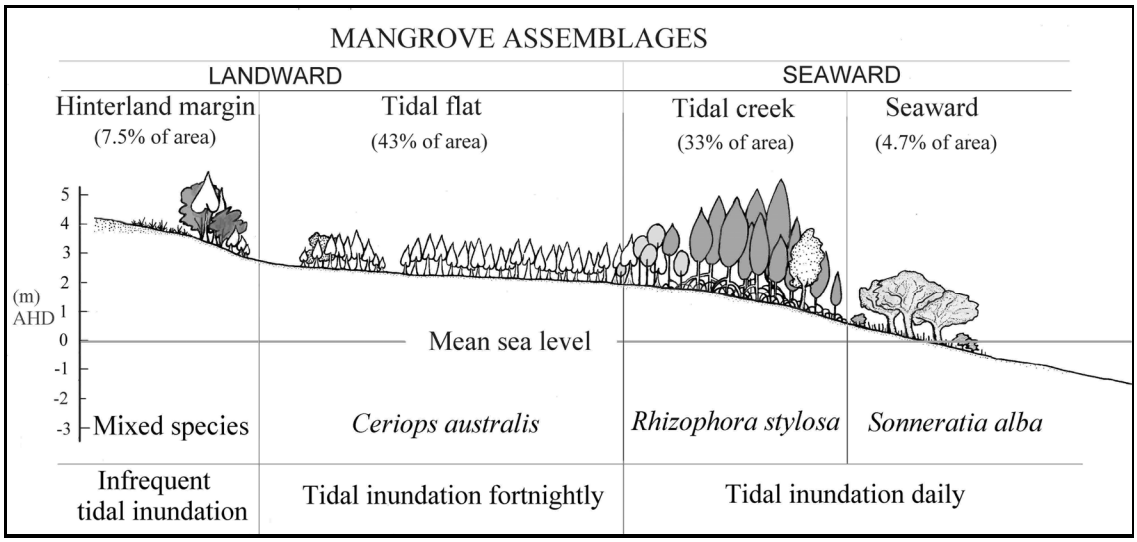


Figure 2-2: Schematic profile diagram of the typical pattern of mangrove zonation in Darwin Harbour, showing the predictable sequence of mangrove assemblages from landward to seaward (L to R). The percentage of the total mangrove area, tidal elevation (AHD or Australian Height Datum) and inundation frequency is also indicated (after Metcalfe, 1999)

Although zonation patterns tend to reflect the outcome of complex physico-chemical and biological interactions, likely factors influencing the distribution and extent of mangrove assemblages in Darwin Harbour include the seasonality of the climate, tidal regime (Woodroffe and Bardsley, 1987; Metcalfe, 1999), freshwater inflow, topography and substrate type (Semeniuk, 1983, 1985). In particular, the combined effects of high dry season evaporation rates and infrequent tidal inundation on soil moisture/salinity levels seems to strongly affect mangrove vegetation structure and composition in the mid- and upper intertidal zone (Woodroffe and Bardsley, 1987).

Indeed, landward mangrove habitats are characteristically more influenced by

terrestrial rather than marine processes, including freshwater seepage, the seasonal deposition of terrestrial sediments, infrequent tidal inundation and desiccation. The mid- to upper tidal flat (3–4 m AHD) is characterised by extremely flat topography. In this habitat, *Ceriops australis* typically forms almost monospecific stands over extensive tidal flats covering approximately 43% of the mangrove area in Darwin Harbour (Brocklehurst and Edmeades, 1996). Upper intertidal habitats in the harbour also may become hypersaline in the dry season (encouraging salt flat formation) and may then be diluted during the wet by rainfall and freshwater runoff from the hinterland. The hinterland margin zone is a mixed species mangrove assemblage, influenced by seasonal freshwater seepage and inflow along the mangrove/hinterland interface, occupying 7.5% or 1,525 ha of the total area.

By contrast, habitats in mid- to lower intertidal zones, are largely shaped by marine processes including wave action, tidal currents and two high tides per day. *Sonneratia alba* is typically dominant on the seaward shore at around mean sea level (0 m AHD). Further to landward and fringing tidal creeks at around 1–2 m elevation, *Rhizophora stylosa* is usually dominant, comprising roughly 33% of the area of Darwin Harbour mangroves (Brocklehurst and Edmeades, 1996). In seaward assemblages (i.e. seaward and tidal creek forests), soil salinities remain around that of seawater for most of the year and tidal scouring maintains relatively steep topographic contours along the banks of tidal channels.

In all, ten mangrove communities or assemblages have been identified and mapped in Darwin Harbour by Brocklehurst and Edmeades (1996) and are summarised in Table 2-1. This classification and numeration of mangrove assemblages (although not consecutive from the seaward to landward margins), has been widely applied in subsequent mangrove research and monitoring studies (Comley, 2002; Martin, 2004; URS Pty Ltd, 2004).

The four main mangrove assemblages found in Darwin harbour were selected for study in this project. From seaward to landward they comprised:

- Seaward (Community 8)
- Tidal creek (Community 2)
- Tidal flat (Community 4)
- Hinterland margin (Community 6)

The seaward assemblage (Community 8) almost exclusively comprises *Sonneratia alba* trees. The mixed species *Rhizophora* assemblage (Community 2), which occurs along both minor and major tidal channels as well as forming monospecific shoreline forest (Community 1), will be referred to as the 'tidal creek' assemblage in this thesis. The very extensive *Ceriops australis (= C. tagal)* dominated forests (Community 4 and 5) will most often be referred to as the 'tidal flat' assemblage, while Community 6 is referred to as the 'hinterland margin' (Figure 2-2).

Collectively the four assemblages under study have an extensive distribution, covering 80.4% of the total mangrove area, and they dominate the mangrove forests of the harbour.

Table 2-1: : Vegetation communities (assemblages) of Darwin Harbour as classified and mapped by Brocklehurst and Edmeades (1996) indicating total area in hectares and the four floristic assemblages studied in this project (shaded).

Map Unit*	**Mangrove Community (Brocklehurst and Edmeades, 1996)**	**Area (ha)**	**Community name in common usage**
1	*Rhizophora stylosa* closed forest	668	Shoreline forest
2	*Rhizophora stylosa*/*Camptostemon schultzii* closed forest	5,965	Tidal creek
3	*Rhizophora*/*Bruguiera*/*Ceriops* closed-forests	734	Transition
4	*Ceriops tagal* low closed forest	7,959	Mid tidal flat
5	*Ceriops tagal*/*Avicennia marina* low closed forest	892	High tidal flat
6	Mixed species low closed forest	1,525	Hinterland margin
7	Mixed species low woodland	288	Low woodland
8	*Sonneratia alba* woodland	968	Seaward
9	*Rhizophora stylosa* low woodland	2.8	Islands, rocky shore
10	Low open woodland	24.2	Low tidal mudflat
11	Samphire/Salt flat	1,377	Salt flat
12	Beach	28	Beach
* Map unit = community. Numbering was adopted to indicate assemblage type in this thesis and used in individual study plot identification codes (e.g. M381 = site M3, community 8, study plot 1).			

Previous research on mangrove productivity included six or more of the ten assemblages described from the harbour (Metcalfe, 1999; Comley, 2002) but logistics and experimental design considerations for this project led to selection of four of these assemblages. Concomitant research on the utilisation of mangroves by fish (Martin, 2004) and the significance of plant-animal interactions (Salgado Kent, 2004) focussed on

the three seaward and the three landward assemblages (of these four dominant zones) respectively. Consequently, the same study plots have now been the focus for several interrelated research projects. The overlap of data from this research is highly valuable and collectively, recent research at Charles Darwin University (CDU) has facilitated the development of mangrove monitoring methodologies by Government (Moritz-Zimmerman et al., 2002) and private enterprise (URS Pty Ltd, 2004; Metcalfe, 2004b).

2.2. Study plots

The majority of field data were collected within 50 m × 50 m (0.25 ha) study plots. Plot size conformed with the standard used for other fauna surveys throughout the Northern Territory by Parks and Wildlife and NRETA (Northern Territory Government department of Natural Resources, Environment and the Arts). Study plots were placed within the four main assemblages at each study site, along an imaginary transect aligned from the landward margin to the seaward edge of the mangroves. Each transect was duplicated and replicate study plots were placed along a second parallel transect, located at least 50 metres distant from the first transect (Figures 2-4 to 2-10).

Study plot identification codes were determined by site (eg E1, M3, BV etc), then assemblage (6, 4, 2 and 8), followed by study plot number (either 1 or 2), listed for example as M381, E122 etc. Thus a total of 24 × 0.25 ha study plots were established on six transects in undisturbed mangroves. To study the effects of disturbance on mangroves, a further four study sites were selected in disturbed mangroves, at which 26 study plots were established along eight transects. Sub-sampling within study plots varied according to the type of survey being conducted and is described in the methodology sections of subsequent chapters.

2.3. Study locations

Three study sites in undisturbed areas of Darwin Harbour were selected: Charles Darwin National Park (Site E1), Elizabeth River (Site E2) and Jones Creek (Site M3). Although areas in Darwin Harbour were damaged during Cyclone Tracy in 1974, the study plots selected at these three sites are effectively undisturbed, having recovered from structural storm damage (Ferwerda, 2000; Metcalfe, unpublished report) and they

are not currently affected by anthropogenic influences. A primary consideration in the selection of the three main study sites, was access—each site is accessible from the land and study locations were selected in both the East and Middle Arms of the harbour. West Arm was not considered for study, as it is largely inaccessible by land.

Four study sites were selected in disturbed mangrove areas: Bayview residential development (BV), bulldozed and cyclone damaged areas of Charles Darwin National Park (DE), the East Arm Port precinct (DP) and Golden Prawn Aquaculture project in Middle Arm (DM). The location of all study sites is shown in Figure 2-3.

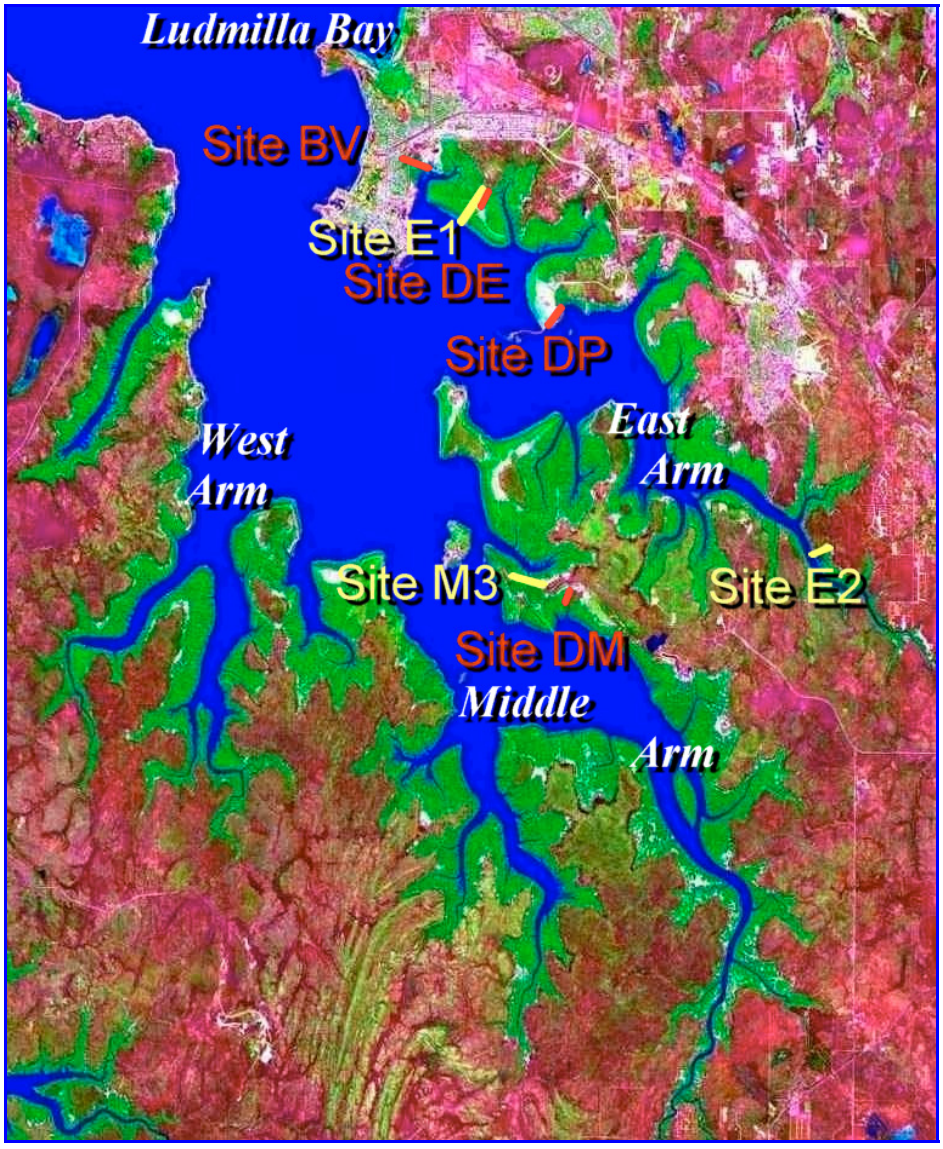


Figure 2-3: Satellite image of Darwin Harbour showing the distribution of mangroves (green) and the location of the 3 undisturbed (yellow) and 4 disturbed (red) study sites.

A pilot study for invertebrate sampling was undertaken during October 2000 in Charles Darwin National Park (Site DE) and a confirmation study was conducted in mangrove

communities in Ludmilla Bay in February 2001 (Figure 2-3). The methodology used for the pilot and confirmation studies is described in sections 5.2.2 and 5.2.3 of Chapter 5.

~2.3.1. Study sites – Undisturbed mangrove areas

Three sampling sites were selected from the nine existing sites established during a previous (1997–1999) research project (Metcalfe, 1999). Study sites in which the four mangrove communities are represented, were selected as follows.

Site E1 – Charles Darwin National Park

The majority of fieldwork for this thesis was done at Site E1, located in Charles Darwin National Park in East Arm. This site is characterised by a very broad, gently shelving intertidal zone—the two parallel transects are approximately 1.5 km long from the landward margin to the seaward edge. During low spring tides, exposed intertidal mudflats extend approximately one kilometre beyond the seaward edge of the mangroves. Sampling sites on the seaward margin were occasionally accessed by boat, particularly to transport heavy or bulky field equipment to study sites.

Development in terrestrial and hinterland areas has been limited to a few roads, some dirt tracks and limited tourist facilities situated amongst natural vegetation cover. The hinterland margin community at Site E1 is barely 50 m in width and comprises *Ceriops australis, Bruguiera exaristata* and *Excoecaria ovalis* to around 6 m tall with dense *Lumnitzera racemosa* on the landward fringe. This assemblage receives tidal inundation to varying extents once every 2 to 4 weeks—when tides exceed 3.2 m AHD.

In contrast, the tidal flat or *Ceriops* zone is extremely extensive, and combined with the associated *Ceriops*/*Avicennia* community (Map Unit 5, Brocklehurst and Edmeades 1996), is over one kilometre in width. Tree height in the mid-tidal flat is typically low (only 2 to 3 m) and where present, *Avicennia marina* typically overtops *C. australis.* This zone can be extremely dense due to patches of dense saplings, regrowth possibly arising from regeneration after Cyclone Tracy, which damaged this section of the harbour's shoreline 30 years ago.

Indeed, much of the *Rhizophora stylosa*-dominated tidal creek assemblage at this location, once the tallest mangrove assemblage, suffered long-term damage during the 1974 cyclone. The area it once occupied still remains bare of mangrove vegetation, clearly

visible on aerial photography, between the *Sonneratia* woodland to seaward and regenerating *Rhizophora* and *Ceriops* to landward (Figure 2-4). The tidal creek assemblage is characterised by deep, unconsolidated mud in areas lacking vegetation and soft, root structured mud in patches of healthy remnant forest. Study plots are however, located in stands of well-developed forest adjacent to a small tidal channel that experienced minimal cyclone damage. *R. stylosa* is the dominant species to 11 m in height with *Bruguiera parviflora* and *Camptostemon schultzii* (4 to 6 m high), particularly common along the banks of the tidal creek.

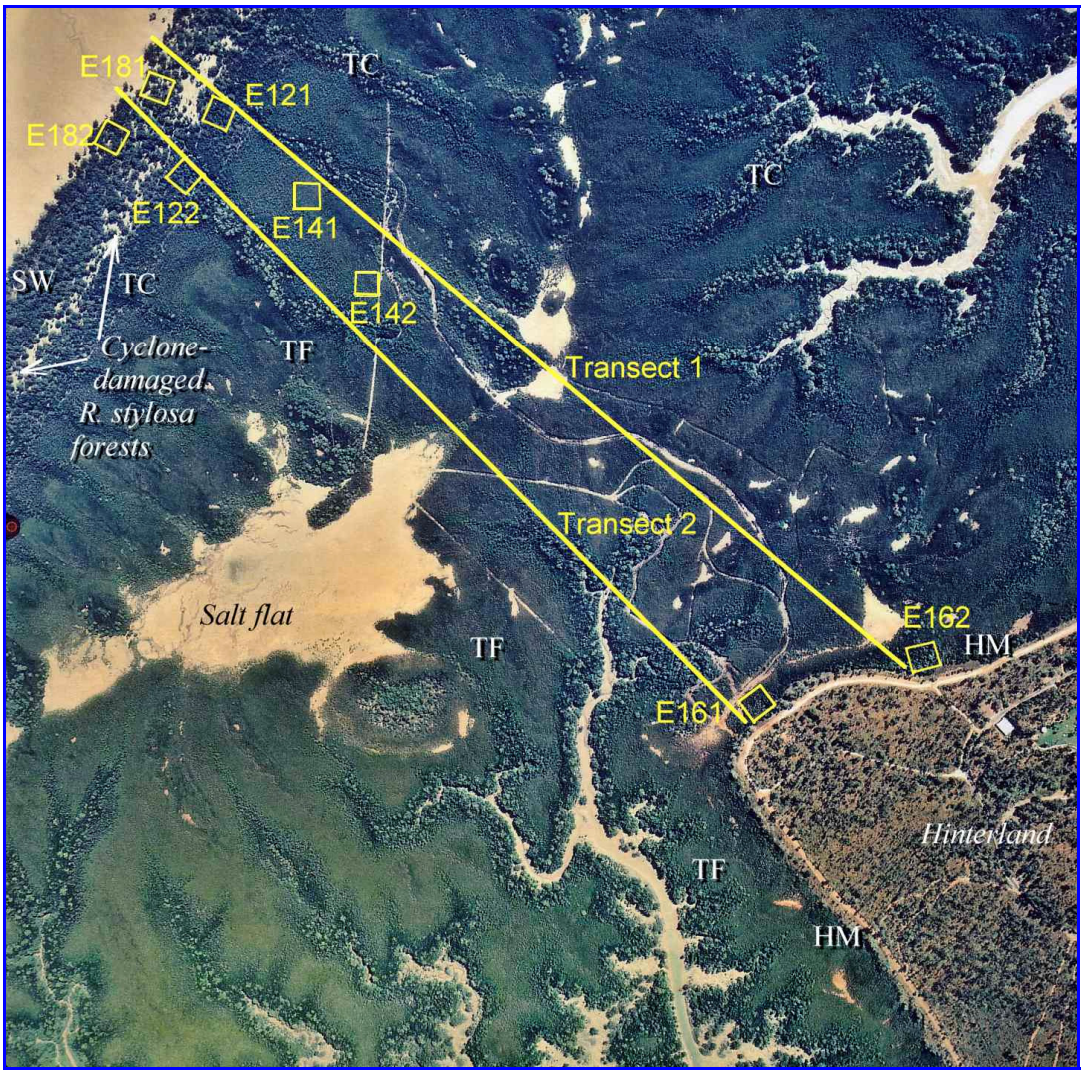


Figure 2-4: Aerial photo of CDNP showing paired transects and the location of 50 m × 50 m study plots in the 4 major assemblages (where SW = seaward, TC = tidal creek, TF = tidal flat and HM =hinterland margin). Also visible is the clearing in the seaward mangroves created by cyclone damage to *Rhizophora stylosa* forests and the network of bulldozed tracks.

The seaward zone comprises large, well-spaced *Sonneratia alba* trees to 10 m high with patches of *Aegiceras corniculatum* to 3 or 4 m high. The substrate is typically deep marine mud interlaced with a network of cable roots and dense, conical pneumatophores.

Site E2 – Elizabeth River

The Elizabeth River study site, also in the East Arm of the harbour is approximately 1 km upstream of the Elizabeth River bridge. This is the most upstream location studied and the intertidal zone is relatively narrow (300–600 m wide) and steep compared to other study sites closer to the main harbour (Figure 2-5).

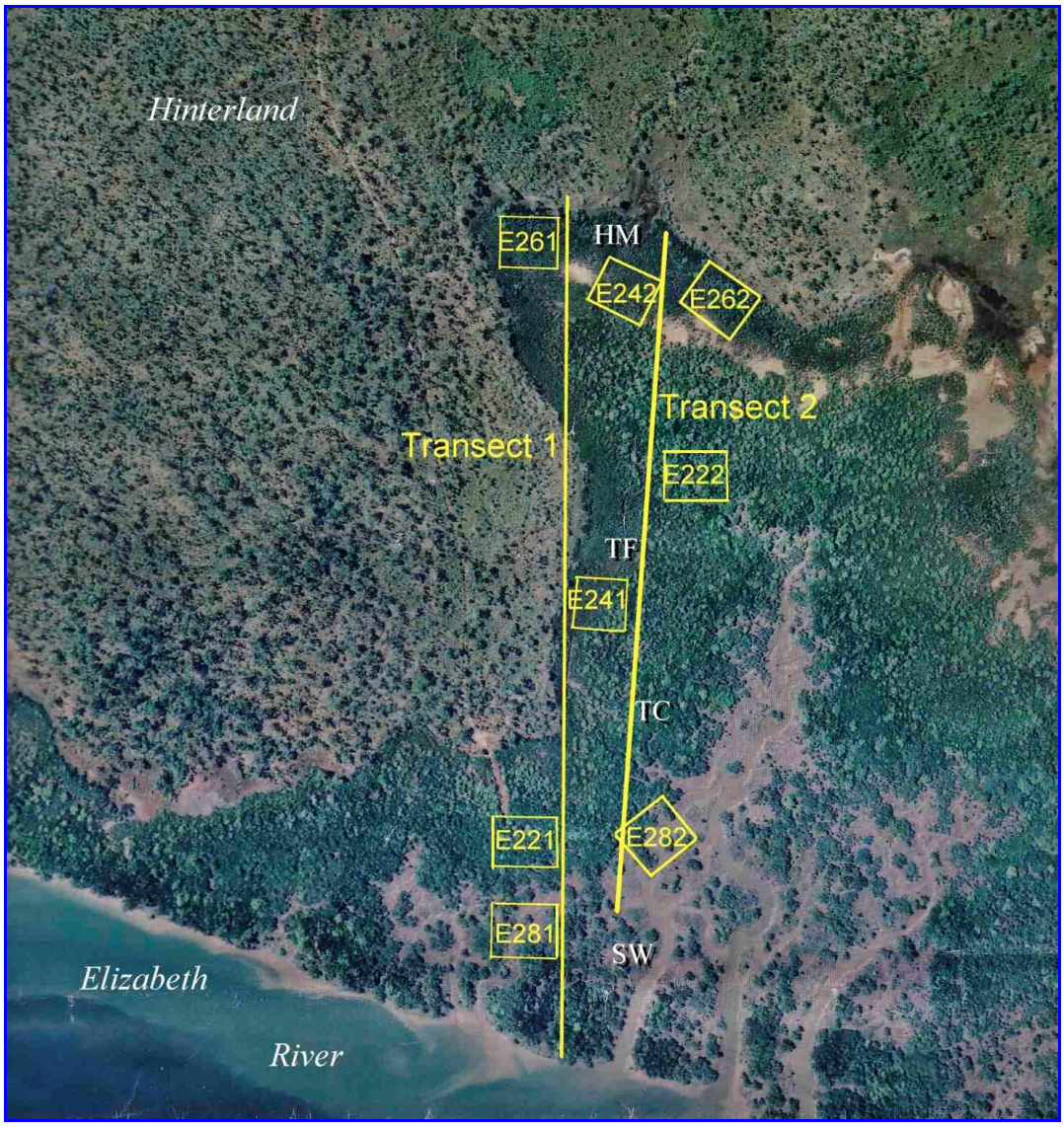


Figure 2-5: Aerial photo of site E2 on the Elizabeth River showing paired transects and the location of 50 m × 50 m study plots in each of the four assemblages (where SW = seaward, TC = tidal creek, TF = tidal flat and HM =hinterland margin).

Site E2 was surrounded by natural bushland and had a single, infrequently used, dirt access track, presumably used only for recreational purposes. The hinterland margin included substantial lateritic outcrops and freshwater seeps into it for several months after the wet season at the interface with terrestrial habitats. Similar to other sites around the harbour, the hinterland margin zone was barely 50 m wide and the seaward

edge of study plots either fringed saltflat vegetation or extended slightly into tidal flat habitat (Figure 2-5).

The tidal flat community was characterised by low *C. australis* and scattered *A. marina* on well-consolidated mud. The tidal creek assemblage was relatively low-growing, multi-stemmed and dense, as is characteristic of upstream areas of East Arm (P. Brocklehurst pers. comm.). *S. alba* trees in the seaward zone were interspersed with low-growing *Aegiceras corniculatum* and *Aegialitis annulata*.

Site M3 – Middle Arm, Jones Creek Site

Site M3 is located in Middle Arm and is largely surrounded by undeveloped bushland. The site is, however, traversed by high voltage transmission lines with an access road beneath them. The road and the base pads for the transmission towers are built on a 2 m high, earthen bund through the mangroves but they appear to have a minimal effect on adjacent mangroves. Minor anthropogenic disturbance was also observed at this location. Furthermore, aboriginal people intermittently use the mangroves in this area to fish, for gathering shellfish (*Telescopium telescopium, Nerita balteata*) and "mangrove worms" (molluscs from the family Teredinidae).

The hinterland margin study plots are situated between terrestrial grassland and sedgeland characteristic of seasonal seepage zones and a band of narrow salt flats (Figure 2-6). The substrate in the hinterland margin zone is typically firm gravelly mud. *C. australis* is the dominant species, occurring as tall (to 7 m high), well-spaced trees interspersed with occasional *Excoecaria ovalis* to 9 m high. Scattered *Thespesia populneoides* and shrubby *Lumnitzera racemosa* occur where the mangroves abut terrestrial environments.

The mid-tidal flat comprises almost monospecific stands of *C. australis* 2–3 m high on relatively firm clayey mud. Canopy height decreases to less than 2 m and multi-trunked, shrubby *A. marina* becomes locally common in the more saline soils fringing salt flat areas. *Aegialitis annulata* is a common understorey species to 1.5 m in these habitats.

The tidal flat community intergrades with well-developed *R. stylosa* forest 8 to 11m high growing along a network of estuarine channels draining into Jones Creek. Along these channels, arching prop roots commonly arise 2 to 3 m above the mud surface—in places

forming nearly impenetrable thickets. Substrates within the *R. stylosa* forests tend to be saturated and root-structured or deep, anoxic and sloppy.

Figure 2-6: Aerial photo of site M3 in the middle arm of Darwin Harbour, indicating the location of 50 m × 50 m study plots and the nearby aerial transmission lines. Assemblages are denoted by SW = seaward, TC = tidal creek, TF = tidal flat and HM =hinterland margin.

The seaward assemblage is not well developed in upper reaches of tidal creeks in Darwin Harbour, becoming pronounced only along the seaward shores of the harbour and the lower reaches of major creeks. Consequently it was necessary to locate the seaward assemblage at M3 some distance along the nearest creek in the direction of the harbour (Figure 2-6). Furthermore, in order to place 50 m study plots wholly within this zone, it was necessary to span the width of the creek. The *Sonneratia alba* trees at this site

were widely spaced and often extremely broad (dbh values to 80.3 cm) with thick limbs that occasionally arch to the mud surface, sprout roots and continue to grow. Substrates between these massive trees are soft, deep marine muds, knee-deep in places, with dense patches of *Aegiceras corniculatum* saplings and low trees.

~2.3.2. Sampling sites – Disturbed mangrove areas

Four sites were selected in disturbed mangrove areas to study the effects of a range of different types of disturbance on mangrove biota. However, disturbed sites in the harbour were not easy to find, as most development typically involved the complete 'reclamation' of mangrove areas. Indeed, heavily polluted or degraded systems, in which all four assemblages were represented, were not found. Consequently the study study sites selected were restricted to the fringes of urban or industrial developments that either impinged on, or traversed, mangrove habitats. Moreover, the nature and degree of anthropogenic disturbance varied from site to site, and amongst study plots at each site.

Disturbance in the intertidal zone was frequently narrow or linear, and the shape of sampling units was adjusted to this configuration, whilst still maintaining the same 0.25 ha sampling area. As it was not always possible to find disturbed sites that encompassed all four of the target assemblages, only two of the four disturbed sites selected had study plots in all four assemblages (East Arm Port and Bayview).

Site BV – Bayview Residential Estate

Construction of the Bayview marina and housing development commenced in the early 1990's and involved the staggered clearing of 103 ha of mangroves in Sadgroves Creek, East Arm. The disturbance to mangroves around the fringes of this development included localised forest death from waterlogging (by impeding tidal drainage during road construction and earthworks) and smothering (by thick in-washed deposits of terrestrial sediments).

Where the Bayview marina estate extends into the seaward zone, only a narrow mangrove fringe remained and several study plots had to be placed alongside steep rock-armoured sea walls (Figure 2-7). The terrestrial sections of Bayview are isolated from other areas of natural bushland as the site is bounded to the north and west by an

arterial road to the city and the development lies adjacent to high-density housing and industrial areas. At the time of the survey, construction was incomplete and several study plots (BV42 and BV22) were situated adjacent to a construction camp.

Figure 2-7: Aerial photo of Bayview residential and marina development under construction in May 2000, indicating location of 33 m × 75 m study plots in four mangrove assemblages. The high turbidity evident in Sadgroves Creek (foreground) is presumably inwashed terriginous sediments from earthworks and clearing of vegetation within the catchment.

Located directly opposite the extensive mangroves of Charles Darwin National Park (Site E1), this study site was well placed for comparative studies of disturbed and undisturbed mangrove habitats in Darwin Harbour.

Site DP – East Arm Port Facility

The East Arm Port Facility, at the mouth of the Elizabeth River, will largely replace the old Darwin Wharf at Stokes Hill, next to the city. Construction of the new port has involved building an extensive wharf with large areas of mangrove reclamation for port infrastructure and associated industries. These developments provided an opportunity to study the effects of industrial construction on adjacent mangroves. Reclamation

techniques at the site typically involved the construction of earthen bund walls that exclude tidal flow and impound mangrove areas, which are then cleared and/or buried beneath terrestrial fill. The seaward edge of bund walls were stabilised with geo-textile matting and granite rock armouring.

Disturbance to surrounding mangroves at Site DP has ranged from complete habitat destruction in reclaimed areas to major changes in hinterland drainage, and alterations to tidal flows from the construction of bund walls and the wharf. The impact of channelling of stormwater runoff into defined outlet points was identified as important. This situation contrasts with pre-construction freshwater drainage, where sheet flow dispersed gradually through the hinterland margin. Creating impervious substrates over vast areas of the terrestrial land surface will have had a marked impact on the quantity and the duration of seasonal freshwater inflow and will have influenced the pattern of erosion/sedimentation in adjacent mangrove habitats. Study plots were scattered around the perimeter of the project and the level of disturbance varied greatly from plot to plot.

In the seaward assemblage one 50 m × 50 m study plot (DP82) was located at the base of a 4 m high sea wall, wedged between the main wharf on one side and a new reclamation bund on the other. The sediments were deep, unconsolidated marine muds and a high proportion of the remaining *S. alba* trees were either dead or deteriorating. The second seaward study plot (DP81), located less than 200 m from the first, was on the other side of the main wharf but showed few obvious signs of degradation despite its proximity to the 1 km long jetty (Figure 2–8). The substrate in this seaward habitat was relatively firm and contained areas of lateritic outcrop. Clearly, the level of disturbance varied from study plot to study plot. However, similar to other disturbed sites, there was little choice in the placement of plots in specific assemblages located as close as possible to the development.

One of the two tidal creek study plots was located just landward of the seaward plot and supported a low, open area of *R. stylosa* with substantial areas of bare mud and regrowth of *A. marina*. A similar low *R. stylosa* formation with sandy-mud to rocky substrates was selected just to the east, also located amidst terrestrial construction activity and areas of previous long-term disturbance. The latter site was the location of a seaplane landing facililty during World War 2—the remains of a steel ramp structure bordered the study plot.

Figure 2-8: Aerial photo of the East Arm Port facility under construction in 2000, indicating location of 25 m ×100 m study sites in four mangrove assemblages (where SW = seaward, TC = tidal creek, TF = tidal flat and HM =hinterland margin.) During 2001 the remaining seaward mangroves (lower left) were also cleared.

Tidal flat study plots were initially established in dead *C. australis* forests disconnected from the sea by earthen bund wall construction the previous year (Sites DP4–1 and DP4–2, indicated in light blue in Figure 2-8). This site was selected to gain an indication of which species if any, remain following extreme disturbance (i.e. removal of the forest and tidal exclusion). However, development of the port progressed rapidly during 2001 and although some surveys had been completed at this site mid-year, it was necessary to select new sites when pumping of dredge spoil into these bunded areas commenced several months later. Hinterland margin sites at the East Arm Port were located on the

fringes of access roads and the new tidal flat sites (DP41 and DP42) were located a short distance from these study plots.

Site DM –Golden Prawns Aquaculture Development

Site DM is located in the middle arm of Darwin harbour. The Golden Prawns Aquaculture project has been under construction and in various phases of development for many years with an unsuccessful record for prawn production. This site included an inlet/outlet channel constructed by excavating mangrove muds to form a channel and an adjacent bund wall largely made of terrestrial fill. The channel and bund runs from the hinterland margin to the *Rhizophora* dominated forest of the tidal creek (Figure 2-9). Disturbance to adjacent forest varies from thick siltation (from steep unconsolidated bund walls constructed adjacent the hinterland margin assemblage), to minor disturbance (clearing) within the *Ceriops* and *Rhizophora* zones, and localised acid sulphate soil formation (J. Hill, DIPE pers. com). The channel is used for both the discharge of pond water and for the intake of saltwater into an adjacent saltwater storage pond.

Although the site does not appear to have had a notable impact on the surrounding mangroves it is an appropriate location to examine the impacts of localised physical disturbance due to prawn farming activities. In recent years, an increasing number of aquaculture projects has been initiated in the harbour. This study site also provided a suitable opportunity to investigate the effectiveness of several rehabilitation techniques trialed as part of this research project. The proponent was keen to see whether such techniques could assist in consolidating the highly unstable muddy banks of the channel.

The channel did not extend as far as the seaward zone and thus study plots could not be established in this assemblage (Figure 2-9). Located some 600 m further downstream, the nearest seaward assemblage forests were too distant from the development to be of relevance to the study. The channel discharges directly into a minor tidal creek fringed with *Camptostemon schultzii, Aegiceras corniculatum* and *Rhizophora stylosa*—all species typical of the tidal creek assemblage. Both the tidal flat and hinterland margin assemblages at Site DM are dominated by *Ceriops australis*. Forest height and species diversity increased in the landward mangrove fringe.

Figure 2-9: Aerial photo of Site DM, fringing the Golden Prawn aquaculture project in Middle Arm showing the location of 25 m ×100 m study plots in three assemblages (indicated by TC = tidal creek, TF = tidal flat and HM =hinterland margin).

Site DE – Bulldozed Tracks (Charles Darwin National Park)

Persistent cleared tracks resulting from bulldozer activity for geotechnical investigations in 1992 (prior to the area being declared a national park) provided an opportunity to study the potential long-term impacts of clearing on mangrove biota and to investigate the processes involved in recovery of the forest. Regeneration of the forest (mainly *C. australis)* along these cleared tracks—over a decade after clearing—has been very slow with little recruitment visible in some areas.

Although the scale of clearing at this location is small, the study may provide an indication of the local impacts of linear clearing on invertebrates, and the potential effects of disturbance on the biota over the longer term. Birds and mammals were not included in the fauna surveys (see Section 4.2.1 and 4.2.2 for a description of survey methods and objectives) at Site DE due to their higher mobility in relation to the extremely narrow disturbance corridor (approx. 10–20 m). However, invertebrate surveys were conducted in both tidal flat and tidal creek assemblages which had been cleared by bulldozer. The network of tracks also provided numerous sites suitable for

studies on recovery from disturbance, rehabilitation and assisted rehabilitation experiments (see Chapters 7 and 8).

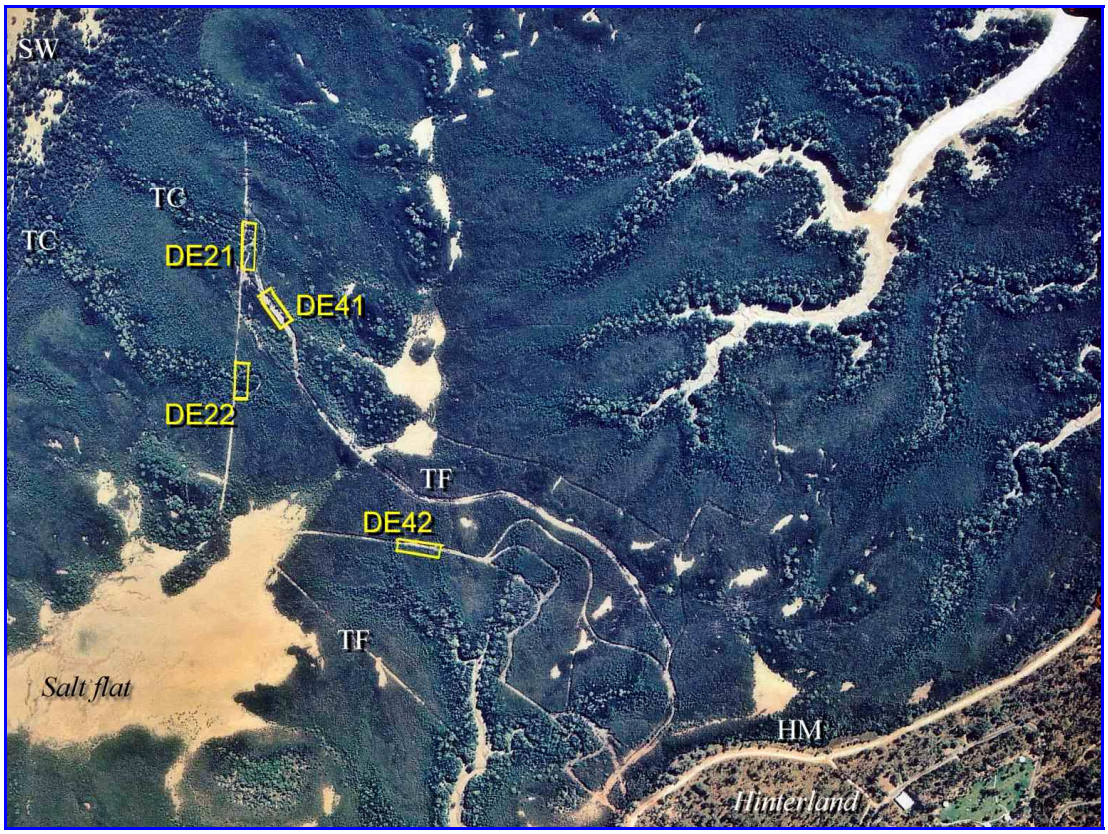


Figure 2-10: Aerial photo of mangroves at Site DE in Charles Darwin National Park in 2001 showing the network of bulldozed tracks. The location of study plots for fauna surveys in two assemblages (tidal flat and tidal creek) are shown. Assemblages are indicated by SW = seaward, TC = tidal creek, TF = tidal flat and HM =hinterland margin.

Bulldozer damage is largely limited to the very extensive tidal flats at Charles Darwin in which *C. australis* is the dominant species, often in association with *A. marina*. Tracks occasionally crossed (or attempted to traverse) tidal channels allowing studies to be undertaken in disturbed tidal creek habitat (Figure 2-10). Surrounding vegetation in these areas mainly comprises *R. stylosa, A. marina* and *Bruguiera exaristata.* Although study plots remained 0.25 ha in extent, plot dimensions at Site DE were altered (15 m × 150 m) to reflect the linear nature of the disturbed mangrove area.

CHAPTER 3. VERTEBRATE FAUNA

PART 1 – BIOLOGICAL DIVERSITY OF MANGROVE ECOSYSTEMS

CHAPTER 3. VERTEBRATE FAUNA

Mangrove communities are dynamic systems in which a fascinating range of organisms may coexist. Species enter from the land, swarm in from the sea at high tide and include highly specialised forms adapted to a wide variety of ecological niches provided by these forests. In no other habitat, do birds, bats and marsupials co-occur with mudskippers, sea turtles, insects, marine worms and crustaceans. Part 1 of this thesis is concerned with documenting some of the rich diversity of terrestrial and marine life within mangrove habitats. Spatial and temporal patterns in richness and abundance of vertebrates and invertebrates are reported in Chapters 3 and 5 and the effects of anthropogenic disturbance are investigated in Chapters 4 and 6.

3.1. Introduction

Despite the challenges posed by regular inundation, salinity and low plant species diversity, the mangrove habitat is used by a diverse range of vertebrates—particularly fish, bats and birds (McKenzie and Rolfe, 1986; Loughland, 1988; Hogarth, 1999; Palmer and Woinarski, 1999). The arboreal faunal community in mangroves is often abundant (Hutchings and Recher, 1983) but there are few obligate mangrove specialists. The majority of terrestrial animals that utilise mangroves are only periodic visitors; the

mangrove environment being just one of an array of habitats used in their overall survival strategies (Macnae, 1968b; Hutchings and Recher, 1983; Lacerda et al., 2001). Terrestrial fauna may use mangroves daily or seasonally, in response to opportunities for feeding or breeding (Hogarth, 1999; Lacerda et al., 2001). To a lesser extent, mangroves may be used as a corridor between habitats or as a refuge (Hogarth, 1999). Some waders for example, seek refuge in mangroves during high tide, returning to feed on adjacent mudflats at low tide, and mangroves are a principal roosting habitat for flying foxes in the Top End of the Northern Territory.

Early research on mangroves largely focussed on plant assemblages and by the 1980's it was recognised that the flora had been relatively well studied, whilst faunal communities were still quite poorly known (Hutchings and Recher, 1983). At this time, it was noted that mangrove fauna in tropical areas, particularly the Northern Territory and the north west of Western Australia had been particularly neglected. Few studies have specifically focussed on mammal fauna in mangrove habitats in Northern Australia. An early review noted "In northern Australia the mammalian populations of rats (native and introduced), of mice, and of flying squirrels (Phalangeridae) have from time to time been seen in mangal forests" (Saenger et al., 1977). Hutchings and Saenger (1987) noted the lack of detailed information on the terrestrial fauna living in mangroves and commented that "terrestrial biologists seem reluctant to work in mangroves!". Surveys of the vertebrate and invertebrate fauna of mangroves in the Kakadu region were conducted between 1979 and 1982 but the final results were never formally reported (Hegerl et al., 1979; Hegerl et al., 1982). Reconnaissance work on the East Alligator river in Kakadu National noted mammal traces indicating that rodents and possums inhabited mangrove habitats (Hegerl et al., 1979). During a later survey in the same area, feral animals were observed in mangroves including buffalo (which grazed a variety of mangrove species), dingoes and pigs, which used the mangroves for shelter (Hegerl et al., 1982). Trapping at four sites by Hegerl et al. (1982) recorded only one mammal species, the native rodent *Melomys burtoni,* which was abundant on a small intertidal island but sparse on adjacent riverbanks.

Our knowledge of mangrove fauna in northern Australia has progressed little in the two decades since Hutchings and Recher (1983) identified the need for basic inventory, distribution and abundance data. Very few studies of mangrove fauna have been

conducted in northern Australia and prior to commencement of the work described here, the Kakadu survey remained the only Northern Territory study of mangrove vertebrate and invertebrate fauna. This situation is not uncommon elsewhere throughout the tropics however, with surveys of biological diversity in mangroves, and wetlands in general, receiving very little scientific attention (Gopal and Junk, 2000; Kathiresan and Bingham, 2001).

Nevertheless, there has been sufficient research (Macnae, 1968b; Hutchings and Recher, 1974, 1982), and synoptic reviews of those studies (Saenger et al., 1977; Hutchings and Recher, 1983; Hutchings and Saenger, 1987), to indicate that a considerable variety of terrestrial fauna utilise mangrove habitats on some occasions. Information on the distribution and abundance of these fauna is, however, needed to improve our understanding of ecological interactions between terrestrial and aquatic species: for instance, the role of terrestrial fauna in mangrove food webs. Such information is a necessary step in understanding the role of mangrove communities in the wider context of estuaries, and the conservation of coastal resources.

Over the last few decades, the conservation of biological diversity has received increasing attention at a global level. Furthermore, Australia ratified the Global Convention on Biological Diversity (CBD) in 1983 and this resulted in the National Strategy for the Conservation of Australia's Biological Diversity (Anon, 1996) and other Commonwealth policies which have increasingly recognised mangroves as centres of biological diversity. In the development of the national strategy, mangrove habitats were identified as one of five special components of Australia's terrestrial biological diversity. Mangrove habitats were considered on a par with the rainforests of north Queensland and the botanical province of South-western Australia (Anon, 1994). Such recognition clearly underscores the need to document adequately the biological diversity of mangrove ecosystems.

Although the terrestrial vertebrate fauna (frogs, reptiles, birds and mammals) of upland habitats in the Top End has been well reported in numerous comprehensive biological surveys over the last 20 years (Woinarski and Braithwaite, 1990; Woinarski, 1998; Fisher and Woinarski, 2002; Brennan et al., 2003; Woinarski et al., 2003), these surveys rarely extended into intertidal areas and data concerning the terrestrial vertebrate fauna of mangroves is sparse. The first specific survey of vertebrates in Northern Territory

mangroves was prompted by the expansion of Kakadu National Park, but this work targeted only the small mammals of the East Alligator River (Hegerl et al., 1982). Although substantial contributions on mangrove birds have been made since that time (Noske, 1996; Franklin and Noske, 2000; Noske, 2001), no comprehensive surveys of the total vertebrate assemblage in mangrove habitats have been conducted.

By contrast, the fauna of monsoon vine-forest (rainforest), for instance, has been relatively well-studied, despite its small total area (258 km^2)—less than 1/5 of the total area of mangrove in the NT (Fensham and Woinarski, 1992; Menkhorst and Woinarski, 1992; Woinarski et al., 2003). Mangroves, however, are not as threatened as rainforests (which are subject to factors such as fire and feral animals) and few vertebrate species are mangrove-specific, most having wider distributions through neighbouring habitats (Hutchings and Saenger, 1987; Hogarth, 1999). Nevertheless, many transient species are dependent on mangroves for resources necessary to complete their life-cycles (Milward, 1982). Mangroves may also provide temporary roosts and shelter for birds and fish, during high tides for instance, or more permanent habitat for species requiring dense vegetation. Indeed, the 'refuge' function of mangroves is likely to be increasing in importance due to widespread clearing in terrestrial habitats—the distributions of several endangered South American species have contracted to mangrove habitats which have become their remaining primary shelter (Lacerda et al., 2001).

In Australia, where large areas of reasonably intact mangroves still remain, it will be difficult to formulate management and conservation priorities without an adequate knowledge of the patterns of faunal diversity and the importance of mangroves for both transient and resident vertebrate species. One of the goals of this research was to increase our knowledge of the diversity, distribution and abundance of the main vertebrate groups occurring in mangrove habitats in the Northern Territory.

Aim

The aim of the work in this chapter was to complete a comprehensive survey of the terrestrial vertebrate fauna occurring in three undisturbed mangrove sites in Darwin Harbour (Sites E1, E2 and M3, described in Chapter 2). The vertebrate groups selected for study were:

- Arboreal and ground mammals
- Bats
- Birds

Bats are considered separately from other mammals due to their high vagility and different sampling techniques. Terrestrial and marine reptiles (crocodiles, turtles, lizards) were not studied and neither were marine mammals (dugongs, dolphins). Fish were studied but are included in Chapter 5 (Invertebrate fauna) with other species of marine origin.

The specific objectives of the survey were:

- To conduct mammal trapping to document the diversity, distribution and abundance of mammals and test for spatial and annual patterns
- To document avian diversity, distribution and abundance and test for spatial, annual and seasonal patterns.
- To investigate avian feeding guilds and the vertical and horizontal partitioning of mangrove bird distribution.
- To conduct a preliminary study of mangrove bat diversity and distribution and to test for spatial and seasonal variation.

Thus the primary aim of these combined surveys was to characterise the diversity, distribution and abundance of vertebrate fauna of undisturbed mangroves. The second aim was to provide results enabling tests of the effects of disturbance (examined in Chapter 4) and which can be placed within the context of terrestrial habitats elsewhere in the Top End.

3.2. Methodology

As far as possible, standard wildlife survey methods (NRETA or Department of Natural Resources, Environment and the Arts) were used for the vertebrate fauna surveys. Methodological consistency allows the data attained to be directly compared with other survey results from terrestrial and wetland habitats elsewhere in the Northern Territory, as well as contributing to the NT fauna database. However, mammal trapping in this study was conducted over 4 nights rather than 3 nights as is usual in NRETA surveys (Woinarski et al., 2003). Due to the huge effort involved in placing over half the traps in trees (due to tidal flooding in low intertidal assemblages), it was decided to maximise the amount of information obtained from each site by trapping for an extra night. Other

minor modifications to the methods employed in terrestrial surveys were essential in mangrove habitats, where the tidal range exceeds 7 m. For instance, the 20 L pitfall traps and drift-lines used to trap small mammals in terrestrial surveys could not be used in areas subject to regular tidal inundation. Also, nocturnal surveys of mammals were not conducted.

Most fauna data were collected from within 50 m × 50 m study plots: this is the standard size used by NRETA for the majority of its fauna and flora surveys across the NT. Study plots were placed along two parallel transects at each site. Each transect consisted of four study plots, one in each of the four mangrove assemblages (Chapter 2, Figures 2-4, 2-5 and 2-6). Incidental observations, made both within and outside the study plots, were used in the compilation of species inventories but this data was not included in statistical analyses.

~3.2.1. Mammal trapping

Fieldwork

Mammal trapping in each study plot used four wire cage traps (56 × 20 × 20 cm, bait-hook mechanism), two large aluminium box-type or 'Elliot' traps (46 × 15.5 × 15 cm, treadle mechanism), and 18 small Elliot traps (33 × 10 × 9 cm, treadle mechanism). The four wire cage traps were placed on the corners of the plot and the 20 Elliot traps were evenly spaced, five on each side, around the perimeter. Trapping was conducted one transect at a time (96 traps total), for four consecutive nights during the neap tidal cycle. Trapping was done in the neap cycle to reduce the number of traps that had to be placed above ground level. Successfully attaching traps to trees was not only difficult but very time-consuming and it was better to have as many traps as possible on the ground in order to catch ground-dwelling species. Consequently, all traps set in the hinterland margin, and the majority of those in the tidal flat, were placed on the ground. In both the tidal creek and seaward assemblages, traps were attached to trees, above the level of predicted overnight high tides.

Traps that were attached to tree branches were secured using a combination of zip-ties, flagging tape and tie-wire. Reconnaissance trips were made by canoe during tides of particular heights in both the tidal creek and seaward communities to select and mark

tree branches at suitable elevations for mammal traps. Care was taken to select branches that could easily be reached by climbing because at the conclusion of each 4–night program the traps were often retrieved on foot at low tide. Typically, both seaward study plots were accessed by canoe during morning high tides. On the fourth day, traps were collected and moved to the adjacent, replicate transect for a further 4 nights trapping.

To attract a range of fauna, several different baits were used: oats and peanut-butter mix; fresh fish; apples; and oats mix plus sardines. Each Elliot trap was labelled to indicate its bait type, to ensure the same proportion of bait types was used each night. Traps were rebaited and reset each morning as they were checked. Mammals caught were marked (fur and/or tail was marked with waterproof felt pen), so that recaptures could be identified, and released, after recording sex and the type of bait. Any species which could not be reliably identified in the field was retained, identified by an authority and released at the same location the following day.

High neap tides (from about 5 to 6 m Darwin Chart Datum) occurred during the middle of the night and the middle of the following day, becoming later by approximately one hour per day. Trapping occurred on eight consecutive days, when tides did not exceed 2.5 m AHD (or 6.5 m Darwin Chart Datum): inundating only those mangrove assemblages occurring to seaward of the tidal flat (see Figure 2-2, Chapter 2).

Trapping only on neap tides may introduce some bias. For instance, some species may move up-shore during spring tides and, although unlikely, it is possible that some vertebrates only enter the mangroves during such times. Spring tides, however, submerge the majority of the tree canopies in the seaward assemblage making trapping impossible. Surveys were run for two years (1999 and 2000) but due to time limitations, only during the dry season.

Prior to commencing fieldwork, approval was gained from the Animal Ethics Committee to undertake non-destructive sampling of vertebrate species for scientific research (No. A99017). A permit to trap animals within a Northern Territory National Park (Permit No. 7663) was also gained from the Parks and Wildlife Commission of the Northern Territory (PWCNT) for research within Charles Darwin National Park.

Analysis

Methods of reporting trap capture data appear to vary among researchers and among projects with different objectives. Trappability has been defined as captures per 100 trap nights (Begg et al., 1983; Kerle, 1998) and a variation of this formula is used to reflect habitat favourability (Kerle, 1985). Trap success has also been reported as the ratio of the total number of captures to the total number of traps set (trap nights), expressed as a percentage (Woinarski and Braithwaite, 1990). The latter measure was adopted in this study to facilitate comparison with PWCNT data, in which trap success is synonymised with mammal abundance (Woinarski et al., 2001).

The total number of species (species richness) and the mean abundance of all animals was tallied for each of the 24 study plots. Mean abundance of individual species was calculated as follows:

$$\text{Mean abundance} = \frac{\text{total captures in all plots (over 4 nights)}}{\text{total number of plots sampled}}$$

Deriving mean abundance from total captures per 0.25 ha study plot, follows standard PWCNT methodology and in this instance, as each survey spanned 4 nights, the value obtained is also the equivalent of the mean number of animals caught per hectare. To establish precise density values for each mammal species would require a population study that permanently identified individuals (using techniques more reliable than waterproof marking pen) to accurately calculate recapture/capture ratios and determine home ranges (Begg et al., 1983; Kerle, 1998). Although recaptured animals were noted and abundance data are slightly lower when this is taken into consideration, only the tallies of total captures per study plot are used so as to be consistent with most NRETA reports and data in the NT fauna database.

Species richness and abundance data from trapping surveys were compared between years, sites and assemblages using a 3 factor nested ANOVA, with year and assemblage as fixed factors and site as a random factor. In this design the data are pooled for the four nights for each study plot. The replicates are thus the transects as there is only one study plot in each assemblage, on each transect. ANOVA assumptions were tested by graphical methods including residual plots and variance *vs* means plots (McGuinness, 2002b). Raw data were examined for homogeneity of the variances by examination of

plots of means *vs* standard deviations and re-examined after transformation. In general, abundance data were transformed ($\log_{10}(x + 1)$). Plots of residuals were also examined before and after transformation as a check for non-normality. ANOVAs for mammal abundance and similar analyses for species richness were calculated using *Statistica* version 5.5 (Statsoft Inc).

To summarise patterns in mangrove mammal composition and abundance, data were analysed using the hierarchical clustering into sample groups (CLUSTER) and ordination by non-metric multi dimensional scaling (NMDS) procedures in the *Primer* version 5 (Primer-E Ltd) program (Clarke, 1993). Study plots were classified according to their species composition using clustering based on a Bray-Curtis sites by species similarity matrix with each analysis run from 50 random restarts.

~3.2.2. Bat surveys

Comprehensive surveys of Microchiropteran bats (micro-bats) require trapping (harp nets, trip lines and mist nets), supplemented by the use of electronic bat detectors, active searches of roost sites (de Oliveira, 1998), and occasional shot sampling (Milne et al., 2005). Due to time and logistical constraints, this survey used only a hand held ultrasonic bat-detector (*Anabat II,* Titley Electronics) operated during censuses of 10–minutes duration conducted within 5 hours of sunset.

Anabat detectors convert ultrasonic calls produced by echolocating micro-bats into audible signals. On hearing a bat call, the detector was pointed in the direction of the call and the signals were recorded onto 90–minute cassette tapes (*Sony* Chrome UX). Dedicated *Anabat* computer software was used to process recorded calls into time frequency graphs from which identification to specific level was generally possible if the acoustic signature was known. All bat calls recorded during this survey were identified by Damian Milne from the Biodiversity Unit (NT Department of Infrastructure, Planning and Environment) through comparison with an extensive library of reference calls from Top End bats (Milne, 2002). Although a substantial body of work on mangrove bats has been done in north Western Australia (McKenzie and Rolfe, 1986; McKenzie and Start, 1989), I am not aware of any previous trapping or electronic surveys of bats in mangrove habitats in the Northern Territory.

Bat surveys were done at each study site between mid 2000 and mid 2001, at three different times of year (June, dry season; November, early wet season; and February, wet season). During each survey, two 10–minute censuses were done within each of the 24 study plots. Environmental variables were recorded at the same time and included temperature and relative humidity (Whirling psychrometer, *G H Zeal Ltd*), visual estimates of cloud cover, moon phase and the relative abundance of flowering trees (all estimates were reported as percentages).

Surveys at the three sites were conducted on consecutive nights and typically completed between 18:45 hours and midnight. A single pre-dawn survey was conducted as an activity comparison, at site E1. A total detection/observation period of one hour per study plot (2 censuses of 10 minutes duration over 3 seasons) was obtained during this study. As such, the study represents a brief snapshot of bat diversity and the results obtained should be interpreted appropriately.

The electronic sampling technique provides data on bat species richness and activity but is not a reliable indicator of abundance. For instance, it is not possible to distinguish the call sequences of a single bat making numerous passes from single passes by several bats. Similarly, numbers of passes is not necessarily an accurate indication of numbers of bats due to possible differences in foraging behaviour: for instance, continuous aerial foraging *vs* hunting from perches (Fenton, 1982). Consequently, abundance data for bats was not generated by these surveys. Furthermore, macro-bats (flying foxes and blossom bats) do not echolocate, and records for these bats could only be obtained visually. If flying foxes (*Pteropus* spp.) were observed within particular mangrove habitats during the 10–minute censuses their presence was noted. Flying foxes merely flying over a site and not utilising the assemblage were not recorded.

Occasionally bat calls could not be reliably identified due to the quality of the recording or an unknown acoustic signature. Unfortunately, the *Anabat* call signatures of two pairs of relatively common species in the Northern Territory cannot be reliably separated: *Scotorepens greyii*/*Chalinolobus nigrogiseus* and *Pipistrellus westralis*/*Miniopterus schreibersii* (Milne, 2002; Milne et al., 2005). Calls attributed to these species pairs were, however, included in analyses of species composition and distribution as the former comprises a substantial proportion of bat activity (Table 3–3). ANOVAs were based on pooled results (from both 10 minute censuses within each 0.25 ha study plot). Analyses were

four factor nested ANOVA comparing bat species richness between seasons (fixed, 3 levels), sites (random, 3 levels), transects (random, 2 levels, nested in site) and assemblages (fixed, 4 levels).

Product-moment correlation in *Statistica v5.5*.was used to examine correlations of bat species richness with environmental variables. Correlations were based on data recorded during each 10–minute census within each study plot. Although the above species pairs were included in all analyses, undetermined bat species were excluded. Relationships between the sampling sites with respect to their bat species composition were examined by ordination techniques using multi-dimensional scaling in the *Primer* version 5 program (Primer-E Ltd). Study plots were classified according to their bat species composition using clustering based on a Bray-Curtis sites by species similarity matrix with each analysis run from 50 random restarts.

~3.2.3. Bird surveys

Bird surveys were conducted concomitantly with mammal trapping during the dry season of 1999, and again in 2000, and were also done in the wet seasons of 1999–2000 and 2000–01. Species were identified and counted by one observer during censuses of ten minutes duration within each 0.25 ha study plot. During each census, the observer remained stationary for the first five minutes then wandered randomly through the study plot for the remaining five minutes. Species were detected by their calls as well as by direct observation. Only birds using the study plot were included. Birds merely flying through or over the site were excluded except in circumstances where aerial species (raptors, martins or wood-swallows) were clearly hawking or hunting overhead.

An *Audubon* bird calling device (which creates a high-pitched squeaky sound) was also used intermittently during each 10 minute census, successfully attracting a range of bird species from within the plot. This technique helped to identify birds in dense vegetation and difficult terrain. It is possible that using the caller could introduce bias (perhaps toward particular bird species) but it was used consistently during all surveys.

Calls and call emulators (such as playback recordings) have been used in avian surveys for many decades and can greatly assist accuracy and efficiency (Johnson et al., 1981). These are a practical way of detecting elusive birds in dense habitats (Marion et al.,

1981). Although Johnson et al. (1981) did not discuss generic bird calling devices such as the *Audubon* caller used in this survey, they did note that auditory broadcasts (tape-recorded calls of particular species) do increase the number of birds counted. They considered, however, that the only birds attracted were those in close proximity that would normally be overlooked in a conventional survey. The same appeared to be true during this survey.

The total observation period per survey at each study plot was 40 minutes (4 censuses of 10 minutes duration). This is a total of 2.5 hours per study plot, over the four sample periods. The majority of censuses were completed between 0645 and 1200 hours, but, consistent with NRETA survey methodology (Woinarski et al., 2003), some counts were done later in the day. Most surveys were done during low tide, but a substantial number of dry season surveys were done at high tide in the seaward assemblage, when mammal traps were being checked by canoe. Any foraging activities observed during censuses were recorded in terms of the foraging niches and techniques listed in Table 3-1. Any species observed nesting within mangrove habitats was also noted.

Table 3-1 :Height, technique and site categories for documenting bird foraging observations, following Noske (1995; 1996)

Height category		**Site**	**Technique & description**	
0			Pounce	Leave perch and grab prey from ground
1	0 – 1.0 m	Flower	Probe	Insert bill into cavity of flower or plant
2	1.1– 2.0 m	Fruit	Glean	Take stationary prey while perched
3	2.1– 4.0 m	Leaf	Hawk	Chase and take flying prey
4	4.1– 8.0 m	Branch	Snatch	Take stationary prey during short flight
5	> 8.0 m	Trunk	Perch	Observing prey while stationary
5		Air	Forage	Search for prey while moving (eg. raptors)

Description of the tests for ANOVA assumptions undertaken prior to analysis of bird data are found in the previous section on mammals. Data for species richness and abundance for birds did not require transformation. Similar to the data for mammals, results from each of the four censuses was tallied for each study plot and the pooled data were used in ANOVA. The degree of heterogeneity of the variances in abundance data for individual species (eg. red-headed and brown honeyeaters) were, however, improved by $\log_{10}(x + 1)$ transformation prior to analyses. Bird species richness and

abundance was compared between years, seasons, sites and assemblages using a 4 factor nested ANOVA with year, season and assemblage as fixed factors and site and transect (nested in site) as random factors. The replicates in this case were the study plots. Non-metric multi dimensional scaling (NMDS) procedures in the *Primer* version 5 program (Primer-E Ltd) were used to generate dendrograms and ordinations to illustrate community patterns in bird species composition. Season and assemblage were used as factors in ordinations to illustrate subsets of the data.

~3.2.4. Incidental records

Birds observed at times not during censuses, either in the vicinity of a study plot or within one of the assemblages under study, were recorded as incidental records for that site. Several incidental records were acquired when ground-dwelling bird species were inadvertently caught in mammal traps (notably the Chestnut Rail and Buff-banded Rail) and several nocturnal species were recorded during bat surveys.

3.3. Results

~3.3.1. Mammal trapping

Trap success

During the 1999–2000 surveys, a total of 558 mammals was captured from the 24 study plots over 4,608 trap nights. Site E1 (Charles Darwin National Park) had over twice the number of captures (296) as sites E2 (140) and M3 (120). Overall trap success for the three sites was 12.1% and of the 24 study plots sampled, the highest mean trap success was 29.2% from tidal flat habitat at site E1 (Table 3-2). The lowest trap success for any study plot was 0.5%, recorded in similar habitat at site M3.

Overall trap success was about 30% higher during 2000 (14.7%) than in 1999 (9.7%). Three animals drowned (two *Melomys burtoni* and one *Trichosurus vulpecula),* when tides reached unexpectedly high levels in the forest.

Table 3-2: Total captures of all species in each assemblage at 3 study sites; trap success (captures per 100 trap nights); and mean trap success (%) in 1999 and 2000.

Site	Assem-blage	captures per assem*	captures per assem*	1999 trap success (%)	2000 trap success (%)	mean trap success (%)
		1999	**2000**	**1999**	**2000**	
E1	HM	18	28	9.4	14.6	**12.0**
E1	TF	39	56	20.3	29.2	**24.7**
E1	TC	43	49	22.4	25.5	**24.0**
E1	SW	32	34	16.7	17.7	**17.2**
E2	HM	6	22	3.1	11.5	**7.3**
E2	TF	9	26	4.7	13.5	**9.1**
E2	TC	20	35	10.4	18.2	**14.3**
E2	SW	4	16	2.1	8.3	**5.2**
M3	HM	8	18	4.2	9.4	**6.8**
M3	TF	14	1	7.3	0.5	**3.9**
M3	TC	17	24	8.9	12.5	**10.7**
M3	SW	9	30	4.7	15.6	**10.2**
	Mean	**219**	**339**	**9.5**	**14.7**	**12.1**
* Data from two study plots pooled for each assemblage**.**						

Species richness

Mean richness was 2.08 (± 0.13 SE) species per plot with a total of nine native and four introduced species recorded. Nine species were captured and four recorded only from tracks and traces (see Table A-1, Appendix A, also containing data from Chapter 4). The most diverse groups were the rodents (4 species) and the dasyurids (2 species). The mangrove mammal fauna was dominated by two native species: Grassland Melomys, *Melomys burtoni* and Common Brushtail Possum, *Trichosurus vulpecula* (Figure 3-1). Together, these two species comprised 89% of all captures (Figure 3-2). *M. burtoni* was trapped in 23 of the 24 study plots and in 64% of 192 replicate study plots. Only two introduced species were trapped (Black Rat, *Rattus rattus* and Feral Cat, *Felis catus)* comprising 0.3% of the fauna.

Although four introduced species were recorded, they did not comprise a large proportion of the fauna. Introduced animals recorded during the current survey included single captures of a cat (*Felis catus*) in the tidal flat assemblage at M3 and a black rat (*Rattus rattus*) on the edge of the hinterland at site E1. In landward mangroves, tracks of dingoes or wild dogs were occasionally observed and less frequently, tracks of wild pigs. Dingo tracks were indistinguishable from those of wild dogs, so were

grouped together (dingo/dog) and assumed to be an introduced species.

Figure 3-1: Mammal species and trapping techniques in mangrove habitats in Darwin Harbour. a) Common brushtail possum (*Trichosurus vulpecula),* b) the Grassland Melomys *(Melomys burtoni); c) M. burtoni* is an agile climber with a partially prehensile tail and d) is an adept swimmer above and below the surface, e) Water rats (*Hydromys chrysogaster)* are cryptic and seldom trapped, f) Elliot traps fixed above high tide level in *Ceriops australis* forest, g) bandicoots (*Isoodon macrourus)* were common in the hinterland margin assemblage, h) Flying foxes (*Pteropus alecto)* visited seaward zones and i) seaward assemblage traps were checked by canoe.

In contrast with *M. burtoni* and *T. vulpecula,* which occurred throughout all mangrove assemblages, the majority of other species were largely restricted to the hinterland margin. The Northern Brown Bandicoot, *Isoodon macrourus* and the Northern Quoll (*Dasyurus hallucatus)* were relatively common in mangroves fringing the hinterland, but the remaining species mostly comprised isolated captures, generally in close proximity to terrestrial habitats. The Black-footed Tree-rat (*Mesembriomys gouldii*), Fawn Antechinus (*Antechinus bellus*) and Pale Field-rat (*Rattus tunneyi)* were represented by less than 5 records each.

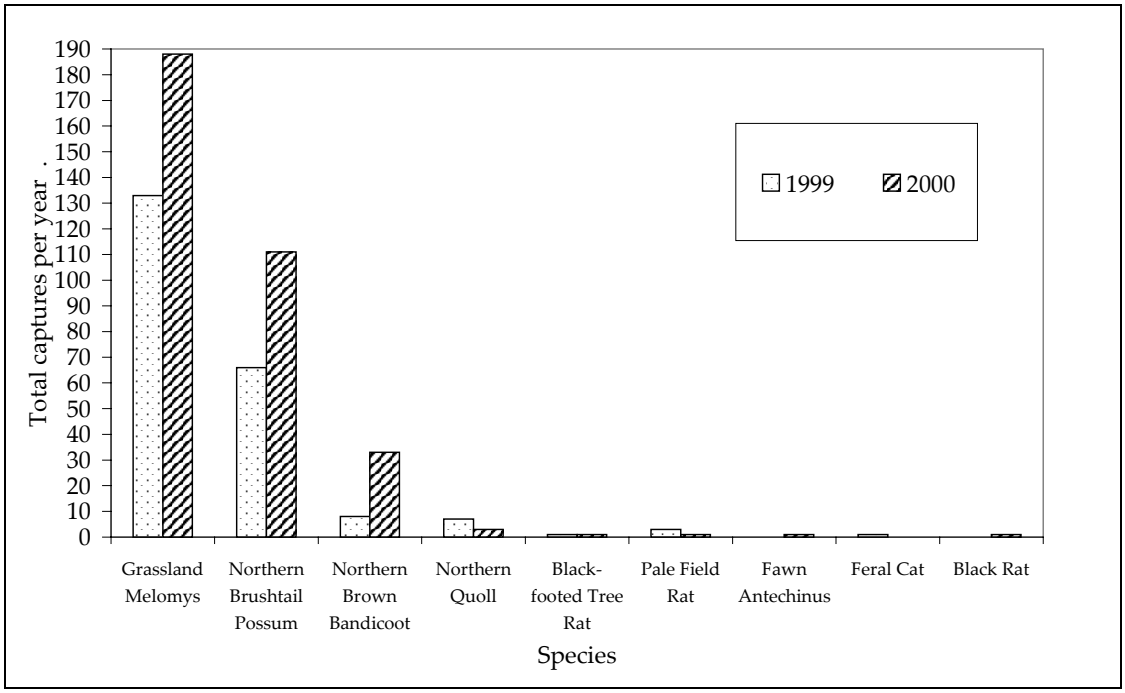


Figure 3-2: Total number of mammal species captured during trapping at 3 undisturbed sites in Darwin Harbour during 1999 and 2000.

While water rats (*Hydromys chrysogaster)* were not captured during these surveys, tracks and other traces indicated they were present in study plots in lower intertidal areas. The rare false water-rat (*Xeromys myoides)* and widespread sugar-gliders (*Petaurus breviceps)* were not recorded from the sites used in this study.

Analysis of variance indicated that species richness varied significantly among assemblages (Figure 3-3a; Appendix A: Table A-2).

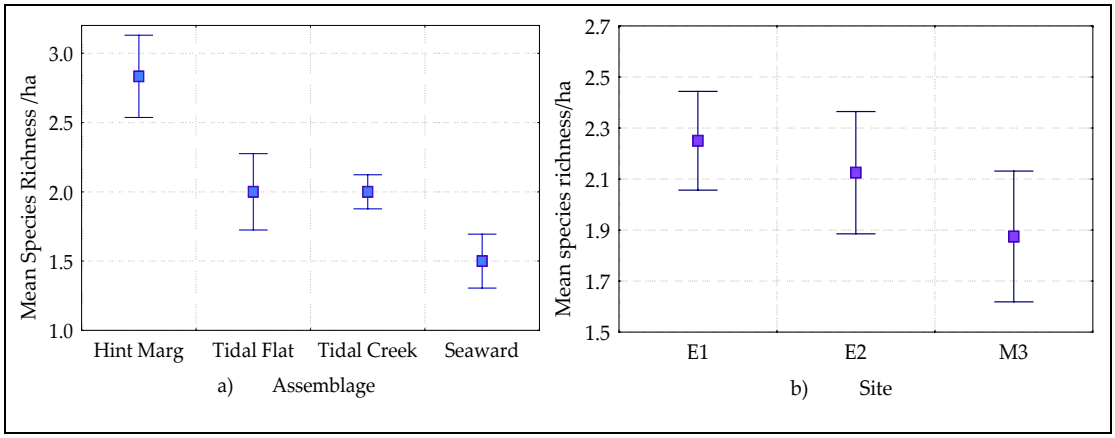


Figure 3-3 : Plots of mean species richness per hectare (± standard error, SE) showing a) significant difference between assemblages, indicating decrease from landward to seaward and b) non-significant differences between 3 study sites.

From the means it appears that richness was greatest in the hinterland margin, least in

the seaward zone and intermediate at the tidal flat and tidal creek assemblages. Species richness was uniform across sites (Figure 3-3b) and did not differ greatly between years (Appendix A: Table A-2; Figure 3-2).

Mammal abundance

Overall, the mean abundance of mammals trapped during 1999 and 2000 was 11.6 animals ha^{-1} (± 1.1 SE) (Table A-1, Appendix A). *M. burtoni* was the most abundant species with 6.7 animals ha^{-1} (± 0.9 SE) followed by *T. vulpecula* at 3.7 ha^{-1} (± 0.6 SE). When recaptured animals were excluded from counts per study plot, the mean abundance decreased to 8.4 animals ha^{-1} (± 0.8 SE). Although mammal species richness clearly decreased along the landward to seaward gradient (Figure 3-3), mammal abundance did not reflect this pattern with surprisingly high mean density (15.7 animals ha^{-1} ± 2.4 SE) recorded in the tidal creek assemblage (Figure 3-4). On several occasions in this assemblage, two *Melomys* were caught in the same Elliot trap, and each of the four cage traps contained *T. vulpecula.*

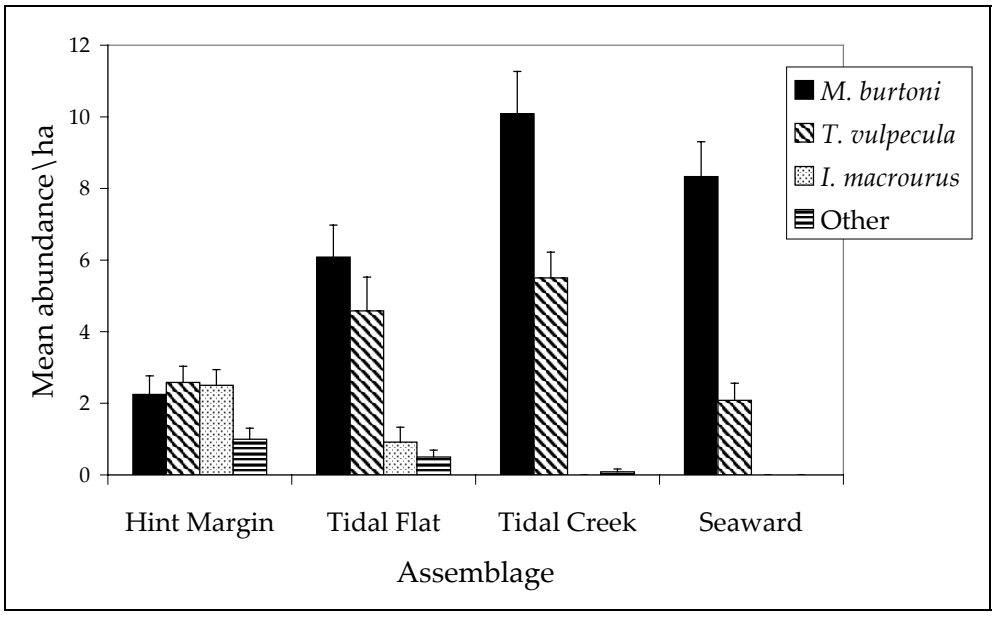


Figure 3-4: Mean abundance of mammals in four assemblages, from landward (L) to seaward (R) during 1999 and 2000. Graph shows means of total captures from 3 study sites (expressed as animals per hectare ± standard error).

ANOVA results indicated mammal abundance was significantly different between sites (Table A-3, Appendix A) and graphs of means show the highest numbers of animals were recorded at site E1 (Figure 3-5a). Annual variation in mammal abundance was also detected between sites, largely due to significantly lower abundance at site E2 in 1999

compared with 2000 (Table A-3, Appendix A; Figure 3-5a). Mammal abundance in assemblages varied between sites and was markedly lower in the tidal flat at site M3 than at sites E1 or E2 (Figure 3-5b).

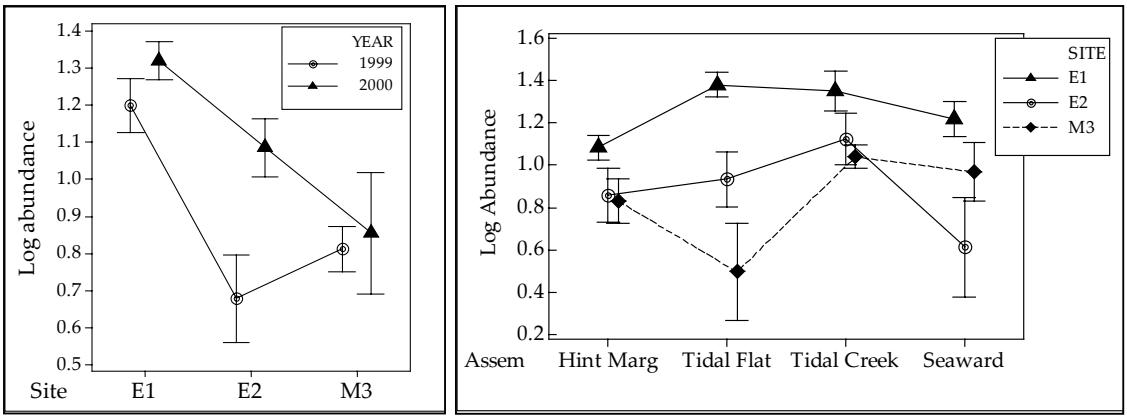


Figure 3-5 : a) Mean abundance ($\log_{10}(x + 1)$ transformed total captures at the three sites, ±SE) over 2 years (left) and b)Mean abundance ($\log_{10}(x + 1)$ transformed total captures over 2 years ±SE) in four assemblages from landward (L) to seaward (R), at the three study sites (right).

The NMDS plot of mammal abundance illustrates the overall patterns in mammal species composition and abundance (Figure 3-6).

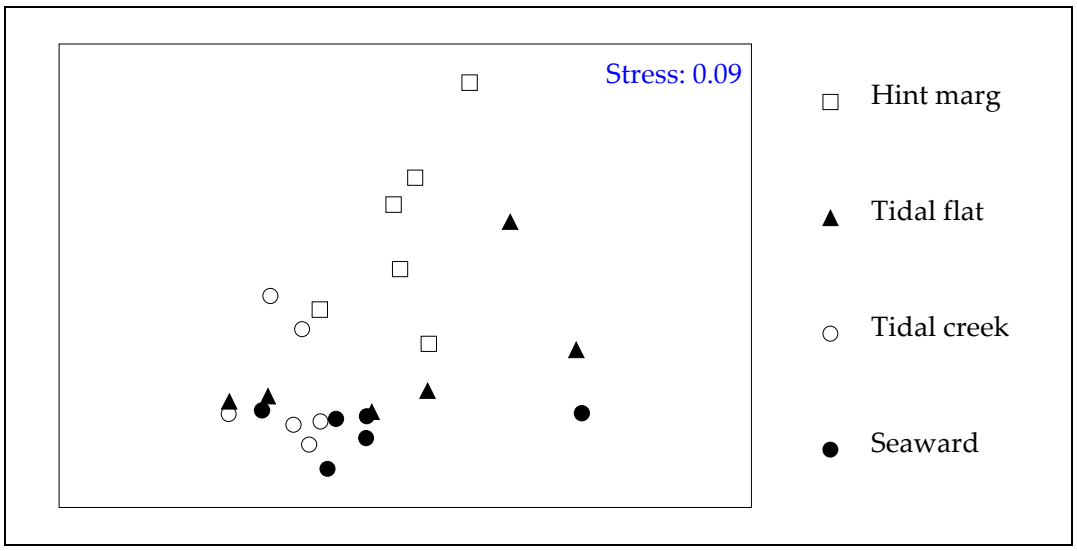


Figure 3–6: NMDS plot of mammal species abundance in the 24 study plots at the three study sites. Ordination is based on total abundance of mammal species within each study plot recorded during trapping in 1999 and 2000.

Each point on the plot represents one of the 24 study plots and these fall roughly along a seaward to landward gradient, from lower left to upper right. Sites with similar faunal assemblages are somewhat grouped, with study plots in the lower intertidal zone (diamonds and upward triangles) more tightly grouped than those to landward

(squares and downward triangles). Some of the tidal flat plots are grouped with those from the tidal creek, and some hinterland margin plots intergrade with those from tidal flat and tidal creek habitats. Overall, the MDS distinguishes the relatively diverse, but sparse fauna of the hinterland margin sites from the less diverse, high density fauna of sites in the lower intertidal zone.

~3.3.2. Mangrove bat diversity

Ten bat species from four families were detected from the three sites (Table A-4, Appendix A). The insectivorous micro-bats (Family Microchiroptera) were the most speciose (8 species). Two species of Megachiropterean bats (Northern Blossom Bat and the Black Flying-fox) were recorded by direct observation. Vesper bats (Family Vespertilionidae) comprised 40% and Freetail bats (Family Molossidae) 30% of the species recorded.

Most bat activity, indicated by the percentage of total number of calls recorded across all 3 surveys, was in the dry (44%) and late dry seasons (32%) and least during the wet season survey (24%). Overall, bat activity (or frequency of calls/observations) was highest in the seaward assemblages (mainly due to the high frequency of macrobats)and least in the tidal flat assemblage (Table 3-3).

Table 3–3 : Frequency of bat species recorded in different assemblages during three surveys

	Assemblage			
Bat Species	**HINT MARGIN**	**TIDAL FLAT**	**TIDAL CREEK**	**SEAWARD**
Unknown	2	4	5	2
Scotorepens greyii/Chalinolobus	10	5	2	
Mormopterus beccarii	1	2	1	2
Pipistrellus westralis	3	2	2	
Miniopterus schreibersii	3			
Pipisrellus westralis/ M. schreibersii			2	
Nyctophilus sp.	2			
Saccolaimus flaviventris	1			
Myotis moluccarum (adversus)	1			
Chaerephon jobensis				1
Mormopterus loriae		4		1
Macroglossus minimus			1	2
Pteropus alecto			9	17
TOTAL	**23**	**17**	**22**	**25**

Analyses of variance of all bat species (excluding unknown call signatures but including indistinguishable species pairs) showed no significant differences in species richness between seasons, sites or assemblages (Table A-5, Appendix A). If the Megachiropterean fruit bats and blossom bats (ie *Macroglossus minimus* and *Pteropus alecto*) are excluded from the analyses however, a different pattern emerges. Mean species richness of micro-bat species varied significantly between assemblages: diversity appeared to decline steadily from the hinterland margin to the lower intertidal assemblages (Figure 3-7, Appendix A: Table A-6).

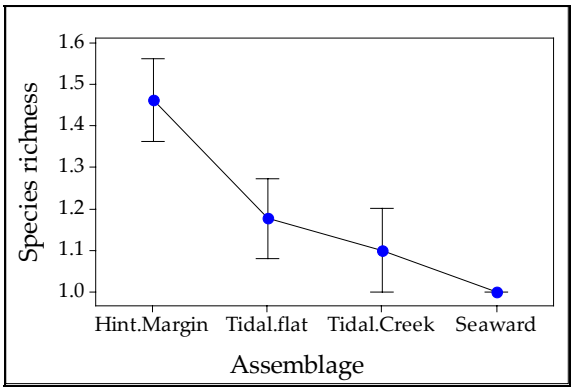


Figure 3–7: Mean species richness (± SE)of microbats recorded within the four assemblages from landward (L) to seaward (R). Points are mean numbers of species per study plot in assemblages, averaged over three seasons.

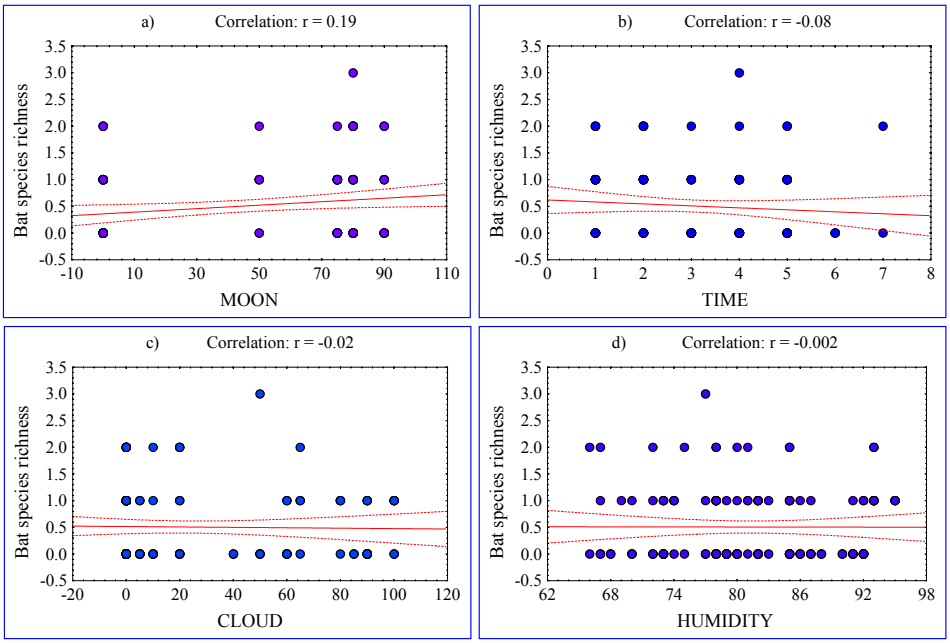


Figure 3-8: a) Significant correlation between bat species richness and phase of the moon (%) and b) non-significant correlation between bat species richness and hours after sunset c) cloud cover and d) humidity. Points represent total numbers of species recorded during individual censuses within study plots at the three sites, during three surveys. Many points are not visible due to overlap.

Correlations between bat species richness and environmental variables (temperature, humidity, flowering of mangrove species, moon, cloud cover and time of night) showed a weak positive correlation with moon phase ($r = 0.19$, $p<0.05$, $n=144$; Figure 3-8). No other significant correlations were found for bat species richness.

Ordination of study plots on the basis of bat composition showed that the bat fauna in each of the four assemblages was reasonably distinct. There was some overlap however, of the bat fauna of the seaward assemblage, with the tidal creek (Figure 3-9).

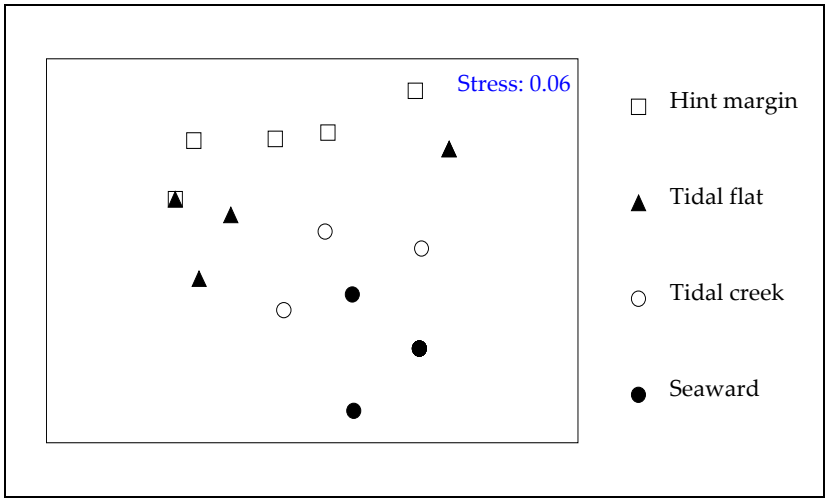


Figure 3-9: Ordination of sites based on bat species composition recorded within each of the 24 study plots, recorded during three surveys at the three study sites. Some plots are not visible due to overlap.

Overall, the sites generally fall along a landward (upper left) to seaward (lower right) gradient, with the bat fauna of the hinterland margin clearly distinguished from sites occurring lower in the intertidal zone.

~3.3.3. Mangrove birds

Bird surveys included 64 hours of observations, and provided a total of 1,101 records including 55 incidental observations. A total of 70 species of birds were recorded from the three undisturbed sites, including nine incidental species (Table A-7, Appendix A; this table also includes data from Chapter 4 on disturbed mangroves). This total included 14 waders, 7 raptors and 2 aerial species (wood-swallows and martins), the remainder being predominantly passerines inhabiting the mangrove forest. There were almost twice as many records during the dry season (621 records) as in the wet (380 records), and more during 2000 (521 records) than 1999 (480 records).

Species richness

All three sites had similar species richness with the number of species ranging between 50 and 54 species per year. Overall, the tidal flat assemblage had rather fewer species than the other three assemblages, all of which had similar diversity (Figure 3-10).

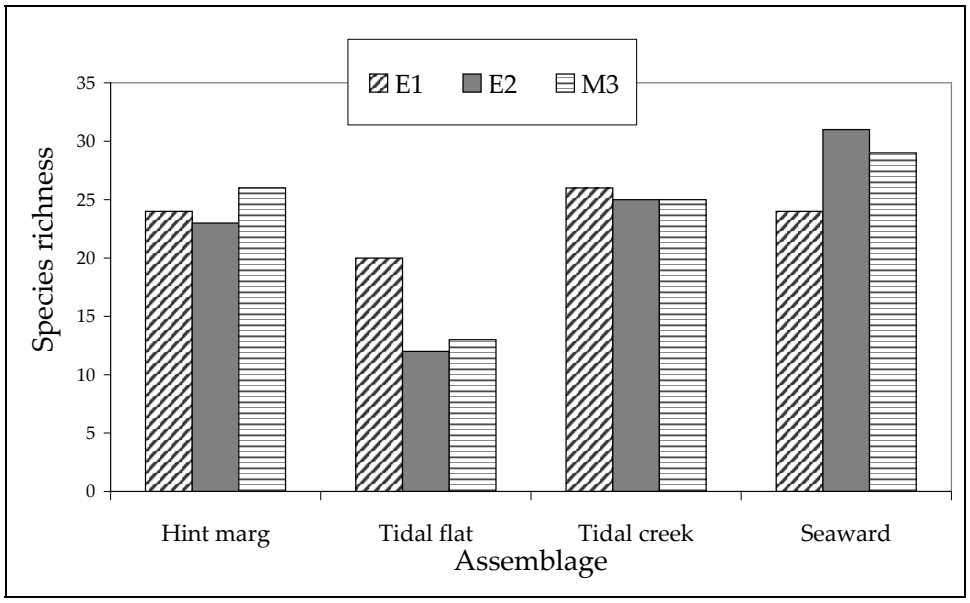


Figure 3-10: Total bird species richness per assemblage, at the 3 sites during 1999-2000

Although mean species richness appeared slightly lower at the three study sites during the wet season (Figure 3-11), the observed differences were not significant (mean dry = 6.8 birds ha^{-1} (± 0.3 SE); mean wet = 5.5 birds ha^{-1} (± 0.4 SE)

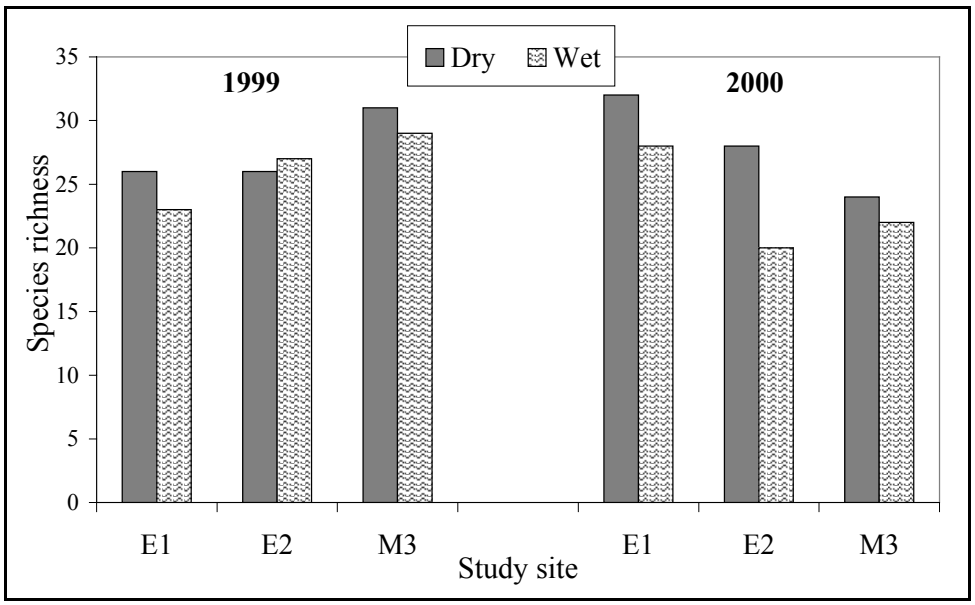


Figure 3-11: Total bird species richness per site (± SE) during wet and dry seasons of 1999 and 2000

Analyses of variance showed two significant main effects indicating differences in species richness between sites and between assemblages (Figure 3-12, Table A-8, Appendix A). From the means, it appears that site E1 had higher species richness than sites E2 and M3 (Figure 3-12, left). Mean species richness per plot was generally highest in assemblages in the lower intertidal zone and least in the tidal flat.

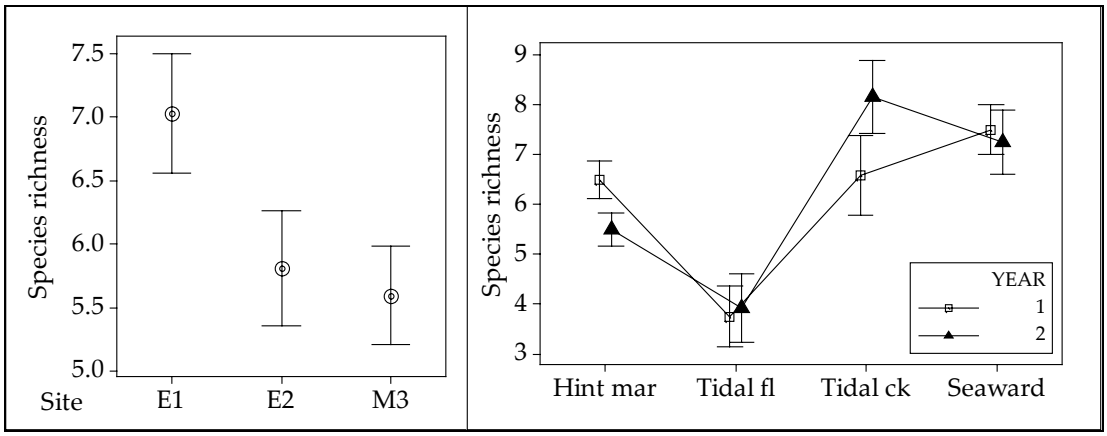


Figure 3-12: Variation in mean bird species richness (±SE) between the three study sites over 2 years (left) and between zones from year 1 (1999) to year 2 (2000). Points are means per study plot, recorded in wet and dry seasons.

There were two significant interactions: a year × assemblage and a year × season × site × assemblage interaction (Table A-8, Appendix A). The significant year × assemblage interaction indicates that bird species richness showed strong and consistent differences among assemblages, despite some differences between years for particular assemblages (Figure 3-12, right). For example, mean species richness was higher in the tidal creek assemblage in 2000 but was lower in the hinterland margin when compared with means for 1999. In general however, the same overall pattern was observed during both years.

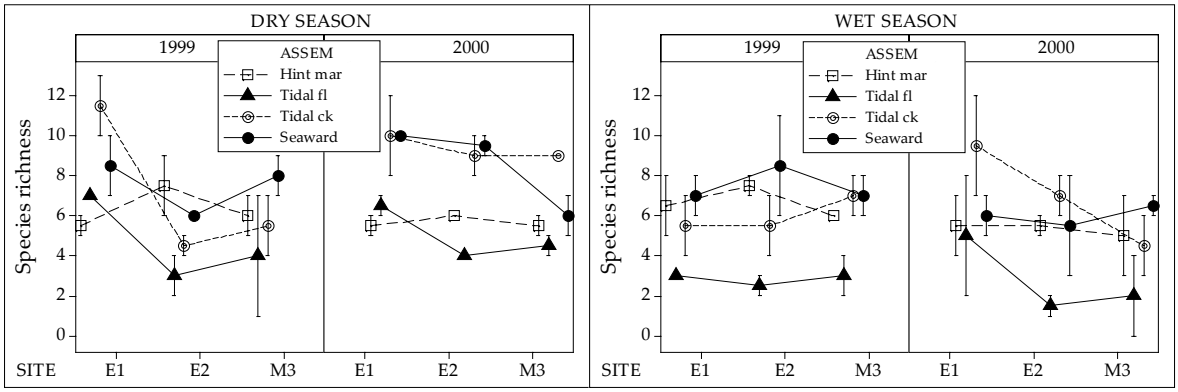


Figure 3-13: Mean species richness in the four assemblages during 1999 and 2000 during wet and dry seasons. Points represent mean species richness per study plot (± SE) at the three study sites.

Examination of graphs illustrating the significant year × season × site × assemblage interaction show no consistent trends in species richness (Figure 3-13).

Mangrove bird abundance

Of the 70 bird species, nine were common, with a mean abundance in any assemblage, of more than 1.0 ha^{-1} (mean abundance of every species is listed in Appendix A: Table A-7). The four most common species—in decreasing order of abundance, the brown honeyeater, red-headed honeyeater, yellow white-eye and lemon-bellied flycatcher—comprised 48% of all the birds counted. Overall, the mean density of birds across all sites was 15.8 (± 1.0 SE) ha^{-1}.

Analyses of variance for log abundance of birds showed a significant main effect for assemblage, season and for site (Table A-9, Appendix A). Mean numbers of birds per hectare were highest in the seaward (21.2 ± 1.8 SE) and tidal creek assemblages (18.6 ± 2.2 SE), and lowest in the tidal flat (10.1 ± 1.8 SE); the hinterland margin assemblage (13.3 ± 1.4 SE) was intermediate (Figure 3-14 left).

Abundance varied between sites and was markedly higher at site E1 than at either sites E2 or M3. Bird abundance showed significant seasonal variation—birds were generally more abundant during the dry season (Table A-9, Appendix A; Figure 3-14 right). Overall, results for abundance are similar to species richness (see Figure 3–12).

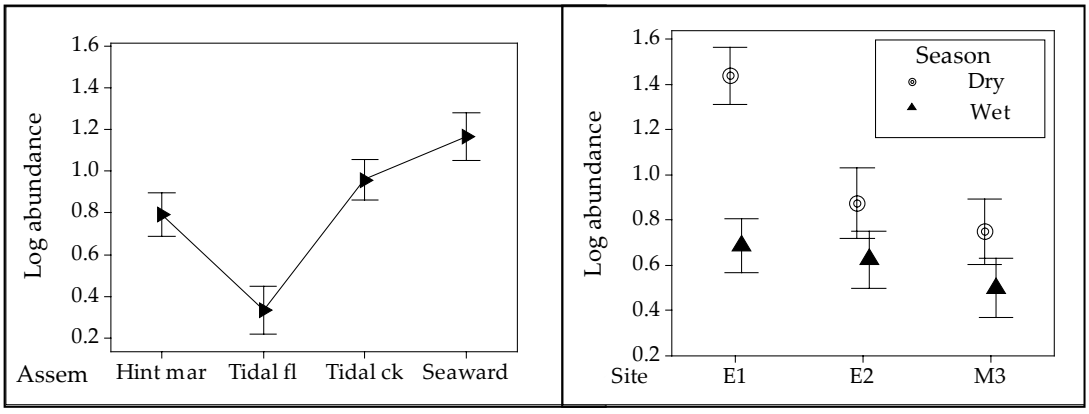


Figure 3-14: (Left) Mean abundance of birds ($\log_{10}(x + 1)$ transformed ±SE) in four assemblages. Points are mean log abundance per hectare (±SE) sampled for two years. (Right) Mean abundance of birds at three study sites in wet (closed triangles) and dry seasons (hollow circles).

Data for the two most common species, the brown honeyeater and the red-headed honeyeater were analysed (Appendix A, Table A-10 and Table A-11). Brown honeyeater

abundance was significantly higher in the dry season than the wet season and varied significantly between sites. Consistent with the overall trend, the abundance of brown honeyeaters at Site E1 was higher than elsewhere. A significant interaction between site and assemblage indicated that while this species was generally more abundant at site E1 than at the other sites, the trend was not consistent across all assemblages. Brown honeyeater abundance in the tidal creek assemblage at E1 was similar to the same assemblage at sites E2 and M3 (Figure 3-15).

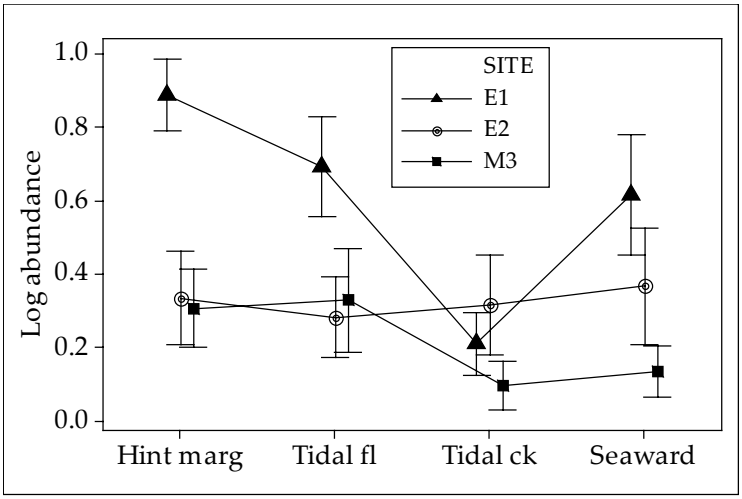


Figure 3–15: Mean abundance of brown honeyeaters ($\log_{10}(x + 1)$ transformed ±SE) within the four major assemblages at three sites in Darwin Harbour

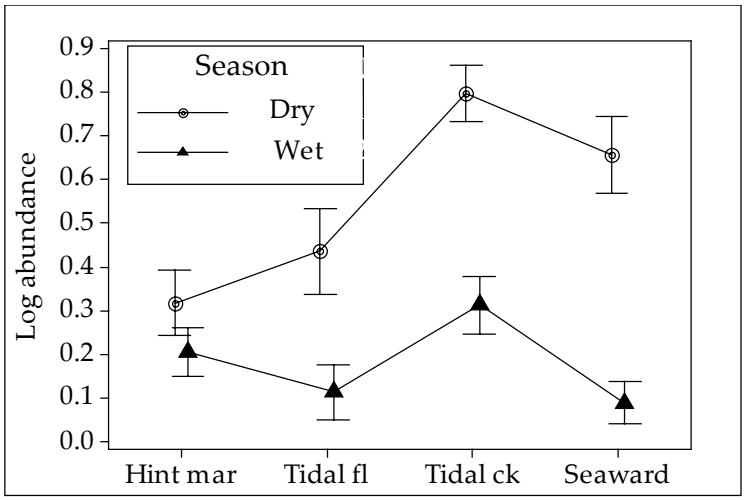


Figure 3-16: Seasonal variation in abundance of red-headed honeyeaters in four mangrove assemblages from landward (left) to seaward (right). Points are mean log abundance at three sites (±SE) in dry and wet seasons. Data for two years pooled.

Numbers of the red-headed honeyeater also varied seasonally, with typically higher abundance in the dry season than the wet. ANOVA results also indicate that abundance of this species is not the same in all zones (Appendix A, Table A-11, Figure 3-16).

Seasonal differences in bird abundance were also found at the community level (Figure 3-17). The ordination of bird abundance shows a distinct separation of study plots sampled during different seasons reflecting the generally higher numbers of birds in the dry compared with the wet season.

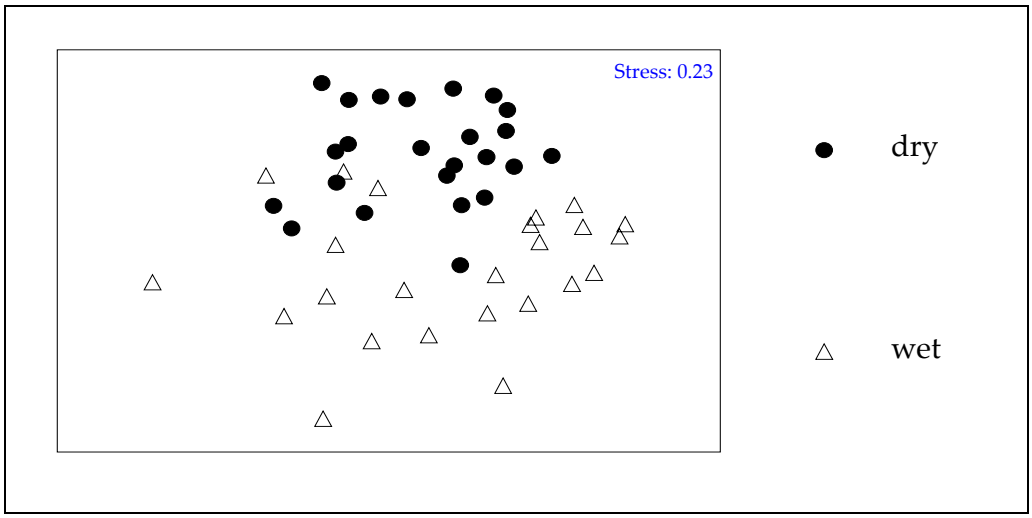


Figure 3-17: Ordination of study plots based on abundance of mangrove bird species during the wet and dry seasons over two years(data not transformed)

Overall, bird species frequency and composition distinctly reflects shoreline zonation (Figure 3-18): the study plots from each mangrove assemblage appear as distinct, non-overlapping clusters.

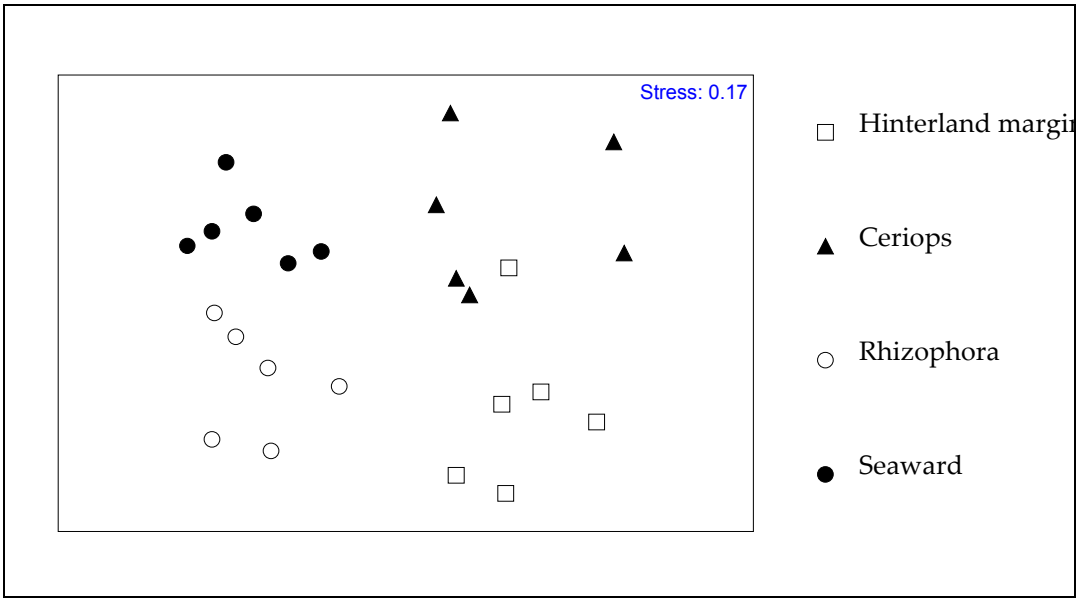


Figure 3-18: Ordination of sites based on frequency of mangrove birds within each assemblage. Data for each study plot pooled over the two years.

Examples of birds exhibiting strong zonal preferences can again be found amongst groups of taxonomically related species; three gerygone (warbler) species display strong

preferences for particular assemblages. The green-backed gerygone is largely restricted to the hinterland margin assemblage, the mangrove gerygone is abundant in the flat and the large-billed gerygone occurs mainly in the lower intertidal zone, especially the tidal creek assemblage (Figure 3-19).

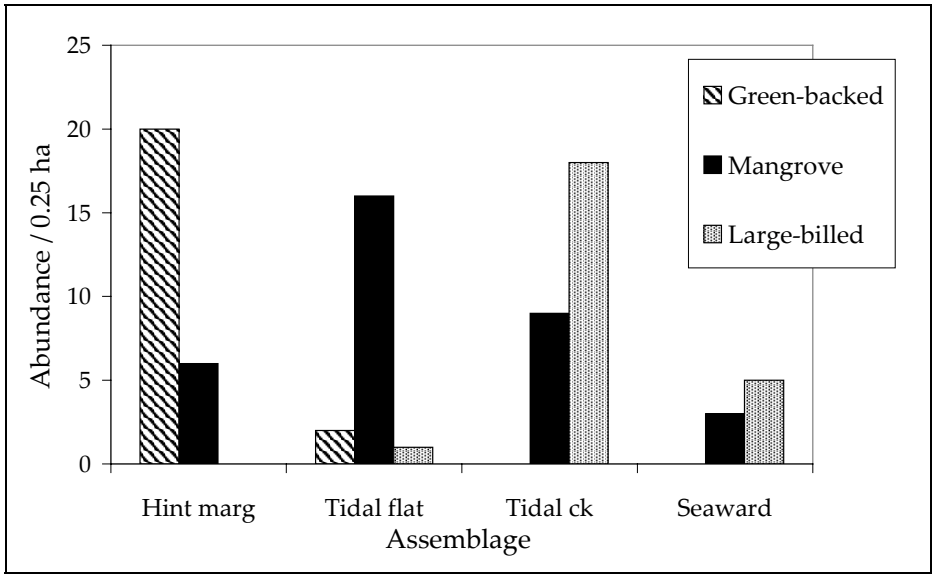


Figure 3-19: Histogram of total abundance per study plot recorded during surveys.indicating the distribution of *Gerygone* species (warblers) in the four major mangrove assemblages.

Foraging ecology

Each of the 70 bird species was assigned to one of ten different feeding guild categories (i.e. piscivore; omnivore; nectivore/insectivore; nectivore; insectivore/frugivore; insectivore/carnivore; insectivore; granivore; frugivore; and carnivore) according to known diets of mangrove birds (Johnstone, 1990; Simpson and Day, 1996). The four most common feeding categories were insectivores (34% of the avifauna), carnivores (24%), nectivore/insectivores, (13%, including 6 species of honeyeater) and insectivore/carnivores (7%, predominantly insectivorous species which supplement their diet with crabs and other crustaceans). Nectivorous/insectivourous species are quite well represented, particularly given the low plant species diversity and the scarcity of species with large, nectar producing flowers. The piscivores, frugivores, granivores and omnivores were the least represented bird categories and collectively they comprised only 17% of the species recorded (Figure 3-20).

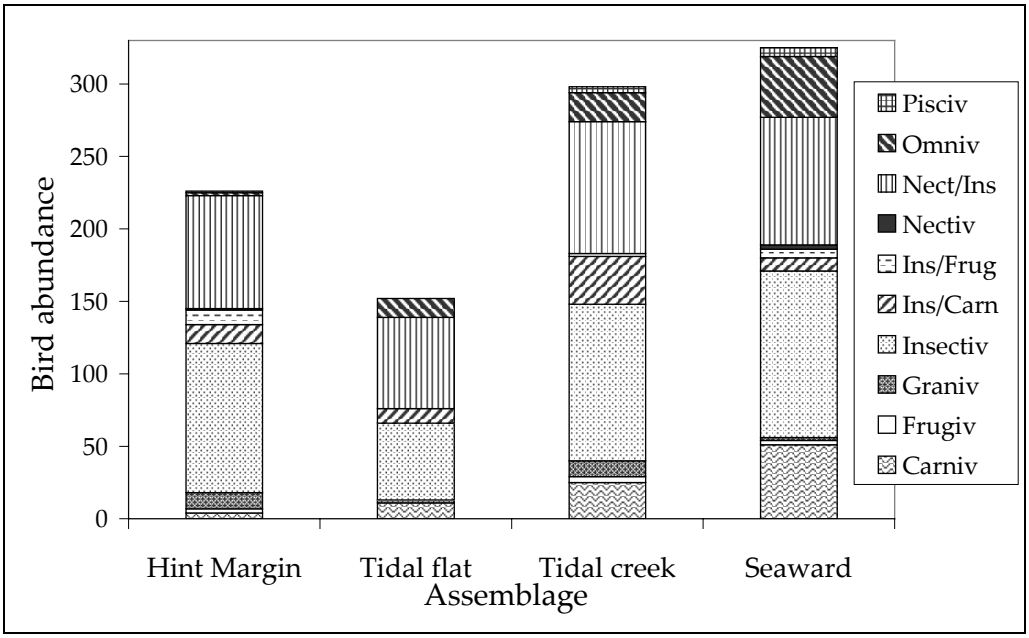


Figure 3-20: Total numbers of bird species in different feeding guilds in different mangrove assemblages in all undisturbed sites during wet and dry seasons.

The data on the foraging heights of mangrove birds indicated that groups of species feed within particular height ranges. A dendrogram of 33 bird species clustered according to similarity in foraging heights distinguishes a discrete group of specialised ground foraging birds from the majority of others that forage generally in the mid to upper canopy between 1.1 and 8.0 m (Figure 3-21). A small number of aerial species also forage above 8.0 m.

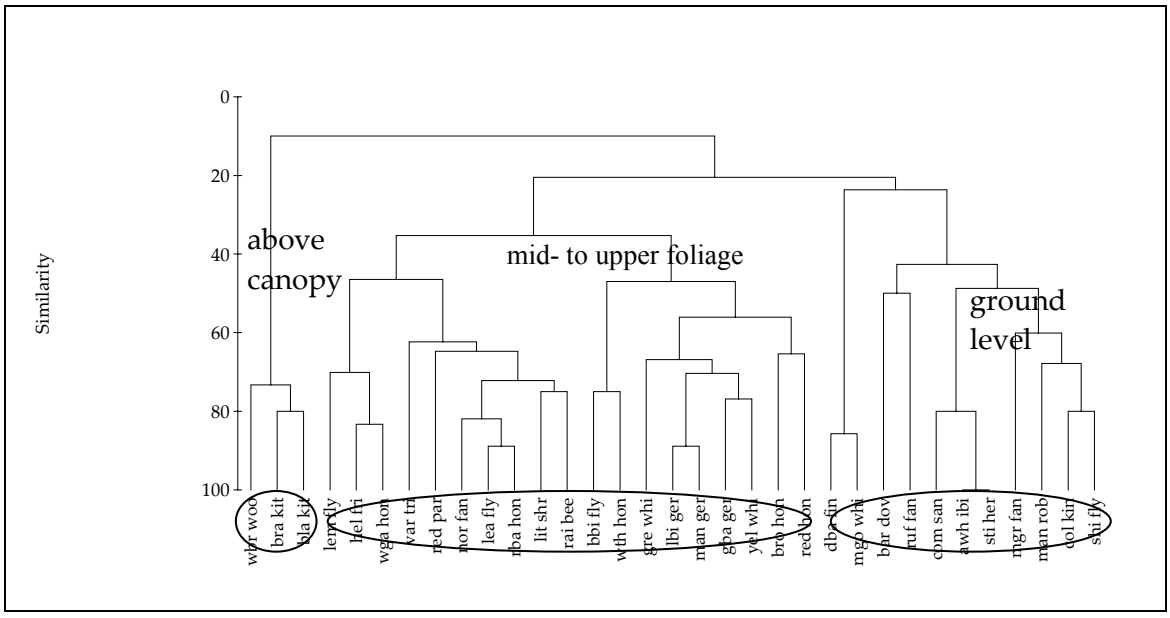


Figure 3-21: Dendrogram of 33 mangrove bird species indicating vertical stratification of foraging activity.

Some groups of birds with close taxonomic ties showed evidence of niche segregation based on vertical stratification in foraging preferences. Four species of flycatcher (genus *Myiagra)* occur within Darwin Harbour mangroves—the broad-billed, leaden, shining and lemon-bellied—and the broad-billed and shining are considered to be mangrove specialists (Hutchings and Saenger, 1987). The latter two species appear to forage in a different height class—low in the canopy under 4 m—to the leaden and lemon-bellied flycatchers, which typically foraged higher—generally between 4 and 8 m (Figure 3-24).

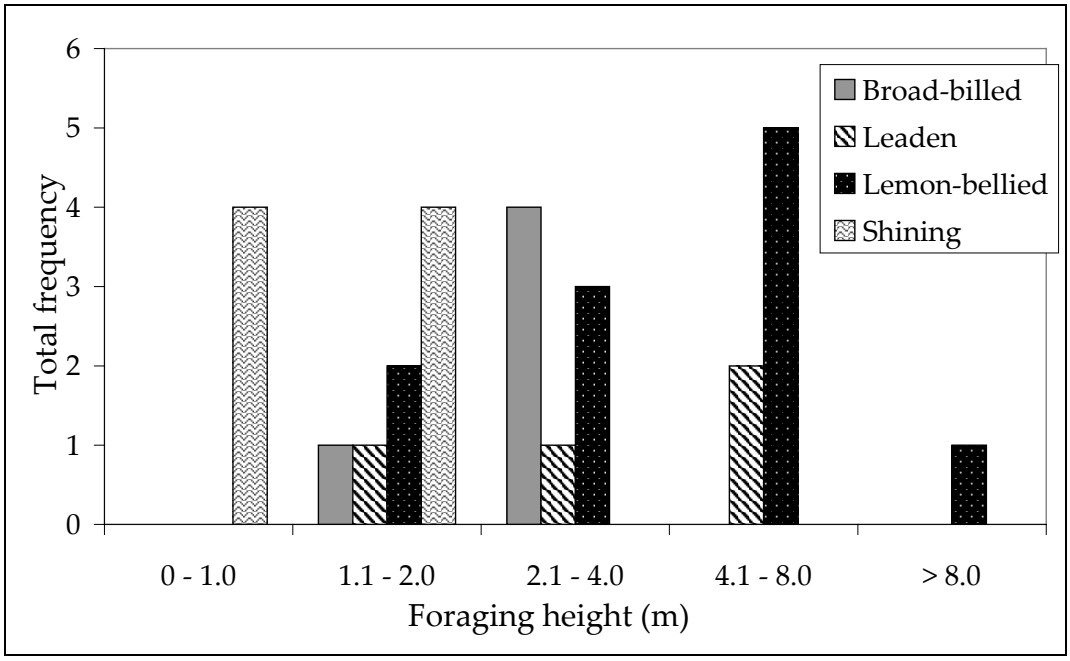


Figure 3-22: Total frequency of mangrove flycatchers foraging at particular heights

The five species of honeyeater (family Meliphagidae) occurring in mangrove habitats appear to demonstrate similar forage height partitioning. The two most ubiquitous species, the red-headed honeyeater and the brown honeyeater, tend to forage mostly at 1 to 2 m and 2 to 4 m respectively. The less-common, larger honeyeaters (white-gaped and helmeted friarbird) tend to frequent the upper canopies of taller trees (Figure 3-23).

The most common mode of foraging (n=184) was foliage gleaning, including leaves and branches (51.1%), which is consistent with the dominance of insectivores in mangrove habitats. Probing of foliage and flowers (27.2%), hawking (15.2%) and snatching (6.5%) were other techniques most commonly used by mangrove birds during foraging. Of 228 foraging observations, 36% involved leaves and twigs as the principal substrate, 20.6 % involved flowers, 14.9% branches and only 1.3% seeds and fruit. Thus 72.8% of foraging by birds observed in this study directly involved the forest trees. Feeding observations

not involving trees included foraging in water (1.8%), on the ground (9.2%), or in the air (16.2%).

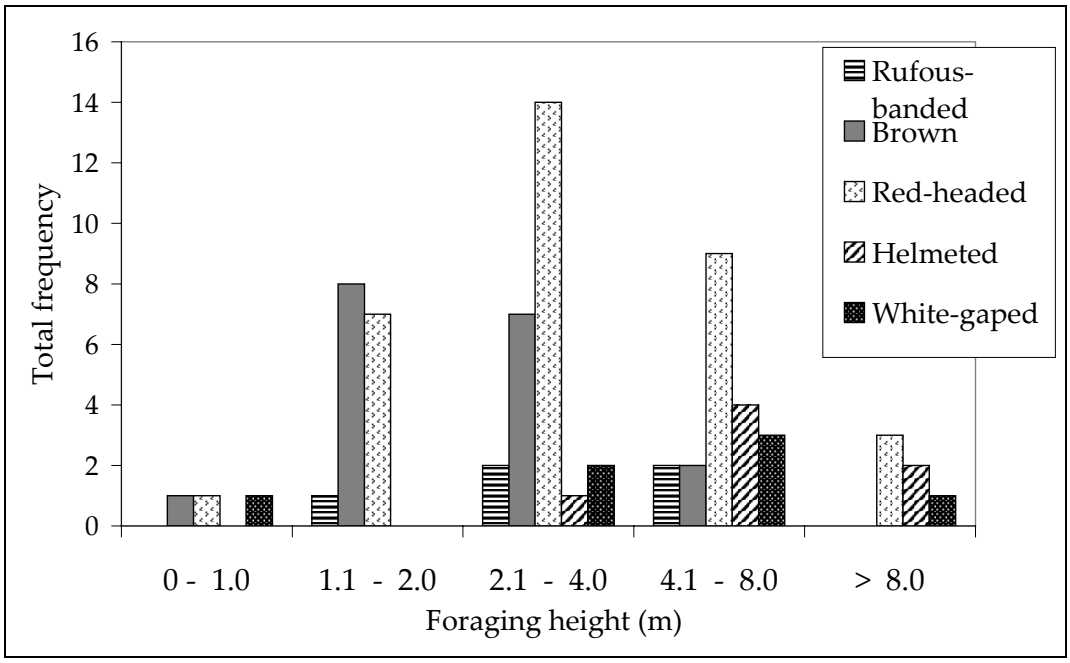


Figure 3-23: Frequency of mangrove honeyeaters foraging at particular heights

Flycatchers also show zonal preferences, with shining flycatchers observed primarily in the tidal flat and tidal creek assemblages, and the lemon-bellied and broad-billed flycatchers occurring in the seaward assemblage.

3.4. Discussion

Diversity of mangrove mammals

This study recorded 9 native and 4 introduced species from the Darwin Harbour sites (from 192 replicate study plots, 4,608 trap nights). Of these, five were recorded on less than 5 occasions (Table A-1, Appendix A). Overall the mean species richness was 2.0 per study plot. Results from elsewhere, where the sampling effort has not been so great, have recorded far fewer species. Fensham and Woinarski (1992) found a total of just 3 species (*M. burtoni, T. vulpecula, P. breviceps)* from mangroves on the Tiwi Islands to the north of Darwin (5 study plots, 360 trap nights) with a mean species richness of 1.0 per study plot.

In the Darwin Harbour mangroves of this study, the mammal fauna was dominated by

M. burtoni and *T. vulpecula*, which were recorded in all assemblages and at nearly all sites. These two species are almost certainly resident. In the most extensive patch at Charles Darwin National Park (Site E1), they were abundant in the seaward assemblage, over 1.5 km from the nearest terrestrial habitat. Based on published home range sizes, it is unlikely that they could be merely visiting on a nightly basis. Begg et al. (1983) found that *M. burtoni* had a home range of between 0.23 ha (females) and 0.43 ha (males) in eucalypt open forest in the Top End. The core mean home range size of *T. vulpecula* in eucalypt open forest is 1.1 ha ± 0.5 and range length is 165 m, though this is known to vary substantially between populations and habitat types (Kerle, 2001). Furthermore, both species were observed to be adept swimmers and *M. burtoni* is able to dive and swim proficiently underwater (pers. obs.). The ability to swim and climb (assisted by its partially prehensile tail) renders *M. burtoni* well adapted for life in intertidal forests. Other recent literature describing Northern Territory wildlife has also noted mangroves as regular habitat for *M. burtoni* (Cole and Woinarski, 2002) and *T. vulpecula* (Miles, 2000; Kerle, 2001).

In this study, the Northern Brown Bandicoot (*Isoodon macrourus*), a ground-dwelling marsupial, comprised about 6% of all captures and was locally common in mangroves fringing the hinterland. These results suggest that they probably only forage in mangroves at low tide at night but shelter in adjacent terrestrial habitat. They did not venture far into the mangroves, rarely occurring seaward of the hinterland margin.

Several other less common species were also recorded during these surveys—all from the hinterland margin—and are probably transients rather than mangrove residents. Quolls (*Dasyurus hallucatus*) were intermittent visitors to the landward fringe, perhaps to feed on *Melomys* or invertebrates. Isolated captures of the Black-footed tree rat (*Mesembriomys gouldii)* suggest that this species may visit mangroves when seasonal conditions—such as widespread fires—render terrestrial habitats less favourable. Similarly, Agile Wallabys (*Macropus agilis)* commonly retreat to the shade and protection of mangrove fringes during the day (pers. obs.) and may forage there (McGuinness, 1997b). *Rattus tunneyi* was uncommon, but appears to actively use mangroves, as it was trapped well within the mangroves (tidal flat assemblage) on several occasions.

Species richness did not vary between sites or between years but there were significant

differences between assemblages. The highest diversity of mammals was recorded on the hinterland fringe and the least in the seaward assemblage. This result may, however, partly have been an artefact of the constraints on sampling techniques that could be used in the seaward assemblage and the subsequent analysis strategy. All traps had to be set in trees in the seaward assemblage, thereby potentially missing predominantly ground dwelling or semi-aquatic species, such as the water rat. This species was detected by tracks and traces, but only records of trapped species were included in later analyses. The use of other sampling techniques such as spotlighting and ground level trapping in the lower intertidal zone between high tides may have given different results.

Mangrove mammal diversity was not high in the mangroves but it may be comparable with that in other common lowland terrestrial habitats. Mean mammal species richness on the Tiwi Islands (Fensham and Woinarski, 1992) ranged from 3 species in paperbark forest (3 study plots, 216 trap nights), through 7 species in monsoon forest (44 study plots, 3,168 trap nights) to 8 species in eucalypt open forest (25 study plots, 1,800 trap nights). The mean species richness per study plot for these same habitats were 3.0, 1.6 and 1.9 respectively, although it is extremely difficult to compare results from different habitats where the sampling intensity differs so greatly.

Virtually none of the mammal species found in the mangroves in this or other studies are restricted to this habitat. In particular, the only two species considered to be resident in mangroves in this study—*Melomys burtoni* and *T. vulpecula*—are also known from a wide range of other terrestrial habitats (Woinarski, 2000; Kerle, 2001). No mammals in Australia are considered to reside exclusively in mangroves. Once thought to be a mangrove specialist, the water mouse *Xeromys myoides*—a rare, nocturnal rodent that forages exclusively at ground level for crabs—has also been recorded in freshwater swamps, floodplain and saltflat habitats (Van Dyck, 1996; Woinarski et al., 2003). Mangroves are not the only habitat lacking a specialised mammal fauna; this has also been noted for monsoon forests (Fensham and Woinarski, 1992; Menkhorst and Woinarski, 1992).

Mangrove mammal abundance

Despite species richness being relatively low, mammals in mangrove habitats were surprisingly abundant. The distribution of resident terrestrial mammals throughout all the main assemblages, including the seaward zone, was also interesting. The overall mean trap success in this study of 12.1 captures per 100 trap nights (Table 3-2) was much higher than is generally reported from terrestrial habitats across the Top End (between 0.8 and 5.0 captures per 100 trap nights) but falls short of results from some more local studies, for instance, 20.2 from the Kakadu conservation zone (Woinarski and Braithwaite, 1990; Woinarski et al., 2001). Limited data from mangroves in other areas suggests that they may consistently support high densities of mammals; Fensham and Woinarski (1992) reported a trap success of 8.7 captures per 100 trap nights from 5 mangrove sites on the Tiwi Islands, just north of Darwin.

The overall density of mammals recorded from the Darwin Harbour sites (11.6 animals ha^{-1}) was almost double that known previously from other mangrove systems in the region (Table 3-4). Mammal abundance differed significantly between these sites ($p<0.05$), and the density of mammals at site E1 was even higher (18.7 ha^{-1}) being more than double that at the other two (8.7 at E2 and 7.6 at M3). There are several possible reasons why site E1 supported such high mammal densities. First, it has been established in earlier work (Metcalfe, 1999) that this site had unusually high primary productivity (as measured by leaf litter fall) with peak productivity recorded in the seaward assemblage. Notably, both *Melomys burtoni* and *Trichosurus vulpecula* feed on the fruits of *Sonneratia alba* (pers. obs.). High population densities of other rodents in wetland habitats in the Top End have been documented (Redhead, 1979; Masden and Shine, 1999) and are thought to reflect the interaction between climatic factors and highly fecund species in the context of extremely productive environments.

Second, the two trapping periods at this site coincided more with mammal breeding periods than at the other sites (Begg et al., 1983). Third, this patch, being exceptionally broad (some 1.5 km from shore to sea, see Figures 2-3 and 2-4), may have been less effectively penetrated by potential predators from the hinterland than at the other sites and may have offered a refuge from terrestrial predators (e.g. feral cats and dogs).

Table 3-4: Mean abundance (per ha) of common mangrove species in this and previous studies, in mangrove (M) and terrestrial eucalypt forest habitats (E). ** Indicates surveys conducted over 3 nights but adjusted to the equivalent of 4 nights and therefore equivalent to density per hectare

Species	**This study (Darwin Harbour)**	**Fensham & Woinarski, 1992** (Tiwi Islands)**		**Woinarski et al., 2003** (mainland)**
Habitat	**M**	**M**	**E**	**E**
Melomys burtoni	6.7	6.4	0.4	2.8
Trichosurus vulpecula	3.7	0.3	0.3	2.8
Isoodon macrourus	0.8	–	0.1	3.5
Dasyurus hallucatus	0.2	–	–	2.7
All mammals	11.6	6.9	4.0	–

Indeed, the unusually low abundance of mammals in the tidal flat assemblage at site M3 during 2000 may be associated with the presence of feral cats, trapped at this site the previous year. The only feral cat recorded during the 2-year survey was trapped at site M342 in 1999 and in the year between its detection and the next survey, the trap success at this site declined greatly from 7.3 to 0.5 captures per 100 trap nights (Figure 3-5b). Presumably, feral cats have decimated the mammal population in the tidal flat assemblage at this location.

Mammals were most dense in the tidal creek assemblage (15.7 animals ha^{-1}). It appears that the tall *Rhizophora stylosa* forests (to 11m high) provide the most suitable habitat for the largely herbivorous, numerically dominant resident mammal assemblage comprising *M. burtoni* and *T. vulpecula*. The presence of large, structurally complex, hollow-bearing refuge trees that are not flooded during spring high tides may be of crucial importance. *M. burtoni* is known to prefer densely wooded habitat (Begg et al., 1983). Mammal abundance decreased in adjacent landward and seaward assemblages where the average tree height was lower (9 m in the seaward assemblage and 2–3 m in the tidal flat) and consequently where there were fewer refuges above the high tide level.

Although the seaward and tidal flat assemblages had less shelter, both were still well populated (12.1 animals ha^{-1} in the tidal flat and 10.4 ha^{-1} in the seaward assemblage). It is possible that some of these animals may have entered these assemblages from adjacent tidal creek habitat, to forage on a nightly basis. In the seaward assemblage, the large, seed-bearing fruits of *Sonneratia alba* were avidly consumed by *M. burtoni* (pers.

obs) and the flowers and leaves of this species are likely to be important in the diet of *T. vulpecula*. Overall, mammals are relatively mobile species and the tidal flat and seaward assemblage mangroves are never particularly distant from taller forests along the dendritic network of tidal creeks. The hinterland margin was the least populous (8.33 ha^{-1}) but this assemblage had the highest diversity of mammals.

In this survey, the mean densities of *T. vulpecula* and *M. burtoni* were 3.69 and 6.69 per hectare respectively. These values are higher than averages reported by Woinarski et al., (2003) for Top End terrestrial habitats (eucalypt forest) in which both species had mean densities of 2.8 ha^{-1} (Table 3-4) but Cole and Woinarski (2002) also note that *M. burtoni* may be very abundant locally. This was certainly evident during this study when at times, on particular study plots, the trap success was as high as 40 captures per 100 trap nights. Hegerl et al. (1982) also reported a relatively high maximum trap success rate for *M. burtoni* (25 captures per 100 trap nights) from a single night's trapping on an intertidal island in the East Alligator River. For *T. vulpecula* the maximum trap success on any one night exceeded 100%: all four cage traps and both large Elliot traps contained a possum and at one trap a young possum was waiting outside the cage containing its mother.

Bat diversity

Although bats comprise over 25% of all Australian mammal species (Friend and Braithwaite, 1986), until recently they have been poorly studied due to sampling difficulties and taxonomic problems. The bat composition of the Northern Territory is most closely related to that in the Kimberley but is also broadly similar to that in north Queensland (Friend and Braithwaite, 1986). This survey, utilising only electronic echolocation detection methods, detected at least 11 of approximately 20 species of bats known from the Darwin area (McKean, 1979). Other surveys that used a range of other survey methods across a number of habitats have had similar results. For instance, a total of just 16 species, including 2 macrobats have been recorded from the Tiwi Islands (Woinarski et al., 2003).

Nine of the species recorded from the Darwin Harbour mangrove belonged to the Suborder Microchiroptera (micro-bats), mostly small, insectivorous bats that use echolocation to navigate and feed. Six of the total of ten microbats recorded were Vesper

bats: Vespertilionidae is the biggest and most widespread of all the bat families with over 300 species, all insectivorous, occurring in a broad range of climates (Richardson, 2002).

The extensive north Australian savannas support a rich microbat fauna comprising approximately 26 of the 63 bat species in Australia (Milne et al., 2005). The other two species recorded during this study, *Pteropus alecto* and *Macroglossus minimus*, were phytophagous Megachiropterans (or mega-bats, including the flying foxes and blossom bats), represented by 13 Australian species, that navigate principally by sight (Hall and Richards, 2000). A third mega-bat species, the little red flying fox, *Pteropus scapulatus,* was not detected but is likely to have been present as it commonly coexists with *Pteropus alecto*. Unlike *P. alecto*, which is a local migrant, the little red flying fox, is highly nomadic across the NT, tracking seasonal patterns of flowering and fruiting (Vardon and Tidemann, 1999).

The bat fauna recorded during this study is very similar to that in mangroves elsewhere in the region. While there have been no detailed surveys of bats in mangroves in the Northern Territory, comprehensive surveys have been undertaken in mangroves in the Kimberley region of Western Australia (McKenzie and Rolfe, 1986; McKenzie and Start, 1989). The West Australian survey, restricted to insectivorous microbats, reported a total of fifteen species. Seven of the nine microbats recorded during the Darwin Harbour surveys were also recorded in the Kimberley mangroves. A more comprehensive future survey of bats in Top End mangroves might further highlight the similarity of the bat fauna between these two regions.

When compared to surveys of bats in other environments in the Northern Territory, it is apparent that all of the bats that were found in mangroves are also known from a range of other environments (Friend and Braithwaite, 1986; Milne et al., 2005). Only one species *Pipistrellus westralis* is generally recognised as being largely restricted to coastal areas, living primarily in mangroves (Churchill, 1998). Friend and Braithwaite (1986) noted that extensive habitats are richer in bat species than those that occupy a smaller area. Thus it follows that bat species richness in mangroves is expected to be less than that observed in open forests (14 species) but more than that recorded in monsoon forests (10 species, Friend and Braithwaite (1986)). The tally of 11 species detected during the Darwin Harbour survey conforms with these predictions.

The landward to seaward gradient had a significant influence on the diversity of mega- and microbats in mangrove habitats. This is illustrated in the ordination of study plots based on the presence or absence of bat species. Hinterland margin sites clearly had a distinct bat fauna and were distinguished from sites in other assemblages, with the seaward assemblage fauna being the least similar. This pronounced pattern of zonation was unexpected in such a mobile group, but the gradient observed may relate to factors such as foraging strategy, body size and flying distance from hinterland areas where microbat roosting sites are likely to be located. This pattern of zonation may also reflect the intermittent use of the seaward assemblage by flocks of flying foxes.

The majority of microbats are continuous flight foragers (McKenzie and Rolfe, 1986) taking insects on the wing beside or just above the tree canopy. It is likely that the open corridor that typically runs along the shoreline between the forests of the hinterland margin and the adjoining upland terrain is used intensively as a foraging flyway by small insectivorous bats. Indeed, the vesper bats (family Vespertilionidae) which were most common in the hinterland margin tend to have smaller body weights (<10 g) than either bats in the Molossidae family (including *Chaerephon jobensis* and *Mormopterus* sp.*)* or the highly mobile Pteropodids which travel long distances to feed (Churchill, 1998). The mollosids, which occur from the tidal flat to the seaward zone, generally forage at greater heights (usually over and above the canopy) and can detect insects at greater ranges (Fenton, 1982) and, based on these observations, appear to hunt more widely.

The data on bat frequency were dominated by the high incidence of black flying foxes (*Pteropus alecto*) which only utilise those assemblages in the lower intertidal zone, where they apparently feed on the flowers and fruit of *S. alba.* Although *S. alba* may flower and fruit almost continuously throughout the year, this is more common during the dry season (Wightman, 1989; Coupland, 2002). It was during this season that the highest *P. alecto* activity was recorded—*P. alecto* were only observed on a few occasions during wet season surveys. The large flocks of flying foxes seen at site E1 in Charles Darwin National Park during the dry season were not recorded at other sites, nor at other times. Several authors have noted the importance of mangroves as roosts for flying foxes in the Top End (Thomson, 1989; Vardon and Tidemann, 1999). Indeed the proximity of favourable roosts in closed canopy mangroves to a range of suitable foraging resources was found to be the major factor influencing the distribution and colony size of this

species in the Top End (Loughland, 1988). No diurnal roosting colonies of *P. alecto* occurred on the sites of this study but foraging activity was observed in the seaward assemblage at night.

In contrast with the phytophagous macro-bats, the species richness and frequency of insectivorous microbats was highest in the hinterland margin assemblage, progressively decreasing through more seaward assemblages. Coupland (2002) found that the *Sonneratia* woodlands of the seaward assemblage in Darwin Harbour mangroves had the highest insect abundance of the four mangrove assemblages and the lowest insect numbers were recorded in *Rhizophora*–dominated assemblages. Insect abundance also appeared to increase during the wet season. The pattern of diversity and distribution of insectivorous bat species observed in this study did not reflect this pattern of insect abundance—bat diversity progressively decreased to seaward and seasonally, was highest during the dry and late dry seasons. However, Coupland (2002) only quantified the abundance of diurnal insects and these may not necessarily reflect the levels and activity of nocturnal insects, preyed on by bats.

In any case, other workers have found it extremely difficult to relate patterns of bat species composition and abundance with any environmental factors in a range of much more comprehensive surveys at both landscape and local scales (Milne et al., 2005). Indeed, McKenzie and Rolfe (1986) note that "the species composition [of bats] of most tropical communities is dynamic rather than static, because of cyclic environmental fluctuations such as seasonal changes in rainfall and humidity or less predictable perturbations."

Mangrove bird diversity

By world standards, Australia has a reasonably rich mangrove avifauna. In Panama and Venezuela, bird species richness ranged between 24 to 80 species (Lefebvre and Poulin, 2000)and 47 species (excluding waders and aerial species) were recorded from Selangor in Malaysia. Despite almost 250 bird species recorded as either visiting, being associated with, or exclusive to Australian mangroves (Milward, 1982) there have been surprisingly few quantitative studies on their diversity, abundance and foraging ecology. The majority of early literature was largely descriptive and mainly concerned composition, distribution and evolutionary origin (Macnae, 1968b; Ford, 1982; Schodde

et al., 1982; Johnstone, 1990). Several authors have noted that north-western Australia (i.e. west of the Gulf of Carpentaria and including the Northern Territory) has a particularly rich mangrove endemic bird fauna (at least 23 species). By contrast, there are only 8 endemics from Eastern Australia and 10 from New Guinea (Hutchings and Saenger, 1987). In the Northern Territory, bird species composition often closely reflects vegetation type and mangrove communities have a distinct avifauna (Woinarski et al., 1988). The mangrove bird community is most closely related to that of monsoon forests both in the diversity (and abundance) of species, despite their relatively small area in the region generally (Ford, 1982; Woinarski et al., 1988).

A total of 70 bird species were recorded from the three sites in Darwin Harbour during this study. If the 14 waders, 7 raptors and 2 aerial species are excluded from this tally, species richness is similar to that recorded by Noske (1996), who listed 52 birds (excluding waders and aerial species) from one site in Darwin Harbour. Of the 70 bird species, at least nine are virtually restricted to mangroves and considered mangrove specialists (chestnut rail, collared kingfisher, mangrove robin, broad-billed flycatcher, mangrove fantail, mangrove gerygone, yellow white-eye, red-headed honeyeater and large-billed gerygone). Several other mangrove restricted species (eg white-breasted whistler) are also known from the region but were not seen during this study (Schodde et al., 1982; Hutchings and Saenger, 1987).

Other less intensive surveys of mangrove birds in the Darwin region have revealed fewer species with 33 species recorded by Woinarski et al. (1988) in mangroves to the east of Darwin and 12 species from mangroves on the Tiwi Islands (Fensham and Woinarski, 1992). Hegerl et. al (1982) recorded 39 species of birds from mangroves and adjacent intertidal mudflats along the East Alligator River.

The current survey is one of the only mangrove studies that has adequately surveyed the tidal creek and seaward mangrove assemblages. The results showed that there was significant variation in species diversity between assemblages and mangrove birds are tightly grouped within different assemblages. The results, particularly the ordinations, indicated that position on the shore was a primary factor determining community species composition. Assemblages which offer the widest range of foraging possibilities (tidal pools, tree canopies, flower/fruit resources and mudflats in the seaward assemblage for example) are likely to have the highest bird diversity. Similarly, the

assemblages that offer few foraging opportunities—the tidal flat for example—are likely to have the lowest bird diversity. For instance, the tidal flat supported birds from only 6 feeding guilds whilst the seaward assemblage had representatives of 10 different guilds. However, unlike studies of mangrove birds in Peninsular Malaysia, in which the greatest number of species occurred along the dry landward edge (Noske, 1995), in Darwin Harbour the two most seaward assemblages were the most speciose. The apparent partitioning of the bird community may reflect preferences for particular regimes of cover, habitat complexity, floristic composition and perhaps insect abundance (see Lefebvre and Poulin, 2000). Most other studies of birds in Darwin Harbour have not examined variation between different assemblages (or have stopped short of the seaward assemblage) and do not provide data for comparison.

Mangrove bird abundance

Prior to the surveys by Woinarski et al.(1988) and Noske (1996) no estimates of the density of birds in Northern Territory mangroves had been published. Recent NRETA surveys have provided detailed quantitative data on birds from numerous coastal regions of the Top End but many of these did not extend into mangrove habitats (Woinarski et al., 2001; Brennan et al., 2003).

The mean density of non-aerial birds recorded in mangroves on the Howard Peninsula was 12–13 ha^{-1} (Woinarski et al. 1988). Noske (1996) noted a mean density of 24 ha^{-1} from a study site near Palmerston in Darwin Harbour and 15 to 26 ha^{-1} in Peninsula Malaysia (Noske, 1995). However, the latter density estimates were derived from fixed width transects not quadrats. Arnold [(1983) as cited in Noske 1996] found that observers walking transects recorded significantly higher numbers of birds than stationary observers at the centre of 1 ha^{-1} quadrats. In mangroves around the islands of Arnhem Land, the overall mean abundance of the 29 most commonly recorded species was similar (26.8 birds per 0.25 ha quadrat), being on a par with coastal thicket and *Melaleuca* forests (Woinarski et al., 2001). The mean density of birds recorded in this survey across all sites and both seasons was 15.8 birds ha^{-1}. These findings do not support earlier views that despite being a conspicuous element of the fauna, mangrove birds are not particularly abundant (Hutchings and Saenger, 1987). Clearly, recent research in tropical regions has shown that bird richness and abundance tends to be high in vegetation

types with dense tree cover; such as mangrove and monsoon forest (Woinarski et al., 2001).

Univariate and multivariate analyses of overall bird abundance showed clear seasonal variation. This may reflect the ingress of birds attracted to resources associated with flowering during the dry season. Indeed, local movements of the ubiquitous brown honeyeater and the significant seasonal difference in density of the equally abundant red-headed honeyeater can be attributed to nectar availability (Franklin and Noske, 1988; Noske, 1996).

Bird abundance was also significantly different between assemblages. In the seaward assemblage, *S. alba* is the only mangrove species considered to be a "main" nectar source, ie one that attracts a range of small to large nectarivores (Franklin and Noske, 2000). All other species including *C. australis, R. stylosa* and, to a lesser extent, *B. exaristata* are only suitable for small nectarivores. Thus the elevated richness and abundance of birds in the seaward zone of Darwin Harbour may be explained by the rich nectar source, abundant *S. alba* fruit and associated high insect abundance (Coupland, 2002). Lefebvre and Poulin (2000) found that arthropod abundance was an important determinant of bird abundance in mangrove forests of Venezuela and Panama. Relationships between nectar sources and bird species also contributes to vertical partitioning of mangrove birds, the larger species of honeyeaters generally feeding on *S. alba* flowers above 4m and the tiny red-headed honeyeater foraging mainly between 1 and 4 m.

Given the extremely low floristic diversity and the paucity of flowers with abundant nectar it is not surprising that the strictly nectarivore guild is poorly represented. Considerably more species belong to the nectarivore/insectivore guild (birds which are not solely dependent on nectar but supplement their diet with insects). Similarly, the low abundance of ground foragers is understandable given the frequency of flooding in the lower intertidal zones; which greatly restricts foraging time for ground feeders. Despite extremely low floristic diversity, the two most abundant birds (the brown and the red-headed honeyeater) are dependent on nectar (nectivorous/insectivorous guild) and the nine species in this category accounted for 32% of all records. Overall, the results confirm that insectivorous species are the most speciose and the 24 species in this guild and comprise 37% of all records from undisturbed mangroves. Foraging

observations in this study were, however, recorded opportunistically and require replication to substantiate these findings. Given the high frequency of fire in terrestrial habitats, mangroves may make an important contribution to the maintenance of avian biodiversity by providing reliable feeding sites for visiting terrestrial insectivores during critical periods.

3.5. Conclusions

This study documented mammal and bird species occurring in mangrove habitats in Darwin Harbour and provides information on their distribution and abundance amongst the four main mangrove assemblages. In all, 558 mammal records, 1,101 bird observations and 89 bat records were attained from 3 undisturbed sites. This survey has contributed a substantial amount of information on the distribution, abundance and ecology of these groups in NT mangrove habitats. In particular, the results contribute to our understanding of spatial and temporal variations in species richness and abundance. Indeed, the four main assemblages support very different faunal communities with remarkable differences in the abundance of species among these assemblages.

Annual variations were observed, with both bird and mammal abundance higher in 2000 than in 1999. Seasonally, both birds and bats were more abundant in the dry season. Pteropodid bats and birds probably compete for the same nectar sources, which are more abundant in the dry season. Mobile species can respond quickly to variations in resources and this is reflected by seasonal variations in the diversity and abundance of these groups.

Moving from landward to seaward, the quite diverse and largely transient mammal fauna (up to 7 species on the hinterland fringe) decreased to only 2 or 3 resident species; including the water rat (*Hydromys chrysogaster)* on the seaward edge. Although mangrove mammals such as *H. chrysogaster* and the false water rat (*Xeromys myoides)* remain elusive, mangrove habitats are clearly important for these species. Two common, hardy and highly versatile species—the grassland melomys (*M. burtoni)* and common brushtail possum (*T. vulpecula)*—maintain substantial resident populations entirely within intertidal areas.

The seaward and tidal creek assemblages, although depauperate in mammal species, support high densities of animals that may be due in part to the greater structural complexity of these forests and lack of predation pressure. It follows that these highly productive seaward communities (foliage and fruit production peaks in these habitats) are also productive habitats in terms of mammals. However, as trapping has not previously been conducted in these assemblages, the composition and density of their mammal populations was largely unknown. The highly mobile bat community broadly reflects the same pattern of species diversity shown by the other mammals, with highest species richness in the hinterland margin assemblage and highest bat activity in the less diverse seaward assemblage. All vertebrate groups show reduced species richness and abundance in the tidal flat assemblage.

Mangrove birds show a different pattern of distribution. Species richness mirrors abundance; the seaward communities are the most diverse and also support the greatest number of birds, drawn from a wide range of feeding guilds. Knowledge of the foraging ecology of mangrove birds appears fundamental to understanding patterns in their distribution and abundance. Finally, unlike other vertebrate groups there is a suite of some 14 bird species that are entirely restricted to mangrove habitat. In general, however, birds, like mammals, are typically not tied to mangroves but also live in other habitats, and use mangroves opportunistically to feed, shelter and occasionally breed.

Overall, mangroves are utilised by many vertebrate species but most of these are opportunistic visitors from adjacent terrestrial environments. Mangrove plants can be viewed as opportunistic colonists of unconsolidated, unstable substrates and, overall, the vertebrate fauna of mangroves appears to share these qualities of opportunism and transience. Mangrove environments have high primary production, are structurally diverse and capable of supporting high densities of vertebrate animals. However, with the exception of birds, they are distinctly lacking in vertebrate species restricted to the habitat. This suggests that the highly dynamic and unstable nature of the mangrove environment clearly favours mobile species that have the ability to shift and recolonise other estuarine environments, in response to either rapid or gradual environmental change. The impacts of change on the vertebrate fauna of mangroves—in particular the effects of anthropogenic changes on diversity and abundance—is the subject of the next chapter.

CHAPTER 4. IMPACTS OF ANTHROPOGENIC DISTURBANCE ON VERTEBRATE FAUNA

CHAPTER 4. IMPACTS OF ANTHROPOGENIC DISTURBANCE ON VERTEBRATE FAUNA

4.1. Introduction

Environmental disturbance can modify the composition, structure and function of marine plant and animal assemblages (Sousa, 1984; Skilleter, 2000; Duke, 2001; Faraco and Lana, 2003; Alongi et al., 2005). Disturbance has been defined as "a fluctuation in the environment that can, but does not always, cause a change in the structure of an ecosystem, an assemblage of species or a population of organisms" (Skilleter, 2000). Disturbances resulting in ecological change characteristically disrupt not only the structure of biotic communities but also lead to changes in "resources, substratum availability, or the physical environment" (Pickett and White 1985, as cited in Dernie et al., 2003). As a consequence, disturbance directly or indirectly creates opportunities for new individuals or colonies to become established (Sousa, 1984), thereby encouraging environmental heterogeneity (Paine and Levin, 1981). Being situated at the land-sea interface, on largely unconsolidated substrates, mangrove habitats may also be vulnerable to geomorphic and climatic disturbances. In locations where anthropogenic development abuts the current high tide level for example, these habitats may vanish if sea level rises substantially. Nevertheless, mangroves have successfully evolved with intermittent natural disturbance (Duke, 2001) and as shown in chapter 3 of this thesis, support a relatively hardy and adaptable vertebrate fauna. Indeed, disturbance may be an important determinant of the distribution and abundance of plant and animal assemblages in mangrove communities (McGuinness, 1992; Smith III et al., 1994; Ellison and Farnsworth, 1996; Allen et al., 2001; Duke, 2001).

Mangrove habitats are subject to a broad range of natural disturbances including storms, cyclones (Craighead and Gilbert, 1962; Smith III et al., 1994; Sherman et al., 2001), lightning (Sherman et al., 2000; Duke, 2001), geomorphic change and variation in sea level (Woodroffe, 1992, 1995; Blasco et al., 1996). In recent times however, natural disturbance to mangrove assemblages have been, in many places, surpassed in scale and severity by anthropogenic disturbance (Ellison and Farnsworth, 1996; Allen et al., 2001). In many parts of the world human activities are threatening the health, and in some

places the existence, of these habitats (Skilleter, 2000). Anthropogenic perturbations include pollution (Dwivedi and Padmakumar, 1983; Mackey and Hodgkinson, 1995; Tam and Wong, 1995; Clark et al., 1996), oil spills (Lewis III, 1983; McGuinness, 1990; Burns et al., 1993; Duke et al., 1997) and clearing and conversion for other land-uses (Blasco, 2001; Diop, 2003). At the global scale, direct and indirect anthropogenic disturbances are now the most important determinants of mangrove community composition and distribution (Ellison and Farnsworth, 1996; Valiela et al., 2001).

Australians, like much of the world's population, tend to live in close proximity to the ocean: over 85% of the population lives within 50 kilometres of the coast (Duke, 2006). Urban centres on the coast often develop on river mouths and associated estuaries, which is also the primary habitat for mangroves. With urban sprawl and pollution now recognised as the two most important threats to Australian estuaries (Anon, 2003), it is not surprising that widespread destruction of mangroves has resulted from infilling for port facilities, industry, residential and recreational purposes (Saenger, 2002). Throughout temperate and sub-tropical Australia, there are few estuaries unaffected by human activities. For example, of the 100 estuaries in New South Wales, only 4 remain in 'pristine' condition (Lindegarth and Hoskin, 2001).

Anthropogenic disturbance to mangroves frequently involves direct impacts such as reclamation for coastal development but urban and industrial expansion that abuts or impinges on mangroves may also have significant consequences. Urban development typically results in a large range of concomitant, potentially negative, but poorly understood, indirect impacts on adjacent natural habitats (McDonnell and Pickett, 1990). Environmental changes associated with urban development may include increased concentrations of contaminants (e.g. metals, pesticides, hydrocarbons and nutrients); siltation or erosion; structural modification; changes in drainage; and the introduction of exotic species (Stark, 1998; Lindegarth and Hoskin, 2001; Lim and Navjot, 2004).

The effects of disturbance on mangrove fauna can range from subtle changes in species composition, through partial or complete defaunation, to the total loss of the habitat and its biological assemblages. Anthropogenic impacts may be complex, however, with intensity varying at different spatial and temporal scales (Lindegarth and Hoskin, 2001), and occasionally unpredictable, due to synergistic effects where several types of disturbance act together (Jones, 1975). Despite the apparent ubiquity of urban

encroachment on mangroves, little research has been undertaken on the effects of urbanisation—defined as the process of city establishment and growth, particularly spatial expansion (Detwyler and Marcus, 1972)—on these ecosystems.

There are substantial gaps in our knowledge of the effects of anthropogenic developments on mangroves. For instance, the ecological impacts of partial clearing, sedimentation and altered patterns of drainage are poorly understood. It is not known whether the biological diversity of fragmented, urbanised mangroves (such as patches of remnant forests fringing coastal developments) is similar to that in undisturbed habitats. Are mobile species such as birds affected by habitat fragmentation? Do some mammals or birds disappear in response to anthropogenic impacts, including the introduction of introduced species? Do native species benefit from aspects of development? The information on the response of mangrove biota to urban encroachment is sparse and the current literature typically concerns benthic invertebrates (Lindegarth and Hoskin, 2001; Holguin et al., 2005). Chapter 3 highlighted the paucity of information on mangrove vertebrate fauna in undisturbed mangrove systems. There have been no studies in tropical Australia on the impacts of anthropogenic disturbance on the vertebrate fauna of mangroves.

These information gaps are problematical, as sound environmental management of coastal resources typically requires assessment of the potential impacts of various development proposals on mangrove habitats. Such assessments are of limited value if knowledge of the structure, function and ecological interactions present in undisturbed mangrove habitats (Underwood, 2000), and the kind of response expected from them to various forms of disturbance (Dernie et al., 2003), are largely unknown. Indeed, predicting the effects of natural and artificial disturbance, and understanding post-disturbance community trajectories, is necessary for conserving these resources (McGuinness, 1992; Skilleter and Warren, 2000; Skilleter, 2000).

In Darwin Harbour, the mangrove forests surrounding the city of Darwin (population 82,000) have been exposed to a range of different natural and anthropogenic disturbances. As such, they offer an ideal opportunity to study the spatial and temporal effects of urbanisation, industrialisation, cyclone disturbance and post-disturbance recovery processes (McGuinness, 1992, 2002a). Cyclone Tracey had a severe but relatively localised impact on Darwin Harbour and mangroves have typically shown progressive

but differential recovery (Burke, 1992; Youssef, 1997; Ferwerda, 2000). Clearing, and other disturbances, to mangroves have also provided opportunities to study the recovery of biotic assemblages (Guinea, 1987; Audas, 1992). It is also fortunate that most of Darwin Harbour appears to be in near-pristine condition (Anon, 2003). At least, it is evident from the fairly extensive aerial photography archive that the majority of mangroves have not been recently disturbed. This has allowed sites for comparison to be located in close proximity to disturbed sites in the same estuary (see Figure 2-3, Chapter 2).

The results presented in Chapter 3 highlighted that the mangroves in Darwin Harbour are productive habitats for terrestrial mammals and birds. In this chapter, the diversity and abundance of vertebrate fauna in mangroves adjacent to three types of anthropogenic developments—urban, industrial and primary production—is investigated. Comparison with the fauna of the undisturbed mangrove sites will provide insights about how disturbance affects faunal diversity—information of practical value for management and conservation purposes.

Aim

The aim of this chapter is to test for direct or indirect effects of anthropogenic disturbance on the terrestrial vertebrate fauna in mangrove forests in Darwin Harbour. The diversity, abundance and distribution of vertebrate fauna within the four main mangrove assemblages (hinterland margin, tidal flat, tidal creek and seaward) was investigated at three sites exposed to different kinds of anthropogenic disturbance. The vertebrate fauna of these disturbed sites will be compared with that of undisturbed mangrove sites (described in detail in Chapter 3). The vertebrate groups studied at disturbed sites were;

- arboreal and ground mammals and
- birds

Bats were not studied due to time constraints and because of their high mobility.

Subsequent chapters of this thesis will examine the invertebrate fauna of the same disturbed and undisturbed sites to gain a more comprehensive picture of faunal diversity and the effects of anthropogenic disturbance.

4.2. Methodology

Wildlife survey methods similar to those practised by the NT Department of Natural Resources, Environment and the Arts (NRETA) were used in the mangrove vertebrate fauna surveys (see Section 3.2). As far as possible, survey methodology in disturbed sites was consistent with that used in undisturbed mangroves. Overall, four disturbed study sites were selected in the East and Middle Arms of Darwin Harbour—Sites BV, DP, DM and DE (see Figure 2-3, Chapter 2). Descriptions of the location, environmental characteristics and the kind of anthropogenic disturbances that affected each of these sites are contained in Chapter 2. A total of 26 study plots on eight transects were established in disturbed mangroves (see Figures 2-7, 2-8, 2-9 and 2-10, Chapter 2).

Vertebrate surveys were only conducted at three of these sites. The fourth site (Site DE in Charles Darwin National Park) was not studied as it comprised only narrow bulldozed tracks through largely undisturbed tidal flat and tidal creek assemblages and the scale of disturbance was deemed inappropriate for studies of vertebrates. This site was only used for invertebrate surveys (see Chapter 6).

Due to the patchy nature of disturbance, it was not possible to study all assemblages at every site. The four assemblages being studied (hinterland margin, tidal flat, tidal creek and seaward) were only present at Sites BV (Bayview) and DP (Darwin Port). The seaward assemblage was absent at Site DM.

All vertebrate surveys at both disturbed and undisturbed sites were completed during the months of June to November (Table 4-1).

The shape of study plots was adjusted to suit the typically linear form of many disturbed areas. For instance, 33 m × 75 m study plots were aligned parallel to rock walls at Sites BV and DP (Figure 4-1). As in all sites however, the rectangular plots had the same total area (0.25 ha) as the standard 50 m × 50 m study plots used elsewhere. Mammals and birds in disturbed sites were surveyed using the same field techniques used in undisturbed sites, except for some minor modifications, described below.

~4.2.1. Mammal trapping

Mammals were surveyed in each of the four assemblages at two disturbed locations—Site BV and Site DP—in the East Arm of Darwin Harbour. It was not possible to survey

Figure 4-1: Photos taken during fauna surveys in disturbed mangroves of Darwin Harbour. a) artificial ponding of water in tidal flat caused localised tree death at Bayview (Site BV, plot BV41); b) vegetation clearing in *Rhizophora*-dominated tidal creek assemblage (Site BV, plot BV22); c) degraded seaward assemblage at the Darwin Port (Site DP, plot DP82); d) Black Rat (*Rattus rattus*) at plot BV42; e) clearing of seaward zone at Site DP in October 2001, f) earthworks near water inlet channel through mangroves at Site DM—prawn farm in Middle Arm; g) Elliot and cage traps in dead tree in seaward assemblage at Site BV (plot BV81); h) rock-armoured walls typically abut seaward mangroves at sites BV and DP; and i) mangrove robin nesting in dead *C. australis* forest at Site BV.

disturbed sites during the same years as undisturbed sites (i.e. 1999 or 2000) and one mammal survey was conducted during the dry season of 2001 (Table 4-1). Due to time and logistical constraints, surveys in disturbed sites were conducted on both transects simultaneously—192 traps were set for four consecutive nights. This differed from undisturbed sites, where one transect (96 traps) was trapped over four nights then the next was trapped over the following four nights. Site BV was surveyed in August 2001, Site DP in November 2001. In all other respects, the methodology for mammal trapping was the same as that for undisturbed sites (described in Section 3.2.1).

Table 4-1: Schedule of sampling in undisturbed and disturbed mangroves in 1999–2001. Symbols (●) indicate timing and frequency for dry season mammal trapping surveys.

MAMMALS	**UNDISTURBED SITES (Aug-Nov 1999, Jun-Aug 2000)**			**DISTURBED SITES (Aug-Nov 2001)**			
Site	E1	E2	M3	BV	DP	DM	DE
Location	Charles Darwin	Elizabeth River	Jones Creek	Bayview	Darwin Port	Prawn Farm	CDNP tracks
Hint/margin	● ●	● ●	● ●	●	●	-	-
Tidal flat	● ●	● ●	● ●	●	●	-	-
Tidal creek	● ●	● ●	● ●	●	●	-	-
Seaward	● ●	● ●	● ●	●	●	-	-

~4.2.2. Bird surveys

Surveys of birds in disturbed sites were also conducted only during the 2001 dry season (Table 4-2).

Although comparisons of disturbed and undisturbed data based on surveys in different years have limitations (see Discussion), time and logistical constraints did not allow all surveys to be conducted during the same year. Bird surveys in all sites were done during replicated ten-minute censuses within each 0.25 ha study plot. The number of bird surveys in disturbed sites was doubled to allow direct comparison with data from undisturbed sites—providing a total observation period of 80 minutes per study plot. These data were compared with the same total observation period (80 minutes) from undisturbed sites—obtained during two consecutive dry season surveys in 1999–2000 (Table 4-2). Incidental species—birds observed within, or in close proximity to, study plots—contributed to the overall tally of species but were excluded from analyses.

Table 4-2 : Bird surveys conducted in disturbed and undisturbed mangrove sites

BIRDS	**UNDISTURBED SITES**			**DISTURBED SITES**			
Site	E1	E2	M3	BV	DP	DM	DE
Location	Charles Darwin	Elizabeth River	Jones Creek	Bayview	Port	Prawn Farm	CDNP tracks
Dry Season (Aug-Nov. 1999)	●	●	●	–	–	–	–
Wet Season (Apr- May 2000)	●	●	●	–	–	–	–
Dry Season (Jun-Aug 2000)	●	●	●	–	–	–	–
Wet season (March-May 2001)	●	●	●	–	–	–	–
Dry Season (Aug-Dec 2001)	–	–	–	●	●	●	–

Analyses

Analysis of variance was used to examine differences in mammal and bird species richness and abundance between the two disturbed sites and for comparison of disturbed and undisturbed sites. Mammal trapping data from disturbed sites (2001) were compared with data from undisturbed sites in 1999, and then with 2000 data. As with ANOVA's for undisturbed sites (Chapter 3), the data from each four night survey were pooled prior to analysis. For birds, results of individual censuses were pooled to obtain total bird species richness and mean abundance per study plot. Wet season data from undisturbed sites were excluded.

Comparisons of disturbed and undisturbed mangroves involved four factor nested analyses with the factors: disturbance (fixed), site (random, nested in disturbance), assemblage (fixed) and transect (random, nested in site). Site is clearly a random factor at undisturbed locations but could be considered fixed in disturbed situations, which were specifically selected for the study. However, aspects of their selection were random, and for consistency with chapter 3, disturbed sites were designated as random.

Tests for ANOVA assumptions were run prior to analysis by examination of normal plots of within-cell residuals and plots of means against standard deviations, before and after transformation. Mammal's abundance was transformed ($\log_{10}(x + 1)$) but transformation

was not necessary for mammal species richness data, nor for bird species richness or abundance data. Analyses were conducted using either the ANOVA/MANOVA module of *Statistica* or the general linear model in *Minitab*.

Ordination by non-metric multi dimensional scaling (MDS), using the procedures in the *Primer* version 5 program (Clarke and Warwick, 1994), were used to examine community patterns in mammal and bird diversity and abundance, and for comparison of disturbed and undisturbed sites. Study plots were classified according to their species composition using clustering based on a Bray-Curtis sites by species similarity matrix with each analysis run from 50 random restarts. Multivariate techniques using *Primer* were also used to examine patterns in bird species composition at the three disturbed sites (22 study plots) and to compare these with undisturbed sites (24 study plots). Wet season data (obtained from undisturbed sites only) was not included in the bird ordinations.

4.3. Results

~4.3.1. Mammals

Trap success

A total of 114 mammals was captured from 16 study plots over 1,536 trap nights during the surveys of disturbed mangroves in 2001 (Table 4-3). The highest mean trap success for any assemblage was 12%—recorded in both the tidal creek at Bayview (BV) and the tidal flat habitat at the Darwin Port site (DP), the lowest trap success was 3.6% in tidal creek habitat at site DP. The overall mean trap success for the two disturbed sites in 2001 was 7.4 %—less than the mean of 12.1% recorded in undisturbed sites (average of three sites over two years). Sampling effort in disturbed sites (1,536 trap nights) was however, only one third of that in undisturbed sites (4,608 trap nights).

During 1,536 trap nights, four animal deaths occurred (two *M. burtoni* and two *H. chrysogaster*), all apparently from dehydration or heat stress during the hot conditions in early November. In retrospect, trapping such a large grid (192 traps) single-handed, in mangroves was too ambitious and unwise, as some traps were not reached until mid-morning.

Table 4-3: Total captures and mean trap success (%) averaged over the two transects in each assemblage in 2001 (L) and at two of the three undisturbed sites in 1999 and 2000 (R)

ASSEM-BLAGE	STUDY PLOT **	TOTAL CAPTURES 2001 (1,536 trap-nights)	MEAN TRAP SUCCESS (%)	STUDY PLOT **	TOTAL CAPTURES 1999 (1,536 trap-nights)	MEAN TRAP SUCCESS (%)
	** See Figs 2-7 to 2-10 for locns	**DISTURBED SITES**		** See Figs 2-4 to 2-6- for locns	**UNDISTURBED SITES**	
Hint margin	BV61 & 62	13	6.8	E161 & 62	18	12.0
Tidal flat	BV41 & 42	15	7.8	E141 & 42	39	24.7
Tidal creek	BV21 & 22	23	12.0	E121 & 22	43	24.0
Seaward	BV81 & 82	11	5.7	E181 & 82	32	17.2
Hint margin	DP61 & 62	13	6.8	M361 & 62	8	6.8
Tidal flat	DP41 & 42	23	12.0	M341 & 42	14	3.9
Tidal creek	DP21 & 22	7	3.6	M321 & 22	17	10.7
Seaward	DP81 & 82	9	4.7	M381 & 82	9	10.2
	Total	**114**	**7.4**		**180**	**13.6**

Species richness

Species richness was not significantly different between the two disturbed mangroves studied—Sites DP and BV (Table A-14; Appendix A)—and appeared fairly uniform across sites, transects and assemblages.

A total of six mammals (4 native and 2 feral species) was recorded from disturbed mangroves (Table A-1, Appendix A) with a mean species richness of 1.81 (± 0.23 SE) per 0.25 ha study plot. The three most common species in disturbed sites (*M. burtoni*, *T. vulpecula* and *I. macrourus*) were the same as for undisturbed sites, but feral species comprised a greater proportion of the rest of the fauna (Figure 4-2). In particular, the percentage capture of feral rats and house mice were far greater in disturbed sites.

Overall, the relatively low species diversity of terrestrial mammals in mangrove habitats was even lower at sites that had been disturbed. Four species of small mammals that were occasional visitors to hinterland margin mangroves in undisturbed sites were absent from the disturbed sites studied (Figure 4-2). These included the Northern Quoll (*Dasyurus hallucatus),* Fawn Antechinus (*Antechinus bellus),* Pale Field Rat *(Rattus tunneyi)* and the Black-footed Tree-Rat (*Mesembriomys gouldii).* In contrast, water rats (*Hydromys*

chrysogaster) were not trapped in undisturbed sites.

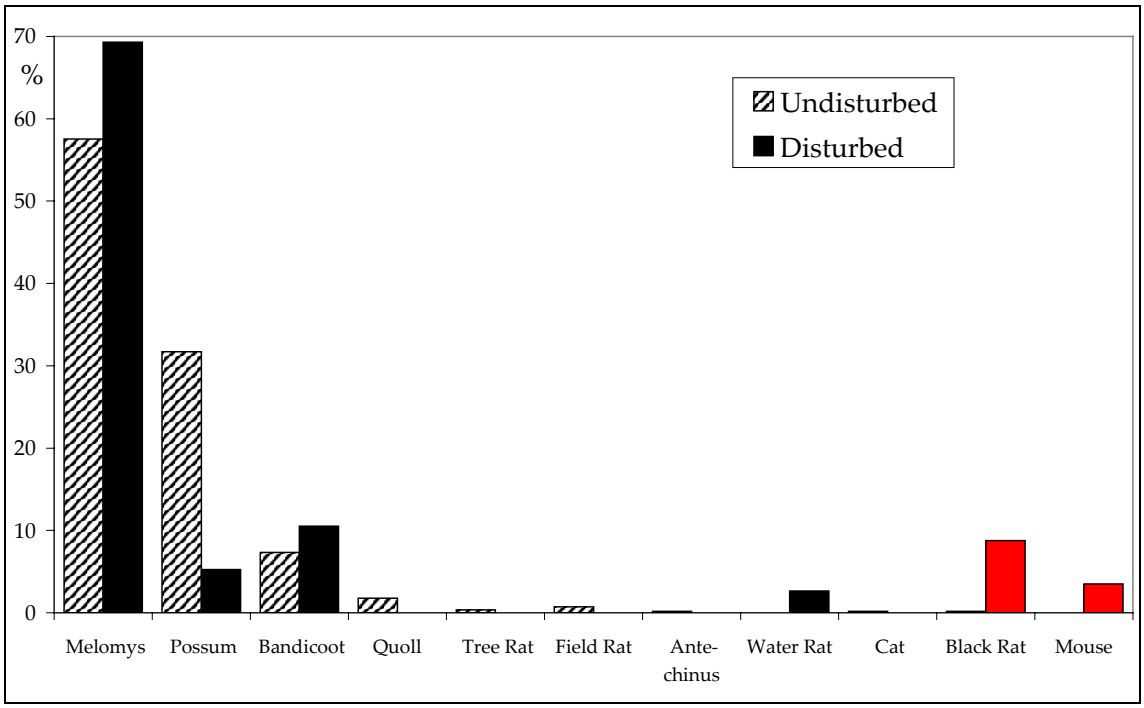


Figure 4-2: Percentage species composition of mammals in disturbed sites (total captures in 2001, indicated by solid bars) and undisturbed sites (sum of total captures from 1999 and 2000, indicated by hatched bars). Introduced species indicated in red.

Despite these overall differences, analysis of plot-based data showed that species richness was not significantly different between the disturbed and undisturbed sites when comparing disturbed sites with undisturbed sites in 1999 (year 1) and 2000 (year 2).

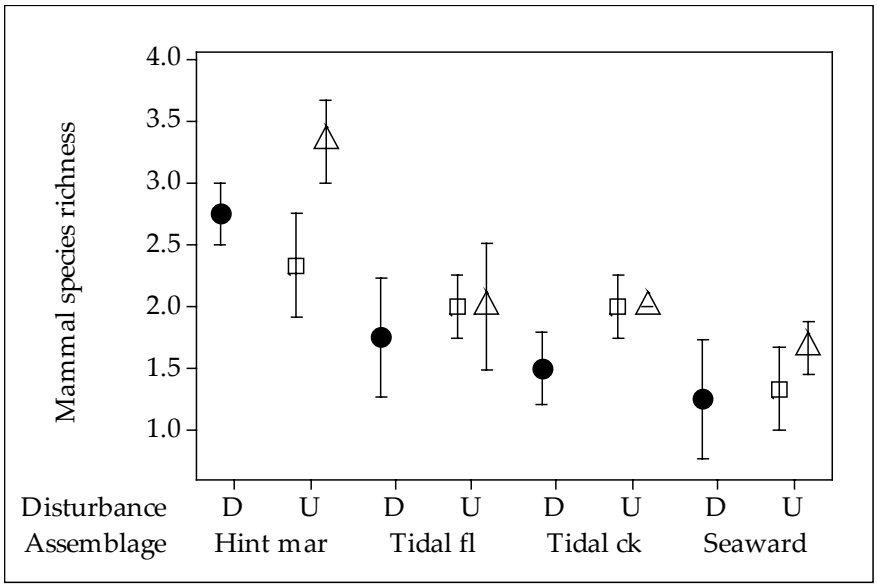


Figure 4-3: Mean species richness of mammals per hectare (± SE) in disturbed (D) and undisturbed assemblages (U). The year of the survey is denoted by symbol shape such that 2001 = circles, 1999 = squares and 2000 = triangles.

However, species richness varied significantly between assemblages (Tables A-16 and A-17, Appendix A). Comparison between assemblages indicates that like undisturbed sites, mammal species richness in disturbed sites is generally greatest in the hinterland margin and decreases to seaward. The most distinct difference in species richness between disturbed and undisturbed mangroves appears to be in the tidal creek (Figure 4-3). Although univariate analyses do not show significant differences between species richness in disturbed and undisturbed mangroves, multivariate analyses indicate they differ in composition. This is illustrated by ordinations based on the presence/absence of mammals in all study plots (Figure 4-4). Although there is overlap in the ordination and many points are not visible due to their similarity (the area of 34 overlapping undisturbed study plots is circled), there is some separation of sites.

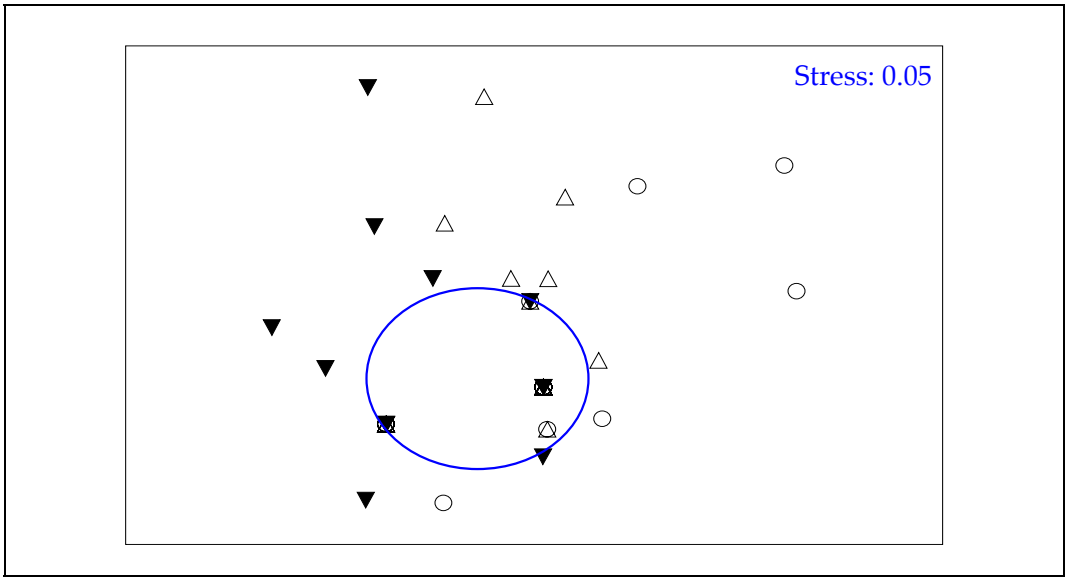


Figure 4-4: Ordination of study plots in undisturbed sites in 1999 (open circles) and 2000 (open triangles) and disturbed sites (closed downward triangles) based on the presence/absence of mammal species. Points are 15 disturbed and 45 undisturbed study plots. NB some points are not visible due to overlap—area of overlap circled in blue.

Mammal abundance

The total abundance of mammals at the two disturbed sites was similar, but there was considerable variation in abundance amongst the three undisturbed sites; from year to year; and between disturbed and undisturbed sites (Table 4-4). Analysis (Table A-15, Appendix A) revealed no significant difference in mean abundance between disturbed Sites BV (7.8 ha $^{-1}$± 1.58 SE) and DP (6.5 ha $^{-1}$ ± 1.76 SE). The mean density of each of the six species trapped in disturbed sites is listed in Table A-1, Appendix A.

Table 4-4 : Total number of captures in undisturbed and disturbed sites in Darwin Harbour. Each annual survey had equal numbers of trap nights per site.

	UNDISTURBED SITES			**DISTURBED SITES**	
	E1 -	**E2 -**	**M3 -**	**BV -**	**DP -**
1999	129	41	47	-	-
2000	167	99	73	-	-
2001	-	-	-	**62**	**52**

The overall mean abundance of mammals in disturbed sites (7.1 ha $^{-1}$ ± 1.2 SE) was less than the mean abundance in undisturbed sites (11.6 ha $^{-1}$ ± 1.2 SE). Graphs of the means suggest that disturbed sites (BV and DP) generally had intermediate mammal abundance (Figure 4-5). Very few mammals were recorded in undisturbed mangroves at site E2 in 1999, but standard errors indicate considerable variability in the data.

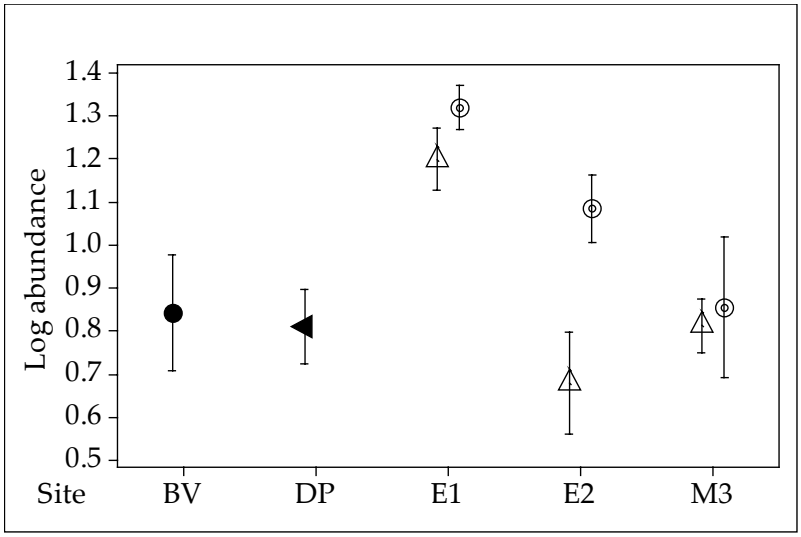


Figure 4-5: Mean mammal abundance ($\log_{10}(x + 1)$ transformed, ± SE) in disturbed sites in 2001 (closed symbols) and undisturbed sites in 1999 (open triangles) and 2000 (open circles)

ANOVA results showed no significant differences in mammal abundance between disturbed and undisturbed mangroves, nor amongst sites or assemblages when comparing 1999 data from undisturbed sites (Table A-18, Appendix A). When comparing 2000 data with disturbed sites, only a significant site × assemblage interaction was found (Table A-19, Appendix A) indicating that mammal abundance in assemblages differed between sites. The main cause of this interaction is due to the unusually low abundance in the tidal flat at site M3 in 2000 (Figure 4-6).

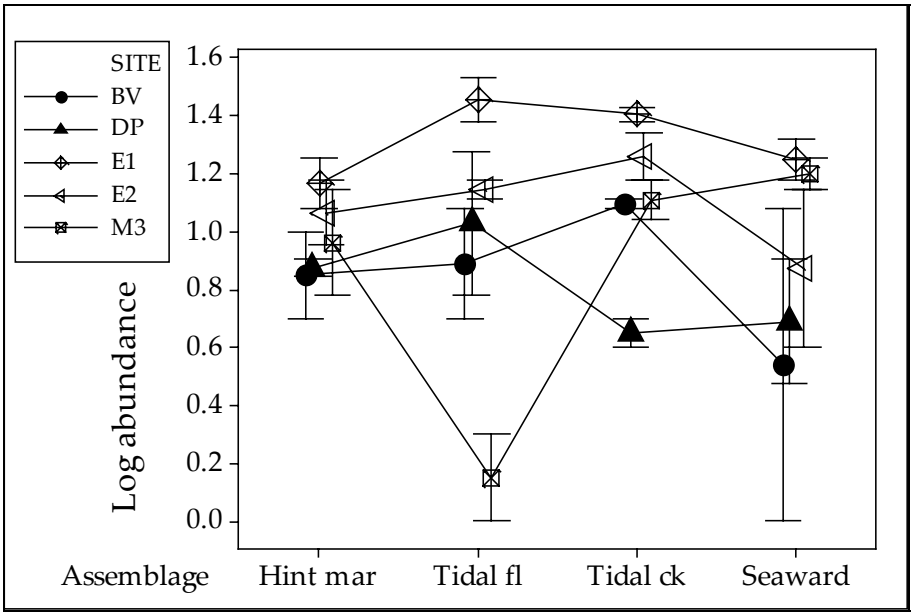


Figure 4-6: Mean mammal abundance ($\log_{10}(x + 1)$ transformed ± SE) in disturbed sites in 2001 (solid symbols) and undisturbed sites (open symbols) in 2000, in assemblages from landward (left) to seaward (right)

From the means it appears that abundance follows a different pattern from species richness—abundance at most sites increases between the hinterland margin and the tidal flat assemblage. Although abundance may increase slightly in the tidal flat and the tidal creek, there is no consistent overall pattern (Figure 4-6). In general, the seaward assemblage in disturbed sites appeared to have the least dense mammal populations (5.0 ha $^{-1}$ ± 2.48 SE) and the highest mean abundance (15.67 ha $^{-1}$ ± 2.36 SE) was recorded in the tidal creek assemblage in undisturbed sites

NMDS ordinations based on the abundance of the two most common individual species—*M. burtoni* and *T. vulpecula* illustrate that at sites with anthropogenic disturbance these species are generally less abundant (Figure 4-7).

NMDS ordination of sites based on the abundance of all mammal species (total captures per study plot) shows the similarity (and overlap) of several sites but clear differences between undisturbed and disturbed mangroves are also evident (Figure 4-8).

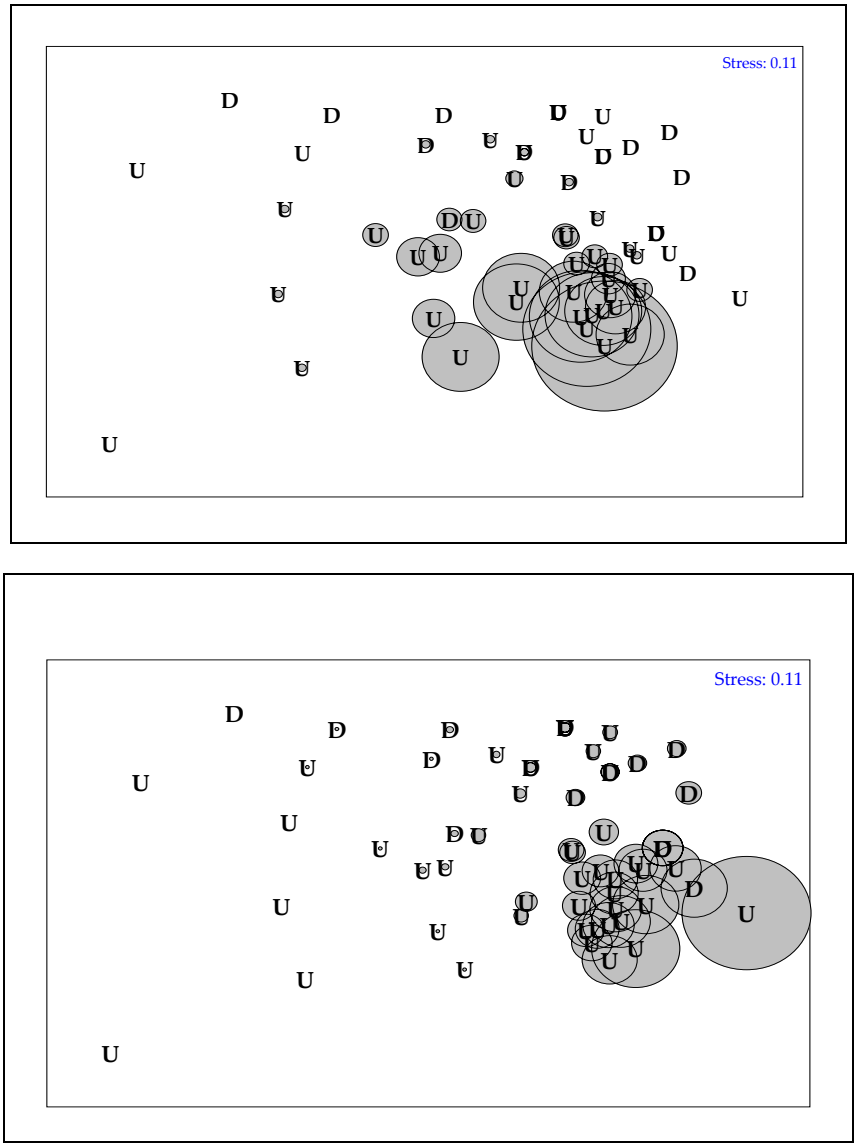


Figure 4-7: Ordination of study plots based on mammal abundance in disturbed (D) and undisturbed (U) mangroves with abundance superimposed [*T. vulpecula* (top) and *M. burtoni* (bottom)].

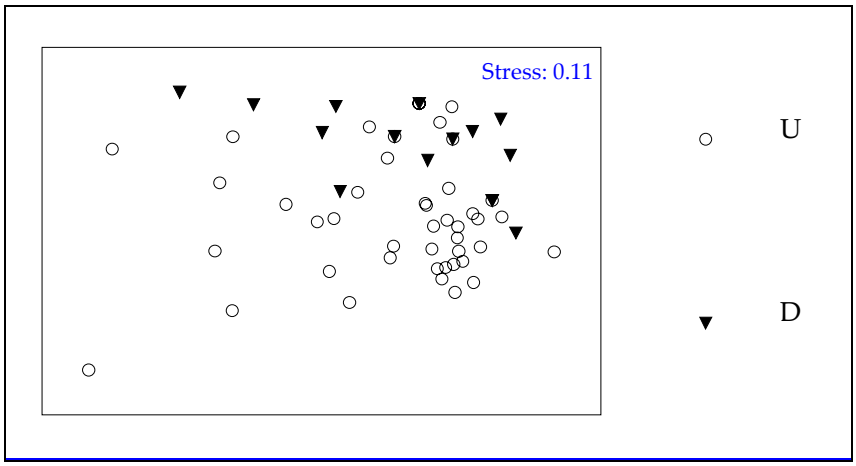


Figure 4-8: NMDS ordination of study plots in disturbed (D) and undisturbed (U) mangroves based on abundance of mammals (total captures per study plot per year)

~4.3.2. Birds

Species richness

A total of 66 species of birds (including 6 incidental species) were recorded in disturbed mangroves in the dry season of 2001 (Table A-9, Appendix A). Analyses comparing species richness in the three landward assemblages (common to each of the three disturbed sites studied) revealed significant differences between sites (Table A-20, Appendix A). Site BV had the highest bird species richness and Site DM the lowest (Figure 4-9 left). However, no difference in species richness was found when data from all four assemblages was compared between only sites BV and DP (Table A-21, Appendix A). The first analysis did not include the seaward assemblage in which high species richness was recorded for site DP. The second analysis included the seaward assemblage in which DP had high species richness and this resulted in BV and DP being, on average, similar when it was included (Figure 4-9, right).

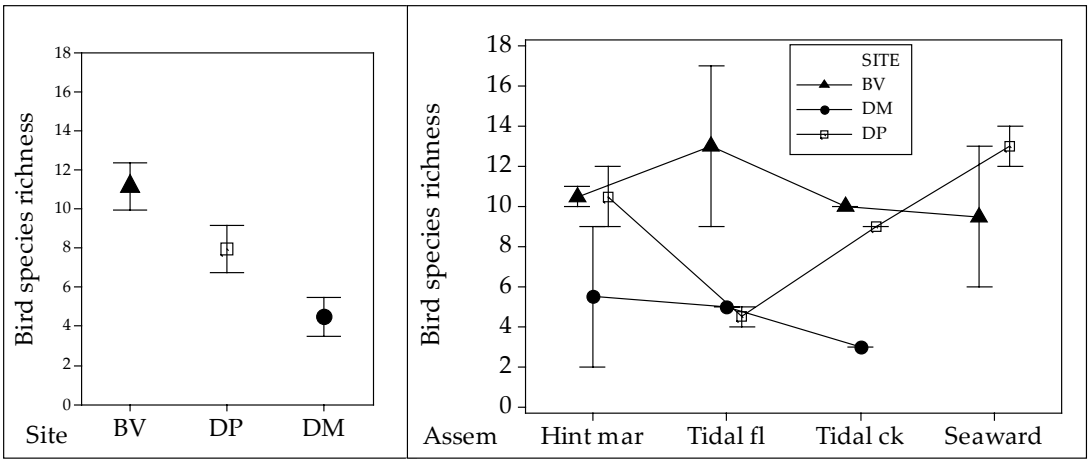


Figure 4-9: Left - Mean species richness of birds at three disturbed sites (BV and DP in East Arm and Site DM in Middle Arm) in three assemblages only. Right - Mean species richness in assemblages at three sites. Points are means per 0.25 ha^{-1} study plot (±SE) during one dry season survey in 2001.

The NMDS plot of bird species richness shows some underlying partitioning of birds into different assemblages (Figure 4-10). At least some components of the avifauna of the seaward, tidal flat and hinterland margin assemblages are distinct from each other but the bird fauna of the tidal creek is not so well defined.

The overall species richness of birds in disturbed sites (66 species) was only slightly less than in undisturbed sites (69 species) and analyses of plot based data also show no significant difference in species richness between disturbed and undisturbed mangroves

(Table A-24, Appendix A)

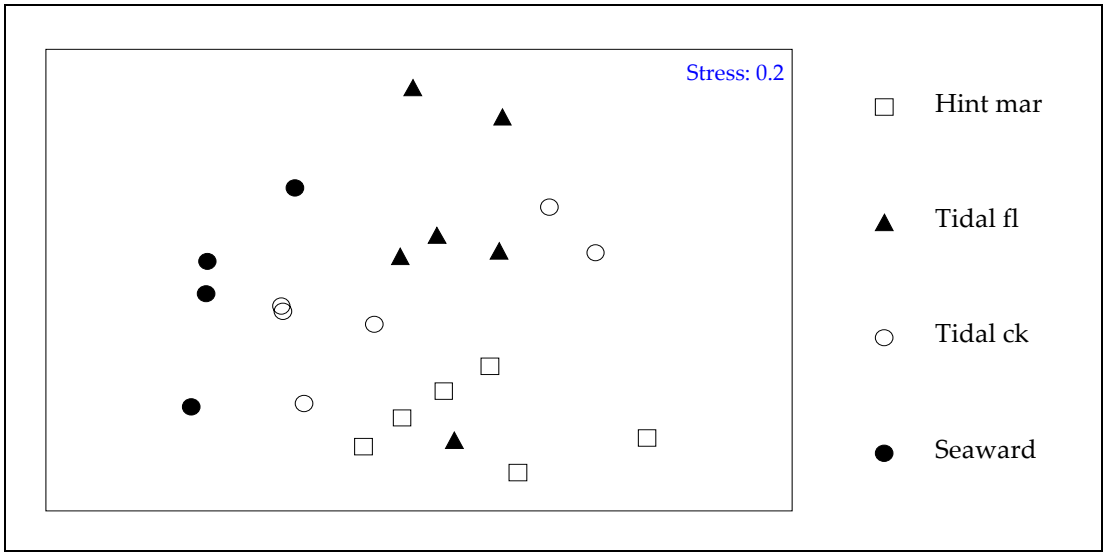


Figure 4-10: NMDS plot of bird species richness in 22 study plots at three disturbed sites. Each point represents one 0.25 ha study plot surveyed in the 2001 dry season.

The differences in species richness between the assemblages were also much the same between disturbed and undisturbed sites, though disturbed sites tended to show greater variability in each assemblage. The only substantial difference in diversity of birds between disturbed and undisturbed sites was in the tidal creek assemblage where disturbed mangroves had considerably fewer species (Figure 4-11).

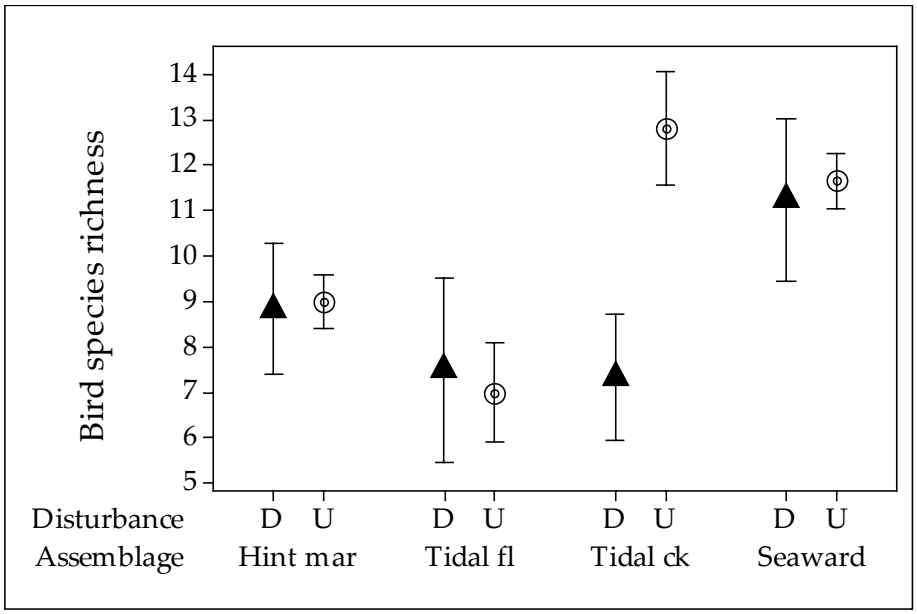


Figure 4-11: Mean bird species richness (±SE) during dry season surveys in assemblages from landward to seaward (L to R) in disturbed (closed symbols) and undisturbed mangroves (open symbols). Points are means per study plot of three sites (U) over two years, compared with means of 2 sites (D) over one year.

While species richness may not change substantially between natural and disturbed mangroves, species composition did. Of the 66 species recorded in disturbed habitats, 16 of these were not recorded in undisturbed sites (Table A-9, Appendix A). Conversely, there were 19 species in undisturbed sites not recorded from disturbed sites—of which only three species were seasonal migrants or visitors to mangroves and therefore likely to be excluded from dry season surveys in disturbed sites. The ordination of all study plots based on the presence and absence of species (Figure 4-12) illustrates that the composition of the avifauna of disturbed encompassed a much greater range of variation than that in undisturbed sites.

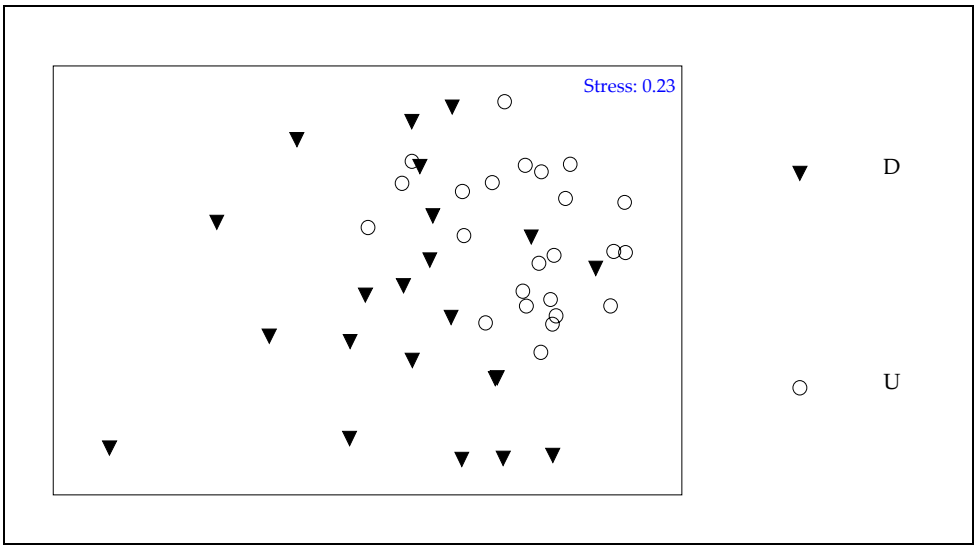


Figure 4-12: Ordination of 22 disturbed and 24 undisturbed study plots based on their bird species composition during dry season surveys conducted in 1999, 2000 (U) and 2001 (D).

Bird Abundance

Overall, the mean density of birds recorded in disturbed mangroves in 2001 was 14 ha^{-1} (Table A-9, Appendix A). There were 10 relatively common species in disturbed sites with densities in any one assemblage greater than 1.0 ha^{-1}. The four most abundant species (the brown honeyeater, red-headed honeyeater, collared kingfisher and rufous-banded honeyeater) comprised 42% of all observations.

Abundance of birds was not significantly different among three disturbed sites when comparing the three landward assemblages common to each site (Figure 4-13, Table A-22, Appendix A). However, bird abundance at Site BV was significantly different from Site DP when all four assemblages were compared (Table A-23, Appendix A).

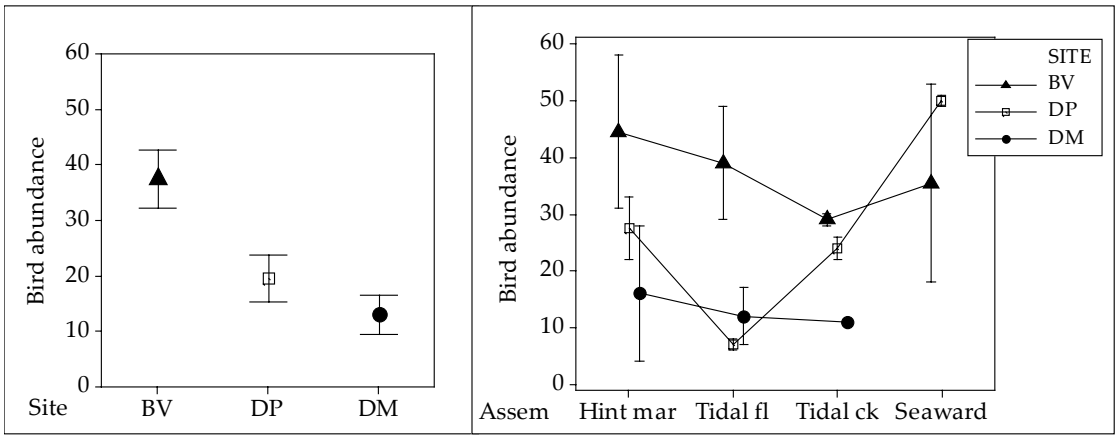


Figure 4-13: Mean bird abundance at three disturbed sites (L) and in assemblages from landward to seaward (R). Points are means per 0.25 ha^{-1} study plot (±SE) recorded during one dry season survey in 2001.

The abundance of birds in the 22 disturbed study plots was partitioned within the major assemblages—with the exception of plots in the tidal flat which are widely dispersed. Plots within other assemblages were grouped from landward (left) to seaward (right) indicating they had similar bird abundance—whereas the scattered position of plots in the tidal flat assemblage indicated wider variation in bird abundance (Figure 4-14).

The four most common species in undisturbed sites—in decreasing order of abundance—brown honeyeater, red-headed honeyeater, yellow white-eye and lemon-bellied flycatcher, differed from those in disturbed sites, listed above. As in disturbed sites, the four most abundant species in undisturbed sites comprised 42% of all observations.

Although the mean density of birds recorded in disturbed mangroves (14 ha $^{-1}$) was lower, but not significantly different from undisturbed mangroves (17 ha $^{-1}$) analyses detected differences between assemblages (Figure 4-15, Table A-25, Appendix A). Overall, bird abundance in disturbed sites tends to follow the same general trend as undisturbed sites—where the highest density of birds typically occurs in the seaward assemblage and the tidal flat had the lowest numbers of birds. As for species richness however, the most marked difference in bird abundance between disturbed and undisturbed mangroves was found in the tidal creek—where abundance was considerably less in disturbed sites.

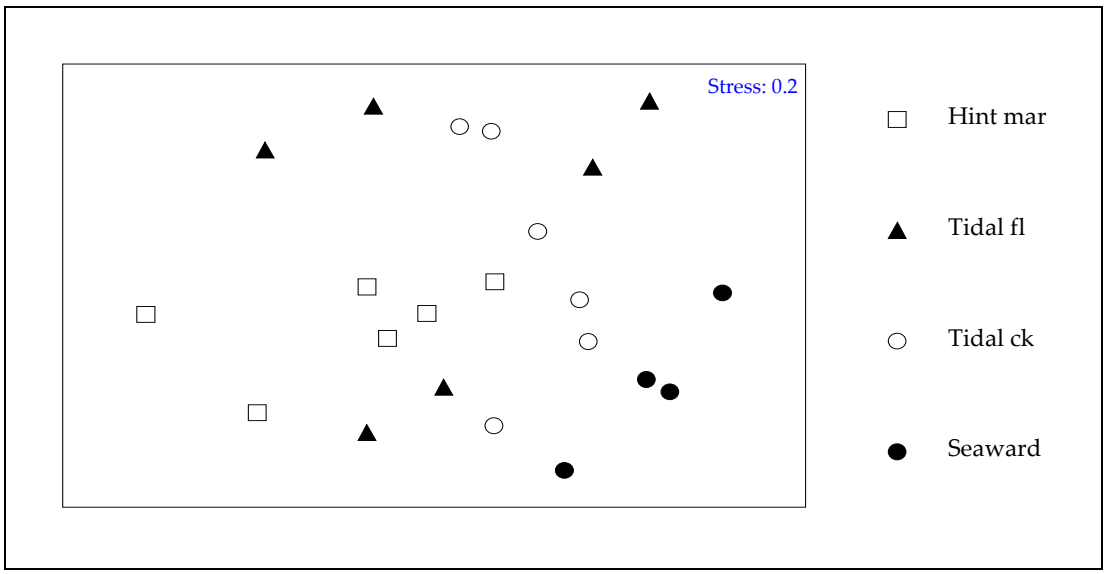


Figure 4-14: NMDS plot of bird abundance in 22 study plots at three disturbed sites. Each point represents one 0.25 ha study plot surveyed in the 2001 dry season.

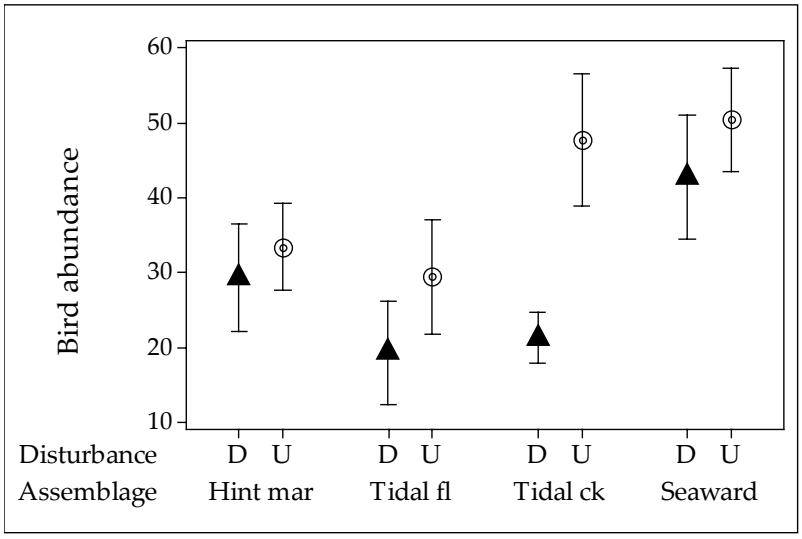


Figure 4-15: Plot of mean bird abundance (±SE) in assemblages at disturbed (solid symbols) and undisturbed sites (hollow symbols), from landward (L) to seaward (R).

Overlap of points in the NMDS ordination indicated that bird abundance is similar in the majority of disturbed and undisturbed sites. Disturbed sites do, however, include a wider range of variation in abundance (Figure 4-16).

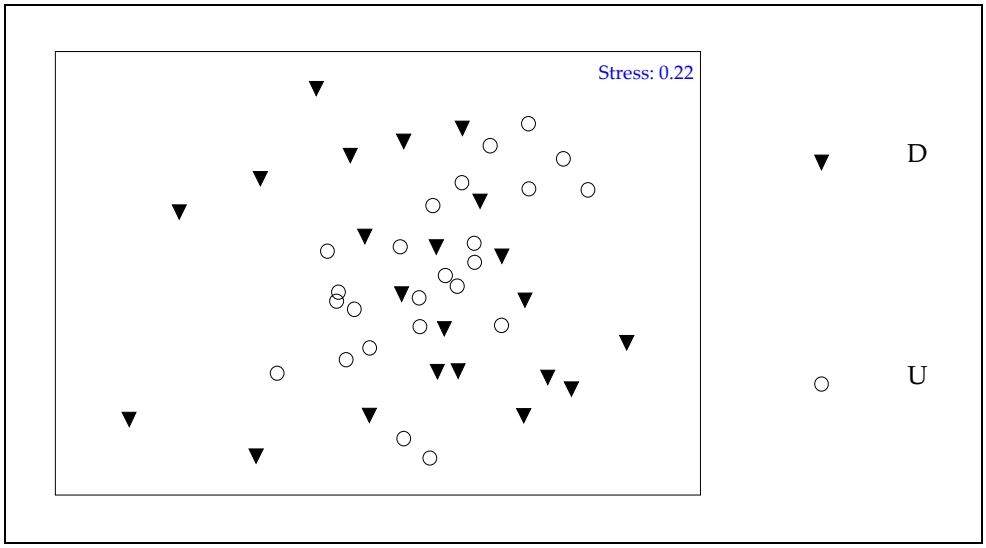


Figure 4-16: Ordination of 22 disturbed (D) and 24 undisturbed (U) study plots based on the abundance of 80 bird species during dry season surveys conducted in 1999, 2000 (U) and 2001 (D).

Foraging ecology

Each of the 66 bird species was assigned to one of the ten different feeding guilds described in Chapter 3. The four most common feeding guilds in disturbed mangroves were carnivores (32%), insectivores (27%), nectivore/insectivores, (12%) and granivores (7.5%,).

Figure 4-17 shows the mean abundance of birds in feeding guilds in disturbed and undisturbed sites. Analyses of the data indicated that abundance of birds in different feeding guilds did not vary significantly between disturbed and undisturbed mangroves (Tables A-26, A-27 and A-28, Appendix A). Abundance of carnivores and insectivores varied between different assemblages, indicated by significant main effect for assemblage. Numbers of carnivorous birds appeared to increase from landward to seaward (Figure 4-18, lower) whereas insectivorous birds, at most sites, tended to be lowest in the tidal flat and reasonably abundant in other assemblages and (Figure 4-18, upper). A significant site × assemblage interaction for carnivorous birds also indicated that abundance varied in assemblages amongst different sites. The main reason for this interaction was the particularly high abundance of carnivorous birds in the tidal flat at Site BV and in the seaward assemblage at Site DP. Abundance of nectivorous/insectivorous birds did not vary significantly between disturbed and undisturbed locations, nor among sites or assemblages.

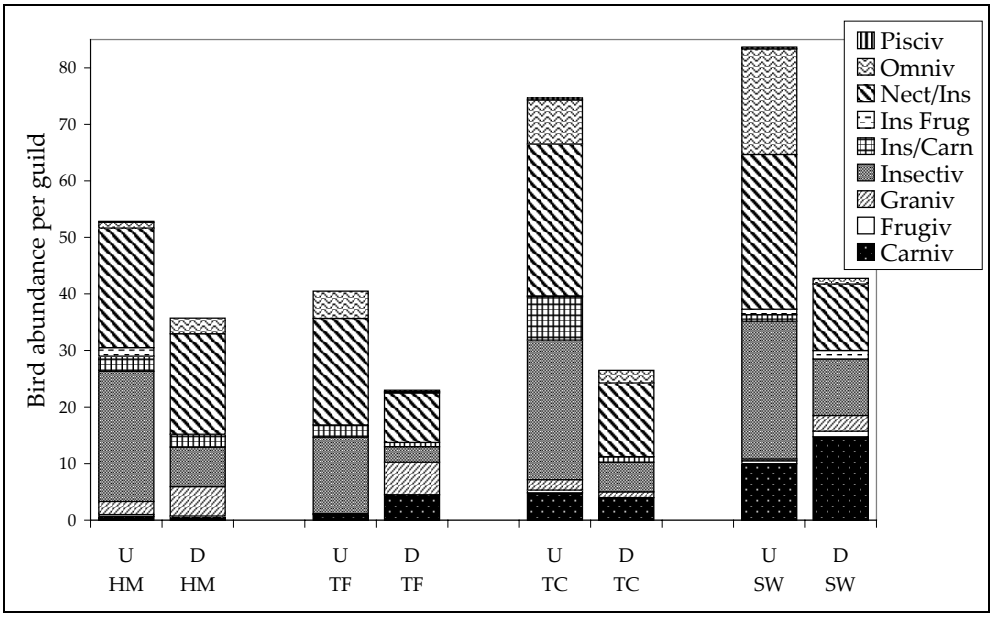


Figure 4-17: Mean abundance of birds in different feeding guilds. Data pooled from two disturbed (D) and three undisturbed (U) sites, graphed in assemblages from landward (left) to seaward (right) where HM denotes hinterland margin, TF - tidal flat, TC - tidal creek and SW - seaward assemblages. Means calculated for each 0.25 ha $^{-1}$ study plot from eight replicate censuses during dry season surveys in 1999-2001.

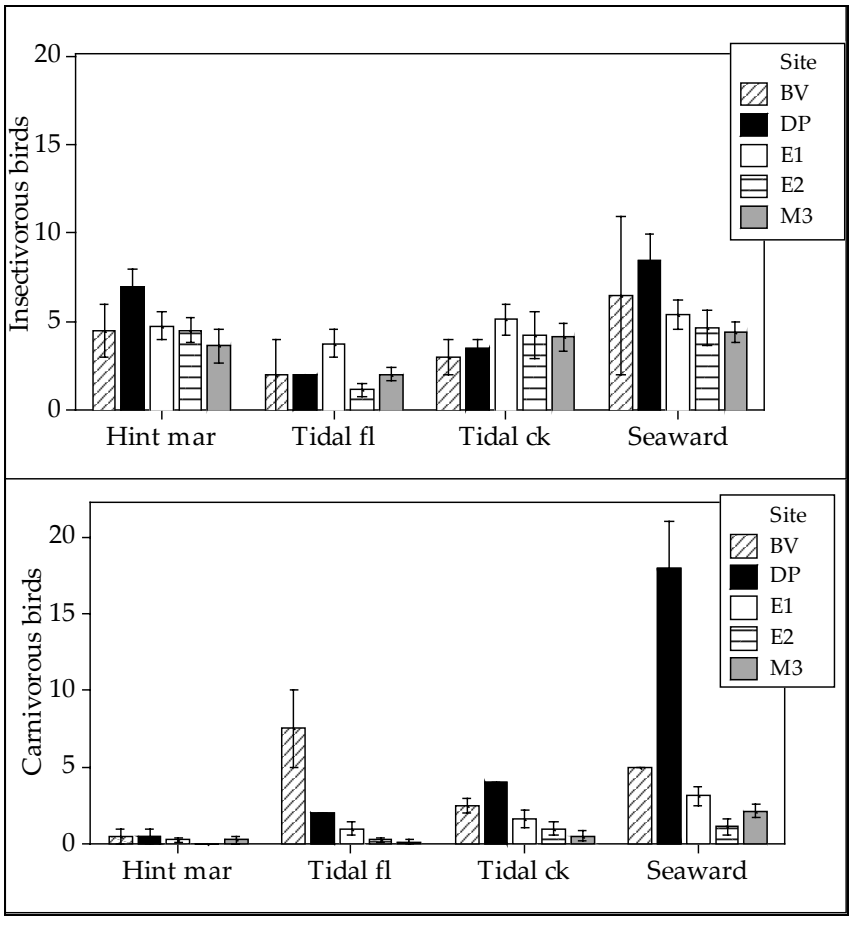


Figure 4-18: Mean abundance (±SE) of insectivorous (upper) and carnivorous birds (lower) in disturbed (BV, DP) and undisturbed sites (E1, E2, M3). Bars represent mean abundance per 0.25 ha^{-1} study plot in assemblages from landward (L) to seaward (R).

4.4. Discussion

Diversity of mammals in disturbed and undisturbed mangroves

This study recorded four native and two introduced species in disturbed sites, whereas in undisturbed sites seven native and two introduced species were found. In all, when incidental observations are included, 13 species were recorded from undisturbed and six species from disturbed mangroves, suggesting that the relatively low species diversity of terrestrial mammals in mangrove habitats is diminished further in disturbed mangroves. Although mean species richness (1.8 ± 0.2 SE) in disturbed sites, was somewhat less than the 2.1 (±0.1 SE) recorded in undisturbed sites, analyses of variance failed to detect significant differences in species richness among disturbed and undisturbed sites. Large differences between the diversity reported from the three undisturbed sites however, presumably contributed to the lack of any significant difference when compared with disturbed sites. Temporal (inter-annual) variation in mammal populations may also have confounded the possible effects of disturbance on mangrove mammals, given that disturbed and undisturbed sites were sampled in different years. The mammal fauna did however, show similar trends in disturbed and in undisturbed sites. The same three species were dominant in all mangroves (*M. burtoni, T vulpecula* and *I. macrourus*). Indeed, *M. burtoni* is ubiquitous in both—comprising 57% and 69% of captures in undisturbed and disturbed mangroves respectively. As in undisturbed sites, mammal species richness tended to decrease progressively through the four assemblages from landward to seaward.

In contrast with undisturbed sites, species richness did not vary significantly between assemblages in disturbed sites. Overall, the lower diversity in disturbed sites may reflect the effects of habitat modification, including development immediately adjacent to mangroves and deforestation, particularly in lower intertidal areas (where tall trees are necessary to prevent drowning of arboreal mammals). Indeed, the most diverse assemblage for vertebrate fauna is typically the hinterland margin and the integrity of this habitat will be important in maintaining species richness in a relatively species-poor environment. Neither site BV or DP intergrades with extensive, healthy native woodland habitat—as in each of the undisturbed sites—so the pool of species that might occasionally visit these mangroves is possibly greatly reduced. In mangrove areas disjunct from natural hinterland habitats, species richness is likely to be reduced to just a

few resident species (e.g. *M. burtoni* and *T. vulpecula*).

Indeed, several native species which were largely restricted to the hinterland margin assemblage in undisturbed mangroves were absent in disturbed sites where the hinterland had been substantially modified. Thus, it was not unexpected that these species—which are relatively uncommon visitors to the hinterland margin assemblage—were not present in urbanised mangroves. In addition, the distribution and abundance of many terrestrial species may be in decline, due to widespread but currently indecipherable environmental change (Woinarski, 2000; Fisher, 2001; Woinarski et al., 2001), which may, in turn, affect populations in adjacent, but interlinked habitats, such as mangroves.

Recent studies in tropical savannas of the Top End have documented declines in the abundance of several native mammals, including the northern quoll *Dasyurus hallucatus, Antechinus bellus* and *Rattus tunneyi* as well as several typically common species such as *I. macrourus* and *T. vulpecula* (Woinarski, 2000). Indeed, the quoll was recently classified as Vulnerable under Northern Territory Legislation (Woinarski, 2003) and listed as Endangered by the Commonwealth (Anon, 2006). These declines are attributed to predation by feral cats, the introduction of cane toads and environmental change, including increased frequency of destructive fires. In general, species with declining distributions are likely to be most affected by urban encroachment and the results of this study support this prediction. Although not a resident mangrove species, the northern quoll declined from 1.8% of captures in undisturbed mangroves to nil in disturbed mangroves—probably indicating not only loss of habitat, but sensitivity of this species to anthropogenic disturbance. Indeed, the disappearance of the four native mammals from disturbed mangroves may well be representative of trends in the wider landscape.

There were no significant differences in mammal diversity in univariate analyses between disturbed and undisturbed mangroves but multivariate analyses indicate there were changes in species composition. Four native mammals that occasionally utilise landward mangrove assemblages in natural mangroves appear to have been replaced by two introduced rodents at disturbed sites (*Mus musculus* and *Rattus rattus*). Moreover, the proportion of the total fauna represented by feral species increased from 0.3% in undisturbed mangroves to 12% in disturbed sites. *M. musculus* and *R. rattus* are virtually restricted to urban and modified areas (Woinarski, 2000), which are rapidly replacing

natural woodland habitats surrounding Sites DP and BV, but these species appear to occasionally venture into the landward mangrove fringe. *R. rattus* is obviously an adept climber and was recorded from *Rhizophora stylosa* trees several meters above ground level. The house mouse *M. musculus*, was recorded several times in disturbed sites but was not trapped in undisturbed mangroves of this survey.

Another factor contributing to an apparently different suite of species between natural and disturbed mangroves is the absence of water rats in trapping results from undisturbed sites. Although this species was obviously common (detected by its tracks and feeding areas) it eluded capture in undisturbed sites. Water rats were however, trapped on several occasions during surveys in disturbed sites—most often amongst man-made rock walls adjacent to the seaward zone—where traps could be placed at ground level, but above the high tide mark. This species is probably reluctant to climb trees (where traps were always placed in undisturbed sites) as it takes most of its prey of live fish from the water, but would likely find refuge amongst the granite boulders fringing both disturbed sites. In this instance, sampling differences may have contributed to the differences in species composition indicated by the ordination. It follows that water rats may, in fact, benefit from anthropogenic habitat modification. Alternatively, the animals caught may simply have been displaced—they were caught during a period of active bulldozing of adjacent habitat, in which extensive *Sonneratia* and *Rhizophora* forests were being cleared for construction of the Port (Figure 4-1e). Several of the animals trapped were recorded away from their usual habitat (i.e. seaward and tidal creek mangroves) and were stressed—with unfortunately more than one trap death from dehydration.

Overall, the mammal species composition in natural mangrove areas differed qualitatively from sites that have been subject to anthropogenic disturbance. Multivariate analyses illustrate these differences in species composition—showing a distinction between disturbed and undisturbed sites in NMDS ordinations based on the presence or absence of mammals. Environmental differences resulted in the loss of some species from disturbed mangroves, but the introduction of other species, so that the overall diversity remained somewhat similar to natural mangroves.

Abundance of mammals in disturbed and undisturbed mangroves

The mean abundance of mammals in disturbed sites was 7.1 ha $^{-1}$ (± 1.2 SE) and although abundance seemed lower than in undisturbed sites (11.6 ha $^{-1}$ ± 1.2 SE), there was no significant difference in mammal abundance between sites or assemblages. In general, the abundance of *M. burtoni* in disturbed mangroves (4.9 ha^{-1} ± 1.2 SE) was relatively high—despite proximity to roads and clearings—and not markedly less than undisturbed sites (6.7 ha^{-1} ± 0.5 SE). Studies in monsoon rainforests of the Top End indicate that *M. burtoni* is very common, being found in over half the patches surveyed and is a generalist species, characteristic of small and disturbed rainforests (Menkhorst and Woinarski, 1992). A recent review of the mammal fauna of savanna woodland habitats in the Top End also associates *M. burtoni* with degraded sites and sites supporting few specialised rodents (Woinarski et al., 2001). Breeding of *M. burtoni* in November 2001 may also have contributed to high mammal abundance in disturbed sites. The timing of surveys at site DP (November) may have coincided with one of the two main bi-annual breeding periods noted by (Begg et al., 1983), that is April – June or October – January. For instance, the proportion of juveniles or breeding females was 13.5% at Site BV in August 2001 and 31% at Site DP in November 2001, suggesting that trapping at the Port coincided with breeding of this species.

Furthermore, the mean density of bandicoots in disturbed sites (0.75 ha^{-1} ± 0.41 SE) was only slightly less than in undisturbed sites (0.85 ha^{-1} ± 0.17 SE) and this species was quite common on the urban fringe. This is consistent with observations in other terrestrial habitats where *I. macrourus* is considered a disturbance-increaser (Winter (1988) as cited in Woinarski, 2000; Woinarski et al., 2001) favouring disturbed rainforest habitats (Menkhorst and Woinarski, 1992). Bandicoots increased from 7.3% of total captures in natural mangroves (n=41) to 10.5% in disturbed sites (n=12). Percentage captures of *M. burtoni* also increased, suggesting that this species may be quite opportunistic and was favoured by disturbance in mangroves—as observed in other habitats (Woinarski et al., 2001)

Thus the predominance of two disturbance-increaser species in mangrove habitats has no doubt contributed to the lack of significant differences in mammal abundance between natural mangroves and disturbed mangroves. These observations provide further strength to the argument that the dynamic and unstable nature of mangrove habitats

favours hardy species, adapted to either rapid or gradual environmental change (see conclusions, Chapter 3). Further, exceptionally low numbers of mammals at undisturbed Site M3 (as indicated by the significant site × assemblage interaction in 2000) reduced the overall mean abundance in undisturbed tidal flat mangroves. This odd result followed the capture (and subsequent release) of a feral cat at the site the previous year. Woinarski (2000) notes that feral cats are now prevalent in the Top End and that it is likely they are having a substantial impact on most rodent populations. Indeed, predation by feral cats is thought to be a major contributor to the decline in small mammal abundance in the Top End (Woinarski et al., 2001). The presence of the feral cat may have been related to the subsequent crash in resident mammal abundance at Site M3.

The majority of mammals however, did not benefit from disturbance. For example, although the northern brushtail possum is also recognised as a hardy, generalist species with remarkable ecological flexibility (Kerle, 1998), it decreased in density from 3.69 animals per ha in undisturbed mangroves (relatively high for Australian brushtails) to 0.38 per ha in disturbed sites. The decline is presumably related to changes in the *R. stylosa* forests of the tidal creek assemblage at disturbed sites—which represent primary habitat for possums in mangroves, providing both food and crucial refuges above high tides. Overall, mammal abundance was generally less in disturbed sites across all assemblages.

Ordinations based on the abundance of all mammals (total captures per study plot) showed the similarity of some sites but also illustrated clear differences in abundance between undisturbed and disturbed mangroves. Undisturbed sites occurred as a dispersed group which had a minor overlap with a small group of disturbed sites (with minor levels of disturbance). The remainder of disturbed sites formed a distinct group, with similar abundance, across the top of the ordination. Ordinations of abundance data for individual species, such as *M. burtoni* and *T. vulpecula* show in more detail that changes to mangroves associated with anthropogenic disturbance have influenced mammal populations—with abundance typically decreasing in disturbed sites.

Although mean trap success for the two disturbed sites in 2001 was 7.4 %—less than the mean of 12.1% recorded in undisturbed sites—this result is still high in the context of other mangrove surveys (Fensham and Woinarski, 1992) and surveys in other terrestrial habitats in the Top End (Woinarski et al., 2001). Sampling effort in disturbed sites (1,536

trap nights—2 sites averaged over one year) was however, only one third of that in undisturbed sites (4,608 trap nights—three sites averaged over 2 years) and the study would have benefited from more sampling in disturbed sites. In addition, surveys in disturbed sites were conducted during a different year and slightly later in the dry season than at most undisturbed sites, which may have influenced the results. Indeed, annual variation in bird and mammal abundance was recorded in undisturbed sites and both birds and bats were more abundance during the dry season. Thus the present comparisons need to be considered in the light of such temporal variability and further studies are needed to substantiate these results. It should be noted that the large annual and spatial differences observed in mammal diversity and abundance at undisturbed sites are partly responsible for the lack of any effects of disturbance in analyses comparing disturbed and undisturbed mangroves.

The results of simultaneous field surveys are needed to confirm the apparent trends toward decreased abundance in anthropogenically disturbed mangroves. Even more pertinent would be before-after, control-impact (BACI) design studies documenting the response of mangrove assemblages to anthropogenic disturbance. Such research would provide unequivocal results concerning the effects of disturbance on faunal diversity and abundance—removing the uncertainly inherent in studies such as this, which compare faunal assemblages at selected sites which may, in fact, be intrinsically different to the undisturbed sites.

Diversity and abundance of birds in disturbed mangroves

Analyses of bird species richness at the three sites showed significant differences between disturbed sites, with Site BV having high diversity while site DM had much lower diversity. Abundance also differed between two sites (BV and DP) but not between landward assemblages at all three sites. It is presumed that some of these differences are related to variations in the response of birds to the type and intensity of disturbance at each site. For example, construction of bund walls and access roads through mangroves at Site BV has created several small pools of semi-permanent water (one brackish) in hinterland margin and tidal flat assemblages—habitats that, prior to disturbance, received only infrequent tidal inundation (Figure 4-1). A range of mangrove and hinterland bird species utilise these ponds to bathe and drink, or to exploit additional foraging opportunities. These birds include species not normally observed in the tidal flat

assemblage, for example double-barred finch, crimson finch, intermediate egret, great egret, sacred kingfisher, common sandpiper, radjah shelduck and pied cormorant (pers. obs.). The localised increases in the abundance of carnivorous birds observed in the tidal flat at site BV can be attributed to the ponding of water from anthropogenic disturbance. Disturbance in this instance, has lead to small-scale habitat heterogeneity, which in turn, has attracted new species—contributing to the high species richness recorded at Site BV and significant differences in bird diversity and abundance between sites.

In contrast, the lower species richness observed at Site DM compared with the other two sites probably reflects the extent and intensity of vegetation clearing, both within the mangroves as well as in the adjacent hinterland. Several of the study plots at Site DM were substantially cleared and included sections of the relatively bare water inlet channel. Overall, the physical effects of anthropogenic disturbance on mangroves are relatively haphazard and the diversity and abundance of birds at each disturbed site probably changes in response to this. This was reflected in the results, which showed a lack of consistent trends between assemblages at sites subject to varying levels and types of disturbance—which may have both positive and negative impacts on mangrove avifauna. As with the results for mammals however, the mean density of bird species was typically less in response to anthropogenic disturbance.

Unlike mammals in mangroves adjacent to anthropogenic developments, the proportion of introduced species did not increase. Only two exotic bird species (feral pigeon and cattle egret) occur in the Darwin region and neither are found in intertidal areas. This contrasts with terrestrial habitats elsewhere in the tropics, where a distinct pattern is emerging in the response of birds to urbanisation—the diversity of exotic species generally increases with expanding urbanisation (Lim and Navjot, 2004). The low incidence of exotic birds in the Darwin Harbour environs is assisted by quarantine and control measures but is primarily because the natural environment remains in relatively intact condition.

Overall, a total of 87 species of birds (including 7 incidental species) were recorded from undisturbed and disturbed mangrove sites during this survey. Noske (1996) recorded over 50 species from Darwin Harbour mangroves, excluding waders and aerial species. This represents a rich avifauna—especially given the depauperate flora—and exceeds that recorded on other continents (Cawkell, 1964; Haverschmidt, 1965; French, 1966;

Field, 1968). Northern Australia also has more mangrove-endemic species than any other region of the world, with 11 species known from the region (Noske, 1996). The overall tally of birds recorded in disturbed mangroves (66 species, including 6 incidentals) was only slightly less than in undisturbed sites (70 species, including 9 incidental species) and analyses confirmed that species richness did not vary significantly between natural mangroves and those influenced by anthropogenic developments. However, of the 66 species recorded in disturbed sites, 24% were not recorded in undisturbed habitats and conversely, 22% of species were only from undisturbed sites—suggesting a different suite of species occurs in sites disturbed by anthropogenic activities.

This is evident in the NMDS ordination of sites based on the presence/absence of birds, which shows a distinct grouping of avifauna in undisturbed mangroves. Sites in undisturbed mangroves overlap with approximately 40% of the disturbed sites, and the remaining disturbed sites are relatively distinct but dispersed—which suggests a different and varied bird fauna inhabits, or utilises, disturbed mangroves. Thus, although avian diversity shows no apparent decline, species composition has changed. Some of the overlapping sites represent disturbed sites that are actually little affected by development—aside from proximity, or perhaps by minor changes in drainage—and have retained their natural vegetation. It is likely that these sites have similar avifauna to that occurring in natural mangroves. The more distant points on the ordination represent sites with more extreme modification or loss of habitat, with associated changes in foraging opportunities and diminished avifauna.

Analyses of the abundance of birds in different feeding guilds found no significant differences in mangroves modified by anthropogenic disturbance. Although the abundance of insectivorous species was not significantly different in disturbed mangroves, high mean square values indicated disturbance was an important factor determining the abundance of birds in this guild. Indeed, the abundance of arthropods is a major determinant of bird species composition and abundance in mangrove forests, as the majority of resident species are insectivorous (Lefebvre and Poulin, 2000). In some assemblages the abundance of carnivorous birds was significantly higher in the disturbed mangroves, particularly at locations where vegetation clearing or localised ponding of water has occurred, increasing foraging opportunities for wading birds. Studies in other terrestrial habitats in the tropics have found that among the dietary guilds, both

insectivores and carnivores are adversely affected by urbanisation (Lim and Navjot, 2004). Graphs of mean abundance indicate that carnivores may actually benefit from anthropogenic change. For example, ten of the 19 birds observed only in disturbed mangroves, were wading or carnivorous species, or species associated with more open habitats (eg radjah shelduck, pied heron, eastern reef egret, little egret, beach stone curlew, buff-banded rail, little pied cormorant and black-necked stork).

Clearing, infilling and fragmentation of mangroves can juxtapose habitats that are normally widely separated, facilitating access of characteristically terrestrial birds. For instance, where infilling has extended into seaward mangrove at Site DP, magpie larks and double-barred finches were observed in the seaward assemblage and brown quail were seen foraging amongst *R. stylosa* forest. Thus it is not surprising that the strong partitioning of species into different assemblages in undisturbed mangroves—was less conspicuous in disturbed mangroves.

It appears that highly mobile species such as birds are able to utilise disturbed mangroves opportunistically, moving in and out of areas in response to resource availability. This may also have contributed to species richness and abundance remaining relatively high in the fragmented mangroves fringing developments surveyed in this study. Indeed, even small remnants provided habitat for birds. Rufous banded honeyeaters were observed nesting in the seaward assemblage at the port, where forests had been reduced to no more than a dozen trees in a degraded condition. Similarly, mangrove robins were observed nesting in a stand of dead *Ceriops* forest in the tidal flat zone at Site BV (Figure 4-1c and 4-1i, respectively).

The mobility of birds and the patchiness of disturbance may also be a factor contributing to the lack of any pattern in bird abundance between disturbed and undisturbed sites—illustrated by the ordination of sites based on bird abundance. In general, disturbed mangroves retained relatively abundant avifauna—the mean density of birds recorded in disturbed mangroves (14 ha $^{-1}$) was lower, but not significantly different, to undisturbed mangroves (17 ha $^{-1}$). Overall bird abundance differed between assemblages however, probably reflecting the higher availability of resources to seaward, despite habitat modification, with the tidal flat assemblage the least populous for birds.

Shifts in the most abundant species of birds were observed between disturbed and

undisturbed sites, although the ubiquitous brown and red-headed honeyeaters were dominant in both. The four most abundant species in undisturbed sites (brown honeyeater, red-headed honeyeater, yellow white-eye and lemon-bellied flycatcher) differed from those in disturbed mangroves (brown honeyeater, red-headed honeyeater, collared kingfisher and rufous-banded honeyeater). A carnivorous species (collared kingfisher) and a honeyeater (rufous-banded honeyeater) took the place of two largely insectivorous species (yellow white-eye and lemon-bellied flycatcher) in undisturbed mangroves. It is apparent from these observations, from analyses of feeding guild, and the ordinations based on species presence/absence, that bird community structure and composition has altered in disturbed mangroves.

That these changes were not detected from comparison of species lists, tallies of species or univariate analyses of species richness warns against the exclusive use of these measures. The sensitivity and power of multivariate methods of data analysis to detect subtle changes in natural communities have been repeatedly demonstrated (Clarke, 1993; Warwick, 1993; Clarke and Warwick, 1994). Although the disturbed mangroves of this study were only moderately degraded and retained a relatively diverse avifauna, NMDS ordination showed that species composition differed to that in undisturbed sites. These results indicate that the use of inventories, total species richness and other simple descriptors to assess and monitor vertebrate diversity may not be adequate for environmental impact detection and monitoring. Important disturbance-induced ecological changes between sites may not be detected by univariate tests alone and are perhaps, best used in conjunction with multivariate techniques as they are clearly sensitive to changes in faunal communities.

Indeed, these observations tend to refute claims arising from research in Mexico on urban encroachment of mangroves stating that the "occurrence of birds in a mangrove could be used as an indicator of mangrove ecosystem health" (Holguin et al., 2005). This appears questionable, particularly when the work is based solely on a list of 38 species and their raw abundance. The results of the current study suggest that by taking a simplistic approach to monitoring, ecosystem health could undergo substantial degradation—with the loss of say, numerous resident bird species for example—yet such losses could remain undetected, if masked by the ingress of other species. Further, although abundant and relatively easy to survey, the highly mobile and occasionally migratory avifauna may

not represent the best indicators of mangrove health—presumably their absence from a mangrove indicating environmental decline. The choice and application of appropriate indicator species is problematical enough when considering sedentary, extremely numerous, and highly sensitive invertebrate organisms (Warwick, 1993).

In terms of biodiversity conservation however, information highlighting those species or assemblages most vulnerable to natural or anthropogenic disturbance is of key practical value. Noske (1996) listed 17 bird species which, to some extent, depend on mangrove habitats in the Northern Territory. Other authors consider Northern Territory mangroves to be primary habitat for fewer species (e.g. 15 species (Morton and Brennan, 1991) and others report more.) (Ford, 1982) notes 14 species exclusively utilising mangroves with 6 others adapted to, and frequently in, mangroves. Comparison of the densities of these species, in the undisturbed and disturbed sites of this survey, identified four species not found in disturbed habitats—the mangrove golden whistler, little shrike-thrush, large-billed gerygone and the great billed heron. Clearly these are species that may be susceptible to widespread coastal development involving the removal of mangroves, especially the tidal creek and the seaward assemblages, which represent primary habitat for these species. In particular, the mangrove golden whistler is rarely observed outside mangrove habitats, where it is seldom seen far from the tidal creek assemblage.

The exclusion of all birds except *mangrove dependent* species—those species classed by Noske (1996) as category A (after Ford 1982) and described as being confined entirely or mainly to mangrove habitats—reduces the list to a group of nine species (Table 4-5).

Table 4-5 : Density of mangrove-dependent bird species in disturbed and undisturbed mangroves(birds ha^{-1}). Species are virtually confined to mangroves (Noske, 1996).

Species	Common Name	Undisturbed (1999-2000)	Disturbed (2001)	Undisturbed Noske (1996)
Cracticus quoyi	Black Butcherbird	**0.21**	**0.18**	**0.32**
Pachycephala lanioides	White-breasted Whistler	**-**	**-**	**-**
Rhipidura phasiana	Mangrove Grey Fantail	**0.20**	**0.03**	**0.15**
Todiramphus chloris	Collared Kingfisher	**0.56**	**1.01**	**-**
Myzomela erythrocephala	Red-headed Honeyeater	**2.30**	**1.91**	**5.5**
Gerygone levigaster	Mangrove Gerygone	**0.37**	**0.33**	**0.91**
Peneoenanthe pulverulenta	Mangrove Robin	**0.22**	**0.13**	**2.12**
Eulabeornis castaneoventris	Chestnut Rail	**0.25**	**0.05**	**-**
Zosterops luteus	Yellow White-eye	**2.12**	**0.88**	**5.02**

Comparison of the densities of these birds in undisturbed and disturbed sites, suggests that three species (Mangrove Robin, Yellow White-eye and Chestnut Rail) may decline in response to anthropogenic disturbance. However, the density values recorded by Noske (1996), indicate that there may be considerable spatial or temporal variation in abundance of these three species. Further studies are required on the response of key species to disturbance to corroborate the findings of this study.

Nevertheless, the eight mangrove dependent species are potentially the most vulnerable to loss of mangrove habitat and increasing urban encroachment. With the exception of the red-headed honeyeater, black butcherbird and the yellow white-eye—which occasionally venture into adjacent terrestrial habitats—these birds are entirely dependent on mangroves. Consequently habitat loss, fragmentation or degradation will have direct implications for these species. Furthermore, the secretive white-breasted whistler and specialised chestnut rail and mangrove grey fantail are either rare or potentially sensitive to disturbance. Monitoring of the populations of these species may contribute to their long-term conservation in Darwin Harbour where clearing and fragmentation of mangroves is occurring due to rapid urban and industrial expansion.

4.5. Conclusions

This chapter investigated the impacts of anthropogenic disturbance on vertebrate fauna by study of the distribution, diversity and abundance of mammal and bird species in mangroves modified by urban and industrial encroachment. Overall, the findings indicate that the vertebrate fauna is relatively resilient. Mammal diversity is not greatly diminished and the two dominant species (*M. burtoni* and *T. vulpecula)* remain the same. The total pool of species declined in response to disturbance, however, as several native species, that are intermittent visitors to the hinterland margin disappeared, and were replaced by introduced mice and rats. Thus significant differences in mean species richness associated with disturbance were not apparent, but the proportion of introduced mammals increased.

As for mammals, the total number of birds was slightly less in disturbed sites (66 species) but univariate analyses also did not detect significant differences in mean species richness between disturbed and undisturbed mangroves. Being highly mobile, and opportunistic, birds can utilise even small patches of habitat, foraging and nesting in

degraded fringes. Indeed, the ingress of species adapted to either clearings or waterbodies appeared to balance the loss of forest species, such that mean bird diversity was not diminished.

The overall abundance of both mammal and bird populations also declined in disturbed sites. Spatial variation or patchiness in populations in undisturbed sites however, contributed to the lack of any significant differences. Lower densities of vertebrates appear to be associated with loss of tall forest trees with crucial refuge hollows for mammals and foraging resources for birds. Small scale habitat heterogeneity in anthropogenically modified habitats (e.g. ponding of water, deforestation) led to varied patterns in diversity and abundance, while contributing to a lack of clear partitioning of species into different assemblages.

Obvious changes in species composition were however, detected by multivariate analyses based on the diversity and abundance of birds and mammals. A different suite of species occurred in disturbed habitats and tended to reflect the nature and intensity of disturbance. Disturbingly, several mangrove dependent birds were either less populous or absent from urbanised mangroves. Nevertheless, these forests remain productive habitats for a diverse range of birds and a few hardy mammals, and are presently relatively free of introduced species and major threats.

The research described in this chapter highlighted the need for studies designed to document the direct effects of anthropogenic disturbance on mangrove mammals and birds—for instance BACI design studies in which the fauna present prior to development is monitored in relation to anthropogenic change. Within the limitations of the current design however, this work has provided some useful indications of the response of mangrove vertebrate fauna to disturbance and highlighted species and faunal groups that may be potentially vulnerable to increasing urbanisation. The diversity, abundance and distribution of invertebrates and the impacts of anthropogenic disturbance are the subject of the next two chapters.

CHAPTER 5. INVERTEBRATE FAUNA

CHAPTER 5. INVERTEBRATE FAUNA

5.1. Introduction

Previous chapters of this thesis have shown that mangroves in Northern Australia support a variety of vertebrate fauna, being particularly rich in birds and having high densities of native rodents. However, as in other intertidal, marine and terrestrial habitats the bulk of biological diversity in mangroves lies chiefly in their ubiquitous and diversified invertebrate fauna (Hutchings and Recher, 1983; Wilson, 1988; Edgar, 2000).

The seminal work of Macnae (Macnae and Kalk, 1962; Macnae, 1963; 1967; 1968b) alerted the scientific community to the extraordinary range of biota residing in, or utilising, mangroves on a regular or transient basis. Although largely descriptive, these studies provided information on the pattern of distribution, and species composition, typical of mangroves throughout Africa and the Indo-West Pacific region, highlighting the trend toward increased faunal diversity with decreasing latitude. Indeed, most early (pre-1975) publications contained some inventories but often focussed on floristic and faunal zonation—describing the changes in species composition at different tidal elevations—and the fascinating adaptations of the mangrove biota. Mangrove ecosystems on the coasts of Mozambique (Macnae and Kalk, 1962), Africa (Macnae, 1963), Singapore (Berry, 1963) and Thailand (Frith et al., 1976) were described in this manner. During the same era, magazine articles vividly extolled the faunal diversity, ecological role and conservation value of mangroves (Macnae, 1968a; Jones, 1972; Gove, 1977; Frith and Frith, 1982; Jones, 1988). These articles clearly aimed to shift widespread negative views of mangroves and to foster interest in these much-maligned environments.

Some of the first quantitative assessments of invertebrate diversity and abundance in Australian mangroves were conducted in Broken Bay, New South Wales (Hutchings and Recher, 1974; Hutchings et al., 1977), in Cairns, Queensland (Hegerl and Davie 1977) and in Kakadu National Park in the Northern Territory (Hegerl et al., 1979).

Comparison of the fauna of Australian and Indo-Malay mangroves (Berry, 1963; Sasekumar, 1974; Frith et al., 1976; Sasekumar and Chong, 1998) revealed three dominant invertebrate groups—crustaceans, molluscs and polychaetes—that exhibited ecological similarities and strong taxonomic links, particularly at the generic level. Despite the geographic separation, there were parallels in the horizontal (i.e. land to sea) and vertical distribution of invertebrates across the Indo-Pacific region, with often the same genus, or species, occupying the same niche in different countries.

Reviewing the status of knowledge on the fauna of Australian mangroves in the early 1980's Hutchings and Recher (1982; 1983) underscored the high diversity of invertebrates and noted the need for more research, particularly on the seasonal and annual variations in faunal populations. Wider recognition of the importance of mangroves in coastal food webs was emerging, and combined with concomitant, rapid habitat loss on the east coast of Australia, provided further incentive for research on trophic links and pathways. The focus of many studies during that decade was on commercially important taxa (Hutchings and Recher, 1982) such as fish (Thayer et al., 1987; Chong et al., 1990; Morton, 1990; Roberston and Duke, 1990; Vance et al., 1996) and penaied prawns (Staples, 1980, 1980a; Vance et al., 1990).

Alongi and Sasekumar (1992) and Hutchings (1999) noted that compared with temperate habitats, estuaries in northern Australia had been poorly studied, both qualitatively and quantitatively. More recently, however, an increasing number of studies have been conducted on mangrove fauna in tropical regions including Africa (Schrijvers et al., 1995), South America (Cantera et al., 1999) and Malaysia (Sasekumar, 1974; Sasekumar and Chong, 1998; Ashton and Macintosh, 2002; Ashton et al., 2003). In relation to this study, conducted in Darwin Harbour, perhaps the most comparable research on mangrove invertebrates has been conducted by Wells on the northwest coast of Western Australia (Wells and Slack-Smith, 1981; Wells, 1983, 1984) and in Hong Kong (Wells, 1986a, 1986b). These papers include quantitative data on diversity, density and biomass of molluscs, crustaceans and other mangrove invertebrates at different tidal elevations across the intertidal zone.

Collectively, these previous studies show that mangroves are rich habitats for invertebrate fauna, and like other estuarine habitats, are dominated by crustaceans, molluscs and polychaete worms, often co-occurring in relatively similar proportions to

each other (Wells, 1983; Hutchings, 1999). Recent research by Ashton *et al*. (2003) also documented the diversity, density and biomass of crab and molluscan fauna in near-pristine mangroves of Sarawak, Malaysia, but such comprehensive, quantitative assessments of intact mangrove systems, are rare (Cantera et al., 1999). Although a lot of work has been done in recent years to document the taxonomy, ecology, structure and dynamics of the highly abundant and varied mangrove invertebrate fauna, there are still major gaps in our understanding. Indeed, although mangroves are recognised as centres of biodiversity (Wilson, 1988; Gopal and Junk, 2000), very little quantitative data has been available to support such assertions (Hutchings and Recher, 1982, 1983; Kathiresan and Bingham, 2001).

In Darwin Harbour, crabs have been relatively well studied (Von Hagen and Jones, 1989; Audas, 1992; Nobbs, 1999; Nobbs and McGuinness, 1999, 2003; Salgado Kent, 2004; Salgado Kent and McGuinness, 2006) and selected groups including polychaetes (Hanley, 1985) and molluscs (Gilham, 1980; Crowe, 1997; Crowe and McMahon, 1997; Willan, in prep) have received some attention, whilst most others have only been sampled sporadically. Prior to this study, but one other project aimed to thoroughly document mangrove biological diversity. Surveys have occasionally been commissioned in response to development proposals for specific projects, (Hanley and Couriel, 1992; Hanley, 1993; McGuinness, 1993). Other, post-disturbance studies in the Darwin region have investigated the effects of vegetation clearing (Guinea, 1987) and cyclone damage (Burke, 1992; Ferwerda, 2000). More recently, pre- and post-disturbance surveys of mangrove invertebrate diversity and abundance have been conducted to monitor the impacts of commercial developments within the harbour (Hanley and Couriel, 1992; Metcalfe, 2004a, 2004b, 2005).

Overall, however, studies in the Darwin region have typically been limited to specific aspects of invertebrate biology, generally focussing on one particular species or taxonomic group. These have included molluscs (Crowe, 1997; Crowe and McMahon, 1997), crabs (Von Hagen and Jones, 1989; Audas, 1992; McGuinness, 1993; Nobbs, 1999; Nobbs and McGuinness, 2003; Salgado Kent, 2004), ants (Clay and Andersen, 1996; Nielsen, 1997b, 2000) and insects (Coupland, 2002). Aside from the doctoral studies of Salgado Kent (2004) and Coupland (2002) most other investigations were experimental and hence were necessarily of limited spatial scale (McGuinness, 2002a). Only a few

surveys have examined the three main phyla occurring in mangroves (Hanley, 1987; Hanley and Couriel, 1992), and even fewer have concerned the invertebrate fauna as a whole (Burke, 1992; Hanley, 1993).

In addition, probably due to logistical constraints, the majority of specimen collection within Darwin Harbour had been restricted either to the seaward zone and fringes of tidal creeks, or to the upper landward assemblages. Consequently, there remained major gaps in our knowledge. Baseline information on faunal diversity and abundance across the full range of mangrove assemblages, was clearly deficient. In particular, the invertebrate fauna of one of the central and most extensive tracts of mangroves—the *Ceriops australis*-dominated tidal flat assemblage which occupies 48% of the total mangrove area—was little studied (but see McGuinness, 1994, 1997a; Salgado Kent, 2004).

Furthermore, previous research on the flora of Darwin Harbour mangroves (Woodroffe, 1985; Woodroffe and Bardsley, 1987; Woodroffe et al., 1988) including a two-year study of leaf litter fall as a measure of primary productivity (Metcalfe, 1999), demonstrated profound differences between the four major—hinterland margin, tidal flat, tidal creek and seaward—and four minor mangrove assemblages (see Table 2-1, Chapter 2). The seaward assemblage for example, was found to be highly productive (1,256 g m^{-2} $year^{-1}$) while productivity of the tidal flat was extremely low (394 g m^{-2} $year^{-1}$). Such dramatic spatial variation in mangrove primary productivity represents valuable information for conservation, planning and has ramifications in terms of resource management. The data on primary productivity does not however, adequately reflect the ecological value of each of the mangrove assemblages. The seemingly unproductive tidal flat for instance, appeared to be a very important environment for invertebrate fauna (pers. obs.), yet its value as a habitat and perhaps a refuge for fauna was seldom recognised. Such observations underpinned the need for detailed fauna studies within each of the major assemblages that would contribute to and balance the body of information previously obtained for flora. Further evidence of the fauna-support role of mangroves was required, particularly given the conflicting motives of development and conservation in the context of rapid urban and industrial development in Darwin Harbour.

Indeed, a major incentive for this research derived from the belief that documenting the

faunal components of these assemblages was necessary to improve our understanding of the ecology and functioning of Darwin Harbour's mangrove environments and that this knowledge was an integral step to more informed management and conservation. Prior to this research, no comprehensive studies in Darwin Harbour, and possibly northern Australia, had systematically investigated spatial and temporal variation in the diversity, distribution and abundance of all the invertebrate groups characteristic of mangroves, across all the major floral assemblages.

Aim

This chapter presents the results of a pilot study, a confirmation study and a comprehensive survey of invertebrate fauna occurring in undisturbed mangroves in Darwin Harbour.

These studies were designed to address the following aims;

- The aim of the **pilot study** was to determine the effectiveness of field techniques in sampling invertebrates and to investigate which target invertebrate groups were sampled by each technique. Secondary objectives were to trial variations in the methodology (the most effective area for anoxic mats, for instance) and to establish the level of replication for the main study.
- The aim of the **confirmation study** was to test whether the selected techniques sampled different groups of organisms (e.g. benthic fauna, infauna, epifauna) and to test the practicality and efficiency of the selected (combined) methodology.
- The primary aim of **invertebrate surveys** was to document the distribution, diversity and abundance of macro-invertebrates within the four major mangrove assemblages. The main invertebrate groups selected for study were:
    - Molluscs
    - Crustaceans
    - Worms
    - Ants
- Invertebrate surveys also tested for spatial and temporal patterns in the diversity and abundance of these faunal groups and other selected taxa.
- The second main aim of invertebrate surveys was to provide data from undisturbed sites for comparison with that from mangroves affected by anthropogenic disturbance (examined in Chapter 6)

5.2. Methodology

Invertebrates were surveyed once during the wet season and once during the dry season of 2001 in three undisturbed mangrove locations (Sites E1, E2 and M3 described in Chapter 2). One survey of invertebrates in disturbed mangroves was also conducted in the 2001 dry season (Table 5-1) and those results are examined in Chapter 6.

Table 5-1: Schedule of invertebrate fauna surveys in undisturbed and disturbed mangroves in 2001. Open circles (○) indicate wet season and closed circles (●) dry season surveys.

	UNDISTURBED SITES (Apr–May & Jul–Aug 2001)			**DISTURBED SITES (Oct–Nov. 2001)**			
Site	**E1**	**E2**	**M3**	**BV**	**DP**	**DM**	**DE**
Location	Charles Darwin	Elizabeth River	Jones Creek	Bayview Haven	East Arm Port	Middle Arm Prawn Farm	CDNP Bulldozed
Hint margin	○ ●	○ ●	○ ●	●	●	●	
Tidal flat	○ ●	○ ●	○ ●	●	●	●	●
Tidal creek	○ ●	○ ●	○ ●	●	●	●	●
Seaward	○ ●	○ ●	○ ●	●	●		

~5.2.1. Invertebrate surveys

The mangroves of Darwin Harbour are structurally complex and dynamic habitats—often comprising dense forests with branching aerial root systems growing in muddy, bioturbated substrates. They are subject to regular tidal inundation and are drained by numerous tidal channels. Consequently, five distinct microhabitats were identified within mangrove forests and a methodology was designed to consistently and thoroughly sample the diversity and abundance of fauna in each of the following niches:

1) the mud surface (benthic fauna)

2) within the substrate (infauna)

3) on the surface of tree trunks, roots and rocks, in tree hollows (epifauna)

4) within and attached to rotting logs (epifauna)

5) small pools or puddles .

Only species visible to the naked eye were sampled. Molluscs, crustaceans (including amphipods, isopods, tanaids, crabs and shrimps), worms, ants and small fish were actively sampled or recorded during surveys. Insects (with the exception of ants), mites and arachnids were excluded. It was considered appropriate to include in these surveys,

the specialised mudskippers and small fish (Phylum Chordata) that commonly inhabit mangrove mud and puddles within the forest. Mangrove-dwelling fish are not covered elsewhere in this thesis, but are a conspicuous and abundant element of the fauna; which were grouped with invertebrate phyla in this study. Fish were also included in two prior studies of mangrove fauna in Darwin Harbour (i.e. Burke, 1992; Hanley, 1993).

Four different field techniques, described in detail below—1 m × 1 m quadrats, pitfall traps, anoxic mat and baits—were used to sample the target invertebrate groups in the five microhabitats identified. The combined methodology was developed progressively during a pilot study (1999) and a confirmation study (2000) which tested and refined the selected field techniques respectively.

All invertebrate surveys were conducted within 50 m × 50 m study plots placed on two transects aligned from the landward to seaward margin (see Figures 2-3 to 2-6, Chapter 2). One 50 m × 50 m study plot was located in each of the four major assemblages at each of the three study sites. Coordinates from random number tables were used to locate three sub-plots, or sampling stations, within each study plot (Figure 5-1).

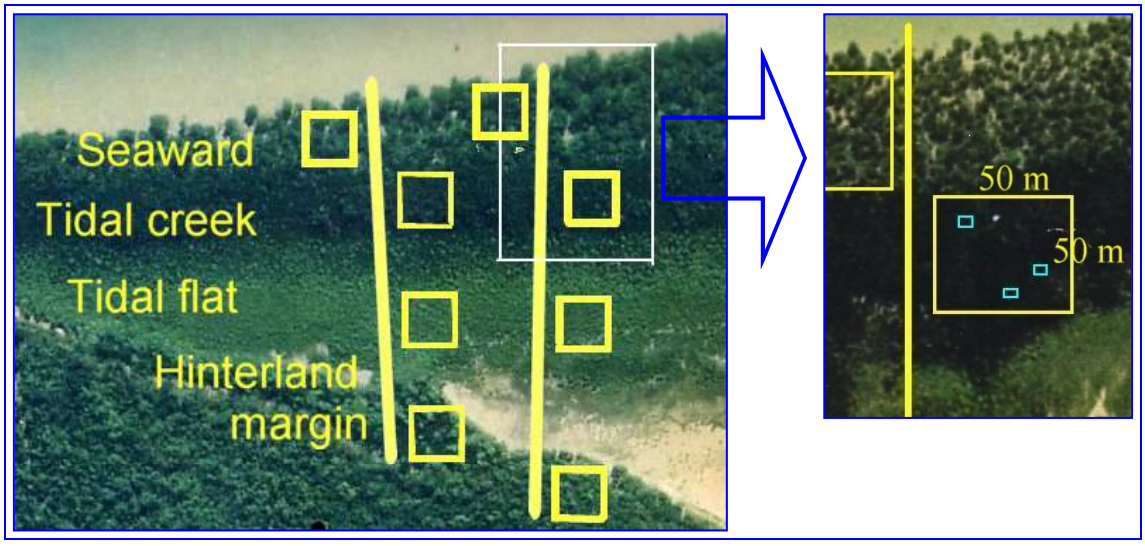


Figure 5-1 : Invertebrate sampling design involved 0.25 ha study plots placed in the four assemblages on two transects. Three randomly placed sampling stations were located in each study plot. At each station, sampling was done within one 1m × 1m quadrat, using baits and by installing one pitfall trap and one anoxic mat (left overnight).

At each of three replicate sampling stations, invertebrates and fish were sampled from the microhabitats listed above using the following techniques:

Benthic fauna

Benthic fauna, or the invertebrates living on the mud surface, were sampled from within 1 m × 1 m quadrats (Figure 5-2). Benthic fauna typically comprised crabs, molluscs, worms and small fish including mudskippers. Quadrats were sampled by passive observation for 2 to 5 minutes followed by active searching of the quadrat, including digging through the sediment to a depth of approximately 5 to 10 cm. All benthic invertebrates observed within the quadrat were either recorded or collected for later identification.

Only living molluscs were documented, as empty shells can be transported considerable distances by wind and/or tidal currents. Mollusc shells were inspected to check if they had been taken over by hermit crabs; as the mollusc originally occupying the shell may have lived within a different estuarine habitat.

Fish within quadrats were sampled by pursuit and capture (mudskippers) and also dug from within burrows in the mud (typically other gobies and mud slitherers).

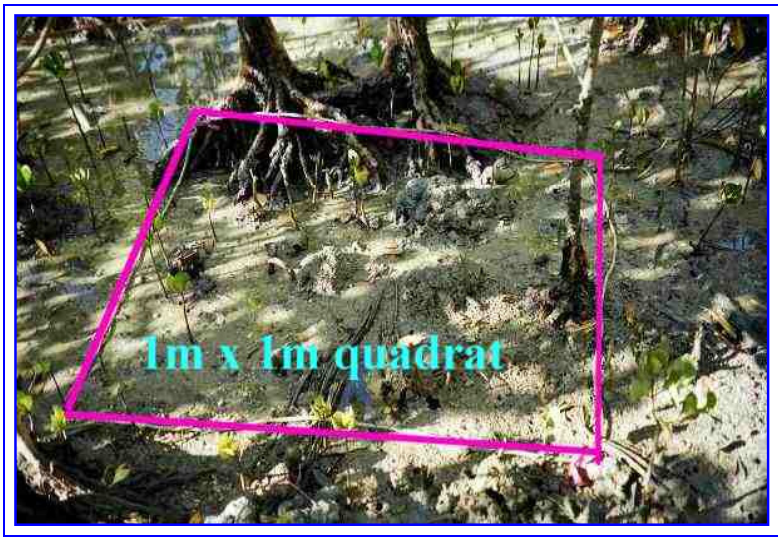


Figure 5-2: Benthic invertebrate fauna was sampled from within 1 m × 1 m quadrats

Epifauna

In this study, epifauna comprised any above ground or tree-dwelling fauna. Quadrats were always placed against the tree nearest to the random number coordinates for that station, to enable sampling of epifauna throughout all assemblages. This introduced a potential bias to the methodology (see Discussion, section 5.5.1); but this technique for

quadrat placement was consistently applied during all surveys and at all locations. Epifauna to a height of 2 m (characteristically comprising molluscs, small crustaceans, including barnacles, and worms) was sampled from the surface of roots, trunks and foliage of all trees within each 1 m ×1 m quadrat. For larger trees, not wholly contained within the quadrat, only the side of the tree facing the quadrat was searched. Mobile, encrusting and cryptic fauna (occurring under loose bark) was sampled using forceps and a knife. Fish were occasionally collected from within rotting logs and hollow roots.

Infauna

Infauna was sampled using an anoxic mat made from a circular plastic disc 0.05 m^2 in area (radius = 12.6 cm). The anoxic mat was placed on the mud surface, secured beneath a mound of mud and left overnight. Invertebrates in the substrate beneath the disc are affected by the localised anoxic conditions and are generally drawn to the mud surface just below the mat, where they become trapped or die. Sampling is completed the following day when the mat is peeled back and specimens are collected from the surface (Figure 5-3). The mud beneath the mat was also searched, by digging with a trowel to a depth of approximately 5 cm.

Figure 5-3: Anoxic mat technique used to sample infauna by creating an area of anoxic mud

Refuge pools, nocturnal and free-ranging fauna

A range of fauna including shrimp, fish, crabs and molluscs occur in small puddles or refuge pools remaining in the mangroves at low tide. These organisms were sampled using a modified pitfall trap, designed and used by other students in concomitant

research projects (Martin, 2004; Salgado Kent, 2004). The trap comprised a 150 mm plastic plant pot, with a smaller, modified plant pot inserted inside it as a collar, to prevent fauna escaping (Figure 5-4). Pitfall traps were dug into the mud until level with the ground surface and left overnight. Depending on the surrounding substrate, pitfalls generally retained water after inundation by two high tides and the contents were carefully sieved the following day.

Figure 5-4: Mangrove pitfall trap for sampling mobile, nocturnal and puddle fauna. Inset: The collar prevents crabs, such as *Neosarmatium meinerti* pictured, from escaping.

Ants

Mangrove ants were sampled using two types of bait (honey and sardine-based catfood) placed in several trees within a 3 m radius of each 1 m × 1 m quadrat. In general, ants present within the sampling station area, rapidly gathered at baits where they were sampled with a small paintbrush. Ants were also sampled opportunistically; for example, when ground nesting species were uncovered during quadrat sampling.

Ant species were listed as either arboreal or ground-dwelling, according to the habitat in which they predominantly foraged and nested (Clay and Andersen, 1996) and according to the habitat (e.g. rainforest, savanna) from which they originated (A. Andersen pers. com., Clay and Andersen, 1996).

Figure 5-5 : Mangrove ants including *Camponotus* sp. 10 (left) and *Polyrachis sokolova* (right) were sampled using sardine-based catfood baits

At each sampling station, data on the abundance of each species (except ants) and a count of crab burrows within the quadrat was entered onto a fieldwork proforma. The height and species of tree within, or adjacent to, the quadrat was also noted. All invertebrate specimens unable to be reliably identified in the field were collected and preserved in 70% ethanol for identification in the laboratory.

The combined methodology enabled the fauna within each of the five microhabitats to be sampled by applying the field techniques described above, at every sampling station. Each sampling station comprised one 1 m^2 quadrat, a pitfall trap, a 0.01 m^2 anoxic mat, epifaunal sampling to 2 m and baiting for ants. The 1 m × 1 m quadrat was however, the only technique that could provide an area-based estimate of species richness and abundance. The species data derived from each sampling technique was combined to obtain an overall value for species richness for each sampling station. Similarly, the abundance of each species (excluding ants) recorded using each technique was summed to obtain a value of total abundance per sampling station. Three replicate sampling stations were sampled per 50 m ×50 m study plot.

Invertebrate species identification

This research was undertaken with the assistance of the Northern Territory Museum of Arts and Sciences (NTM) and where possible, all specimens were identified to species level. Rough sorting of samples into the major taxonomic groups (ie. worms, crabs, molluscs and fish) was done in the laboratory, prior to forwarding specimens to specialists at the NTM. Dr Chris Glasby did the worm identifications, Dr Richard Willan the molluscs and Dr Helen Larson the fish. Several invertebrate specimens were sent to

specialists interstate, namely Dr Dianne Jones (Western Australian Museum), who identified two barnacle species, and Dr Tim O'Hara (Victorian Museum) who identified two undescribed Ophiuroids (brittle stars). A bryozoan found on the undersurface of mangrove leaves was also forwarded to Dr Dennis Gordon (NIWA, New Zealand). Ants were identified by Dr Alan Andersen of the Tropical Ecosystems Research Centre of the CSIRO in Darwin. The NTM does not have a crustacean taxonomist, so with the assistance of taxonomic keys I undertook the majority of crab identifications. Dr Russell Hanley and Peter Davie (Queensland Museum) identified crabs sampled during the pilot study; and a selection of crab reference specimens and other crustaceans.

~5.2.2. Pilot study

A pilot study was conducted during four days from 12th to 15th October 2000 in four assemblages (hinterland margin, tidal flat, tidal creek, seaward) in Charles Darwin National Park (Site E1). Three sampling methods were tested in the pilot study: mud cores, anoxic mats and pitfall traps. Quadrats were not trialed during the pilot study largely because previous mangrove studies in Darwin Harbour have used square 1 m × 1 m quadrats (Burke, 1992), or circular plots of similar dimensions (Hanley, 1987) and a previous study comparing the efficacy of different quadrat sizes (0.25 m^2, 1 m^2, 25 m^2 and 625 m^2) had confirmed that 1 m^2 quadrats satisfactorily sampled crabs in mangrove habitats (Smith et al., 1997). Thus for consistency, and for practical reasons, a quadrat size of 1 m × 1 m was chosen. A confirmation study later examined the efficacy of sampling using quadrats of this size (Section 5.2.3).

For the pilot study, randomly selected sub-plots were located within 50 m × 50 m study plots, where up to ten replicate pitfall traps, and anoxic mats and mud cores of differing dimensions, were used to sample fauna (Table 5-2). Replication of the sampling techniques varied between assemblages with sampling effort focussed in the two seaward assemblages.

Pitfall traps

The pitfall traps used in this study were specifically designed for use in mangroves and had been successfully applied in previous research in Darwin Harbour on fish (Martin, 2004) and crabs (Salgado Kent, 2004; Salgado Kent and McGuinness, 2006).

Consequently the application of this technique did not require extensive testing and pilot study field trials were conducted mainly to determine the number of replicates required for adequate sampling. Three pitfalls were sampled in both landward assemblages for two consecutive nights and six pitfalls were set for three nights in the tidal creek and seaward assemblages (Table 5-2).

Mud cores

To enable comparison of the effectiveness of sampling using anoxic mats with mud cores, cores of two sizes—0.5 and 1.0 litre—were collected immediately adjacent to anoxic mats of 0.05 and 0.1 m^2 area respectively. Mud to a depth of 15 cm was removed using a 5 cm diameter yabby pump (cylindrical suction coring device), transferred to a plastic container to measure the volume, stored in plastic bags and kept cold. Five replicate samples of approximately 0.5 litre and three replicate samples at 1.0 litre were taken from the four assemblages (Table 5-2). Mud cores of greater volume, and additional replicates of mid-sized and small cores, could not be sampled however, due to practical constraints (the weight of mud was too great to be carried by one person for roughly 1.2 km).

Table 5-2: Numbers of replicate samples trialed in each assemblage using three techniques investigated during the pilot study., October 1999.

Sampling technique	**Mangrove Assemblage**			
	Hinterland margin	**Tidal flat**	**Tidal creek**	**Seaward**
Pitfall traps				
	3 **	3 **	6 ***	6 ***
Anoxic mat -				
0.05 m^2	5	5	10	10
0.25 m^2	-	-	3	3
0.5 m^2	-	-	3	3
0.1 m^2	3	3	3	3
1.0 m^2	-	-	1	1
Mud cores				
0.5 litre	5	5	5	5
1.0 litre	3	3	3	3
** denotes sampled for 2 consecutive nights, *** sampled for 3 consecutive nights				

In the laboratory, mud samples were stored at approximately 4°C prior to sieving under running water through a nest of four sieves to a minimum size of 1.1 mm. Retained matter on each sieve was inspected and invertebrate fauna was transferred to sample jars containing 70% ethanol.

Anoxic mat

Sampling effort was focussed in the lower intertidal zones where substrates were most suitable for the use of this technique. In the seaward and tidal creek assemblages, anoxic mats of five sizes—0.05, 0.25, 0.5, 0.1 and 1.0 m^2—were trialed (Table 5-2). In the hinterland margin and tidal flat assemblages, anoxic mats of only two sizes (0.05 and 0.1 m^2) were tested. Placement of mats larger than 0.25 m^2 (or 56.4 cm diameter) was problematic as it was difficult to find a sufficient area of mud without trees, and pneumatophores often had to be removed with secateurs, to create a suitably flat area. Further, substantial quantities of mud were required to secure mid- to large sized mats to help maintain anoxic conditions beneath.

~5.2.3. Confirmation study

The confirmation study was conducted over three days from 4th to 6th February 2001 in the tidal creek assemblage of Ludmilla Bay, in the outer region of Darwin Harbour (see Figure 2-3, Chapter 2). The combined methodology—comprising quadrat and epifaunal sampling, anoxic mats of two sizes (0.05 and 0.1 m^2) and pitfall traps—was trialed at ten replicate sampling stations, randomly placed throughout the tidal creek assemblage.

Analyses

After species identification was completed, species names were reconciled with field records of abundance and entered into a *Microsoft Access* database. Unidentified specimens that could be identified to generic level, but not species level, were included in univariate and multivariate analyses and species tallies. Specimens identified only to family or phylum level were deleted from analyses unless they represented the only member of that family, or phylum. Juvenile taxa (e.g. *Perisesarma* immature and Grapsidae immature) were included in analyses of abundance but not species richness. Selected subsets of the raw data were transferred to *Microsoft Excel* spreadsheets and

Minitab 14 for examination of means and graphical presentation of data. Species abundance data for the pilot and confirmation studies was also examined in *Primer vers. 5* after compiling a Bray-Curtis similarity matrix with untransformed data. For the main invertebrate surveys, NMDS ordinations involving abundance of individual species occasionally required exclusion of study plots containing only a single species in order to gain an interpretable outcome. Sites by species matrices were formulated using the Bray-Curtis similarity measure on untransformed data for ordinations based on abundance and presence-absence transformed data for species richness ordinations. Data was not standardised prior to NMDS analyses and each ordination was plotted after 50 random restarts.

Univariate analyses of the invertebrate community as a whole; for the main faunal groups; for selected taxa and for individual species, involved four factor analyses of variance with the factors: season (fixed), site (random), transect (random, nested in site) and assemblage (fixed). Analyses of the invertebrate fauna as a whole, excluded ants for abundance data, but species richness data included ants.

The procedures described by Winer et al. (1991) and Underwood (1996) were used in preliminary tests on complex ANOVA models to determine if any higher order interactions could be dropped. Following the recommendations of these authors, a conservative approach was adopted and terms were only dropped if the relevant F-ratio was non-significant at $p = 0.25$.

5.3. Results & Discussion—Pilot & Confirmation Studies

~5.3.1. Pilot study

A total of 68 taxa were recorded during the pilot study, comprising 24 molluscs, nine worms, eight fish and 27 crustaceans (including two amphipods, one mud lobster, 21 crabs and three shrimps). A total of 171 records were obtained from pitfall traps, 203 from anoxic mats and 48 from mud cores but sampling effort for the different methods was not equal (see Table 5-2).

Species richness and composition

Overall, mean species richness across all assemblages was highest for anoxic mats and pitfalls, and least for mud cores (Figure 5-6). No data were obtained for the largest anoxic mat (1.0 m^2) as they could not be secured adequately and were washed away. In general, pitfall traps consistently sampled an average of over two species per trap (mean 2.4 ± 0.3 SE, n=48) and the anoxic mat appeared to sample more infauna (mean 2.3 ± 0.3 SE, n=62) than mud cores (mean 1.0 ± 0.2 SE, n=32).

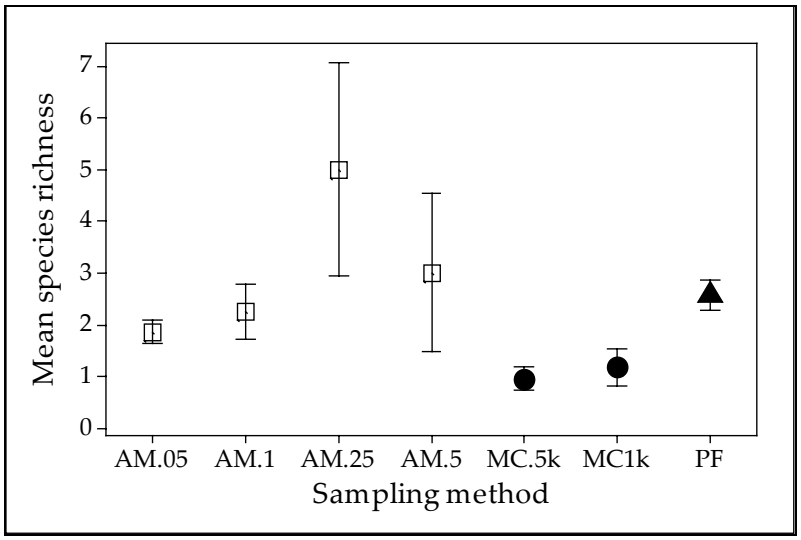


Figure 5-6: Mean species richness (± SE) for sampling methods trialled during the pilot study, where AM = anoxic mats (of 0.5, 0.1, 0.25 and 0.5m^2 size); MC = mudcore (0.5 and 1 *l*) and PF = pitfall trap. Means are pooled for replicates across all assemblages.

Examination of the percentage of species in faunal groups sampled by each technique showed that pitfall traps sampled four main taxonomic groups including a high diversity of crabs, as well as molluscs, fish and other crustaceans. The latter two groups were not sampled by the anoxic mat or the mud cores in the pilot study (Figure 5-7).

Sampling with anoxic mats resulted in high species richness of molluscs, crabs and worms. In comparison, mud cores sampled relatively few species and appeared less effective in sampling worms than the anoxic mat.

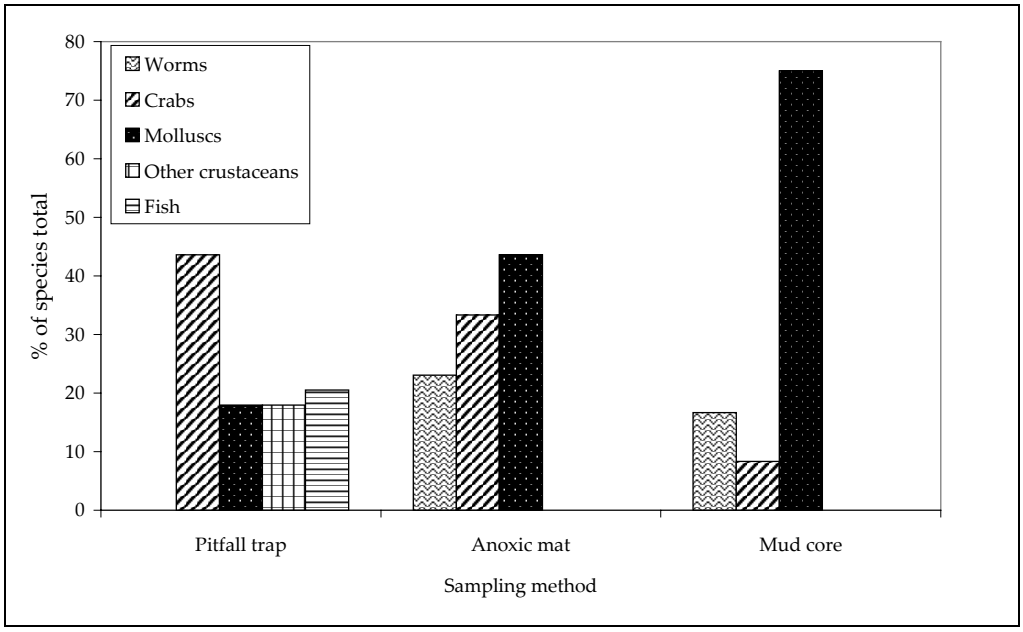


Figure 5-7: Total number of species in different faunal groups sampled by three sampling methods trialed in the pilot study, pooled across four assemblages.

Abundance

Each method appeared to sample a different percentage abundance (numbers of individuals) of the faunal groups (Figure 5-8).

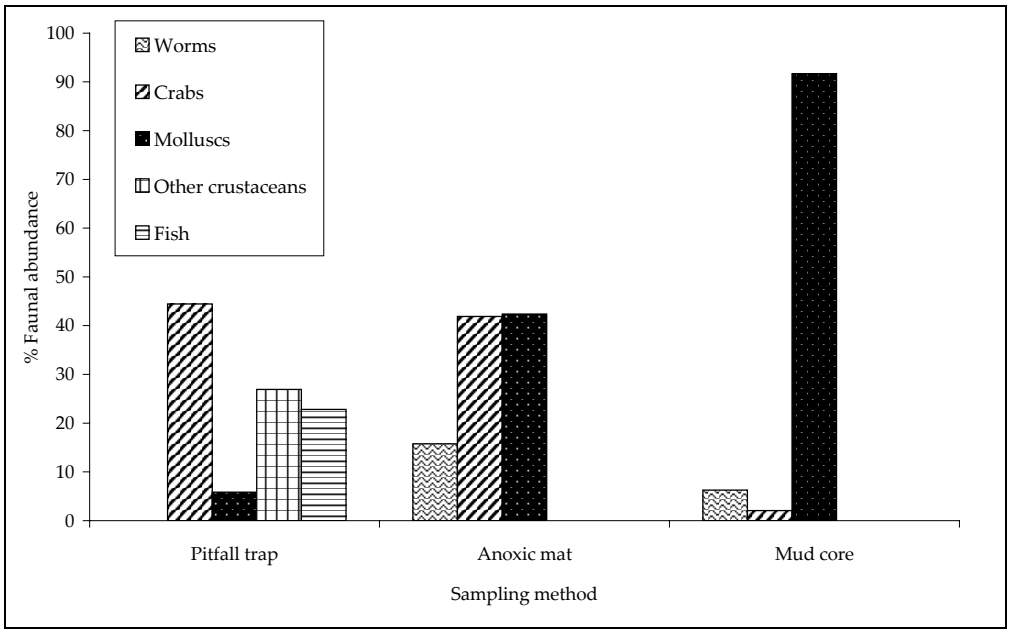


Figure 5-8: Abundance of different faunal groups (% of total recorded for each method) for three sampling techniques trailled in the pilot study, pooled across four assemblages.

Across the four assemblages, pitfall traps mainly sampled crabs (44%), other crustaceans

(27%) and fish (23%). Occasionally mobile gastropods and bivalves would be sampled in pitfall traps. The anoxic mat sampled worms (16%) as well as crabs and molluscs in equal abundance (approx. 42%). In contrast, specimens obtained from mud cores mainly comprised molluscs (92%), few worms (6%) and even fewer crabs (2%). It was apparent that the coring and sieving procedure detected species with hard shells but undersampled delicate and soft-bodied organisms. Thus overall, pitfalls effectively sampled crustaceans and fish, and anoxic mats sampled worms, crabs and molluscs. The process of mud coring and sieving mainly yielded molluscs.

NMDS ordination of the different sampling methods on the basis of abundance of 68 species (Figure 5-9) illustrated a clear distinction in the composition and abundance of fauna sampled by pitfall traps, from that sampled by the anoxic mat and by mud cores. Presumably, pitfalls mainly sampled mobile fauna and the other two techniques sampled sedentary benthic and infaunal species. The infauna sampled by mud cores and by the anoxic mat shows considerable overlap, but the anoxic mat also sampled fauna not found in mud cores, for instance, worms. Overall, mud cores appear to result in a subsample of the fauna sampled by anoxic mats.

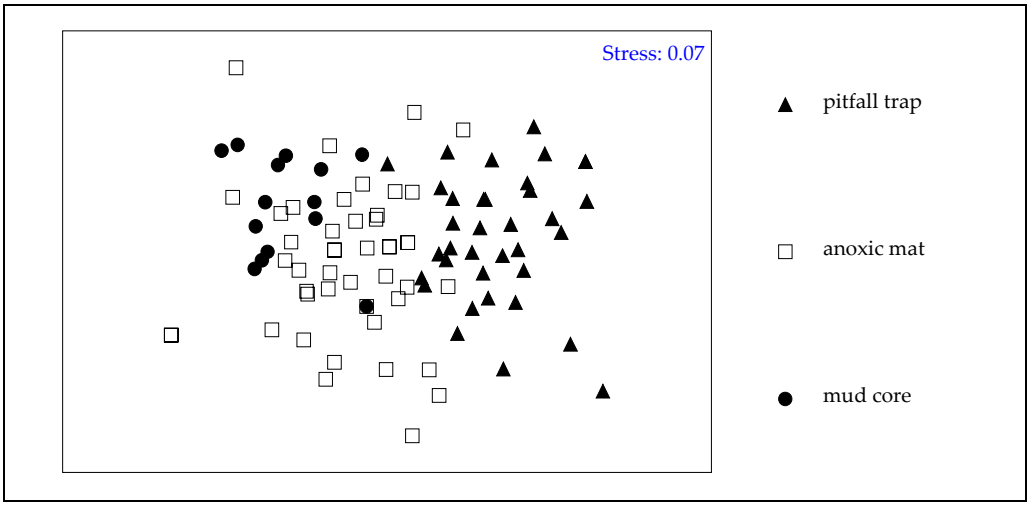


Figure 5-9: Ordination of three sampling methods based on abundance of species recorded in individual pitfall traps; five sizes of anoxic mats, and mud cores of different volumes.

The results show that each technique sampled a different range and abundance of fauna, suggesting that for assessment of macro-invertebrate biodiversity, a methodology combining pitfall traps with anoxic mats would be complementary. Mud cores appeared less efficient than anoxic mats and sampled lower numbers of relatively few species (see below).

Pitfall traps

Pitfall traps effectively sampled fauna in the four assemblages, but few species were recorded in pitfall traps in the hinterland margin (Figure 5-10)

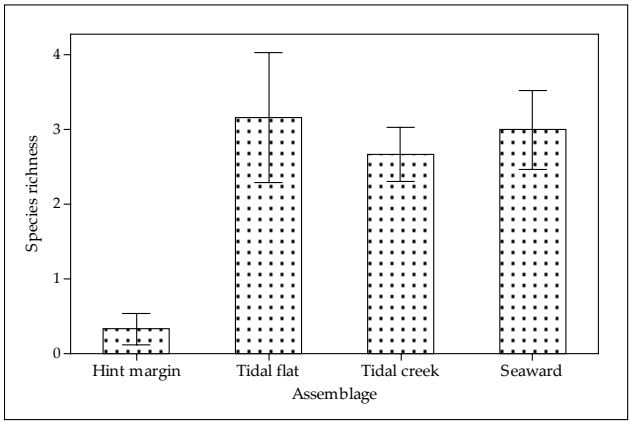


Figure 5-10: Mean species richness of invertebrates and fish (± SE) recorded per pitfall trap, pooled across four assemblages during the pilot study. Sampling intensity was greater in the tidal creek and seaward assemblages (n=16) than in two landward assemblages (n=8).

Results for the tidal creek and seaward assemblages showed no trends toward fewer species on the second or third consecutive day—suggesting that the local area did not become 'fished out' by repeated sampling over three days (Figures 5-11 and 5-12). Results from the hinterland margin and tidal flat assemblages were inconclusive however, due to only two nights of trapping (Figure 5-13). Surveys in these two assemblages were abbreviated for logistical reasons.

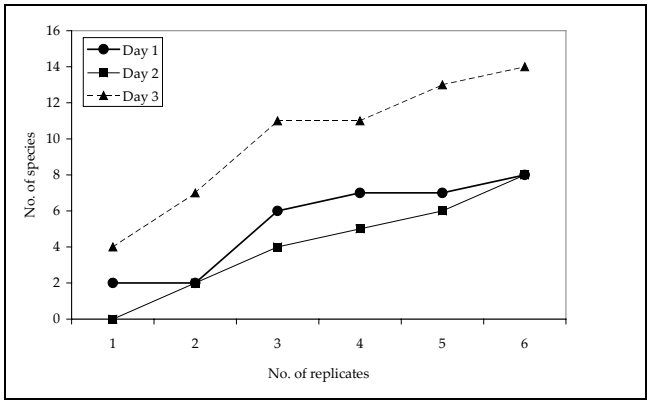


Figure 5-11: Cumulative number of species recorded in six replicate pitfall traps over three consecutive nights in the tidal creek assemblage, Charles Darwin Park.

Figures 5-11 and 5-12 show some evidence of a plateau, and indicate that five to six replicate pitfall traps appears to be adequate to sample the majority of species in the two seaward assemblages. Results for landward assemblages are less conclusive—as the plot

of cumulative species richness against number of replicates in the tidal flat was still increasing after three replicates. Too few species were recorded in the hinterland margin assemblage to draw any conclusions in this regard (Figure 5-13). Increased replication and sampling for three nights would have improved the usefulness of these results.

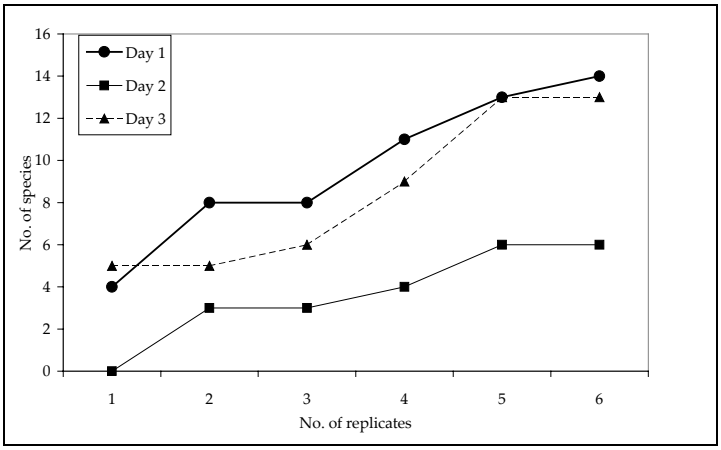


Figure 5-12: Cumulative number of species recorded in six replicate pitfall traps over three consecutive nights in the seaward assemblage, Charles Darwin Park.

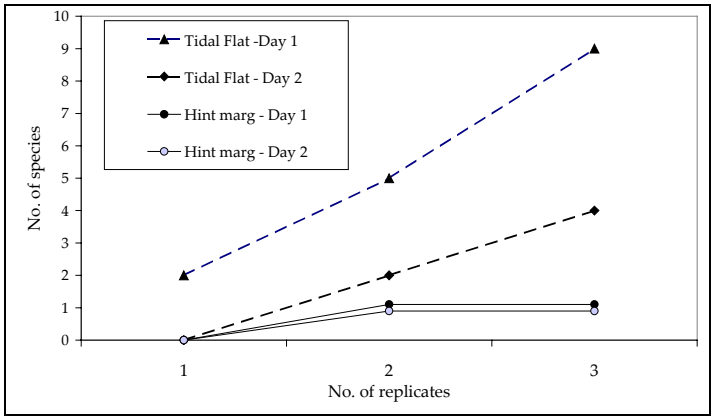


Figure 5-13: Cumulative number of species recorded in three replicate pitfall traps over two consecutive nights in the tidal flat (dashed line) and hinterland margin (solid line).

On the basis of these results, six replicate pitfall traps per assemblage (ie. three per study plot on two replicate transects) were sampled during the invertebrate fauna surveys in undisturbed and disturbed mangroves (see Section. 5.4).

Anoxic mats

Although anoxic mats of five sizes were investigated, all the largest mats (ie 1.0 m^2 area) were washed away. Due to practical difficulties, results for other large mat sizes — including 0.25 m^2 (n=6) and 0.5 m^2 (n=3)—were based on only a few samples. It was generally very difficult to secure large mats and to maintain anoxic conditions beneath

the entire mat. Air would often bubble out of larger crab burrows during a rising tide and if this occurred beneath a mat, it could break the anoxic seal and allow fauna to escape. Adequate replication of the two smallest anoxic mats (0.05, n=41 and 0.1 m^2, n=12) was successfully achieved, as these mats were easier to install (Figure 5-14).

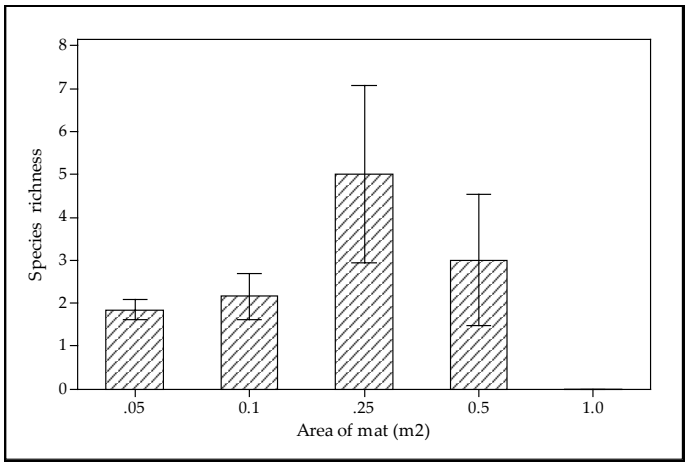


Figure 5-14: Invertebrate species richness (±SE) for anoxic mats of five different areas. Points represent mean numbers of species per mat size pooled across all assemblages.

Overall, the results reflected the impracticality of larger anoxic mats in the field. Intermediate sized mats (e.g.0.25 and 0.5 m^2) resulted in the highest mean species richness but required much time to sample. Indeed, mean species richness declined for the mats of 0.5 m^2 area- probably due to reduced sampling effort associated with the long time required to sample large areas as well as the difficulty in maintaining anoxic conditions beneath large discs. In contrast, small sized anoxic mats (0.05 and 0.1m^2) were practical to use and provided consistent results for sampling diversity and abundance of infauna. Given the small increase in species richness gained using the 0.1m^2 mat, the 0.05 m^2 mat was selected for use in this survey.

A plot of cumulative species richness for anoxic mats of different areas indicates that cumulative species richness in the seaward assemblage increases rapidly between one and three replicates and after five replicates, increments of new species apparently occur less often (Figure 5-15). Due to time constraints, only three replicate samples were obtained for larger anoxic mats so it was not possible to determine if this trend was the same for large mats. In the tidal creek assemblage, a similar pattern was observed with few additional species recorded after three to five replicates (Figure 5-16). Data from the tidal flat and hinterland margin assemblages was more sparse but followed the same trends suggesting that a minimum of five replicate anoxic mats were required to sample

infauna in all assemblages.

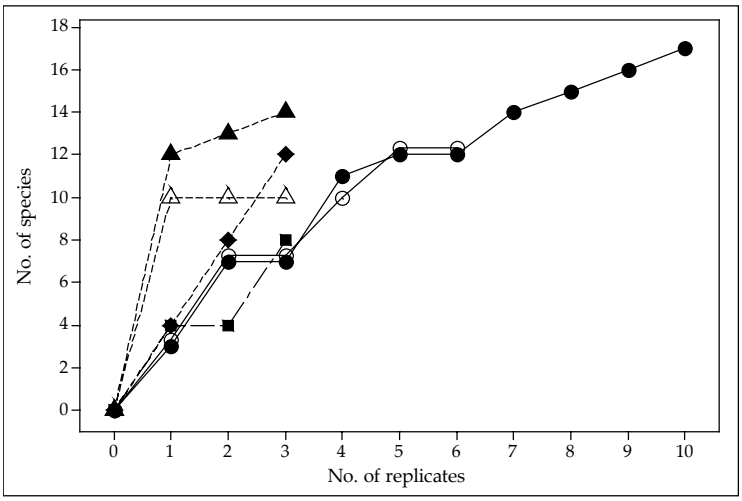


Figure 5-15: Cumulative species richness recorded in the seaward assemblage using anoxic mats of differing sizes—where circles=0.05 m^2; diamonds=0.1 m^2; triangles= 0.25 m^2 and squares=0.5 m^2. Solid symbols denote day 1 of sampling and open symbols denote day 2.

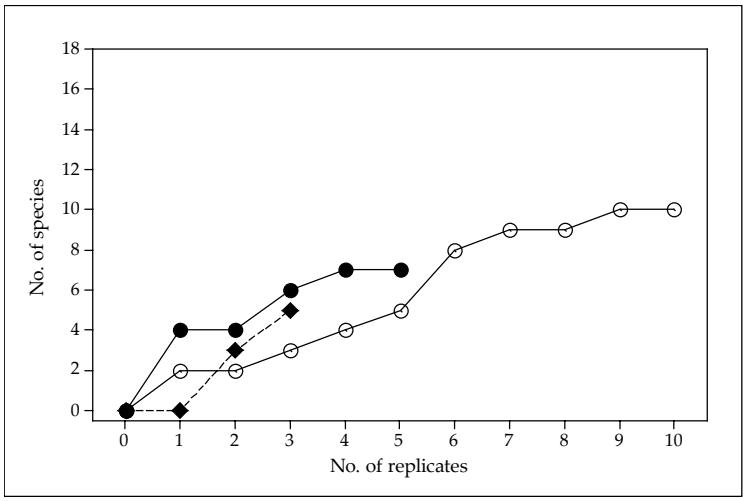


Figure 5-16: Cumulative species richness recorded in the tidal creek assemblage using anoxic mats of two sizes—where circles=0.05 m^2 and diamonds=0.1 m^2; Solid symbols denote day 1 of sampling and open symbols denote day 2.

It should be noted that the anoxic mat sizes trialed during this study were largely ineffective in sampling large invertebrates (e.g. crabs with carapace widths between approximately 3 to 6 cm). Unlike smaller fauna, which typically became trapped and died beneath the mat, large animals apparently had the strength to burrow away from and avoid anoxic mats.

Overall, the pilot study results indicated that the 0.05 m^2 anoxic mat was the most practical size to use in the field, sufficient to sample infauna in all assemblages and that a minimum of three replicates should be used in the main survey.

Mud cores

Infauna recorded from mud cores was very sparse and mean species richness for both 0.5 and 1.0 litre cores was low (< 3 species). No infauna was recorded for the hinterland margin assemblage and there was high variability in all assemblages (Figure 5-17).

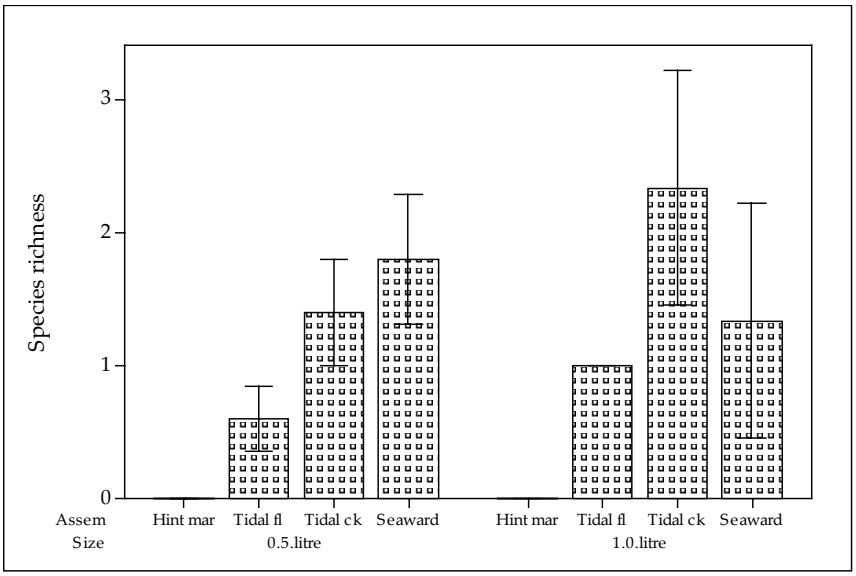


Figure 5-17: Mean species richness (±SE) recorded from mud cores of two sizes sampled from four assemblages during the pilot study.

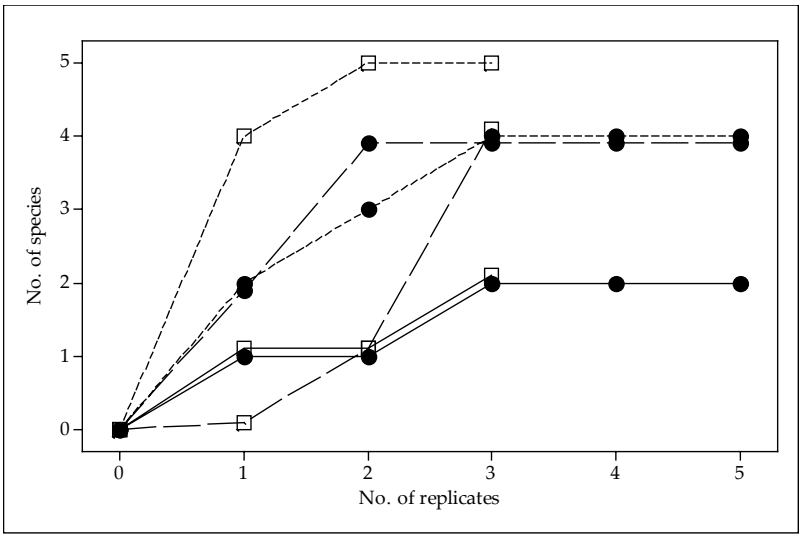


Figure 5-18: Cumulative number of species recorded in mud cores of 0.5 litre volume (solid circles) and 1.0 litre volume (open squares). The three assemblages are denoted by differing connect lines, where tidal flat=solid line, tidal creek=finely dashed line and seaward=large dashed line.

Comparison of anoxic mats (n=52) and mud cores (n=32) of equivalent area and volume respectively indicated that, in general, anoxic mats sampled higher abundance of infauna (Figure 5-19). Neither technique was fruitful in the hinterland margin

assemblage where infauna is naturally expected to very sparse. In other assemblages however, anoxic mats were typically more effective, sampling a greater diversity and abundance of infauna.

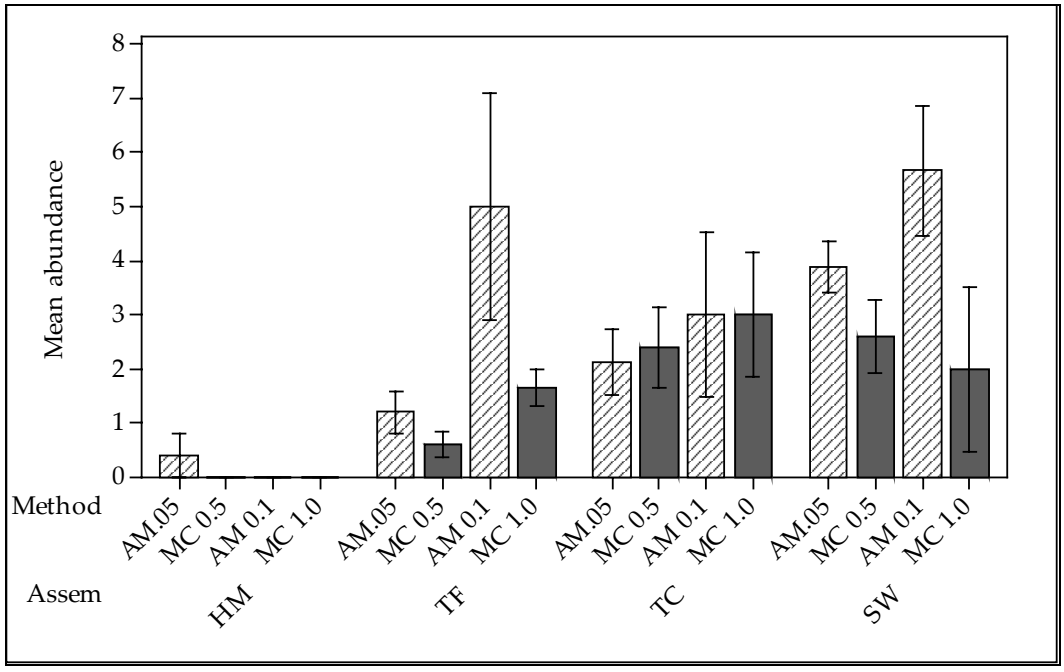


Figure 5-19: Mean species richness (± SE) for anoxic mats (AM, hatched) and mud cores (MC, solid) of two dimensions. Anoxic mats of 0.05m² are compared with 0.5 litre mud cores and 0.1 m² mats with 1.0 litre cores. Mean values shown for four assemblages from L to R where HM= Hinterland margin, TF= Tidal flat, TC= Tidal creek and SW= Seaward.

The yield of fauna sampled from mud cores may have been higher had the samples been sieved immediately, rather than being stored in the cool room for several weeks. It is likely that the elapsed time allowed deterioration of soft-bodied taxa such as worms. Based on these preliminary results however, and comparative efficiency of the sampling techniques, anoxic mats were used in preference to mud coring in the confirmation study and in the main fauna survey.

~5.3.2. Confirmation study

The confirmation study was a brief trial of the selected sampling methodology comprising 1m × 1m quadrats; epifaunal sampling to 2m; a pitfall trap and an anoxic mat. It was conducted to examine whether the selected techniques sampled different groups of organisms (e.g. benthic fauna, infauna, epifauna) and to test the practicality and efficiency of the combined methodology. The study also aimed to establish which of two anoxic mat sizes—0.05 or 0.1m²—was the most practical and productive.

The study site in Ludmilla Bay, in the outer region of Darwin Harbour proved to be relatively unsuitable for conducting this trial. The substrate was sandy mud rather than the fine marine mud generally found throughout the majority of mangroves elsewhere in the harbour. The site is also more coastal, and thus more exposed, than other study sites in the harbour and the unfortunate combination of wave action, heavy rain and sandy substrates led to the disruption of numerous anoxic mats (>55%) and pitfall traps (75%), with resultant loss of data. Although sampling was planned for three consecutive days, the third day was cancelled due to the unsuitable conditions.

Nevertheless, a total of 130 records of fauna comprising 43 species was obtained over two days (4th and 5th February 2001). Of that total, crustaceans comprised 51.1%, molluscs 37.2% and worms, fish and other fauna the remaining 11.1%. As in the pilot study, each sampling method captured a different range of species drawing from different faunal groups (Figure 5-20). Overall, crabs were mainly sampled from quadrats, epifauna mainly comprised molluscs, while pitfall traps sampled crabs and some fish. The widest variety of fauna was recorded from anoxic mats and included numerous species of worms and molluscs. This may have been influenced by increased sampling effort however—as two anoxic mats per station were installed for the confirmation study.

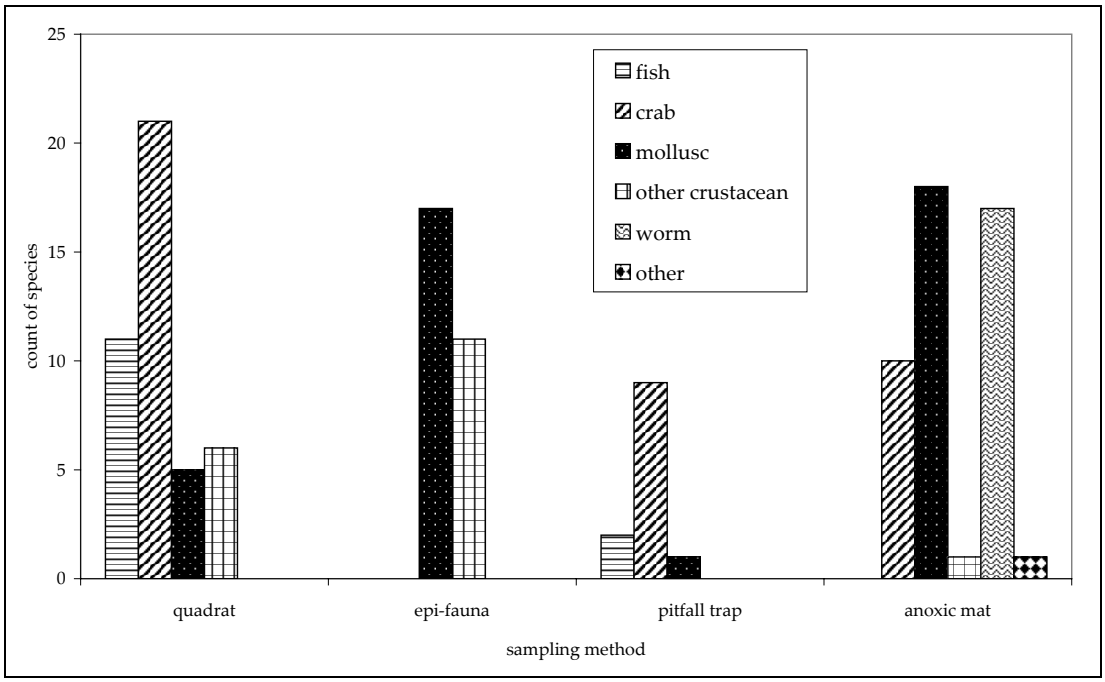


Figure 5-20: Count of species in faunal groups sampled by different techniques in the confirmation study.

Thus, despite the difficulties in implementing this brief study, the findings indicated that each method provided data on different groups of species drawn from different microhabitats. Examination of the data using NMDS multivariate analysis indicated that the epifaunal species sampled from the tree trunks and roots were clearly distinct from fauna sampled using the other techniques (Figure 5-21). Re-analysing the data after exclusion of epifuana confirmed the trend suggested by Figure 5-20—that there was some overlap in the species sampled within quadrats and by pitfall traps, but anoxic mats sampled a distinctly different range of species (Figure 5-22).

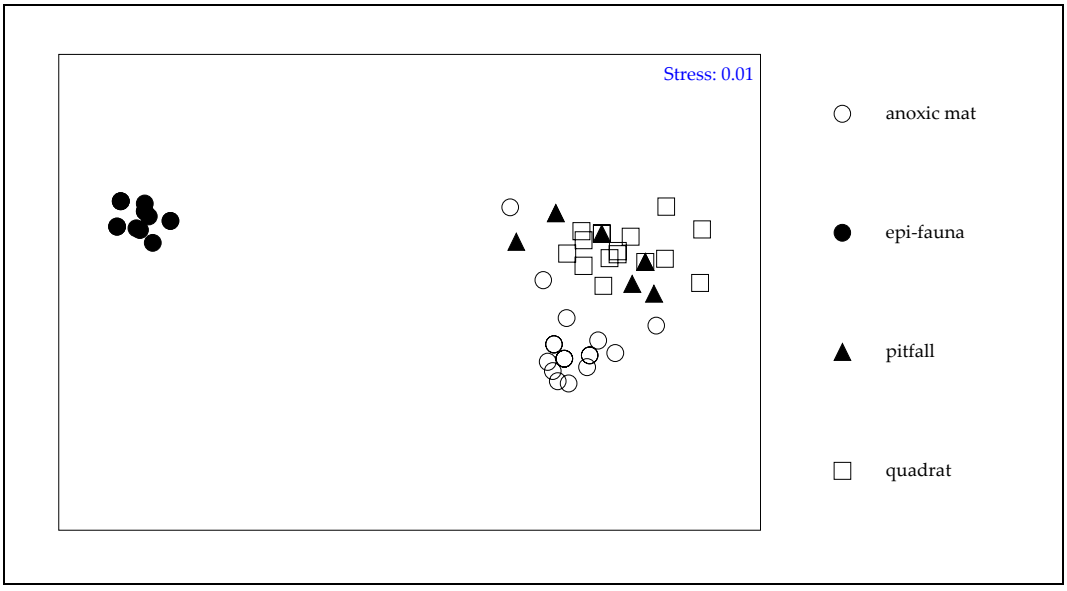


Figure 5-21: NMDS ordination based on the frequency of species sampled by four selected sampling methods. Each point represents one of ten replicate sampling methods.

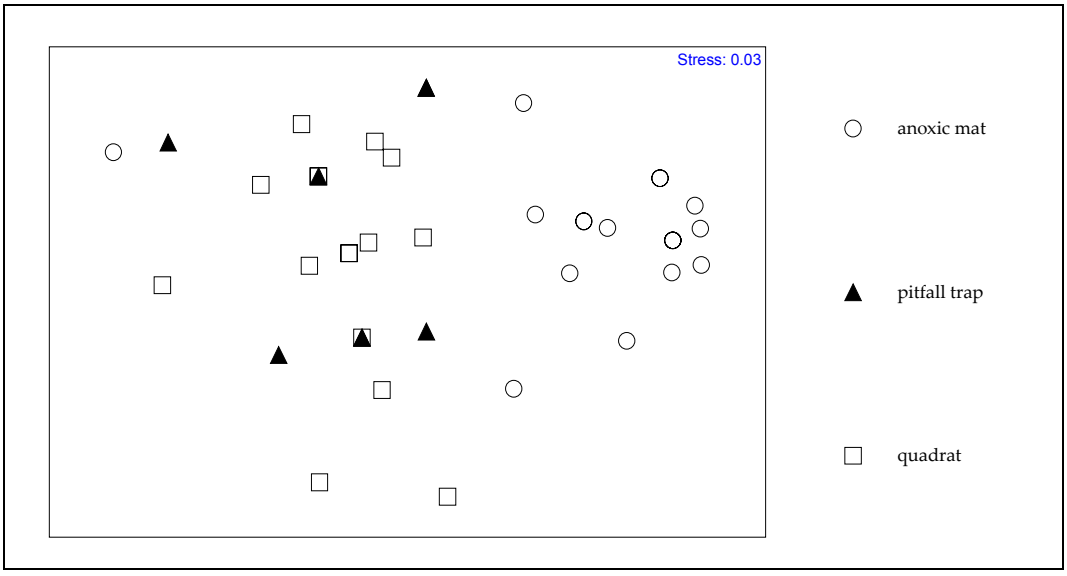


Figure 5-22: NMDS ordination based on the frequency of species sampled using three methods—data for epifauna excluded. All methods were sampled for two consecutive days.

Finally, a comparison of the count of species recorded with small (0.05 m^2, ie. 25.2 cm diameter) and slightly larger (0.1 m^2, ie. 35.6 cm diameter) mats indicated no consistent trends (Figure 5-23). More molluscs were apparently sampled using the larger mat size but more crabs and worms were recorded using the smaller mat. This result is unexpected but the lack of consistency is not surprising, as so many anoxic mats were disrupted by waves during the confirmation study. Thus for the main survey, the smaller mats were selected on the basis of time taken to sample each one—approximately 15-20 minutes. Indeed, the anticipated time to adequately sample each of the four sampling techniques took longer than first expected.

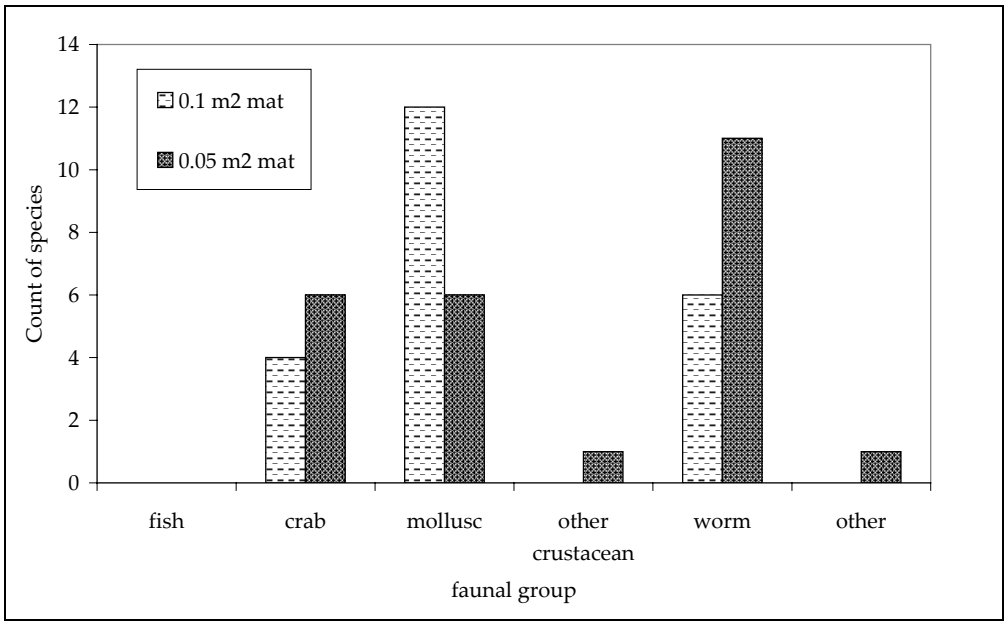


Figure 5-23: Count of species in different faunal groups recorded using anoxic mats of two sizes

5.4. Results –Invertebrate Fauna Surveys

A total of 1,690 records were obtained during wet and dry season surveys at three sites (E1, E2 and M3, described in Chapter 2) using the combined sampling techniques described in section 5.3. For simplicity, fish are grouped with invertebrates in the following sections and are occasionally included under the term 'invertebrate' in figures and tables in the following sections.

~5.4.1. Invertebrate species richness

A total of 191 species from 81 families were recorded from the three sites (Tables B-1 to

B-8, Appendix B. NB these tables also include data from disturbed sites examined in Chapter 6). An additional seventeen species were recorded during the pilot and confirmation studies, increasing the species tally for undisturbed mangroves to 208 (pilot and confirmation study data are not, however, included in subsequent species totals). The invertebrate fauna of the region is relatively poorly known and 72 taxa (38% of the total recorded), are described only to generic or family level. Due to the paucity of previous surveys, this study resulted in several new distributional records for Darwin Harbour. Furthermore, a new genus of bryozoan (Phylum Bryozoa, Family Beaniidae) and a new species of chiton (Phylum Mollusca, Family Acanthochitonidae) were documented during this survey.

Table 5-3 summarises the findings on the diversity and abundance of invertebrates recorded in undisturbed mangroves of this survey. The most speciose invertebrate groups were the crustaceans and molluscs, both comprising 60 species. Thirty-one species of worms, 25 species of ants, 12 fish, 2 sea anemones and one bryozoan were also recorded (Table 5-3). The diversity and abundance of the invertebrate fauna as a whole is presented below and the fauna in each of the taxonomic groups will be considered separately in sections 5.4.3 to 5.4.8.

Overall, mean invertebrate species richness per sampling station during the dry season was 9.9 (± 0.7 SE) and 8.3 (± 0.4 SE) during the wet season. Although the graph of total species richness per study plot (Figure 5-24) indicated no consistent seasonal patterns in the landward assemblages, species richness appeared to decline on most transects in seaward assemblages during the wet season.

Univariate analyses showed no significant differences in mean species richness between the three sites, nor between wet and dry seasons, when averaged across all assemblages. Variation between transects and assemblages was evident however, indicated by significant main effects for these factors (Table B-9, Appendix B). Mean diversity per sampling station increased from a minimum in the most landward assemblage (4.1 ± 0.4 SE) to a maximum in the seaward assemblage (13.7 ± 0.7 SE). Analyses also showed significant season × assemblage and transect × assemblage interactions, the latter indicating that there were differences in species richness between the two transects at each site, in some assemblages.

Table 5-3: Total invertebrate species richness per assemblage, mean species richness per sampling station (± SE) and mean density per station (± SE) for three undisturbed sites.

TAXA	Total species	Mean species richness/ station*	Range	Mean abundance/ station*	Range
ALL ASSEMBLAGES					
Molluscs	60	2.6 ± 0.2	0 - 10	5.4 ± 0.5	0-26
Crustaceans	60	3.8 ± 0.2	0 - 12	15.0 ± 1.5	0 - 91
Worms	31	0.7 ± 0.1	0 - 7	1.3 ± 0.2	0 - 11
Fish	12	0.9 ± 0.1	0 - 4	1.2 ± 0.2	0 - 13
Ants	25	1.1 ± 0.1		-	
Other	3	-		-	
TOTAL	191	9.1 ± 0.4	1 – 24	23.1 ± 1.7	0 - 102
SEAWARD					
Molluscs	39	3.4 ± 0.4	0 - 10	6.7 ± 0.9	0 - 21
Crustaceans	40	6.2 ± 0.3	3 - 12	32.3 ± 3.8	6 - 91
Worms	20	1.7 ± 0.3	0 - 7	2.8 ± 0.5	0 - 11
Fish	7	1.2 ± 0.2	0 - 4	1.4 ± 0.3	0 - 5
Ants	8	1.2 ± 0.2	0 - 4	-	
Other	1	-		-	
Total	115	13.7 ± 0.7	7-24	43.2 ± 4.1	18 - 103
TIDAL CREEK					
Molluscs	27	2.4 ± 0.3	0 - 9	4.9 ± 0.7	0 - 22
Crustaceans	36	4.3 ± 0.3	1 - 8	14.8 ± 2.4	1 - 86
Worms	16	0.8 ±0.2	0 - 6	1.1 ± 0.3	0 - 8
Fish	9	1.3 ± 0.2	0 - 4	1.4 ± 0.3	0 - 8
Ants	6	0.7 ± 0.1	0 - 3	-	
Other	2	-		-	
Total	96	9.5 ± 0.7	4 - 19	22.8 ± 3.0	7 - 104
TIDAL FLAT					
Molluscs	24	3.9 ± 0.4	0 - 9	8.9 ± 1.1	0 - 26
Crustaceans	26	3.1 ± 0.2	1 - 6	9.1 ± 0.7	3 - 20
Worms	8	0.5 ± 0.1	0 - 3	0.9 ±0.3	0 - 7
Fish	6	1.0 ± 0.2	0 - 3	1.6 ± 0.4	0 - 13
Ants	5	0.6± 0.1	0 - 3	-	
Total	69	9.1 ± 0.5	2 - 16	20.6 ± 1.3	6 - 37
HINTERLAND MARGIN					
Molluscs	13	0.7 ± 0.2	0 - 6	1.3 ± 0.5	0 - 16
Crustaceans	16	1.3 ± 0.2	0 - 5	3.8 ± 0.7	0 - 18
Worms	3	0.3 ± 0.1	0 - 1	0.3 ± 0.1	0 - 3
Fish	2	0.1 ± 0.1	0 - 2	0.3 ± 0.2	0 - 6
Ants	18	1.7 ± 0.2	0 - 4	-	
Total	52	4.1 ± 0.4	1 - 10	5.7 ± 0.9	1 - 21

*NB Each station comprised one 1 m^2quadrat, a pitfall trap, a 0.01 m^2 anoxic mat and epifaunal sampling to 2m. Three replicates were sampled per plot.

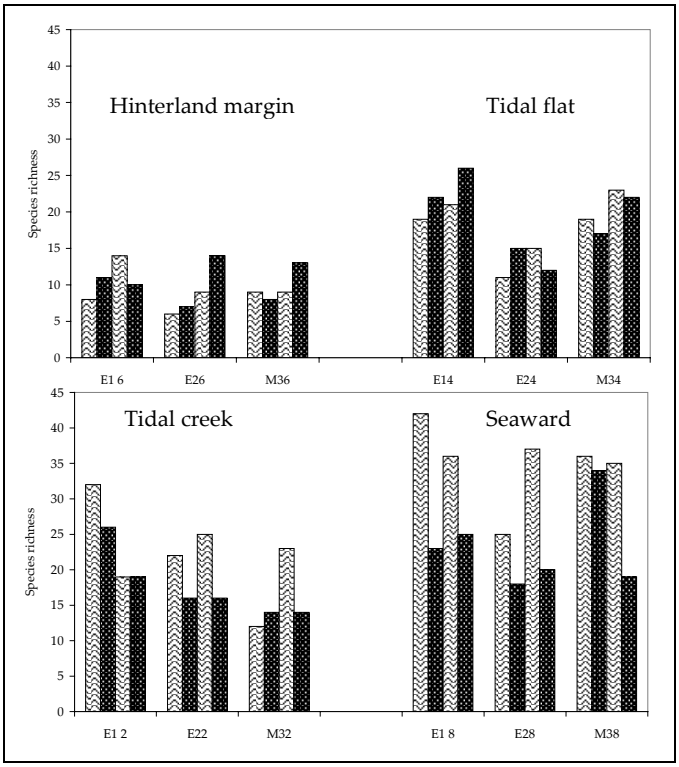


Figure 5-24: Histogram of total species richness of invertebrates during wet season (black) and dry season surveys (grey). Graph shows totals per 0.25 ha study plot, at each of the two transects per site, in the two landward mangrove assemblages (upper) and the two seaward assemblages (lower).

The significant season × assemblage interaction revealed significant seasonal differences in species richness, which varied between assemblages. In the seaward assemblage, mean species richness of invertebrates was higher in the dry season (16.3 ± 1.0) than in the wet (11.1 ± 0.7 SE); but such marked seasonal differences were not recorded in other assemblages (Figure 5-25).

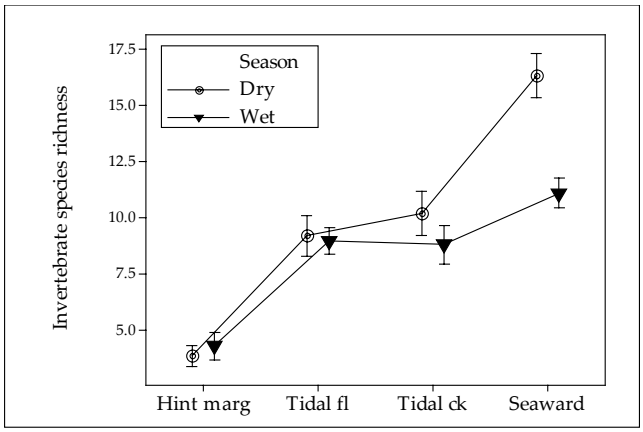


Figure 5-25: Mean species richness of invertebrates in the four assemblages from landward (left) to seaward (right) sampled during wet and dry seasons. Points represent means per study plot (± SE), averaged across paired transects at three sites, using combined sampling methodology.

Mean species richness was only slightly higher during the dry season in the tidal creek assemblage, but seasonal differences were negligible in the two landward assemblages.

The clustering of study plots in the MDS ordination based on the presence or absence of species demonstrated that invertebrate faunas were strikingly different between the four assemblages. Plots within each of the four assemblages are tightly grouped, with only minor overlap of a few plots in the tidal creek and seaward assemblages (Figure 5-26); indicating the discrete species composition and species richness of each assemblage. The ordination shows the clear distinction between the invertebrate fauna of landward assemblages (left) and seaward assemblages (right).

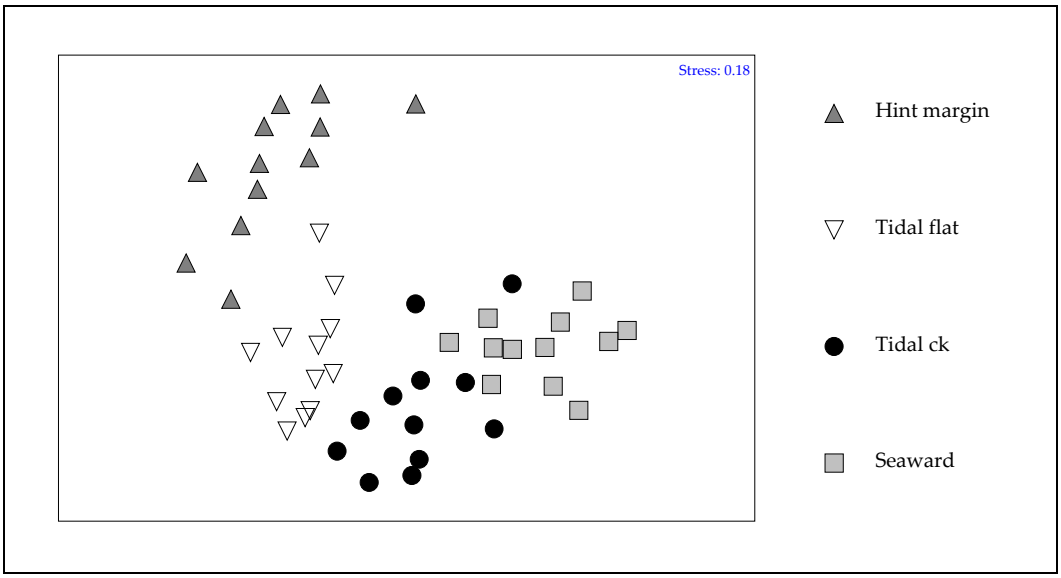


Figure 5-26: NMDS ordination of study plots indicating assemblage. Points represent 24 study plots sampled in wet and dry seasons based on the presence or absence of 191 invertebrate species, sampled at three replicate sampling stations per plot.

~5.4.2. Invertebrate abundance

Overall, the mean abundance of invertebrates per sampling station, (excluding ants, which were recorded only as present, or absent) was 24.1 ± 2.6 SE during the dry season and 22.0 ± 2.3 SE during the wet. Of the 3,323 marine animals recorded during this survey, crustaceans were most abundant (65.1%); far exceeding the numbers of molluscs (23.6%) and worms (5.5%). Crustaceans were the dominant faunal group in each of the four assemblages studied (Table 5-3).

In general, invertebrate abundance displayed similar spatial patterns to that observed for species richness. Total abundance was highest at the seaward margin and least at the

landward mangrove fringe (Figure 5-27). ANOVA's revealed no differences between means of invertebrate abundance at the three sites, nor between wet and dry seasons, averaged across all assemblages. Significant main effects were found for transect and for assemblage (Table B-10, Appendix B).

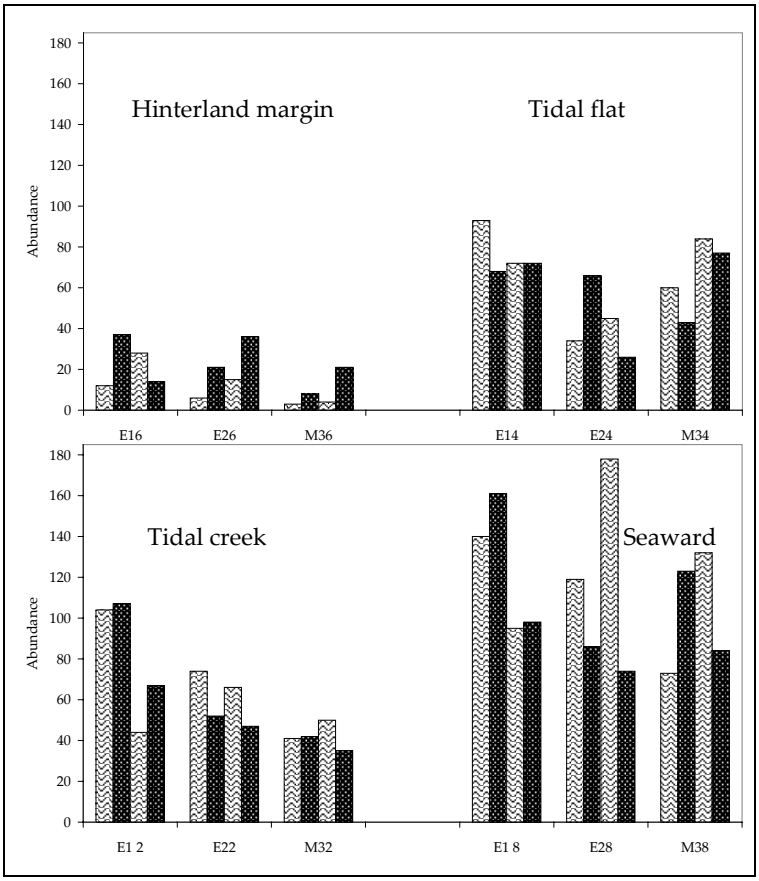


Figure 5-27: Total abundance of invertebrates per study plot during dry season (grey) and wet season surveys (black) in the two landward (upper) and two seaward assemblages (lower). The histogram shows totals for 183 taxa (excluding ants) for each 0.25 ha study plot, at each of the two transects per site.

Mean abundance was highest in the seaward assemblage (43.2 ± 4.1 SE), lowest in the hinterland margin (5.7 ± 0.9 SE) and intermediate in the tidal flat (20.6 ± 1.3 SE) and tidal creek assemblages (22.8 ± 3.0 SE).

In contrast with the pattern observed for species richness, no significant seasonal differences in invertebrate abundance were detected (Figure 5-28). Although mean dry season abundance declined in the hinterland margin assemblage (mean wet, 7.7 ± 1.4 SE; mean dry 3.8 ± 1.1) the difference was not significant.

The MDS of all study plots based on raw abundance revealed a strong gradient of change from the landward fringe to the seaward edge of the mangroves (Figure 5-29).

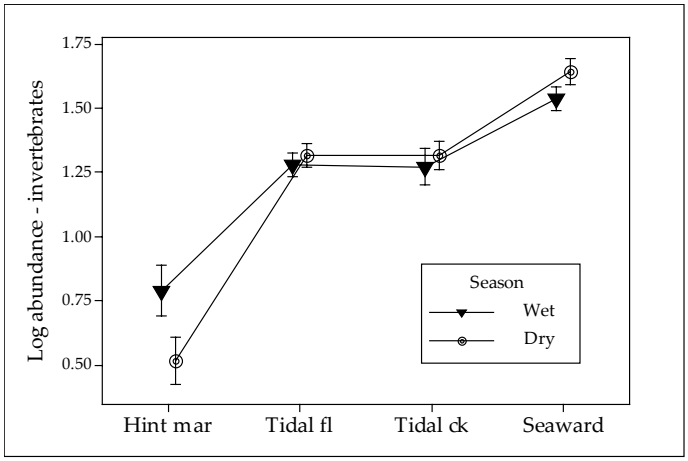


Figure 5-28: Mean invertebrate abundance ($\log_{10}(x + 1)$ transformed) in assemblages from landward (left) to seaward (right) sampled during wet and dry seasons. Means per study plot (± SE) averaged across paired transects at three sites.

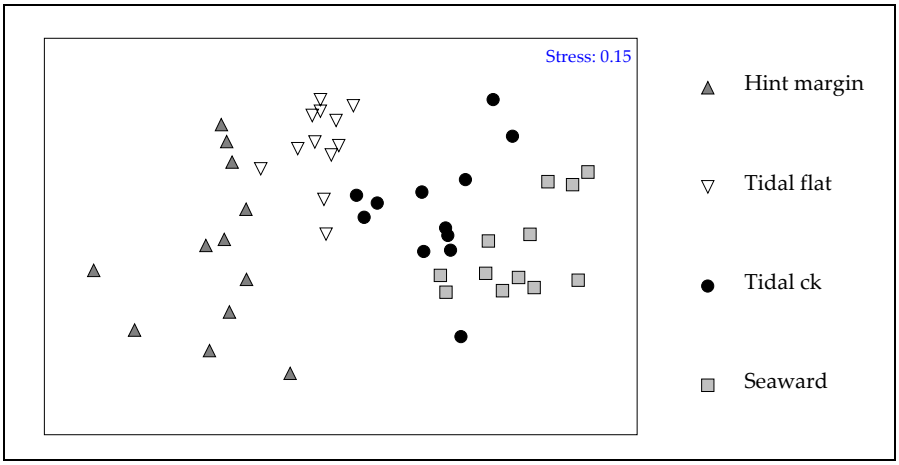


Figure 5-29: MDS based on the abundance of 183 invertebrate species in 24 study plots sampled in wet and dry seasons in four assemblages.

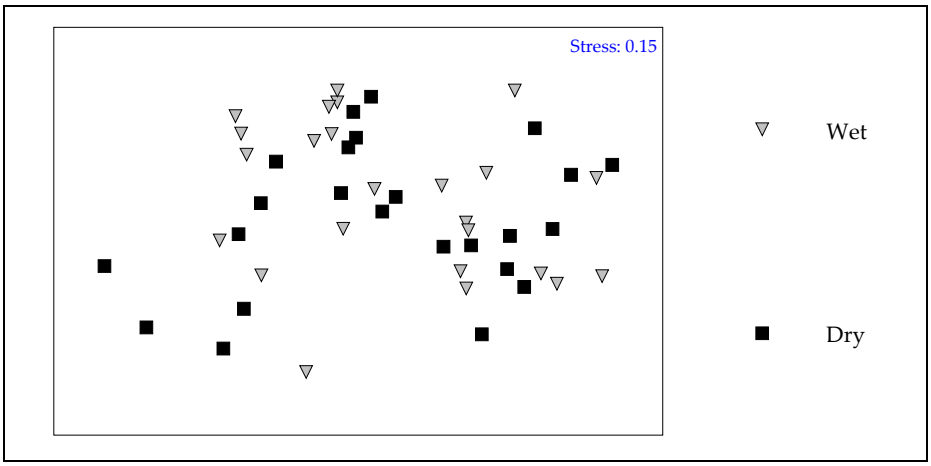


Figure 5-30: MDS of study plots shown in Figure 29 with season superimposed.

The arch effect shown by the ordination further emphasised the single, strong environmental gradient (p. 11-4, Clarke and Warwick, 1994). The ordination illustrates

that each assemblage had distinctive faunal density and species composition. Superimposing season (ie the season during which sampling was conducted) for each of the study plots shown in Figure 5-29, indicated that the influence of season was not important in determining invertebrate abundance (Figure 5-30). This finding was supported by the ANOVA results in which assemblage was a significant factor, but not season.

Tables B-2 to B-9 list all invertebrate species according to faunal group, indicating the frequency (count of abundance) recorded during wet and dry season surveys.

~5.4.3. Worm diversity and abundance

Paraleonnates bolus • *Listriolobus bulbocaudatus* • *Perinereis* sp. • *Sternapsis* sp. • *Namalycastis nicolea* •*P. bolus*

Worm species richness

A total of 130 records for worms, comprising 31 species from 16 families were documented from the four assemblages at three undisturbed sites, during one wet and one dry season survey in 2001. Polychaetes (Phylum Annelida, Class Polychaeta) predominated, comprising 80.6% of all worms sampled. Three polychaete families—Nereididae, Capitellidae and Spionidae—accounted for 45.2% of all species and the remaining taxa comprised worms from other polychaete families and the phlya Platyhelminthes, Nemertea, Echiura and Sipuncula (Appendix B-1).

Univariate analyses revealed seasonal variation in the species richness of mangrove worms (Table B-11, Appendix B). The effects of season on worm diversity varied between assemblages however, with opposing patterns observed in the most landward and most seaward habitats. Mean worm species richness was significantly higher during the dry season than the wet in the seaward and tidal creek assemblages, whereas it was lower in the hinterland margin during the same season (Figure 5-31).

Overall, the seaward assemblage had a high diversity of worms, while few species were

sampled from the hinterland margin. One hinterland margin polychaete, *Namanereis malaitae,* had not been recorded from mangrove habitats previously. Prior records of this species (as *Cryptonereis malaitae)* were from an intertidally-stranded decomposing coconut leaf frond on the Solomon Islands (Gibbs, 1971).

Species richness of worms did not vary between locations, but ANOVA detected a significant transect × assemblage interaction, indicating that differences between assemblages varied between the two transects at each site (Figure 5-32). The latter appears to represent patchiness in worm diversity in the seaward assemblage, as the interaction is due largely to high species richness in this assemblage on transect one at site M3.

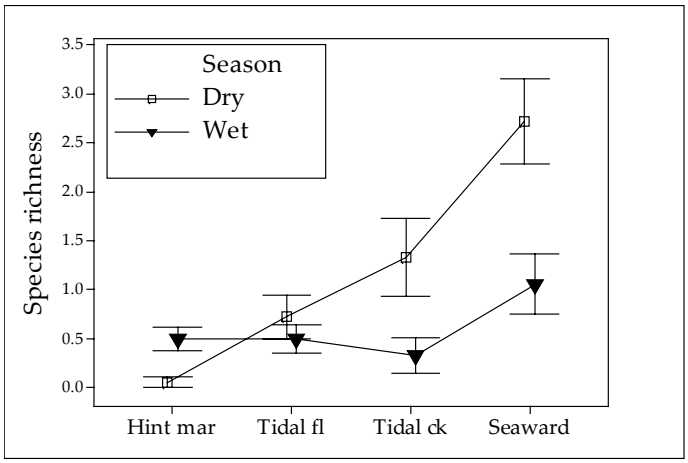


Figure 5-31: Mean worm species richness per sampling station (±SE) in assemblages from landward (left) to seaward (right), averaged across three sites, during wet and dry seasons.

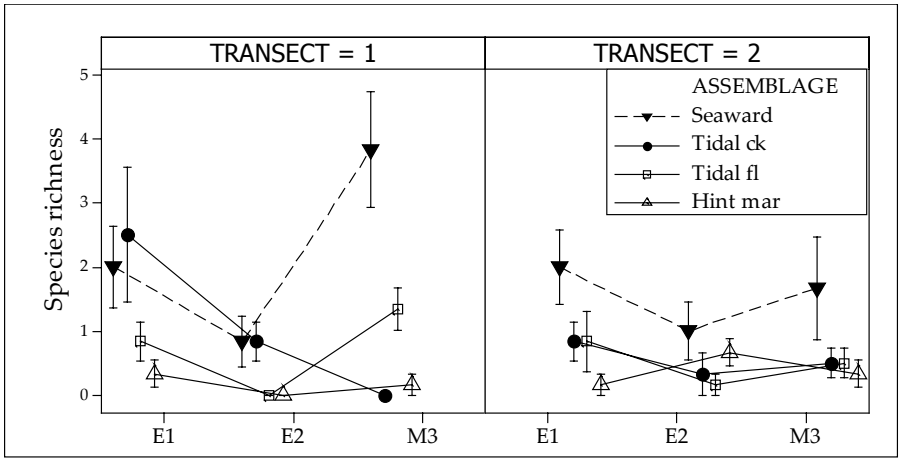


Figure 5-32: Mean worm species richness (±SE) in four assemblages and threee locations indicating variation between transect 1 and 2.

The primary microhabitat for worms was the mud substrate and the highest diversity of

infaunal species was recorded in the seaward (total 18 species, mean 1.1 ± 0.2 per station) and tidal creek (total 20 species, mean 0.5 ± 0.2 per station) assemblages (Figure 5-33). A range of epifaunal worms were recorded in the seaward assemblage, but these were rare elsewhere. Typical epifaunal species included the nereidids *Neanthes cf biseriata*, *Perinereis singaporiensis* and the scaleworm *Lepidonotus* sp. 1. The pattern of abundance in the three main microhabitats mirrors that for species richness, with the density of infaunal worms increasing progressively from landward to seaward.

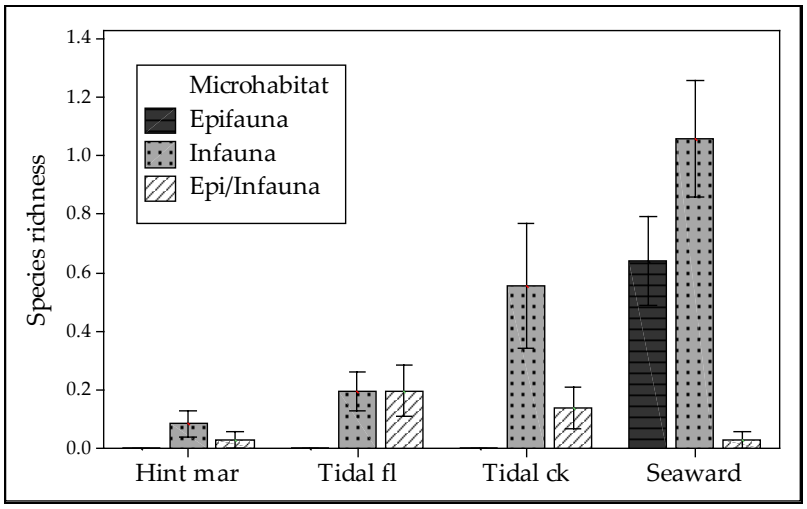


Figure 5-33: Mean species richness of worms (±SE) per sampling station, sampled from three microhabitats in the four assemblages from landward (left) to seaward (right). Epifauna = worms from the surface of trees and within rotting wood; Infauna = worms sampled with the anoxic mat; and Epi/infauna = worms sampled from within 1m^2 quadrat.

Worm abundance

The mean abundance of worms across all assemblages was 1.3 ± 0.2 per station (Table 5-3) with maximum abundance recorded from the seaward assemblage (2.8 ± 0.5, range 0-11 per station). The most abundant worm species were: *Scoletoma* sp. 1 (over 100 individuals/m^2), *Perinereis singaporiensis*, *Glycera nicobarica, Phyllodoce* sp. 1, *Perinereis aibuhitensis* and *Nereis* sp. 1. Many worm species (35.5 % of records) were apparently uncommon, being recorded only once during the surveys, but further sampling may reveal different results.

As for species richness, univariate analyses detected significant seasonal variation in worm abundance. Overall mean abundance of worms per sampling station in the wet season (0.8 ± 0.2 SE) was less than half the mean abundance during the dry season (1.7 +0.3 SE). The most marked seasonal differences in abundance were recorded in the two

seaward assemblages (Figure 5-34).

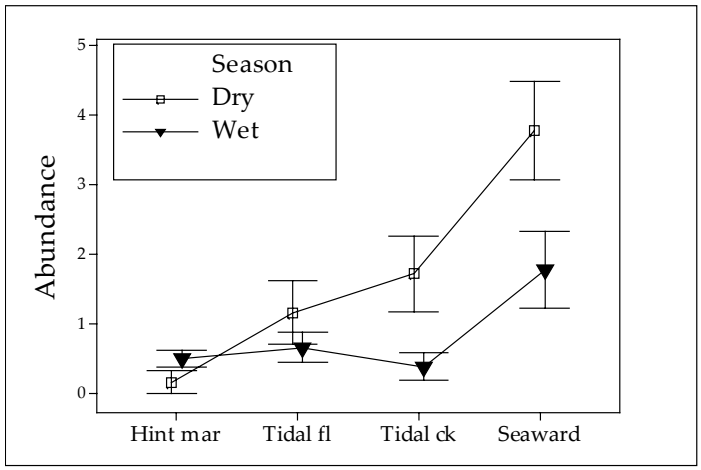


Figure 5-34 : Mean abundance of worms during the wet and dry seasons across four assemblages. Means were pooled from three sampling stations and averaged across three sites.

Overall, abundance of worms in the two landward assemblages was typically lower than in the two seaward habitats. Similar to the results for species richness, a significant transect × assemblage interaction indicated worm abundance varied between the two transects at each site, in some assemblages (Figure 5-35). It appears this interaction is mainly due to particularly high worm abundance from transect one in the seaward assemblage at site M3.

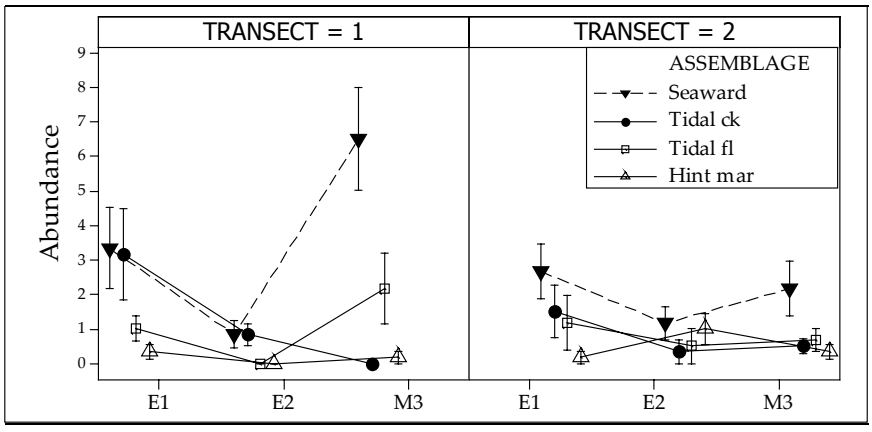


Figure 5-35: Mean worm abundance (±SE) in four assemblages and threee locations indicating variation between transects 1 and 2.

The above results, and the high mean square estimates for season and assemblage, indicate that seasonality and shoreline position were important factors determining worm diversity and density (Table B-11 and B-12, Appendix B).

Multivariate analyses based on the abundance of 31 species indicated the strong

similarity of the worm fauna in study plots in the seaward mangrove assemblage (Figure 5-36). The worm fauna of the other assemblages shows less similarity and less affinity to a particular habitat, as indicated by the scatter of points. The ordination suggests the worm fauna in landward habitats, is not as prolific as that of the seaward assemblage, and is apparently less influenced by shoreline position.

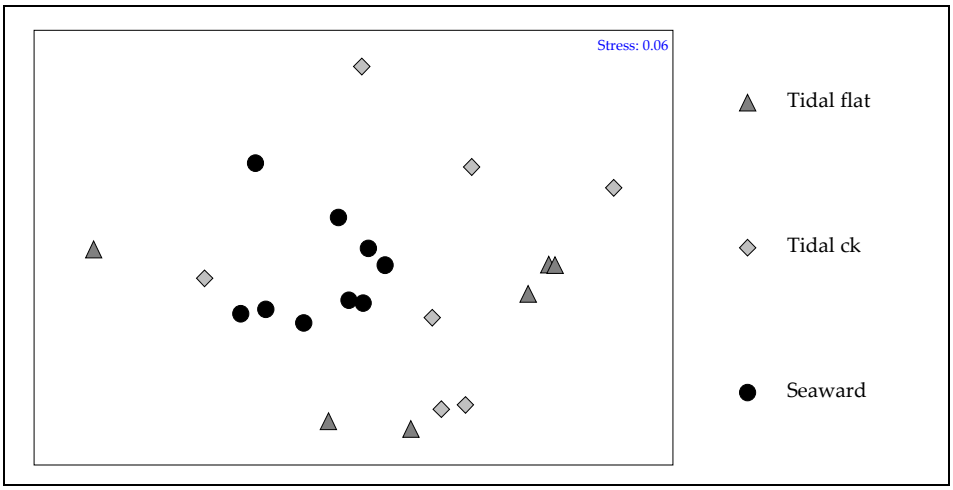


Figure 5-36: Ordination of the abundance of 31 species of worms in three mangrove assemblages. Each point represents one 0.25 ha study plot, at three sites, sampled during wet and dry seasons.

Highlighting season in the same ordination of worm abundance shown in Figure 5-36, indicated that season did influence worm abundance (Figure 5-37). These findings are in accordance with ANOVA results where a significant main effect for season was found for both worm species richness and abundance. The MDS shows study plots sampled during the dry are quite distinctly grouped, showing only minor overlap with plots sampled during the wet season (Figure 5-37).

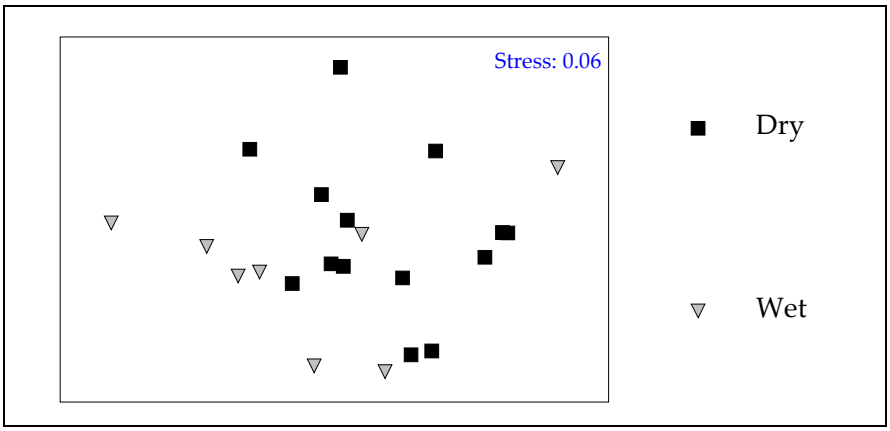


Figure 5-37: Ordination of worm abundance in wet and dry seasons. Each point represents the abundance of worms recorded within 0.25 ha study plots using all sampling techniques, during one wet and one dry season survey.

Worm feeding guilds

All five trophic categories and 14 of the 22 specialised worm feeding guilds described by Fauchald and Jumars (1979) and Pagliosa (2005) were identified among the worm taxa collected in this study (Table B-2, Appendix B). In the following, trophic category is considered equivalent to feeding guild, and worms were classified and examined in the context of five main guilds: carnivores, herbivores (including detritivores), filter feeders, surface deposit feeders and sub-surface deposit feeders.

Surface deposit feeders (10 species) and herbivores (8) were predominant among the worms of undisturbed mangroves, and filter feeders were the only guild not well represented in the study (1 species). Overall, herbivores were the most numerous, with carnivores, sub-surface deposit feeders, surface deposit feeders and filter feeders in decreasing order of abundance (Figure 5-38).

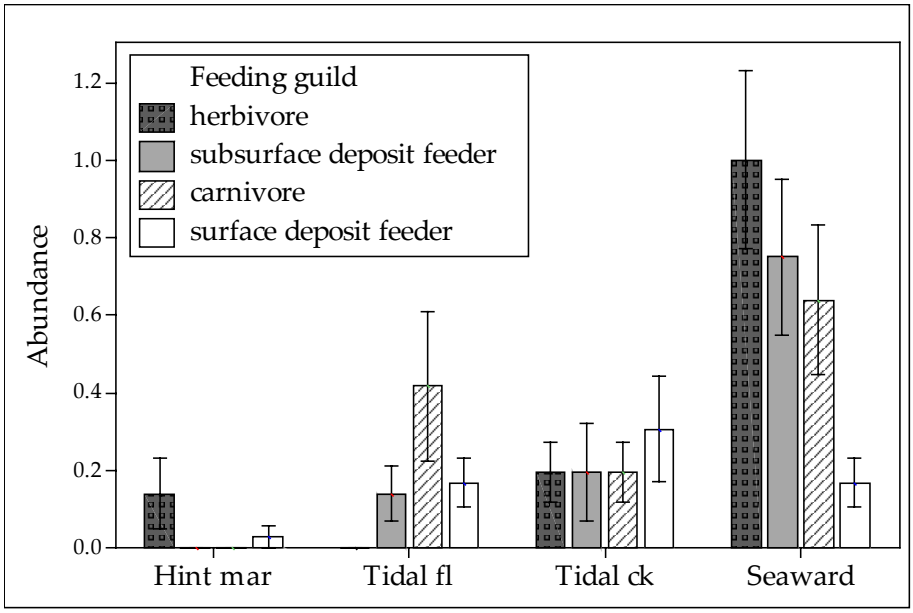


Figure 5-38: Mean abundance of worms (± SE) in the five main trophic categories at three sites in Darwin Harbour. Means per mangrove assemblage are shown from landward (L) to seaward (R).

Analyses of worm feeding guild indicated significant seasonal variation in the abundance of carnivorous worms, which declined during the wet season, as did the abundance of herbivorous species at some sites (Figure 5-39, Tables B-13 to B-16, Appendix B). The abundance of carnivorous and surface deposit feeding worms also varied significantly between sites. The proportion of worms per guild was not consistent between each of the main assemblages at the three sites studied (Figure 5-38)

but the results are not based on a large data set. Carnivores were the most abundant guild in the tidal flat, surface deposit feeders were most abundant in the tidal creek and herbivores in the seaward assemblage. ANOVA results however, indicated that only carnivorous and sub-surface deposit feeders varied significantly in abundance between assemblages (Figure 5-39; Table B-16, Appendix B). The abundance of these worms decreased from a maximum in the soft sediments of the seaward assemblage to a minimum in the seasonally dry substrates of the hinterland margin (Figure 5-38).

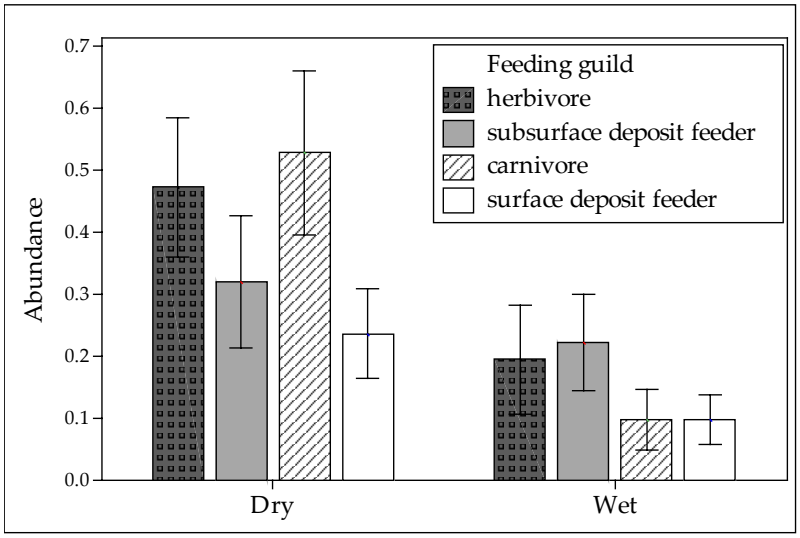


Figure 5-39: Mean abundance (±SE) of worms in different feeding guilds pooled across the four assemblages in wet and dry seasons.

For herbivorous worms, a significant main effect for transect and a significant transect × assemblage interaction indicated that abundance of worms in this guild varied between the two transects per site, amongst assemblages (Figure 5-40, Table B-14, Appendix B).

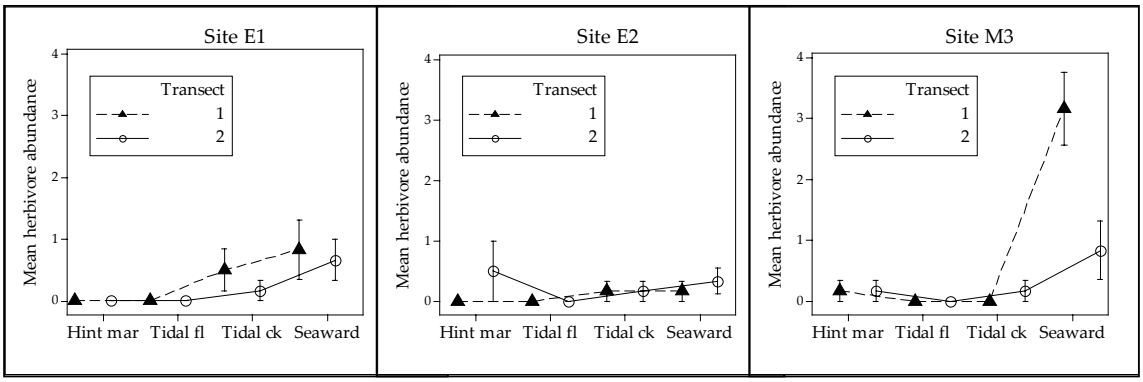


Figure 5-40: Mean abundance (± SE) of herbivorous worms in assemblages on the two transects at three locations.

~5.4.4. Ants

Camponotus sp.10 • Tetraponera punctulata • Oecophylla smaragdina • Polyrhachis sokolova

At the three undisturbed sites a total of 177 records were obtained for 25 species of ants from 12 genera. One introduced ant species (*Paratrechina longicornis*) was recorded (Table B-3, Appendix B, NB this list also contains data from disturbed sites, discussed in Chapter 6).

Ant species comprised a mixture of savanna (36%) rainforest (28%) and mangrove specialists (28%). The primary habitat of two species—*Polyrhachis sp. (*subgenus Chariomyrma) and *Pheidole* sp. A—was unknown, and with *Opisthopsis major*, they represent three new records for mangrove habitats. *Polyrhachis* (6 species), *Camponotus* (4 species) and *Crematogaster* (4 species) were the richest genera in the three undisturbed sites.

Two species, *Crematogaster* sp. 9 and the mud-nesting *Polyrhachis sokolova* were common and recorded across the four assemblages studied (Figure 5-41). The majority of species were uncommon, however, with 32% of species recorded only once in the hinterland margin assemblage. A small suite of species, including *Tetraponera punctulata, Camponotus* sp. 10 and *Camponotus anderseni* were restricted to the seaward assemblage where they were reasonably common. Green ants (*Oecophylla smaragdina)* were only recorded in the tall *Rhizophora stylosa* forests of the tidal creek assemblage where their woven leaf nests were situated safely above the high tide mark. One species *Crematogaster* sp. 3 was found only in the tidal flat assemblage.

Overall, mean species richness of ants was 1.2 species (± 0.1 SE) per sampling station in undisturbed mangroves (n=144). Seasonal variation in ant diversity differed between sites (Table B-17, Appendix B) but there were no differences in species richness between

assemblages, nor between the three sites studied (Figure 5-42 right, Table B-17, Appendix B). The highest mean species richness was recorded in the hinterland margin, followed by the seaward assemblage (Figure 5-42 left).

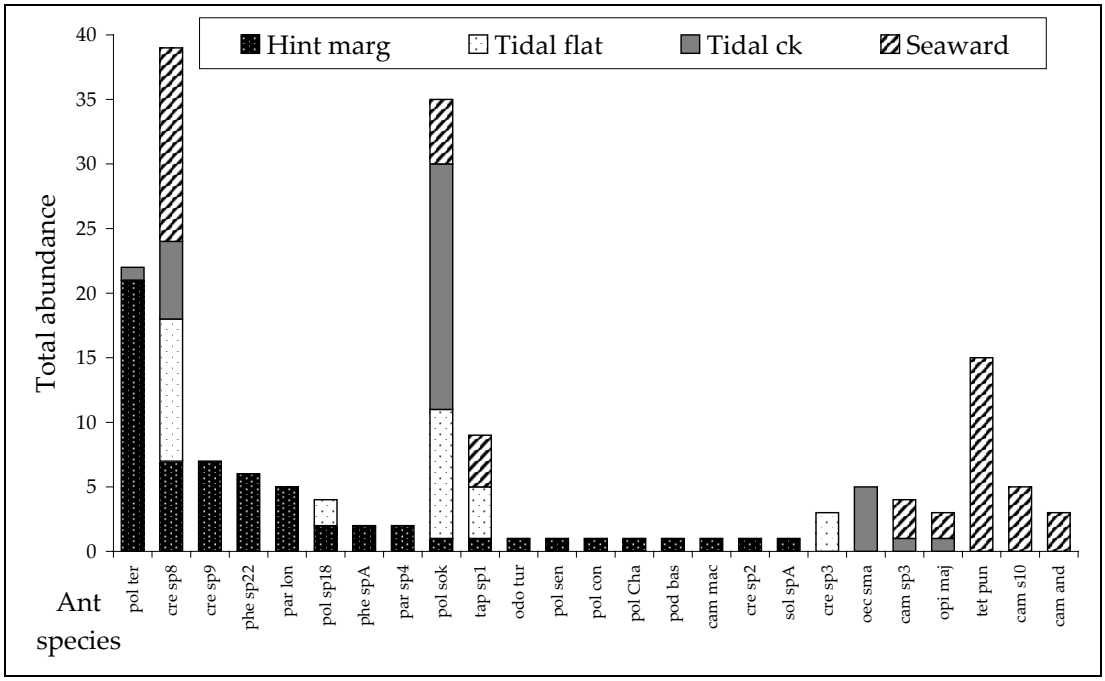


Figure 5-41: Distribution and abundance of 25 ant species (± SE) in the four assemblages in undisturbed mangroves from landward (left) to seaward (right).

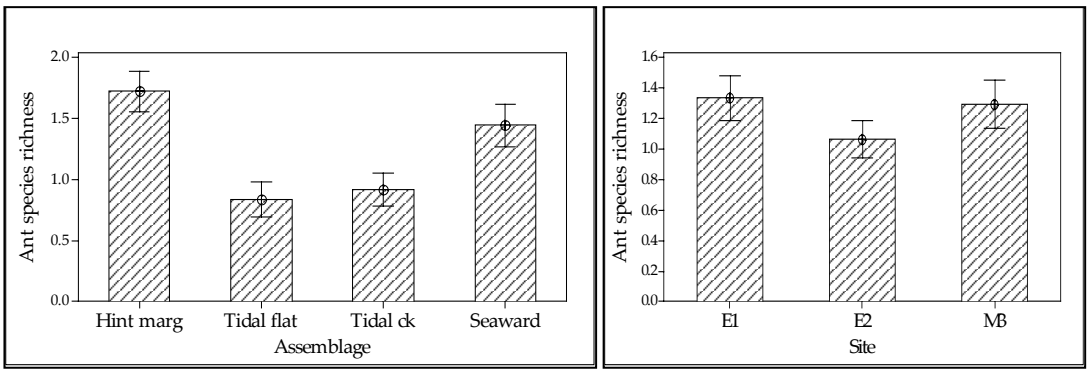


Figure 5-42: Mean species richness of ants in assemblages (left) and locations (right) in undisurbed sites. Points represent means (± SE) per sampling station pooled for wet and dry seasons for one year.

The frequency of ground dwelling ants sampled was highest in the hinterland margin and the tidal creek assemblages. Arboreal ants (i.e. species with arboreal nests) were most frequently sampled in the seaward assemblage (Figure 5-43).

The distribution of the six *Polyrhachis* species shows highest species richness in the hinterland margin and least in the seaward assemblage, with habitat partitioning

amongst the different species (Figure 5-44). *P. terpsichore* (arboreal, rainforest species) is most numerous and virtually confined to the hinterland margin, but occasionally occurred in the tidal creek. Of the two mangrove specialists, *P. constricta* was restricted to the hinterland margin, but *P. sokolova* occurred throughout all assemblages and was sampled most frequently in the tidal creek assemblage. Due to their high frequency, the distribution of these two ground–dwelling species has influenced the overall pattern of distribution of arboreal and ground species observed in Figure 5-43.

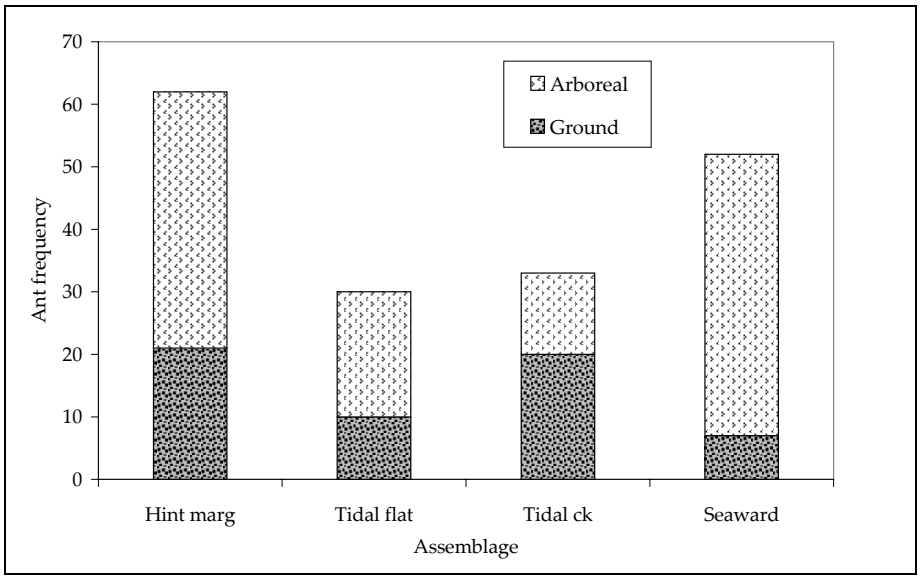


Figure 5-43: Frequency of arboreal and ground dwelling ants recorded in the four assemblages from landward (L) to seaward (R) at three undisturbed sites during wet and dry season surveys.

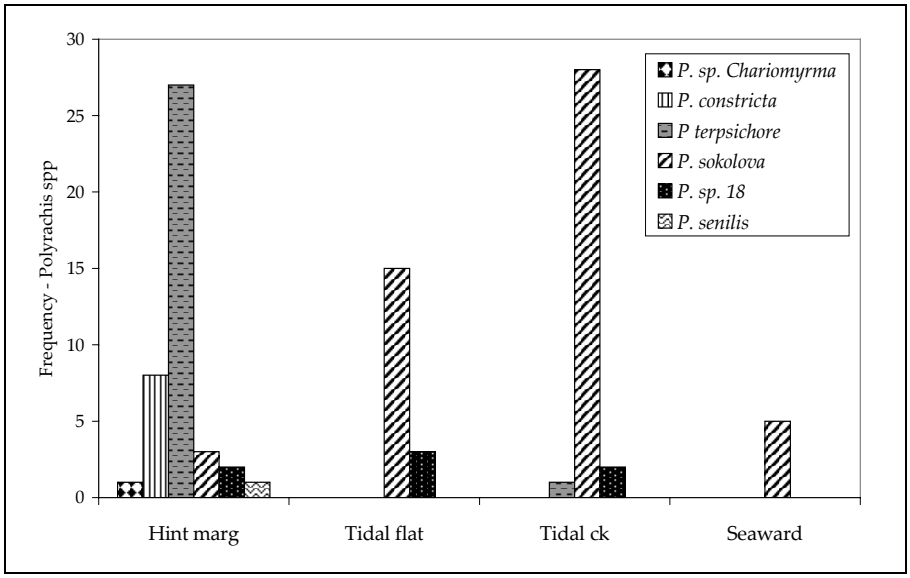


Figure 5-44: Frequency of ant species in the genus *Polyrhachis,* in assemblages from landward (L) to seaward (R). Total frequency data pooled from all surveys (disturbed and undisturbed sites) during three surveys in 2001.

Multivariate analysis of the ant fauna based on the presence or absence of species in the 46 study plots shows a discrete hinterland margin ant fauna (bottom left of ordination) from that occurring in other assemblages (Figure 5-45). Study plots in the seaward assemblage were also fairly tightly grouped (top left) indicating quite distinctive species composition, while tidal flat plots are generally grouped with, and most similar to, those in the tidal creek assemblage.

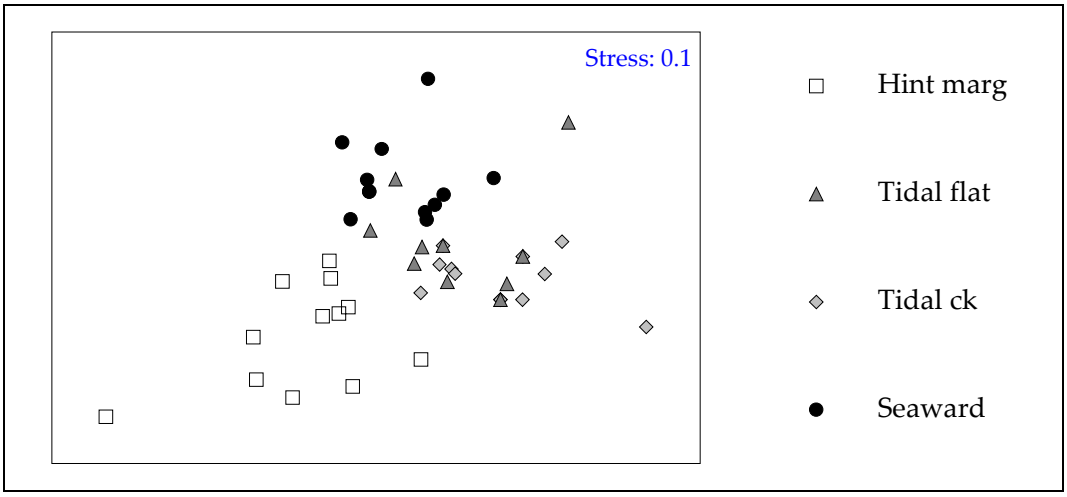


Figure 5-45: Ordination of 46 study plots in four assemblages based on frequency of 25 ant species during one wet and one dry season survey. Data pooled from 3 replicate sampling stations per study plot, at the three undisturbed sites.

~5.4.5. Crustaceans

Periclimenes suvadivensis • *Microeuraphia withersi* • *Thalassina squamifera* • Oniscidae • *Potomalpheops hanleyi*

Crustaceans dominated the mangrove invertebrate fauna. Of the total of 1,609 records from undisturbed mangroves, 48.7% were crustaceans. These records included 60 species at the three study sites (Table 5-3) and comprised seven amphipods, two barnacles, forty species of crabs, three isopods, one mud lobster, five shrimp, one tanaid and one upogebiid (Tables B-1, B-4 and B-5, Appendix B).

In the following sections, firstly the species richness and abundance of all crustacean taxa will be examined. The two main taxonomic groups of crabs (family Ocypodidae

and family Grapsidae) will then be analysed; and finally, the most abundant species of crab in these two families will be dealt with.

Crustacean species richness

Crustacean diversity differed between assemblages; decreasing progressively from a mean of 6.2 (± 0.3 SE) species per sampling station in the seaward assemblage to 1.3 (± 0.2 SE) in the hinterland margin (Figure 5-46 left, Table B-18, Appendix B). Seasonal differences in crustacean species richness amongst the different assemblages were also found. Diversity of crustaceans declined in landward assemblages during the dry season and also diminished in the seaward assemblage during the wet (Figure 5-46 left). Generally there was strong similarity between transects, except for a low value for mean species richness in the tidal creek assemblage on transect two, at site E1 (Figure 46 right, Table B-18, Appendix B).

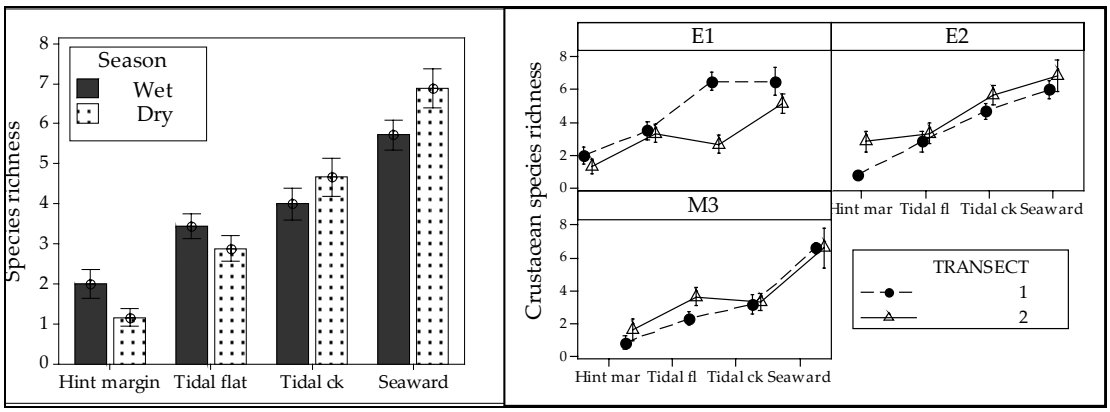


Figure 5-46: Mean crustacean species richness (±SE) in the four assemblages, pooled across the three sites during wet and dry season surveys (left) and on paired transects at each site (right).

Crustacean abundance

Crustaceans had the highest abundance of any of the faunal groups (mean 15.0 ± 1.5 per sampling station). Maximum numbers of crustaceans were recorded in the seaward assemblage (mean 32.3 ± 3.8 per station, range 6-91) and least in the hinterland margin (3.8 ± 0.7, range 0-18). This pattern was thus similar to that observed for species richness but was more pronounced. No seasonal differences were detected and abundance was not significantly different between sites (Table B-19, Appendix B). As for species richness, significant main effects for assemblage and transect were detected for

crustacean abundance ($\log_{10}(x + 1)$ transformed). The mean abundance of crustaceans increased progressively from the landward to seaward margin and was markedly higher in the seaward assemblage than in all other assemblages (Figure 5-47 left). Abundance on transect two at site E1 was lower than on transect one, contributing to the significant main effect for transect (Figure 5-47 right).

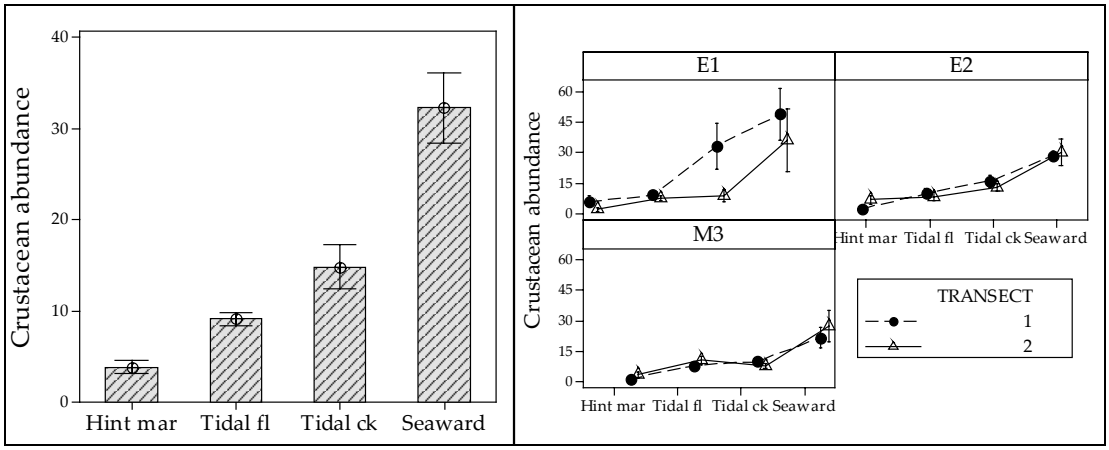


Figure 5-47: Mean crustacean abundance (±SE) in four assemblages, pooled across three sites during wet and dry seasons (left) and on paired transects at each site (right).

Multivariate analysis of the crustacean fauna indicated pronounced differences in species composition between specific habitats within mangrove forests. NMDS ordination of 48 study plots from wet and dry season surveys based on the abundance of crustacean fauna illustrated a distinct fauna occurred in each of the four assemblages sampled (Figure 5-48).

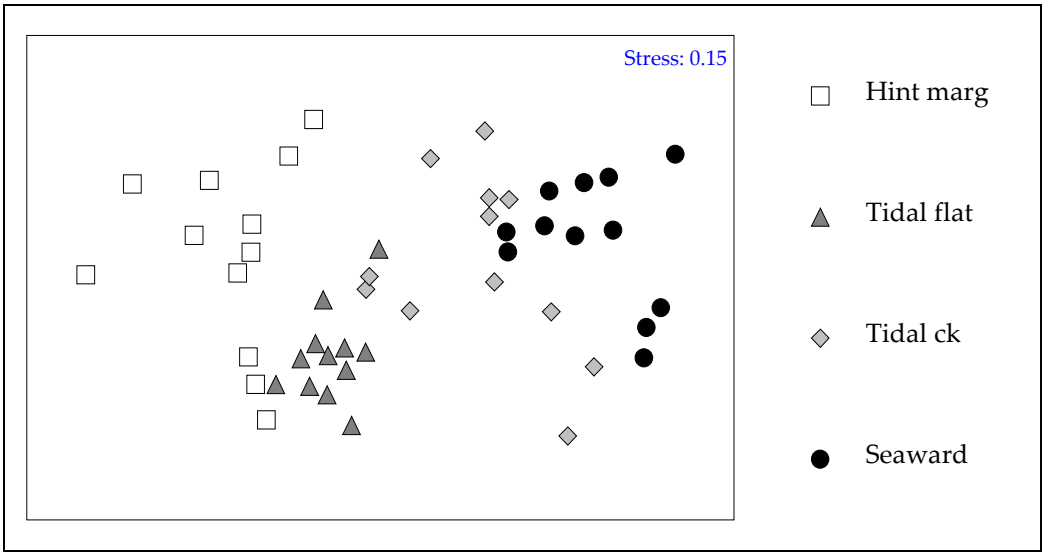


Figure 5-48: Ordination of 48 study plots in undisturbed mangroves based on the abundance of 60 crustacean species indicating assemblages from landward (left) to seaward (right). Data was pooled for each sampling technique and for three replicate sampling stations per study plot.

Crab species richness and abundance

Metapograpsus frontalis •*Uca capricornis* •*Neorynchoplax* sp. nov. •*Uca capricornis*. •*Neosarmatium meinerti*

Of the sixty species of crustacean recorded in undisturbed mangroves, 66.7% (40 species) were crabs (Tables B-1 and B-5, Appendix B). The majority of these belonged to the family Grapsidae (13 species, 11 of which were sesarmids), with Ocypocidae (9 species) and Camptandriidae (7 species) also well represented. Figures 5-49 and 5-50 are descriptive profile diagrams of the four main assemblages depicting the habitat in which the common grapsid and other crabs respectively most often occur (see Figure 2-2, Chapter 2 for delineation and description of the four assemblages shown in the profile diagram).

The most conspicuous and prolific species of crab within the mangroves were the sesarmids *Perisesarma darwinenis* and *Perisesarma semperi. P. darwinensis* was virtually restricted to the two landward habitats and *P. semperi* to the two seaward assemblages (Figure 5-49). Although the numerous, large, hooded burrows of *Neosarmatium meinerti* were characteristic of the hinterland margin, this largely nocturnal species was seldom seen, unless captured in pitfall traps. In the tidal creek and seaward assemblages, juvenile *Metapograpsus frontalis* were very common on the tree trunks while the adults—which are agile predators of mudskippers and invertebrates—were most often found in burrows at the base of trees. The small epifaunal grapsid, *Nanosesarma batavicum,* was only sampled from within hollow logs and beneath the bark of trees in the two seaward assemblages (Figure 5-49). Porcellanid crabs (e.g. *Petrolisthes krangiensis* and *P. haplodactylus)* occur as cryptofauna or epifauna in the seaward assemblages and the hermit crab *Clibanarius longitarsus* were also commonly sampled above the ground on low branches and the crooks of tree trunks.

Analyses of all crab taxa revealed differences between assemblages and crab populations varied in assemblages from wet to dry seasons (Figure 5-51, left,

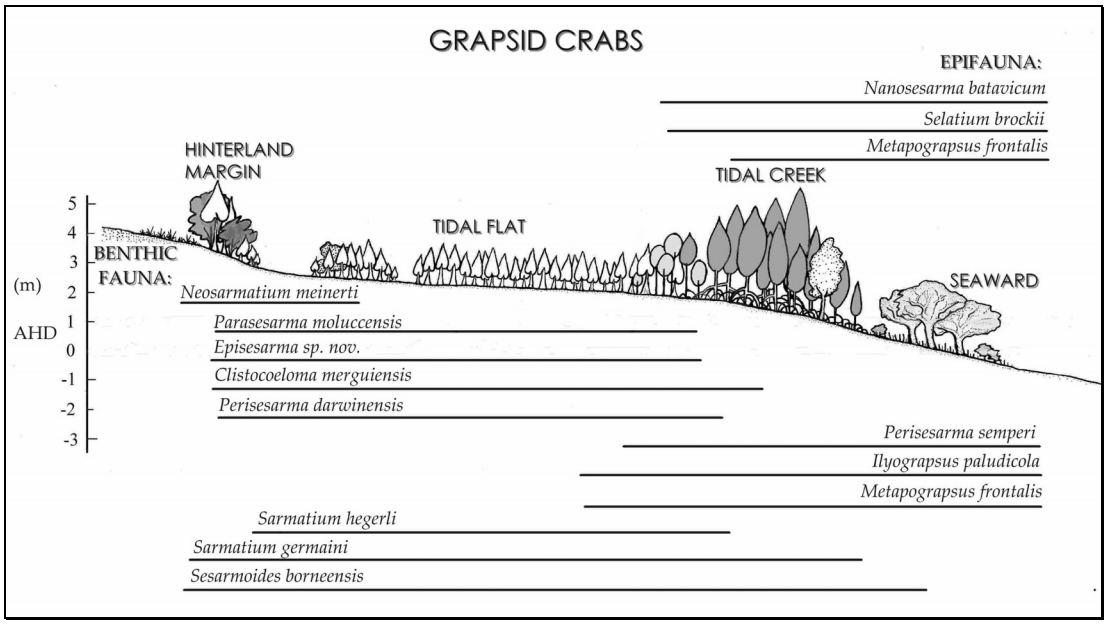


Figure 5-49: Profile diagram showing the habitats in which crabs from the family Grapsidae are most commonly found, in mangroves from landward (left) to seaward (right). Distribution data collected during wet and dry season surveys at three sites in Darwin Harbour (Table B-5, Appendix B, indicating benthic and epifaunal species.

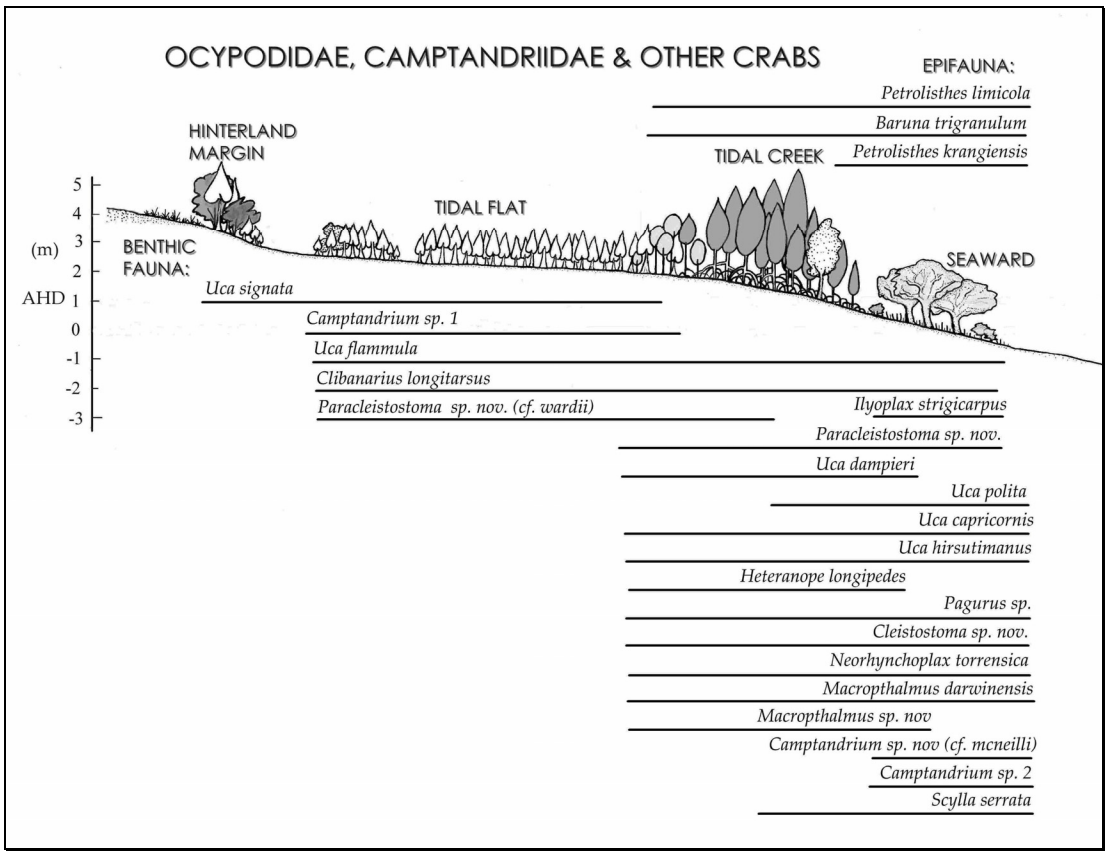


Figure 5-50: Profile diagram showing the habitats in which crabs from the Ocypodidae, Camptandriidae and other families are most commonly found, in mangroves from landward (left) to seaward (right). Distribution data collected during wet and dry season surveys at three sites in Darwin Harbour (Table B-5, Appendix B).

Table B-20 and B-21, Appendix B). Crab diversity and abundance was highest in the seaward assemblage and decreased progressively landward. The dominance of crabs amongst the crustaceans clearly contributed to the similar spatial pattern found for the crustacean fauna as a whole. In hinterland margin habitats, crab diversity and abundance was highest during the wet season. In the seaward assemblage, however, crab diversity and abundance, was lower during the wet season (Figure 5-51).

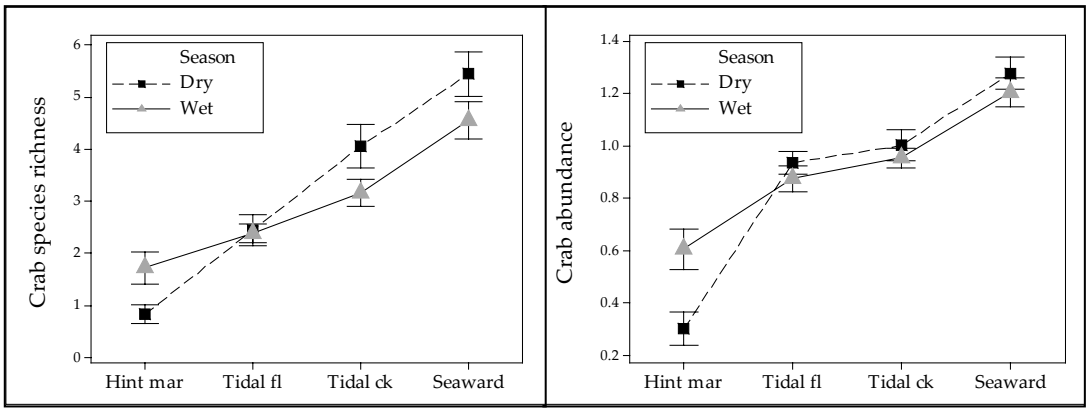


Figure 5-51: Mean crab species richness (left) and $\log_{10}(x+1)$ transformed) abundance (right) in assemblages in wet and dry seasons. Points represent means for each study plot (± SE) averaged across three sampling stations, on the two transects at three study sites.

Abundance of crabs also varied between the three study sites and significantly more crabs were recorded at site E2 than at other sites (Figure 5-52).

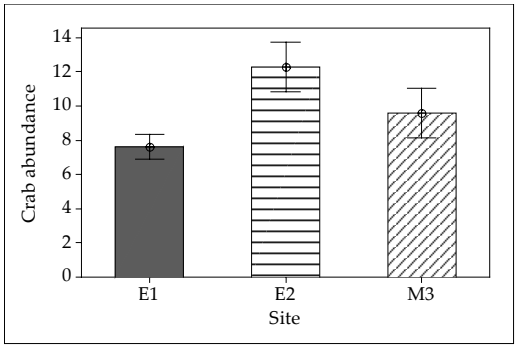


Figure 5-52: Mean abundance (± SE) of crabs at three study sites. Data pooled for four assemblages during wet and dry seasons.

Species richness and abundance of the 13 species of crabs from the Grapsidae family differed between assemblages, declining in assemblages from seaward to landward (Figure 5-53 left). Grapsid richness and abundance in assemblages also varied from wet to dry season (Figure 5-53 right, Table B-22 and B-23, Appendix B). Numbers of species and numbers of individual grapsid crabs fell during the dry season in the hinterland margin, but remained reasonably high during the wet season. An apparent reversal of

this seasonal pattern was seen in the tidal creek assemblage and seaward assemblages and little seasonal difference was observed in the tidal flat (Figure 5-53 right). Particularly high richness of grapsids was recorded from the seaward assemblages at sites E2 and M3 (Figure 5-54, Table B-22, Appendix B). The abundance of grapsid crabs exhibited a similar overall pattern to that for species richness, with populations clearly higher at sites E2 and M3, than at site E1 (Table B-23, Appendix B).

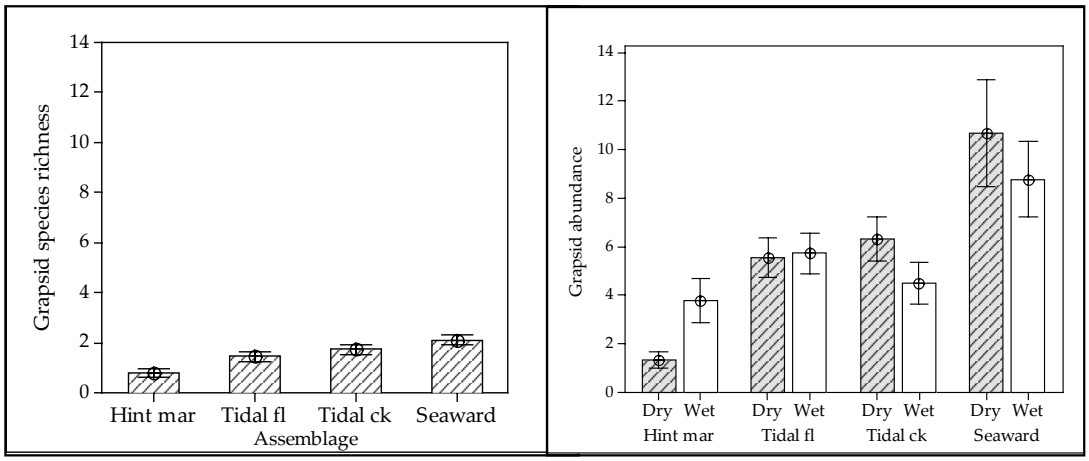


Figure 5-53: Mean species richness (± SE) of grapsid crabs averaged across three sites and two seasons (left) and raw abundance in assemblages during wet and dry seasons (right)

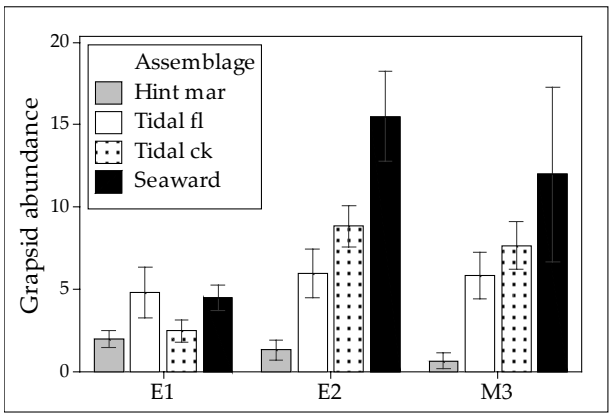


Figure 5-54: Mean abundance of grapsid crabs (± SE) in assemblages at the three study sites. Data pooled for wet and dry seasons.

Ocypodid crab species richness varied between assemblages, and diversity and abundance in assemblages varied between sites. Crabs from this family were rarely recorded in the hinterland margin assemblage, being most speciose and abundant in the seaward assemblages (Figure 5-55 left, Table B-24 and B-25, Appendix B). A season × assemblage interaction indicated elevated ocypodid abundance in the tidal flat assemblage during the dry season (Figure 5-55 right, Table B-25, Appendix B). Overall, ocypodid crabs were less numerous than the grapsid crabs, which dominated the crab

fauna. Ocypodid abundance varied amongst assemblages at the sites studied, evident by greater populations in the seaward assemblage at sites E2 and M3 than at site E1. Site E1, on the other hand, had higher ocypodid numbers in the tidal creek than found at the other two sites (Figure 5-56).

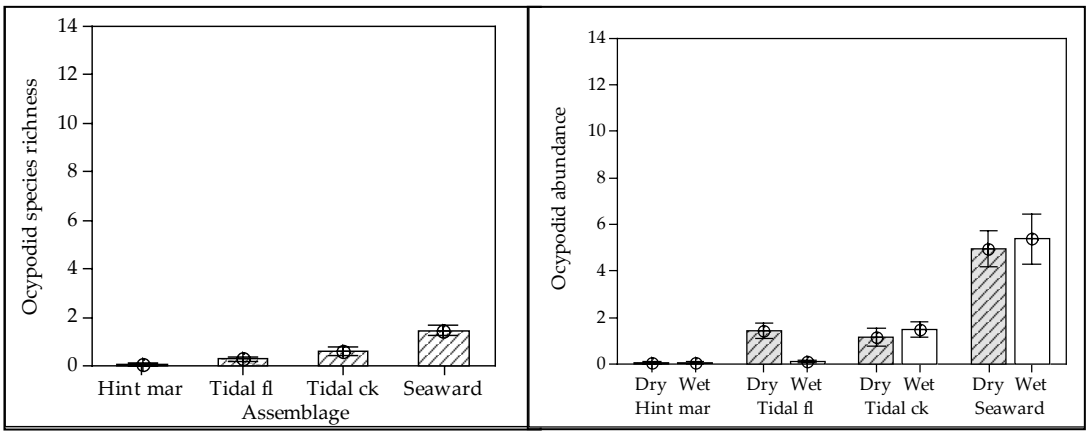


Figure 5-55: Mean species richness (±SE) of ocypodid crabs averaged across three sites and two seasons (left) and mean abundance (±SE) in assemblages during wet and dry seasons (right)

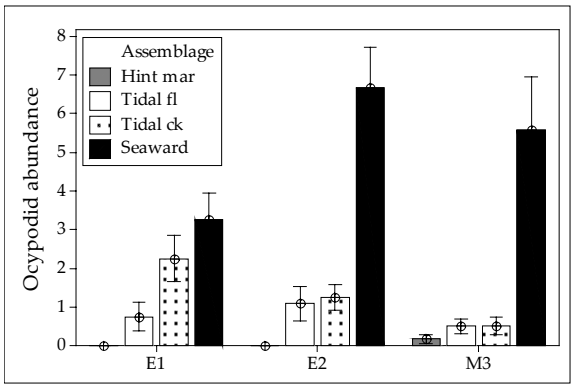


Figure 5-56: Abundance of ocypodid crabs (±SE) in assemblages at three study sited. Data pooled for wet and dry season surveys.

The abundance of the most common crab in the landward mangrove assemblages, *Perisesearma darwinensis* did not vary between the two assemblages in which it occurs, and did not differ between locations, but populations were significantly diminished in landward habitats during the dry season (Figure 5-57).

P. darwinensis was virtually restricted to the two landward assemblages (hinterland margin and tidal flat) and in the two seaward assemblages *Perisesarma semperi* was the dominant grapsid crab (Figures 5-50 and 5-58). The distribution of the two species very rarely overlapped. The abundance of *Perisesearma semperi* did not vary between seasons

or locations but mean abundance was significantly higher in the seaward assemblage than in the tidal creek (Figure 5-58 right, Table B-27, Appendix B).

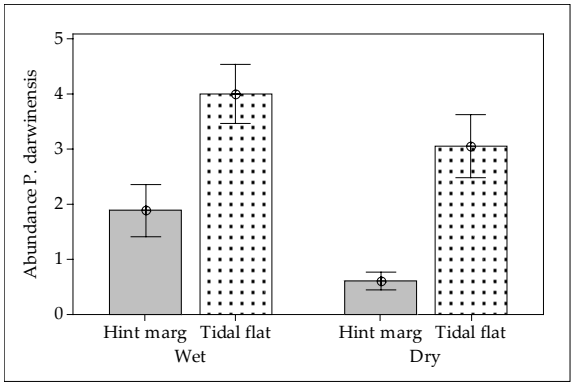


Figure 5-57: Mean abundance (±SE) of *Perisesarma darwinensis* in the two landward assemblages during wet and dry seasons.

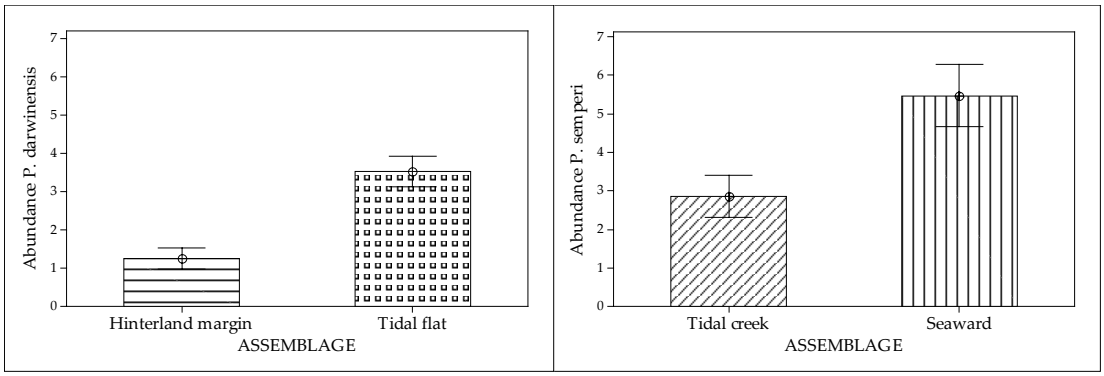


Figure 5-58: Mean abundance (± SE) of *P. darwinensis* (left) and *P. semperi* (right).Values are averaged from all sampling techniques across three sites during wet and dry seasons.

Uca hirsutimanus was one of the most common ocypodid crabs and was only recorded from the two seaward assemblages. The abundance of this species was not significantly different between seasons, locations or assemblages (Table B-28, Appendix B).

The use of burrow counts as a reliable method for estimating the field density of crabs was investigated by counting active or open burrows within each 1 m × 1 m quadrat at every sampling station, prior to quantitative sampling. A significant positive correlation (r= 0.49) was also obtained for the regression for burrow counts *vs* crab count for the seaward assemblage only—the habitat in which crabs were consistently the most numerous (Figure 5-59). A significant correlation (r=0.70, $p < 0.05$) between burrow count and total crab abundance was also obtained for the regression based on all quadrats from all assemblages (Figure 5-60). R-squared values are, however, not particularly high, indicating that burrow counts are not giving a particularly good estimate of

abundance.

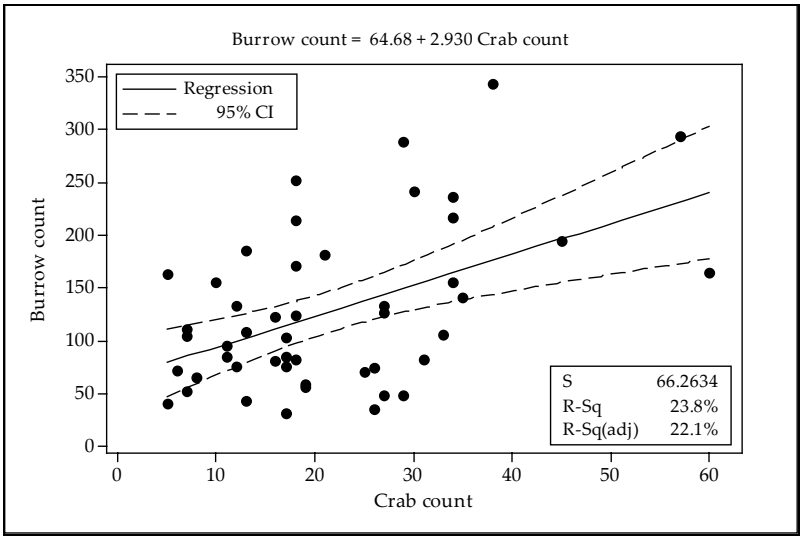


Figure 5-59: Significant correlation (r= 0.49, p,0.05) between burrow count per 1 m × 1 m quadrat and total count of crabs recorded for only the seaward assemblage, at three locations.

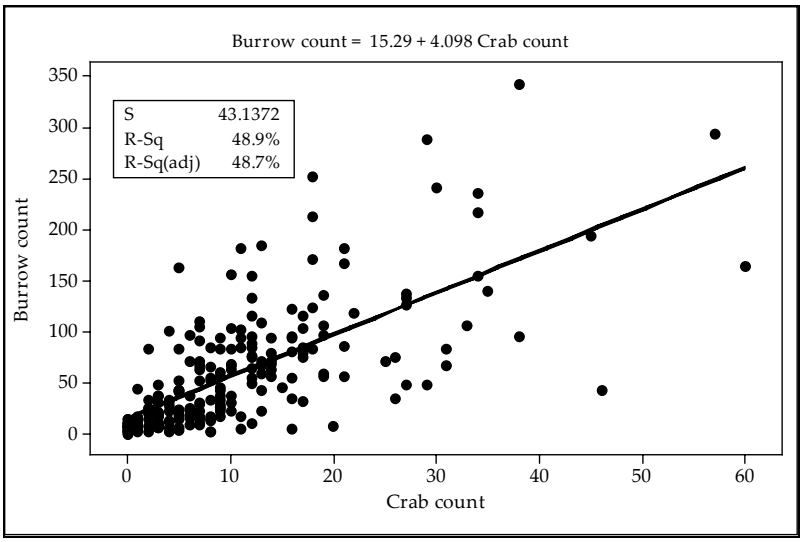


Figure 5-60: Significant correlation (r=0.70, p <0.05) between burrow count per 1m × 1m quadrat and count of crabs recorded from all assemblages at all locations.

~5.4.6. Molluscs

Of the three main macro-invertebrate groups occurring in mangroves (crustaceans, molluscs and worms), the molluscs were found to be the most diverse. Mangrove molluscs occur in a wide range of body forms, found in an extraordinary variety of microhabitats—including wood-boring bivalves living entirely within the tree trunks, to tiny ectoparasites of the abundant mudwhelks, and fist-sized bivalves buried deep within the mud. Many species construct intricately beautiful shells. In terms of

secondary production, molluscs represent a critical element of mangrove food webs (Martin, 2004) as they are fundamental elements of the diet of many vertebrate and invertebrate predators (Peterson, 1991).

A total of 60 species of mollusc was recorded from the three undisturbed sites during wet and dry season surveys conducted for this thesis in 2001 (Table B-1, Appendix B). Forty-eight species were recorded during the wet and 49 during the dry season. Of the overall total, 38 species were gastropods (univalves, class Gastropoda, Table B-6, Appendix B) and 22 species were bivalves (class Bivalvia, Table B-7, Appendix B). Two chitons (class Polyplacophora) were also recorded, one of which was a new species (family Acanthochitonidae, *Craspedoplax* sp. nov.). In the following analyses, the chitons are grouped with the gastropods, so they were not omitted from the data set. Being characteristic of hard substrates, chitons were uncommon in mangroves, but were occasionally observed on the trunks of trees. Indeed, the new species, *Craspdeoplax* sp. nov., was found attached to the shell of another large gastropod *Thais trigonus.*

Distribution of molluscs

The distribution of molluscs within mangrove habitats in the Northern Territory has not been previously documented and no studies have systematically sampled molluscs in assemblages across a mangal from the landward to the seaward margin. Figures 5-61 and 5-62 present schematic distribution and microhabitat information for the majority of bivalve and gastropod molluscs, describing the assemblages in which they are most commonly found (see Figure 2-2, Chapter 2 for delineation and description of the four assemblages shown in the profile diagram). Molluscs represented by very few records were omitted from the profile diagrams.

Molluscs of the seaward assemblage

Seven undescribed species of pulmonate slug in the genus *Onchidium* occurred throughout the mangroves and in the seaward assemblage, several *Onchidium* species were common on the mud surface, on logs, and occasionally on trees. The red bubble snail (*Haminoea* sp.) can occur in high aggregations amongst *Sonneratia alba* trees where it appears to graze microalgae from the mud surface. Also on the mud surface, small gastropods were occasionally observed in abundance, including *Cassidula* aff. *doliolum*.

In contrast with the dense populations of other *Terebralia* species in landward assemblages, *Terebralia sulcata* occurred sporadically throughout the seaward and tidal creek assemblages. The microscopic snails (*Salinator fragilis* and *Assiminea* sp) were frequently recorded on the mud surface in the seaward assemblage. *Assiminea* sp. is unusual in that it can occur across all assemblages, spanning both landward and seaward zones (Figure 5-61). This species is, however, probably a complex of cryptic, sibling (= microsympatric) species (R. Willan pers. comm.).

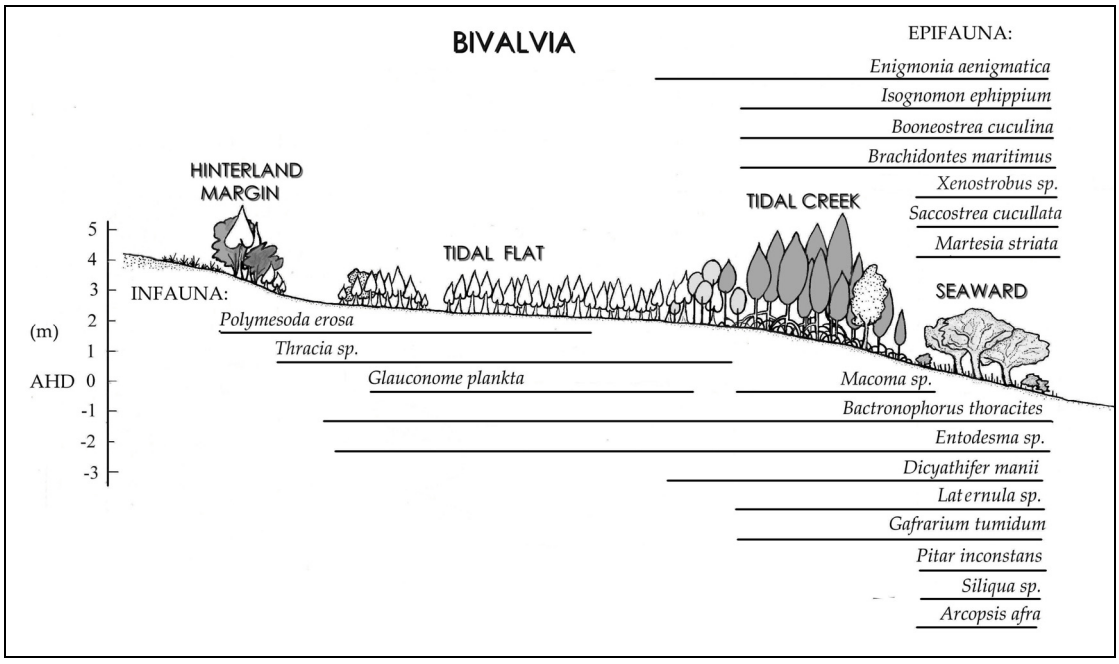


Figure 5-61: Profile diagram showing the habitat in which 19 bivalve mollusc species (of the total of 22 recorded) are most commonly found, in mangroves from landward (left) to seaward (right). Distribution data collected during wet and dry season surveys at three sites in Darwin Harbour (Table B-7, Appendix B). Uncommon and rare species are omitted.

Bivalves tend to be prolific within the relatively sparse forest and soft mud of the seaward assemblage. It is likely that several small species (e.g. *Macoma* sp., *Siliqua* sp.*)* collected with the use of the anoxic mat, may have been overlooked or damaged by other sampling techniques (e.g. mud coring and sieving). Other infaunal bivalves from the seaward assemblage included *Laternula* sp., *Pitar inconstans* and *Arcopsis afra.*

A diverse range of epifaunal bivalves were also sampled from beneath flakes of bark and from the trunks of living *Sonneratia alba* trees in the seaward assemblage. Oysters were not common, but two species (*Saccostrea cucullata, Booneostrea cuculina*) were recorded on tree trunks. The colourful Magic Jingle Shell, *Enigmonia aenigmatica,* was frequently observed on a range of surfaces including leaves, twigs and branches.

Burrowing bivalves (pholads) including *Martesia striata* were found partially buried within both living and dead trees and teredinid bivalves (commonly known as 'ship worms' or teredo 'worms') including *Dicyathifer mannii*, were generally prolific in dead trees or rotting timber. Clusters of the oyster-like *Isognomon ephippium* invariably occupied tree crevices and other sheltered microhabitats while very small mussels, *Brachydontes maritimus* and *Xenostrobus* sp., attached themselves to trees with byssal threads.

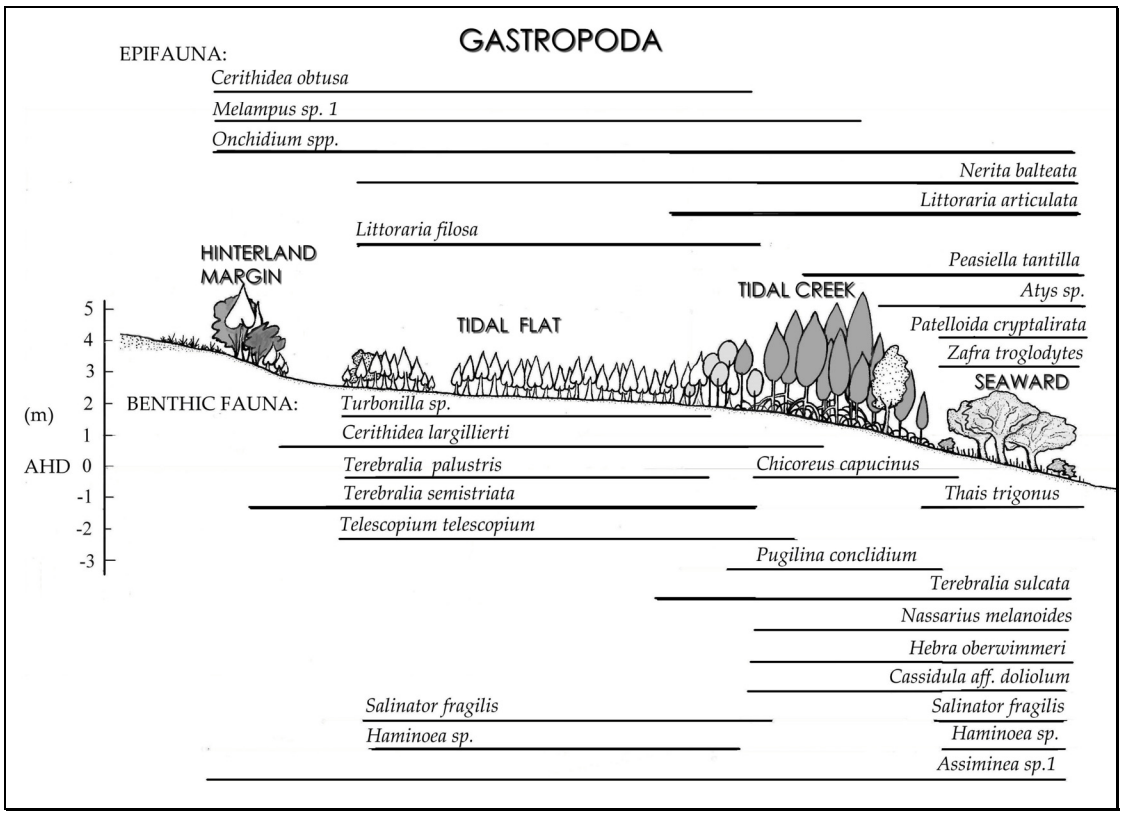


Figure 5-62: Profile diagram showing the habitat in which 27 gastropod mollusc species (of the total of 38 recorded) are most commonly found, in mangroves from landward (left) to seaward (right). Distribution data collected during wet and dry season surveys at three sites in Darwin Harbour (Table B-6, Appendix B).

Epifaunal gastropods in the seaward assemblage typically included juvenile *Nerita balteata* and the chequer-board patterned periwinkle, *Littoraria articulata.* Microscopic gastropod species such as *Atys* sp., *Peasiella tantilla* and *Patelloida cryptalirata* were most often sampled from beneath flakes of bark on *Sonneratia alba* trees.

Molluscs of the tidal creek assemblage

Despite the extensive surface area provided by the branching root systems of *Rhizophora stylosa*, these forests support a relatively sparse molluscan epifauna; particularly in

contrast with *Sonneratia alba* which provided habitat to a diverse range of species. The most characteristic mollusc species from the tidal creek assemblage were the large tree-dwelling nerite snails, *Nerita balteata.* This species is one of several mangrove gastropods which climb up trunks of trees during high tides (pers.obs.). Sparse numbers of oysters (including *Booneostrea cuculina)* and clusters of the periwinkle gastropod *Littoraria articulata* also occurred on tree trunks. The large murex *Chicoreus capucinus* was only recorded within *Rhizophora stylosa* forests, where it is a specific predator of burrowing bivalves such as *Bactinophorous thoracites* and *Dicyathifer manii* (R. Willan, pers. com.). These wood boring bivalves probably comprise the greatest biomass of any mollusc in the mangal, not only in the tidal creek, but throughout other assemblages. A large proportion of living trees in *Ceriops australis* forests appear to be hollowed by a single, large wood-boring teredinid, and senescent trees in the tidal creek and seaward assemblages are invariably riddled with vast numbers of teredinids.

Molluscs of the tidal flat assemblage

Molluscs appeared to reach their greatest diversity and abundance in the extensive tidal flat assemblage. The almost monospecific, dense stands of *Ceriops australis* provide habitat for the arboreal and epifaunal species *Littoraria filosa* and *Cerithidea obtusa,* with the former often occurring in extremely high densities amongst the foliage of the canopy. These two species were rarely found on the ground in the tidal flat, mainly foraging low in the trees when conditions were suitably moist, but during the drier months they remained quiescent in the upper canopy (see McGuinness, 1994). The families Potamididae (mud creepers) and Ellobiidae (ear snails) are well represented in the tidal flat assemblage by 3 and 5 species respectively. Potamidid species such as *Telescopium telescopium* and *Terebralia semistriata* were often very abundant on the shaded mud surface beneath the dense *Ceriops* canopy. Indeed, the high overall densities recorded for the tidal flat are, in part, due to high numbers of gastropods from the family Potamididae (Table 5-4).

Like *Nerita balteata, Cassidula angulifera* and *Cerithidea obtusa* also climb the trunks of trees during high water. During low tide, these molluscs tend to congregate around the fluted bases of *Ceriops* trees. *Nerita balteata* was not uncommon in this moist and protected niche, as were *Melampus* sp. and *Cerithidea largillierti.* Often during the wet season, the mud surface was alive with two species of gastropod; the minute *Assiminea*

sp. 1 and *Salinator fragilis.* The mounds created by the burrowing of mud lobsters (*Thalassina squamifera*) generally contained numerous smaller burrows, made by crabs and worms, which were also habitat for small molluscs (e.g. *Auriculastra subula).*

Table 5-4: Frequency of species recorded from the four main gastropod families in the four assemblages. Values are total counts of individuals at the three sites studied.

Family	Hinterland margin	Tidal flat	Tidal creek	Seaward	Total
Ellobiidae	2	22	2	12	38
Potamididae	13	70	10	9	102
Littoriniidae	-	6	6	5	17
Neritidae	2	23	28	13	66

Molluscs of the hinterland margin

The most conspicuous mollusc in this assemblage was the potamidid gastropod *Cerithidea obtusa.* During the mid-dry season *C. obtusa* retreats to the upper trunk and branches of trees and a single tree might support tens of individuals. Other small gastropods are occasionally found around the bases of trees, under bark and amongst leaf litter. The substrate in this assemblage becomes extremely dry and impenetrable for several months during the dry season when both freshwater inflow and tidal activity cease (the latter due to seasonal variation in tidal amplitude). Thus small or delicate bivalves, common in the soft muds of the seaward assemblage, are very rare or absent in this habitat. The large mud mussel *Polymesoda erosa* (up to 10 cm in width) is one of few bivalves tolerant of such conditions, and was occasionally recorded just below the mud surface in the hinterland margin. During the wet season, this assemblage often receives substantial freshwater flows, is inundated by more regular (fortnightly) tides, and the molluscs become more active in response to the more favourable conditions.

Overall, the pattern of molluscan distribution and density showed that although the species richness of molluscs increased progressively from landward to seaward, the tidal flat had the highest total abundance of molluscs (Figure 5-63). Both diversity and abundance of molluscs were least in the hinterland margin assemblage. Gastropods largely contributed to the peak in abundance observed in the tidal flat (Figure 5-64), whereas only intermediate numbers of gastropods were recorded from the two

assemblages to seaward. In contrast, the total abundance of bivalves decreased steadily from seaward to landward.

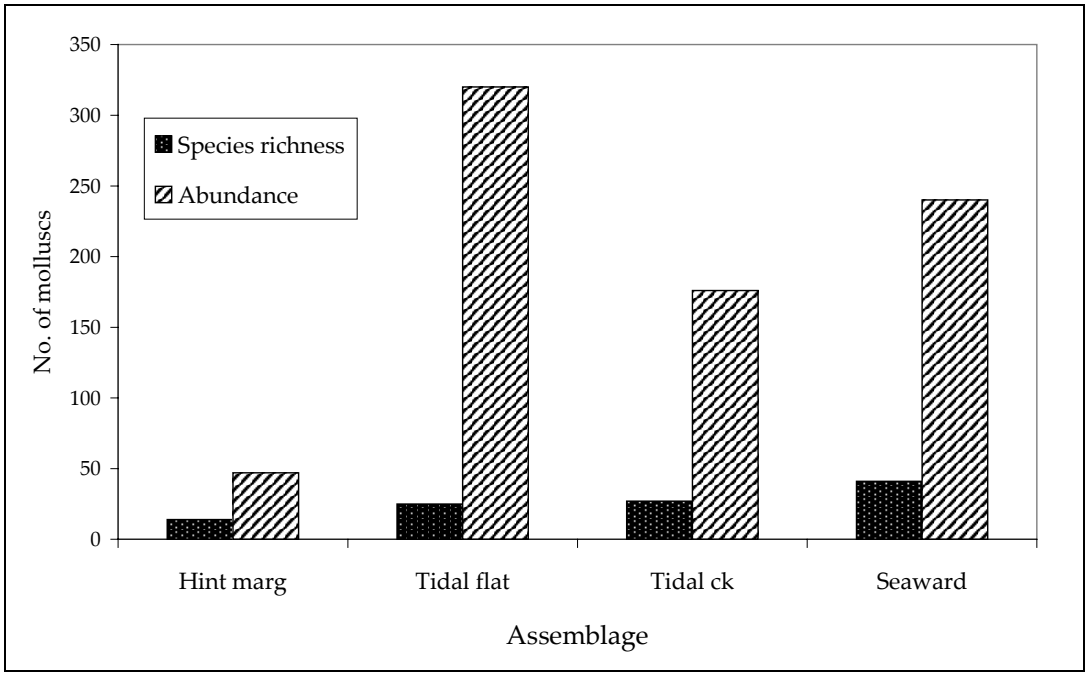


Figure 5-63: Mollusc species richness and total abundance in the four assemblages from landward (left) to seaward (right). Data pooled from wet and dry season surveys at three undisturbed sites in 2001.

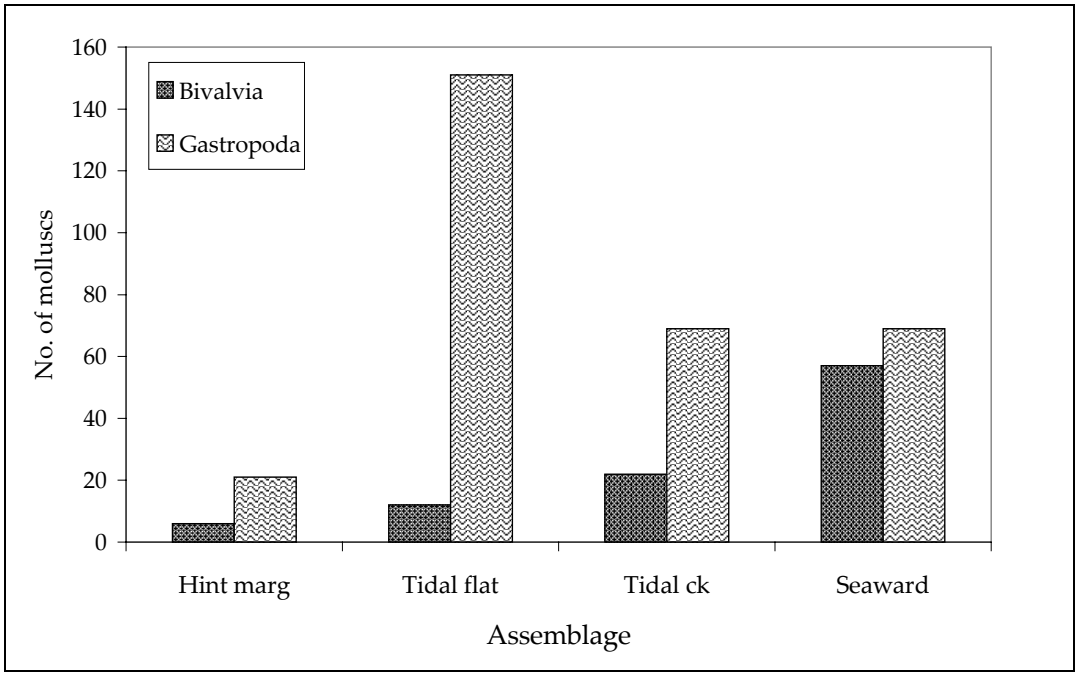


Figure 5-64: Total numbers of bivalves and gastropods recorded in assemblages at the three undisturbed sites, during wet and dry seasons in 2001.

Due to the intrinsic differences between the two classes of mollusc, these groups have been analysed separately, as follows.

Gastropods

Chicoreus capucinus • *Onchidium* sp. 6 • *Littoraria articulata* • *Nerita balteata* • *Haminoea* sp.

Gastropod species richness

Species richness of gastropods differed between sites and assemblages with significant variations in diversity evident in assemblages both from site to site, and between wet and dry seasons (Table B-29, Appendix B). Gastropod diversity was lower at Site E2 than at the other two sites and higher in the tidal flat than in other assemblages (Figure 5-65).

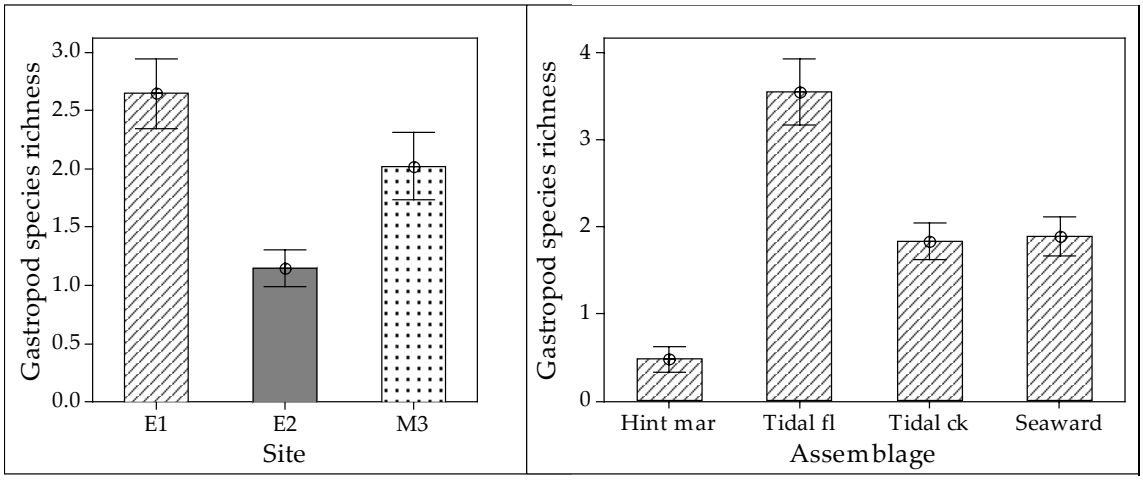


Figure 5-65: Mean gastropod species richness (±SE) per study plot at three locations and in four assemblages in undisturbed mangroves. Values averaged across wet and dry seasons using all sampling techniques at three replicate sampling stations per plot.

Seasonal variation in gastropod diversity amongst assemblages on the two transects at each location was also evident (Table B-29, Appendix B). The season × assemblage interaction was largely due to higher species richness in the tidal flat and the seaward assemblage during the dry season, while the converse was true in the adjacent tidal creek assemblage; where gastropod diversity apparently declined during the dry (Figure 5-66).

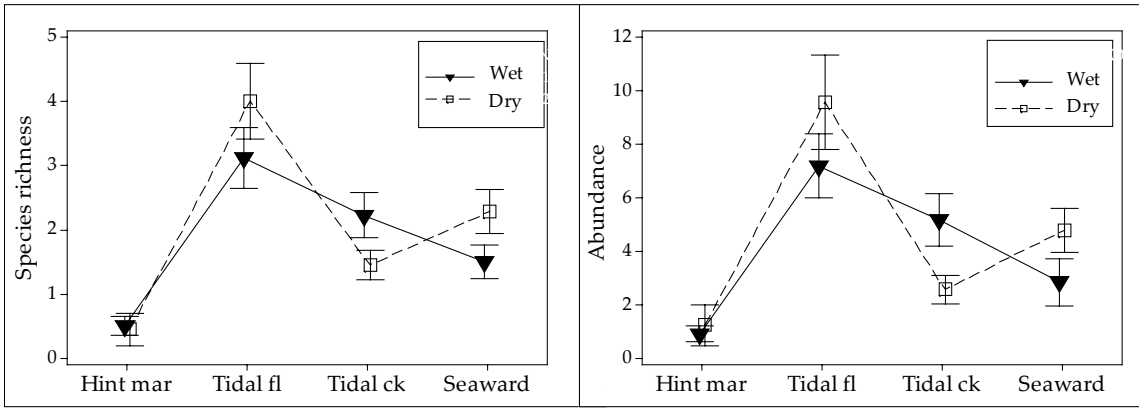


Figure 5-66: Mean gastropod species richness (± SE) per study plot (left) and gastropod abundance (right) during wet and dry seasons in the four assemblages.

Gastropod abundance

The pattern for gastropod abundance largely mirrored that for diversity, with the exception of seasonal differences in gastropod populations amongst transects (Table B-30, Appendix B). Gastropod abundance peaked in the tidal flat, while intermediate numbers were found in the tidal creek and seaward assemblages and the lowest abundance of gastropods occurred in the hinterland margin. The same seasonal pattern observed for diversity, with declines in numbers of gastropod species in the tidal flat and seaward assemblages during the wet season, was also found for gastropod abundance (Figure 5-66 right). A site × assemblage interaction was mostly due to low abundance in the tidal flat at site E2 (Figure 5-67).

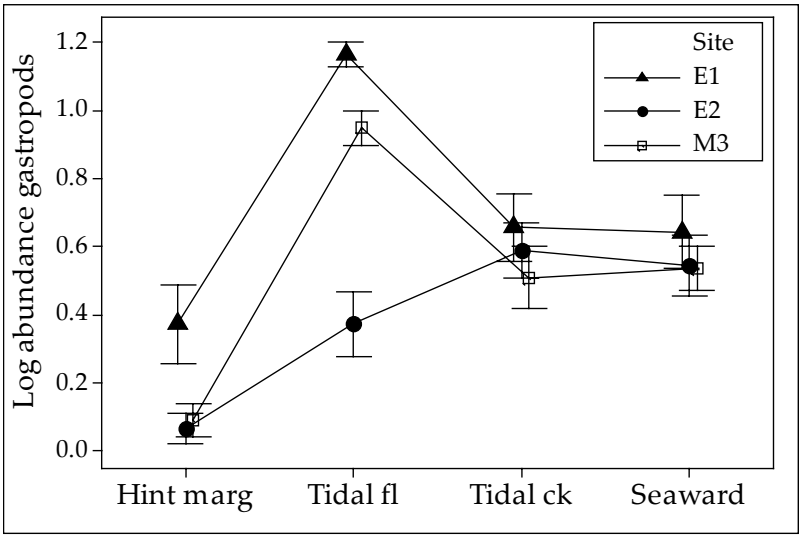


Figure 5-67: Mean abundance (±SE) of gastropods ($\log_{10}(x + 1)$ transformed) in assemblages from landward (left) to seaward (right) at the three study sites.

Ordination of the abundance of 38 gastropod mollusc species in 40 study plots (24 study

plots sampled during wet and dry season surveys, less plots in which the sum of species ≤ 1) indicated little difference in species composition and abundance between the wet and dry seasons (Figure 5-68). In contrast, the same ordination, with assemblage highlighted, indicated the strong influence of shoreline position on gastropod diversity and abundance (Figure 5-69). The plot shows the clear partitioning of the two landward assemblages (left) from the two seaward assemblages (right).

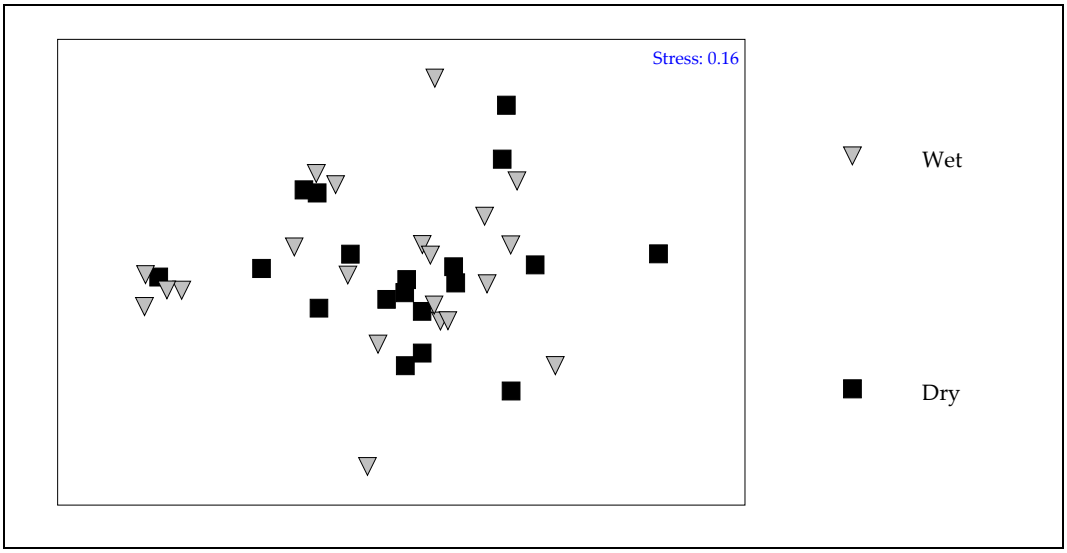


Figure 5-68: Ordination of 40 study plots based on gastropod abundance indicating wet and dry season sampling.

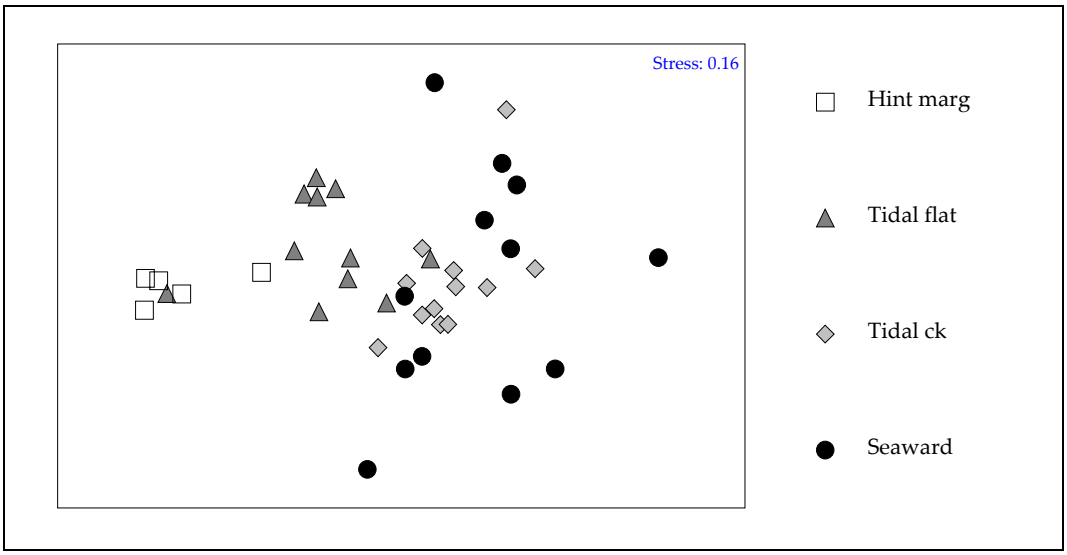


Figure 5-69: Ordination of 40 study plots based on abundance of 38 species of gastropod, indicating four assemblages, sampled in wet and dry seasons.

Bivalves

Gafrarium tumidum•Bactrinophorus thoracites•Polymesoda erosa•Brachydontes maritimus•Enigmonia aenigmatica

Bivalve molluscs were neither as speciose, nor as abundant, as gastropods at the sites studied during this survey. Bivalve diversity and abundance was appreciably higher in the seaward assemblage than in any other habitat (Figure 5-70, left; Table B-31, Appendix B). Bivalves were least populous at site M3, where the lowest numbers of individuals were recorded (Figure 5-70, right).

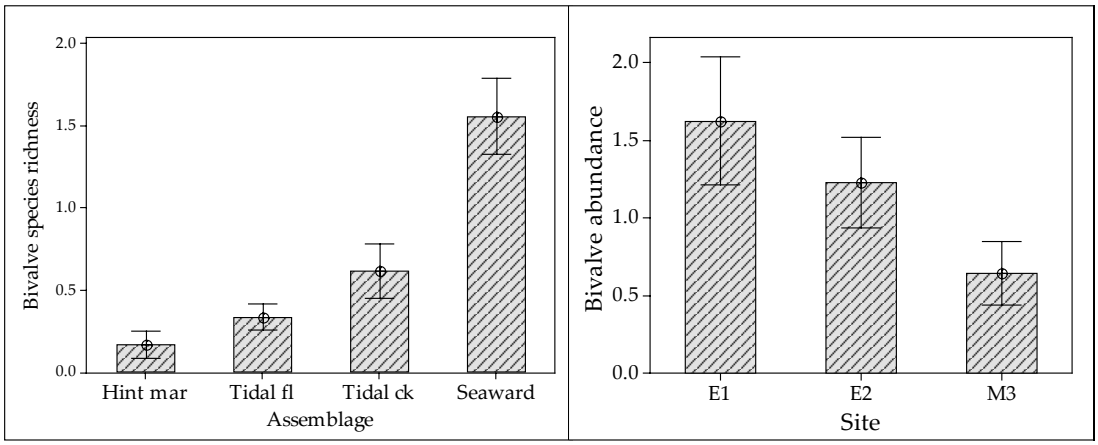


Figure 5-70: Mean species richness (±SE) of bivalve molluscs per study plot, in the four assemblages (left) and abundance at three study sites (right). Data pooled for wet and dry seasons.

Analyses also revealed significant season × assemblage and season × transect interactions for diversity, which highlighted differences in species richness of bivalves from wet to dry, in some assemblages, and seasonal variation in bivalve diversity amongst some transects, respectively. It appears that diversity of bivalves was markedly lower, during the wet season in the two assemblages to seaward (Figure 5-71, left). The season × transect interaction appears to relate to site M3 where mean species richness on transect 1 was lower during the dry than during the wet—at odds with the seasonal pattern in mean diversity (grouped across the four assemblages) observed at the other two sites (Figure 5-71, right).

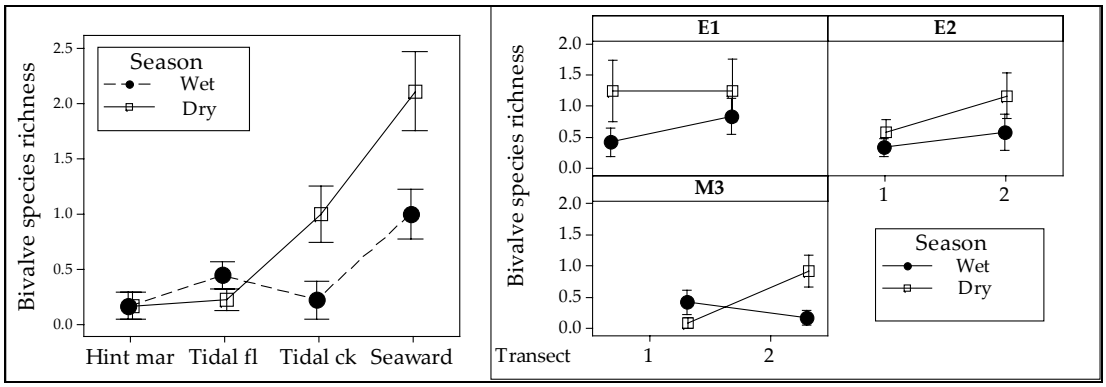


Figure 5-71: Mean species richness of bivalves (±SE) in assemblages during wet and dry seasons, averaged across three sites (left) and seasonal patterns in bivalve diversity recorded on the two transects at the three locations (right).

Ordination of 19 study plots based on the abundance of 22 bivalve species (wet and dry season data for the 24 study plots were pooled due to lack of data for either season alone), shows that the bivalve fauna in the two seaward assemblages is reasonably distinct from that of the two landward assemblages (Figure 5-72); a pattern also evident in the gastropods (Figure 5-69).

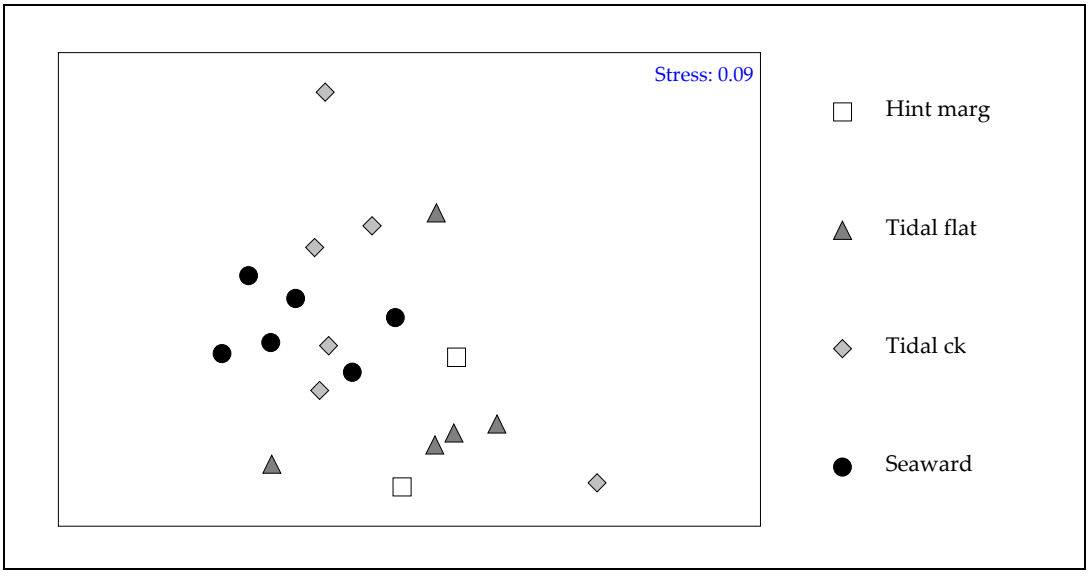


Figure 5-72: Ordination of 19 study plots based on the abundance of 22 species of bivalve mollusc. Wet and dry season surveys were grouped and each point represents data pooled for three replicate sampling stations in study plots in four assemblages.

~5.4.7. Fish

Periophthalmus argentilineatus • *Bostrychus sinensis* • *Periophthalmus sp.* • *Amoya gracilis*

A total of 12 species of small fish (ie. adult size smaller than 150 mm and generally less than 25 mm) were recorded from undisturbed mangroves during wet and dry season surveys. The fish were all resident mangal species, sampled during low tide from pitfall traps (swimming species); by hand from within mud burrows (mud-slitherers and mudskippers); from within tree hollows or fallen timber (epifauna) or from the mud surface (mudskippers). With the exception of two species—the shortkeel pipefish *Hippichthys parvicarinatus (*family Syngnathidae) and the primitive, burrow-digging *Bostrychus sinensis* (family Eleotridae)—all the fish recorded were gobies (family Gobiidae).

The most abundant fish were commonly known as mudskippers, comprising three species of the genus *Periopthalmus*, the species of which are entirely restricted to mangroves and adjacent mudflats (Murdy, 1989). Although these amphibious fish are well known and have long fascinated ichthyologists, they have been notoriously difficult to identify (Macnae, 1968b; Murdy, 1989). Since this current survey was completed however, two new species have been identified, both of which occur in Darwin Harbour mangroves (H. Larson, pers. comm.). On the basis of this revision, the fish named in this survey as *Periopthalmus* sp., *P. novaeguineaensis* and *P. argentilineatus* have largely been replaced by *Periopthalmus darwini,* a semi- terrestrial species from the lower intertidal zone and *Periopthalmus minutus,* which inhabits saltflats and landward mangrove assemblages. Unfortunately, it was not possible to retrieve and re-identify specimens that had previously been lodged with the Northern Territory Museum, as many had been placed in containers with numerous other *Periopthalmus* specimens awaiting classification.

Analyses revealed no differences in the species richness of fish between seasons or between the three locations studied, but differences were detected between the four

assemblages (Figure 5-73 left, Table B-33, Appendix B). The hinterland margin had the lowest diversity while the other assemblages had similarly high fish populations (Table 5-5). Several species were sampled only from particular assemblages, including *Amoya gracilis* (seaward), *Parioglossus palustris* (tidal creek) and *Gobiopterus* sp. (tidal flat).

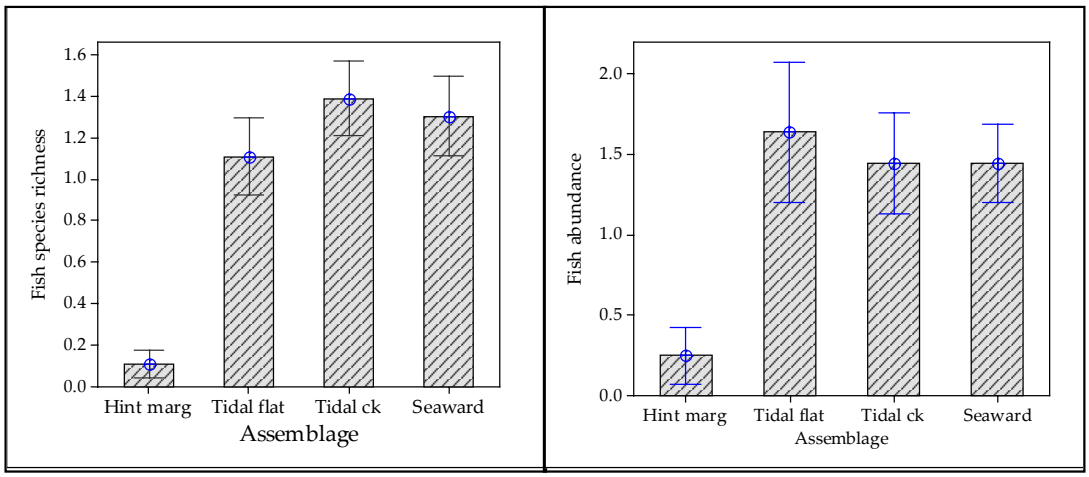


Figure 5-73: Mean species richness (left) and abundance (right) of resident fish (±SE) in study plots in four assemblages, averaged across three sites and wet and dry seasons.

Table 5-5: Distribution of resident fish species in the four assemblages. Values are total abundances pooled across three sites during wet and dry seasons.

Species	**Seaward**	**Tidal creek**	**Tidal flat**	**Hinterland margin**
Amoya gracilis	26	-	-	-
Hippichthes parvicarinatus	1	-	-	-
Amoya sp.	2	1	-	-
Pseudogobius sp. 3	2	2	-	-
Pandaka lidwilli	3	14	-	-
Periopthalmus darwini	3	1	2	-
Periopthalmus sp.	15	18	8	2
Parioglossus palustris	-	2	-	-
Bostrychus sinensis	-	1	1	-
Periopthalmus argentilineatus	-	3	6	-
Gobiopterus sp.	-	-	20	-
Mugilogobius filifer	-	10	22	1

A transect × assemblage interaction highlighted variation in species richness between transects, in several assemblages at the three sites (Figure 5-74). The differences between transects however, appeared to mainly be due to haphazard variation from place to place within the forest.

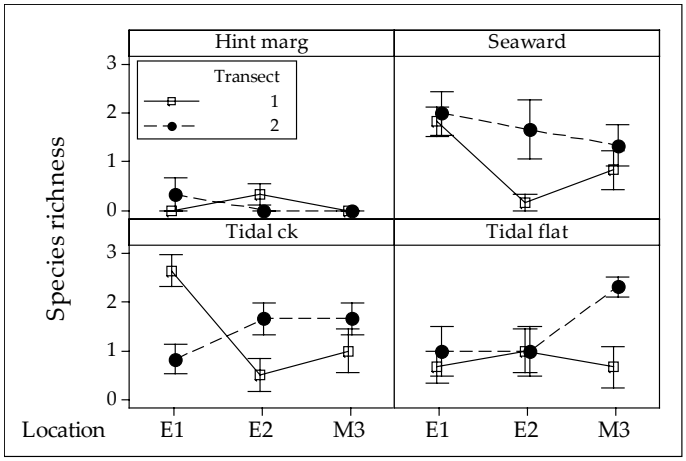


Figure 5-74: Mean species richness (±SE) of fish on two transects at each of three locations in the four assemblages. Data pooled for wet and dry season surveys.

A transect × assemblage and a season × transect × assemblage interaction for analyses of fish abundance indicated variation in the density of fish amongst transects within the different assemblages, which also varied seasonally (Table B-34, Appendix B). The results appear to reflect the random variation within sites (between transect 1 and transect 2) and the patchy distribution of the various fish microhabitats within the forest (Figure 5-75 left). Seasonal differences appear to be due mainly to the increase in mean fish abundance on some transects in the landward assemblages during the wet season, particularly at site E2 (Figure 5-75 left).

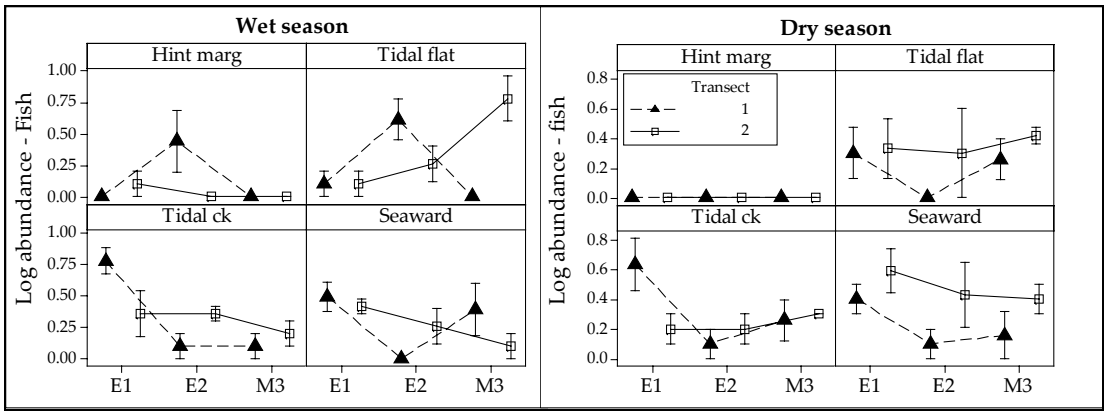


Figure 5-75: Mean abundance ($\log_{10}(x + 1)$ transformed of fish (±SE) on the two transects at three sites, in wet (left) and dry (right) seasons.

Examination of the mean abundance of fish sampled per trap type during the wet season and dry season suggests that fish entering the hinterland margin during the wet season, comprised mudskippers sampled from quadrats and swimming species trapped in pitfall traps. The numbers of swimming fish were also higher in the tidal flat during

the wet, than during the dry. In contrast, fish caught in quadrats in the seaward assemblage (mud slitherers and mudskippers) were more numerous during the dry season (Figure 5-76).

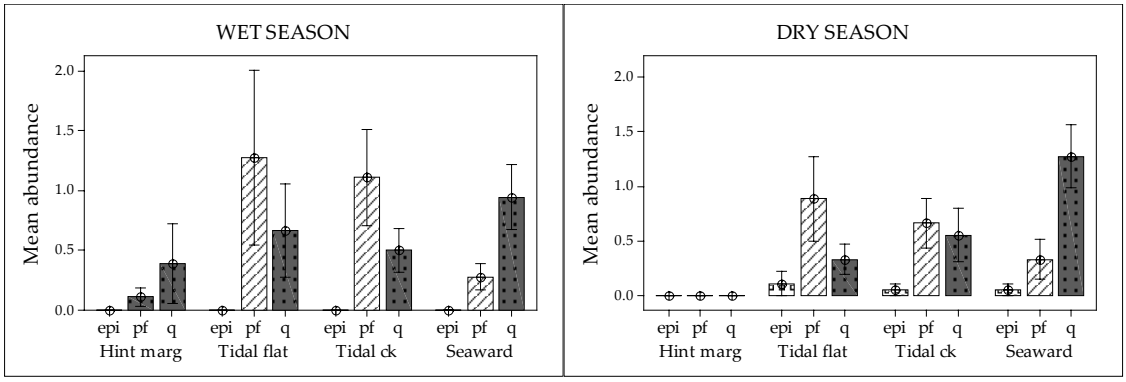


Figure 5-76: Mean abundance of fish (± SE) sampled from different trap types during wet and dry season surveys. Means were pooled for the two transects at three sites.

~5.4.8. Other invertebrate fauna

Amphibiobeania epiphylla sp. nov. • *A. epiphylla* •Unidentified sea anemone • *Amphiodia* sp.

The focus of this study was on macro-invertebrates of marine origin. Numerous species from other groups, particularly insects such as midges, flies, spiders, crickets and centipedes, were encountered, but not sampled or recorded during field surveys, due to time and logistical constraints. Aside from the major faunal groups already considered in previous sections, a small number of marine species from other faunal groups were also recorded during surveys (Table B-1, Appendix B).

Two undescribed anthozoans, including a sea anemone and a tube anemone were recorded from the seaward and tidal creek assemblages. Sea anemones were typcially found on tree trunks in lower intertidal habitats and the extensive tentacles of the tube anemone (Class Anthozoa, Order Ceriantharia) were occasionally sampled from beneath anoxic mats and within quadrats. The taxonomy of these organisms is very poorly known in tropical Australia and further taxonomic resolution was not possible.

Flat worms (Phylum Platyhelminthes, Order Turbellaria) were amongst a diverse cryptofauna sampled from within rotting logs, under bark and within the burrows of crabs. These worms, along with species from the Phylum Nemertea have been grouped with worms from the Phylum Annelida, described in Section 5.4.3. Two undescribed species of brittle star (Phylum Echinodermata: Family Amphiuridae) were also sampled from seaward habitats; one species was sampled from beneath the bark of *S. alba* and the other from the surface layer of fine silty mud in the *Rhizophora stylosa* dominated forest of the tidal creek assemblage.

An unusual bryozoan (*Amphibiobeania epiphylla* sp. nov.) that encrusts the surface of leaves, was first sampled from saplings of *Rhizophora stylosa*, in the tidal creek assemblage at Site E1. The bryozoan is unique in its markedly amphibious habit and morphology and has been described as a new genus (see Appendix D, published in *Zoological Science*, 2007).

In summary, the major findings of these invertebrate surveys are summarised in Table 5-6 which lists, for each of the main faunal groups, significant ANOVA results for the main spatial (site and assemblage) and temporal (season) factors. To clarify seasonal patterns, the table also shows the taxa in which diversity and density among assemblages changed with season (indicated by a significant season × assemblage interaction). Finally, the table indicates those groups for which mean diversity and abundance in the seaward assemblage declined during the wet season

Table 5-6: Summary table of significant ANOVA results for all invertebrate taxa.

TAXA	Season	Site	Assemblage	Season × Assemblage	Wet season decrease in seaward zone
WORMS	□ ●				□ ●
CRUSTACEANS			□ ●	□	
—CRABS		●	□ ●	□ ●	□ ●
◦ GRAPSIDS		●	□ ●	□ ●	●
◦ OCYPODIDS			□ ●	●	
BIVALVES		●	□ ●	□ ●	□
GASTROPODS		□ ●	□ ●	□ ●	□
FISH			□		
ANTS					
ALL TAXA			□ ●	□	□
NB Mean diversity = □ Mean abundance = ●					

A recent environmental monitoring program using near identical methodology to this one year study, yielded another three years of data on mangrove invertebrate fauna from Darwin Harbour, expanding further our knowledge of species diversity, abundance, spatial and temporal variation (Metcalfe, 2005). It thus provided the opportunity to test and examine further the findings of this study during six consecutive, wet and dry season surveys. In particular, this represents information of value for clarifying spatial (between assemblages) and temporal (between year and seasonal) trends that emerged in this study (Figure 5-77)

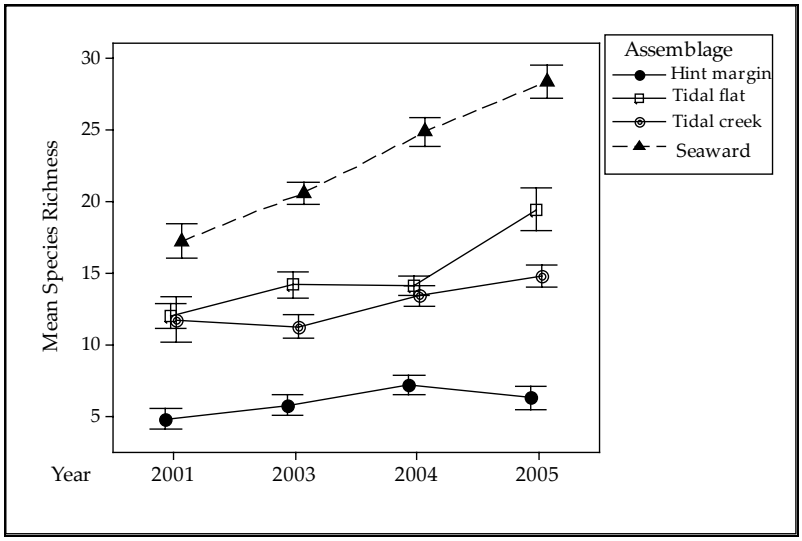


Figure 5-77: Mean invertebrate species richness (± SE) at two study sites (E1 and M3) during four years. Data from 2001 was collected during this survey and 2003 to 2005 data for a commercial monitoring program. Data for one wet and one dry season survey pooled for each year (Source: Metcalfe 2005).

5.5. Discussion

The preceding section presented the results of quantitative surveys of the species composition, abundance and dynamics of mangrove invertebrate assemblages. The following section examines and summarises these findings and where possible, draws comparisons with previous research as well as placing the Darwin Harbour results within a wider geographical context. Firstly, the development of the field methodology used to survey mangrove invertebrates, and the limitations of these techniques, is discussed (section 5.5.1) prior to discussion of the main findings on species richness and abundance in relation to tidal elevation (section 5.5.2). Secondly, the results for each of the main faunal groups (worms, molluscs, crustaceans, ants and fish) are addressed

(section 5.5.3) and seasonal patterns are discussed (section 5.5.4).

Although sites and sampling stations were well replicated in this study, there was a lack of seasonal replication. Time and logistical reasons limited surveys to one wet season and one dry season survey during 2001. Hence to occasionally clarify temporal patterns in invertebrate populations, particularly the seasonal trends suggested by the current findings, data from a three-year survey, conducted during wet and dry seasons from 2003 to 2005 (Metcalfe, 2004a, 2005), may occasionally be referred to.

~5.5.1. Assessment of mangrove invertebrate diversity and abundance

The pilot and confirmation studies developed a combined methodology for sampling mangrove biological diversity that was implemented during the main invertebrate fauna surveys. The following section discusses the formulation of the sampling methodology, prior to discussion of the main survey findings (Section 5.5.2).

Although the initial intention of this study was to develop a system for the rapid assessment of mangrove biodiversity, conversant with literature on this topic (Beattie et al., 1993), implementation of the survey methodology proved quite time consuming. Each transect (four study plots) generally took two days to sample—pitfalls and anoxic mats were left overnight—and surveys could only be conducted during spring tides; when the lower intertidal zone was exposed for several hours each day (i.e. during two weeks of every month). The first transect at each site was typically surveyed during one spring tidal cycle and the second transect, during the next spring tides, a fortnight later. Further, the work in sorting and identifying samples to species level was labour-intensive and time-consuming. Indeed, the time and expertise required to conduct biological surveys at this level of taxonomic resolution has been much debated (Warwick, 1988; James et al., 1995; Hutchings, 1999) and is often viewed as a considerable drawback.

Nevertheless, despite the time required to conduct field sampling and species identification, the methodology, with little modification, has since been applied in a commercial context for three projects in the Top End (Metcalfe, 2004b, 2004c, 2005). The methodology proved effective for environmental assessment and monitoring purposes and has the capacity to provide detailed information capable of detecting small changes

in diversity and abundance of invertebrate fauna. Both univariate and multivariate analyses have been used in the current and subsequent monitoring studies to determine and describe patterns of variation and the results are highly complementary. In accordance with previous research, multivariate analyses appear sensitive to spatial and temporal variation in the structure of invertebrate faunal assemblages (Clarke, 1993; James et al., 1995) and univariate analyses provide definitive tests for differences between means.

Several aspects of the current methodology need to be considered when comparing the results with other surveys. For instance, the consistent placing of quadrats against the nearest tree enabled comparison of epifaunal diversity and abundance between assemblages and sites. This practice meant that epifauna was well represented in these surveys and in habitats such as the seaward assemblage, where trees are widely spaced, abundance data may be somewhat inflated due to over-representation of epifauna.

The combined methodology adopted for use in this survey involved techniques (i.e. pitfall trapping) that provide an indication of invertebrate activity, but not density (Smith III et al., 1991; Salgado Kent, 2004). Density estimates, or total number of individuals per square metre can be derived solely from quadrat data, and are thus comparable with other studies, whereas the abundance values obtained per sampling station during this survey, are not. A major advantage of sampling the majority of species from quadrats, was that it largely avoided the problem of unreliable species identifications from visual estimates.

The anoxic mat technique has had limited previous application in a different scientific context—defaunation by anoxia. Large mats were used on subtidal marine substrates in studies investigating patterns in larval settlement and post-defaunation recolonisation. (Thrush et al., 1996; Beukema et al., 1999). Anoxic mats were trialed in this study after a colleague mentioned that plastic sheeting, otherwise known as the 'carpet of death', had been used to sample invertebrates on intertidal mudflats (M. Guinea, pers. com.). The technique was adapted for use in mangroves and appears to have excellent potential for wider application. I am not aware of any previous studies that have used this technique to sample infauna in mangrove habitats. Indeed, no literature on its application in studies of intertidal benthic invertebrates was found.

Infaunal invertebrates are often soft-bodied and delicate—and generally require careful handling with fine forceps. Anoxic mats avoided the use of sampling techniques that involved live capture and sieving, both of which can easily damage specimens (Peterson, 1991). Indeed, the excavation of sediment within cores or quadrats, followed by elutriation and sieving has been described as "highly intrusive and labour intensive" (Ashton et al., 2003) and is often highly impractical in mangrove habitats where dense root mats commonly occur. The anoxic mat facilitated the sampling of very delicate worms, tiny bivalves and crustaceans, which most likely would have been crushed or overlooked by mechanical sieving.

The pilot study demonstrated that anoxic mats enabled retrieval of a range of species from the substrate, including fauna not recorded from the mud cores. Sampling intensity during the pilot study was, however, greater for anoxic mats than for mud cores. During the main surveys, the technique was effective for sampling worms, a range of small crustaceans (including crabs, tanaids, upogebids, isopods, amphipods) and molluscs, but not larger crustaceans, which generally escaped by burrowing away from the mat. The anoxic mat was not effective in porous substrates—such as dry and gravelly sediments found in the hinterland margin assemblage during the dry season.

The pilot study demonstrated that sampling using anoxic mats of large area involved a number of physical difficulties; including finding a large enough space, free of holes, pneumatophores and other obstacles, in which to place the mat. Further, the time required to adequately search large areas was prohibitive. Even the smallest mat size used in the current surveys (0.05 m^2) generally took over 20 minutes to sample and larger mat sizes would also considerably increase the time required to process and identify specimens.

Invertebrates occurring in the small pools or puddles remaining in the mangroves at low tide are an important component of the resident fauna. Pitfall traps were effective in sampling this microhabitat and represented a good technique for sampling free-ranging, nocturnal and the more cryptic species, not usually sampled by other techniques. For example the rare pipefish *Hippycthes parvicarinatus,* mud crabs *Scylla serrata,* several fish (*Bostrychus sinensis, Hemigobius hoeveni, Calameana* sp. 24), shrimps (*Acetes* sp. *Potomalpheops hanleyi, Palaemon serrifer)* and two molluscs (*Hebra oberwimmeri, Melanoides tuberculatus)* were only recorded from pitfall traps in this study.

Although pitfall traps underestimate crab populations and provide inadequate estimates of density (Skilleter and Warren, 2000; Ashton et al., 2003), in the absence of a satisfactory method of estimating crab numbers, they provide consistent and convenient measure of relative abundance (McIvor and Smith III, 1995; Lee, 1998). Indeed, a recent study comparing different techniques for sampling crabs in mangroves concluded that pitfall traps were the best method for measuring relative abundance (Salgado Kent and McGuinness, 2006). Data from pitfall traps was supplementary to that from quadrats, the latter enabled crab density to be reliably estimated. One of the primary aims of the survey was to document biological diversity, and a broad range of biota (including fish, molluscs, errant polychaetes, shrimp, crabs and other crustaceans) were recorded using pitfalls. The size of fauna sampled from pitfall traps also varied from mud crabs (*Scylla serrata*) that were too large to be concealed within the pot, to tiny spider crabs less than 4 mm across the carapace.

A limitation of the current methodology was that infauna from depths greater than 5 to 10 cm were rarely recorded, unless they were observed on the mud surface during visual surveys prior to active sampling, or if they emerged in the course of quadrat sampling. Large crabs, particularly *Uca* spp., often resumed foraging activities shortly after the random placement of quadrats, but were rarely sampled during excavation, apparently retreating to the safety of deep burrows. The larger grapsid crabs and burrowing polychaetes were similarly wary and given that these taxa may occasionally occur deeper than 20 cm in some mangroves (Frith et al., 1976), these species may have been inadequately sampled during the current survey. However, an investigation of a range of sampling techniques for *Uca* crabs in the Darwin region, found that over 90% of crabs emerged from burrows during the first 10 minutes of observation (Nobbs and McGuinness, 1999). These findings suggest the majority of crabs is likely to have been detected by the current methodology. Further, the majority of mangrove infauna is generally thought to be restricted to the upper 20 cm layer of the mud (Alongi and Sasekumar, 1992), as below this, tree roots may form an almost impenetrable barrier (Hutchings and Recher, 1983; Wells, 1983). Indeed, Wells (1983) sampled to a depth of 5 cm, noting that spot-checks to deeper levels did not result in any small animals—also noting that only larger crab burrows went below the top 5 cm.

Other areas of potential bias include the sampling period; all surveys were conducted

during daylight and during the spring tidal cycle. Although the use of pitfall traps may in part, redress the lack of nocturnal surveys, there is a chance that species only active or present during neap tides may have been missed by the current sampling regime. Ashton *et al.* (2003) however, found no significant differences in the abundance, biomass and diversity of either crab or molluscan fauna sampled during spring tides compared with sampling during neap tides.

Overall, the combined approach used in this study—utilising visual estimates from scans of approximately five minutes duration; thorough quadrat sampling; epifaunal searches to 2 m; an anoxic mat; two types of bait; and a pitfall trap at each of three replicate sampling stations—appeared adequate to meet the aims of the survey. Indeed, this methodology could be readily applied to other environmental assessment and monitoring projects and has subsequently been applied, with little modification, to pre- and post-construction monitoring for two major industrial developments in Darwin Harbour during 2003-2005 (Metcalfe, 2004a, 2004b, 2005). Such studies—which span several annual and seasonal cycles—are extremely valuable in expanding our knowledge of temporal variations in invertebrate diversity and abundance (McGuinness, 2002a).

~5.5.2. Invertebrate species richness & abundance

Striking parallels are evident between the Darwin Harbour invertebrate fauna and that elsewhere in the Indo-West Pacific. Many common genera are shared, community structure is often similar and there has been a parallel speciation of common genera, where similar species in the same genus commonly occupy the same niches at different locations (see Macnae and Kalk, 1962; Macnae, 1968b; Sasekumar, 1974; Hanley, 1993; Sasekumar and Chong, 1998). Hence, the invertebrate fauna appears relatively specialised, and the similarities between mangrove faunas across the Indo-West Pacific region may indicate long-standing adaptation to this type of environment (Warner, 1969; Sasekumar, 1974).

The present study investigated spatial and seasonal variation in invertebrate diversity and abundance amongst mangrove vegetation of the upper intertidal zone. Overall, faunal assemblages reflect the intrinsic homogeneity of these environments; often characterised by extensive forests comprising only a single species of tree. However this

broad homogeneity may belie substantial variation, particularly in faunal abundance, between locations (sites) and patches (transects) of forest (Table 5-6). Indeed, the locally homogeneous nature of the forest was also indicated by previous studies on leaf litter fall in mangrove assemblages in Darwin Harbour, in which near-identical litter fall values were frequently obtained from paired litter fall traps within several metres of each other (Metcalfe, 1999). There was however, substantial variation in litterfall among similar assemblages in different locations around the harbour. A similar trend was observed in this study of secondary productivity, (i.e. consistency on the small scale but significant spatial variation on the larger scale), evident in current analyses, by the numerous interactions with transect. Furthermore, pronounced differences were invariably found in the taxonomic composition and density of fauna between the four assemblages. Indeed, of all the taxonomic groups studied, significant differences in species richness amongst the four assemblages were evident for all taxa, except ants and worms (Table 5-6).

The overall pattern for invertebrate diversity and abundance was a progressive increase from landward to seaward. The lowest invertebrate diversity and abundance was recorded in the hinterland margin, while the tidal flat and tidal creek had intermediate species richness. Species richness and abundance in the seaward assemblage was substantially higher than in all other assemblages, during both seasons. Surprisingly, the tidal flat had similar to the tidal creek assemblage—situated lower in the intertidal zone—and mean abundance of molluscs was in fact higher in the tidal flat than in all other assemblages. Indeed, it was evident from subsequent surveys in Darwin Harbour that species richness in the tidal flat may often be higher than the tidal creek (see Figure 5-77). Due to these distinctive patterns in faunal distribution, invertebrate diversity and abundance is discussed in terms of habitat or assemblage, as follows.

The seaward assemblage

The most seaward mangrove assemblage, dominated by *Sonneratia alba* was by far, the most rich and productive habitat for invertebrate fauna. Mean diversity (13.7 ± 0.7 SE) in the seaward assemblage was higher than in the other assemblages studied with a peak during the dry season (mean 16.3 ± 1.0 SE); declining substantially at all sites studied during the wet season (mean 11.1 ± 0.7 SE). Wind-generated waves and heavy rainfall during the wet season may lead to substantial erosion of the soft substrates in the

seaward zone (pers. obs.) and consequent displacement of benthic species. At low tide, small pools within this assemblage represent an important microhabitat for resident fish and crustaceans. Mangrove habitats at low tide do not, however, appear to be refuges for any fish or prawn species of commercial significance.

Tidal creek assemblage

The lower invertebrate diversity observed in the tidal creek may be due to more intense predation by marine predators (Martin, 2004). *Rhizophora stylosa* forests typically grow along regularly flushed tidal channels through which fish enter to feed at high tide. Alternatively, the lower diversity may be due, in part, to fewer suitable microhabitats. For instance, the mud in the tidal creek assemblage typically comprises a dense network of above and below ground roots, with only minor areas of bare mud suitable for burrows. In fact, due to the paucity of clear substrate in this assemblage it was generally difficult to find enough area to install pitfall traps and anoxic mats in close proximity to randomly selected sampling stations. In addition, the large surface area of the anastamosing system of *R. stylosa* prop-roots is often covered with a thick layer of short foliose algae—which appears to retard the establishment of epifaunal invertebrates. Unlike studies in South American mangroves (Cantera et al., 1999), which found that mangrove roots with algal turf supported a diverse array of invertebrates (32 species), relatively few species were sampled from amongst the algae in this study. Algae generally covered only the lower roots of *R. stylosa,* extending to a height of approximately 1 m above ground level. Alternatively, the inherent difficulties in sampling the tidal creek assemblage; may have contributed to fewer records from this assemblage. Indeed, the dense tangle of roots often assisted invertebrates to elude capture during surveys as well as consistently hindering sampling activities.

Tidal flat assemblage

Despite being higher in the intertidal zone, and receiving substantially less frequent tidal inundation, diversity was only slightly lower in the tidal flat (mean 9.1 ± 0.5) than in the tidal creek (9.5 ± 0.7). Further, mean invertebrate abundance was very similar between the two assemblages (mean tidal creek, 22.8 ±.3.0; tidal flat, 20.6 ± 1.3). The results suggest that the mid-mangrove zone, may represent more of a temporal refuge to invertebrates than say the tidal creek, which is inundated by two high tides daily.

Less frequent (daily tides, every fortnight) inundation of the tidal flat may offer protection from subtidal predators that move into these areas at high tide. In particular, the tidal flat was clearly suitable habitat for numerous juvenile gastropods and immature crabs, which appeared to be more abundant in this assemblage (pers. obs.). Concomitant research has demonstrated that a wide variety of fish enter mangroves during high tide to forage, venturing well into the two landward assemblages (Martin, 2004). Predators other than fish, including stingrays and mudcrabs were also commonly observed entering mangroves with the incoming tide (pers. obs).

Hinterland margin

The low diversity and abundance of invertebrates sampled from the hinterland margin was not unexpected, given the extreme environmental conditions and infrequent tidal inundation characteristic of this assemblage. Desiccation of coarse substrates and hypersalinity arising from dry conditions and infrequent tides would prohibit many burrowing species for example. Furthermore, prolonged freshwater inflow during the wet season could lead to osmotic shock in species unable to osmoregulate.

The strong seasonal decline in diversity in the hinterland margin is presumably associated with prolonged desiccation during the dry season; when both freshwater inflow and tidal inundation may cease for several months. Higher tidal amplitude and freshwater flows during the wet, appear to rejuvenate the hinterland margin as a habitat for invertebrates. Tidal inundation not only sustains resident invertebrate fauna, but facilitates recruitment and dispersal into landward mangroves. The large leaf-burying, grapsid crab *Neosarmatium meinerti* is perhaps the most important species in this assemblage. It is largely restricted to hinterland fringe, which is one of three highly productive mangrove habitats in terms of leaf litter production (Metcalfe, 1999), where it plays an important role in the processing of considerable quantities of leaves (McGuinness, 2002a; Salgado Kent, 2004).

Diversity and abundance of all invertebrate taxa

Overall, mangroves appear to be part of a continuum in which diversity tends to increase from the upper intertidal to the lower intertidal, and perhaps to the subtidal. Although this study did not extend beyond the seaward limit of the mangroves, Hanley

(1987) proposed that an even greater variety of taxa occurs subtidally. This claim is supported by studies at North-West Cape in Western Australia where the richest diversity of invertebrates were recorded on intertidal mudflats just seaward of the mangroves. By contrast, Hutchings (1999) and Hutchings and Recher (1983) suggested that the protection from desiccation, reduced predation and habitat diversity afforded by mangrove forests explains why diversity is "typically higher in mangroves and associated sediments than on nearby bare mudflats." Their observations are not referenced however, and may be anecdotal or based on findings from temperate mangroves. In order to investigate this in Darwin Harbour, systematic, quantitative studies of the invertebrate fauna of the extensive intertidal mudflats, in front of the mangroves, are a clear priority for future research.

Sampling over three more years for a recent environmental monitoring program (Metcalfe, 2005) increased the tally of species to 332, including two new species of false spider crabs (Family Hymenosomatidae). Increased sampling, spanning four years did not however, greatly alter the percentage of the total fauna each group represented; molluscs remain the most diverse faunal group (Table 5-7).

Table 5-7 : Total species richness and percentage of total fauna represented by each faunal group recorded during Darwin Harbour fauna surveys using the current methodology. Totals for PhD research include species from disturbed and undisturbed sites, pilot and confirmation studies in wet and dry seasons. Mangrove monitoring data includes wet and dry season surveys at six sites over three years.

TAXA	This study 2000-2001* *includes disturbed sites	Mangrove Monitoring Program 2003-05	TOTAL No. SPECIES (all surveys)
MOLLUSCA	82 (32.2%)	74 (26.0%)	95 (28.6%)
WORMS	51 (20.1%)	68 (23.9%)	75 (22.6%)
ANTS	32 (12.6%)	36 (12.6%)	44 (13.3%)
CRUSTACEA	69 (27.2%)	80 (28%)	85 (25.6%)
FISH	16 (6.3%)	22 (7.7%)	27 (8.1%)
OTHER SPECIES	4 (1.6%)	5 (1.8%)	6 (1.8%)
TOTAL	254	285	332
Survey duration & no. of records	1 year (2,993 records)	3 years (6,512 records)	4 years (8,754 records)

Inevitably, the data for species richness is an underestimate of the total diversity of macro-invertebrates utilising mangroves, as it comprises only the groups selectively sampled by this methodology, and those species remaining in the mangroves at low

tide. An unknown number of invertebrates, not sampled by these surveys, move in and out of mangroves during high tides. The majority of penaeid prawns for example, and some portunids or swimming crabs are pelagic and utilise mangrove habitats in this way. Nevertheless, the baseline data obtained during this study of near-pristine mangroves in Darwin Harbour represents a sound basis for future monitoring studies and may be of value for future research, environmental assessment and management projects.

In the context of other intertidal habitats, mangrove infaunal densities appear to be relatively low (Alongi and Sasekumar, 1992). The highest abundances are generally recorded not from mangroves, but from adjacent intertidal mudflats (Wells, 1983; Kurian, 1984; Cantera et al., 1999). Indeed, Wells (1983) noted 61% of the total biomass for a macro-tidal bay in NW Australia was contained in bare mudflats of the lower intertidal zone and suggested that—based on their high secondary production—mudflats must play a critical role in the estuarine food web. Investigation of the reasons for a seemingly sparse mangrove fauna lies beyond the scope of this study, but comparisons of mangrove invertebrate faunas in other estuarine systems throughout the world revealed mixed results (Table 5-8). Other studies have noted strong faunal zonation and the diversity and abundance of infaunal macro-invertebrates varies widely in relation to tidal elevation (Table 5-8). Similar gradients in species richness and density have been documented elsewhere but patterns vary markedly with latitude, climate and degree of anthropogenic disturbance. The lack of a consistent pattern is perhaps not surprising, given the wide variation in physical and climatic factors between regions and at different tidal elevations on mangrove shores.

Nonetheless, invertebrate faunal diversity recorded during this survey is considerably higher than that recorded from mangrove habitats elsewhere in the Indo-Pacific region (Table 5-8). The results imply the considerable significance of the biologically diverse mangroves of Darwin Harbour in both the regional and global contexts. A total of 208 species were recorded during the pilot, confirmation and main surveys of undisturbed mangroves in 2000 and 2001; excluding ants, a total of 183 species was derived from this work. With subsequent sampling in the harbour over another three years, many more species were found, and the tally of mangrove invertebrates (excluding ants) was brought to 290 species (Table 5-8).

Table 5-8: Species richness and densities of macro-benthic invertebrates in mangrove habitats from the Indo-West Pacific region (adapted from Alongi and Sasekumar, 1992). Values are totals or means (± SD)

Location	Habitat/ Assemblage	Species richness	Mean abundance (individuals/m^2)	Reference
Surin Island, Thailand	Low intertidal Mid intertidal High intertidal	5 8 34	4 10 28	Frith *et al.*, 1976
Phuket Island, Thailand	Low intertidal Mid intertidal High intertidal	26 92 60	80 ± 28 218 ± 34 129 ± 65	Frith *et al.*, 1977
Northwest Cape, N.W. Australia	Rhizophora forest Avicennia forest High tidal flat	31 59 5	473 ± 319 257 ± 390 1 ± 3	Wells, 1983
Cochin estuary, India	Low intertidal	N A	5,872 (pre-monsoon) 420 (monsoon)	Kurain, 1984
Kw Yao Yai, Thailand	Low intertidal Mid intertidal High intertidal	43 55 70	49 107 142-178	Nateewathana and Tantichodock, 1984
Missionary Bay, N.E. Australia	Mid- intertidal	1-7 1-3 19-31	2.1 (epifauna) 89 (infauna) 62 (cryptofauna)	Cragg, Robertson & Sasekumar, unpublished
Darwin Harbour, North Australia	Low intertidal (*S. alba*) Low intertidal (*R. stylosa*) Mid –intertidal High-intertidal	115 96 69 52	43.2* 22.8* 20.6* 5.7*	This study, 2001
* Denotes mean per sampling station not per m^2				

In both the regional and global contexts, the total of 290 species is high, but few other studies have had equivalent sampling effort—most surveys are of only one to two years duration and rarely span both seasons and all assemblages. Two previous surveys in Darwin Harbour mangroves recorded 133 taxa, including insects and 2 gobies (Hanley, 1993) and 93 taxa, including resident fish (Burke, 1992). Intertidal habitats at North-West Cape yielded a total of 163 invertebrates, but this tally also included 112 species from the species rich mudflats beyond the mangroves (Wells, 1983).

Comprehensive surveys of mangroves in equatorial South America comprising epifaunal and infaunal sampling over several years resulted in 70 species including 18 gastropods, 15 bivalves, 15 crabs, 6 caridean shrimps and 7 fish (Cantera et al., 1999). Other studies, limited to crabs and molluscs, documented 129 species from far north Queensland (Hutchings and Recher, 1982) and 75 species from Sarawak (Ashton *et al*.

2003). The total of 75 identified mollusc and crab species documented from Sarawak (Ashton and Macintosh, 2002; Ashton et al., 2003) was considered high compared with other studies of mangrove macrofauna in South-East Asia. Their species tally is, however, considerably lower than the 105 crab and mollusc species recorded from undisturbed sites in Darwin Harbour during this survey. Their study was of limited scope, however, and they acknowledged that the study plots sampled were not representative of the whole Sematan mangrove ecosystem (Ashton et al., 2003).

Aside from Hanley (1993) and Burke (1992) few studies of all mangrove invertebrates have been done in the Northern Territory, and there are no comparable quantitative surveys of fauna in all assemblages, making it difficult to place these results in a local context. Most information arises from Western Australia or Queensland and often relates to one specific component of the fauna such as molluscs (e.g. Wells and Slack-Smith, 1981; Wells, 1986; Wells, 1986). Hence, the main findings of this research and those of other previous studies are considered under the headings of the main faunal groups.

Mangrove polychaetes and other worm taxa

Mangrove worm faunas have seldom been recognised as an integral part of the macroinvertebrate fauna and they have often been neglected in invertebrate faunal surveys (e.g. Berry, 1963; Wells, 1984; Ashton and Macintosh, 2002; Ashton et al., 2003). Worms have been omitted from recent volumes on mangrove biology (e.g. Hogarth, 1999; Kathiresan and Bingham, 2001) and until recently, their pivotal role in the trophic dynamics of estuaries around the world was not widely understood (Sarkar et al., 2005). This neglect may have been perpetuated by the misconception that mangrove environments do not generally support rich worm faunas (Milward, 1982; Hanley, 1985) as well as inherent sampling difficulties and taxonomic challenges. Thus the high diversity and densities of these organisms in mangroves and other intertidal habitats has been poorly documented—particularly in comparison with other taxonomic groups such as the crustaceans. Recent research is gradually redressing this situation and the ecological importance of the worm fauna of mangroves is becoming increasingly recognised.

Polychaetes in some mangroves may comprise the dominant proportion of the

invertebrate biomass (Kumar, 1995; Sheridan, 1997) and they represent a critical link between organic material at the base of the food web and a variety of secondary consumers (Bailey-Brock, 1995; Dittmann, 2001). Polychaetes comprise part of the diet of a wide range of macro-invertebrates, fish and wading birds. Their collective burrowing and foraging activities oxygenate, condition and enrich mangrove substrates (Kumar, 2003) and in systems polluted by excessive nutrients, such as in many estuaries in India, polychaetes are profuse re-cyclers of organic matter, and their populations may reach phenomenal densities of 100,000 m^{-2} (Hsieh, 1995). Although poorly studied, the mangrove worm fauna is clearly a very important component of mangrove biodiversity and ecosystem function.

Diversity and abundance of mangrove worms

Worms were the third most diverse (and abundant) faunal group in the mangroves of Darwin Harbour. Along with crustaceans and molluscs, the worms were one of the dominant faunal groups with a total of 31 species recorded from undisturbed mangroves. In general, the worm fauna of mangrove habitats is dominated by polychaetes (Phylum Annelida, Class Polychaeta) (Hutchings and Recher, 1982, 1983; Hutchings, 1997, 1999; Kumar, 2003) although in some rare instances, oligochaetes may dominate the macrobenthic fauna (Schrijvers et al., 1995). In this study, polychaetes comprised 80% of the worm fauna from three undisturbed sites and 89% of worms from six monitoring sites, sampled over three years, in Darwin Harbour (Metcalfe and Glasby, in press). Similar to mangrove habitats elsewhere, three polychaete families—Nereididae, Capitellidae and Spionidae—were dominant (Hutchings and Recher, 1983) accounting for 41.5% of all records in this survey. Although nemertean worms (proboscis or ribbon worms) were also quite abundant, their taxonomy is not sufficiently advanced to readily distinguish species, so data for this worm phylum was pooled (Nemertea spp.). Relatively few sipunculids, echiurans and turbellarians, and no oligochaetes, were recorded during the one-year survey for this thesis.

Previous information on mangrove polychaetes is scant, with only 60 species listed for Australian mangroves in 1982 (Hutchings and Recher, 1982) and knowledge of the worm fauna of Darwin Harbour mangroves is only just emerging. For instance in 1987, worms belonging to the phyla Echiura, Platyhelminthes and Nemertea had not been recorded and the harbour's mangrove habitats were considered species poor (Hanley,

1985). By 1993 however, 33 polychaete taxa (including 25 undescribed species) had been recorded from the tidal creek and seaward mangrove assemblages (Hanley, 1987). Prior to the current surveys, no detailed systematic surveys of mangrove worms and no quantitative assessments of worms within the main mangrove assemblages had been attempted.

In all, a total of 31 species was recorded from undisturbed habitats; 51 species were recorded from both undisturbed and disturbed habitats (see chapter 6); and the species tally increased to 75 species with the addition of the three years of sampling at monitoring sites (Table 5-7). Clearly, the apparently sparse worm fauna was due to a lack of survey effort. Surveys conducted elsewhere report wide variation in mangrove worm diversity and densities. Mangrove invertebrate studies in Thailand (Frith et al., 1976) report 32 species (22 polychaetes, 1 platyhelminthes, 6 nemerteans, 3 sipunculids) but only four polychaetes were sampled from Selangor in Malaysia (Sasekumar, 1974) and eight species (6 polychaetes, 1 nemertean, 1 sipunculid) from Matang in Malaysia (Sasekumar and Chong, 1998). In temperate regions, 46 polychaetes (including 21 identified to species level) were collected from Careel Bay in New South Wales (Hutchings and Recher, 1974), while Hsieh (1995) documented 9 polychaete species from mangroves in Taiwan. A recent review (Kumar, 2003) listed a total of 87 polychaetes from India, Thailand, Malaysia and Japan, noting that India was a 'hotspot' for polychaete diversity with 62 species. Direct comparisons among studies are difficult however, owing to variations in sampling methodologies (Alfaro, 2006), taxonomic expertise and regional differences. The high diversity of mangroves worms (75 species) from all Darwin Harbour studies may reflect the large extent and habitat diversity of the mangroves, but could also be the result of more intensive sampling effort, spanning wet and dry seasons over several years.

Ideas based on the findings of mangrove studies in temperate regions combined with a lack of systematic surveys in the past, contributed to the misconception that polychaetes were restricted to the seaward margin of the mangroves, or to habitats with permanent water (Hutchings and Recher, 1983; Hanley, 1993). More recent studies (Cantera et al., 1999), including the current Darwin Harbour surveys (Metcalfe and Glasby, in press) and existing data from equatorial regions (Frith et al., 1976) have shown that polychaetes occur throughout low, mid- and high-intertidal mangrove assemblages—

albeit with reduced diversity and abundance in landward habitats. In the landward assemblages of Darwin Harbour, the worm fauna was cryptic and seldom sampled during the dry season, but a relatively discrete group of species was revealed by sampling during seasonally wet conditions (see Appendix, Appendix C). Seasonal patterns in worm abundance are discussed in section 5.4.

Overall, however, it appears that a distinctive polychaete fauna in mangroves is lacking—most species occurring at similar heights on the shore in other habitats. Furthermore, most polychaetes recorded in Darwin Harbour are widely distributed throughout the Indo-Pacific region—only seven species appear restricted to the mangroves of Darwin Harbour, and this needs corroboration from ongoing taxonomic studies (Metcalfe and Glasby, in press).

Worm feeding guilds

Surface deposit feeders (10 species) and herbivores (8) were predominant among the worms of undisturbed mangroves, and filter feeders were the only guild not well represented (1 species). The abundance of sub-surface deposit feeders differed significantly between assemblages, presumably in response to seasonality and marked variations in soil moisture, texture and organic content with tidal elevation (Alongi and Sasekumar, 1992) and from wet to dry seasons. Overall, herbivores were the most numerous, with carnivores, sub-surface deposit feeders, surface deposit feeders and filter feeders in decreasing order of abundance. The observed partitioning of species amongst these families and within these feeding guilds appears to reflect the high primary productivity and sedimentary characteristics of mangrove habitats. For instance, nereidid worms—the most abundant polychaetes comprising 29% of all records in this study—were all herbivorous or surface deposit feeders. The diet of nereids is known to include fine plant detritus of mangrove leaf origin, algae and tiny crustaceans (Odum and Heald, 1972) and their diversity and abundance in the mangroves of Darwin Harbour is indicative of the characteristically high organic detrital content of these systems (Hsieh, 1995). Further, such observations substantiate the importance of polychaetes as re-cyclers of mangrove litter and as pivotal links in trophic pathways (Kumar, 2003; Sarkar et al., 2005).

Crustacean diversity and abundance

Crab diversity and distribution

Although mangrove faunal assemblages comprise many phyla, the decapod crabs are almost always the dominant group (Alongi and Sasekumar, 1992). Of the 60 species of crustacean recorded in this survey 42 were decapod crabs (Table B-1, Appendix B) and two families, the Grapsidae and the Ocypodidae contained the majority of mangrove crab species (Jones, 1984; Davie, 1993; Tan and Ng, 1994). Davie (1985) recorded 60 species of crab associated with mangroves in NW Australia, listing 56 species from the Northern Territory. Recent research in Sarawak, Malaysia reported 31 crab species in near pristine mangroves (Ashton et al., 2003) and 46 brachyuran crabs from the Pichavaram mangroves in India (Ravichandran, 2006). Lee (1998) suggested the global centre of diversity of mangrove crabs was the Malaysian peninsular where Tan and Ng (1994) listed 76 mangal species, including 44 sesarmines. Thus, in the context of the Indo-West Pacific, the mangrove habitats of Darwin Harbour are clearly a rich habitat for crabs.

Crabs are the best known, taxonomically (e.g. Jones, 1984; Davie, 1994; Frusher et al., 1994; Tan and Ng, 1994) and the most studied of the mangrove invertebrate groups (Roberston, 1986; Wilson, 1989; Smith III et al., 1991; Lee, 1999). This is not surprising, given how conspicuous, ubiquitous and relatively straightforward they are to study. Consequently studies have been conducted describing the significant role of crabs in the transfer of energy between mangroves and forest sediments (Roberston and Daniel, 1989; Smith III et al., 1991; Lee, 1998; Nordhaus, 2006), the effects of their burrowing on forest productivity (Smith III et al., 1991), soil texture and chemistry including the prevention anaerobic or toxic conditions (Alongi and Sasekumar, 1992; Kristensen, 2006). Crabs are also important competitors and consumers that can influence the structure of forests by seed predation (Smith III, 1987c; Smith III, 1988; McGuinness, 1997; Salgado Kent, 2004).

Although crabs from 11 different families were recorded in Darwin Harbour; only Grapsidae, Ocypodidae and Camptandriidae were both abundant and speciose, comprising 13, 10 and 7 species respectively. Indeed, ocypodids and sesarmines (family Grapsidae; subfamily Sesarminae) comprise the dominant taxa in the majority of

mangrove environments worldwide (Lee, 1998; Kristensen, 2006), including the mangroves of Malaysia and Singapore (Macintosh, 1984; Tan and Ng, 1994), Jamaica (Warner, 1969), north-east Australia (Roberston, 1991; Smith III et al., 1991). Mozambique (Macnae and Kalk, 1962), Africa (Macnae, 1963) and the Arabian Gulf (Al-Khayat and Jones, 1999; Apel and Turkay, 1999). In mangroves in the Caribbean region however, the sesarmine crab fauna is poorly developed (McIvor and Smith III, 1995) but a diverse ocypodid fauna has largely filled this niche (Jones, 1984) .

The general pattern of crab distribution in Darwin Harbour (Figures 5-49 and 5-50) suggests that although grapsid crabs are found throughout the mangrove, predation pressure may pose some limitations on diversity in lower intertidal assemblages: grapsids were more speciose (8 spp) in landward habitats than seaward habitats (6 spp). Furthermore, the sesarmines in particular, which are voracious consumers of mangrove litter, congregate where leaves accumulate in the less frequently flushed, landward assemblages. Crabs of the genus *Neosarmatium* are primarily herbivorous and are among the largest mangrove sesarmines (Davie, 1992) and along with *Perisesarma* sp. are responsible for consuming a large percentage of the annual leaf fall (Roberston, 1991; Salgado Kent, 2004). Indeed, in tropical Australia, over 70% of annual leaf litter was consumed by grapsids in the hinterland margin zone (Roberston and Daniel, 1989). The same intertidal gradient—in which the importance of litter consumption by crabs increases with height above low tide mark—was also observed in Malaysia (Leh and Sasekumar (1985) as cited in Roberston and Daniel, 1989). Leaf litter is consumed by sesarmines, either directly, or after leaves pulled into their burrows have decomposed (Kristensen, 2006).

The other crab families, particularly the Ocypodids, are relatively rare in landward assemblages (2 species) and better adapted to the conditions in seaward habitats (8 species) where they consume microrganisms including microalgae from the mud surface. Differences in feeding preferences, osmoregulatory ability and tolerance of terrestrial conditions may, to some extent, have contributed to the striking affinity of the crab fauna to particular mangrove assemblages observed in this survey. Several other studies have also reported this same pattern of distribution with grapsids to landward and ocypodids to seaward (Warner, 1969; Machiwa and Hallberg, 1995). Others have noted strong faunal zonation of mangrove crab fauna (Frusher et al., 1994) and the

striking parallels between the fauna of intertidal zones in other parts of the world (Macnae and Kalk, 1962; Warner, 1969; Jones, 1984). The structure of crab communities in pristine mangroves of Sarawak in Malaysia, was found to be correlated with topographic elevation and surface water salinity (Ashton et al., 2003). However, the factors underlying distinct zonation patterns in grapsid crabs in studies conducted in North Queensland were complex, in the latter study, neither pore-water salinity, nor osmoregulatory ability adequately explained patterns of crab distribution, though sediment characteristics were important in determining crab abundance (Frusher et al., 1994).

Crab abundance

Crab abundance was significantly influenced by shoreline position and by season, although seasonal effects were dependent on assemblage. Other important factors influencing crab abundance may include substrate type, soil moisture and salinity, and spatial and temporal patterns in larval recruitment (Macnae, 1968b; Jones, 1984; Frusher et al., 1994; Machiwa and Hallberg, 1995). The overall mean density of crabs in mangrove habitats of Darwin Harbour from surveys for this thesis was 9.8 ± 0.7 SE crabs m^{-2}. For comparative purposes, the mean was based solely on quadrat data, and excluded crabs sampled epifaunally. The mean abundance of 16.1 ± 0.7 SE crabs per sampling station, obtained from the 3 year monitoring study, is perhaps more representative of crab populations in Darwin Harbour.

There is clearly considerable variation in the abundance of mangrove crabs between species, assemblages and locations. Jones (1984) lists density estimates for individual mangrove crab species which range from 0.06 m^{-2} for *Ucides cordatus* in the landward fringe in Puerto Rico to 84 crabs m^{-2} for *Ilyoplax obliqua* in the *Rhizophora* zone in Malaysia. A mean density of 18.8 individuals m^{-2} (± 23.2 SD, ± 4.49 SE) can be derived from the 28 mean values listed (Jones, 1984). In Darwin Harbour, much of the recorded crab abundance can be attributed to a few, very common species. *Perisesarma darwinensis* and *P. semperi* for example, dominated the crab fauna of Darwin Harbour, representing 35.2% of all records during the one-year survey and 22.7% of the three-year study. Similarly, Ashton *et al*. (2003) found *Perisesarma eumope* contributed the greatest biomass of any crab in the tropical mangroves of Sarawak.

Due to intrinsic differences between the two main groups of crabs (grapsids and ocypodids) the response of each group to seasonality is considered separately, and data from the three year monitoring program (Metcalfe, 2005) is used to examine possible trends found in this study. Ocypodids showed little seasonal variation in diversity and abundance in the seaward assemblages during the one year survey but were more numerous in the tidal flat in the dry (1.4 ± 0.3 SE) than in the wet season (0.1 ± 0.1 SE). The rise in abundance was due to a mid-year increase in the population of *Uca signata* in this assemblage. Fiddler crabs (genus *Uca*) feed by filtering surface sediments with specialised feeding apparatus and each species tends to be specifically adapted to a particular sediment type and substrate particle size (Icely and Jones, 1977; Frith and Brunenmeister, 1980). It is suggested that the seasonal influx of terriginous sediment (associated with freshwater flooding during the monsoon) may deposit a fine veneer of sediment across landward mangrove assemblages, which may favour the proliferation of *U. signata* in the tidal flat during the subsequent dry season. An alternative explanation, which could have the same effect, is that tidally transported sediment of marine origin may gradually accumulate across the tidal flat during the dry season. Either process could result in a build up of fine silt or sand in the mid-tidal zone that might trigger an increase in *U. signata* abundance. Further work is needed to distinguish among such alternative explanations and to investigate the factors influencing the abundance of *Uca* in the tidal flat assemblage.

The three year study demonstrated a similar seasonal pattern in ocypodid abundance to that found in this study (Metcalfe, 2005). Overall, no consistent patterns were observed in the seaward assemblages but a sharp increase in dry season ocypodid abundance was sometimes observed in the tidal flat assemblage. Unlike the grapsids, ocypodids were rarely recorded in the hinterland margin assemblage, in either season.

Abundance of grapsid crabs during the one year study for this thesis was highest in the seaward assemblage during the dry (10.7 ± 2.2 SE) and somewhat lower during the wet (mean 8.8 ± 1.6 SE). Examination of data for grapsid diversity and abundance over three years however, indicates no consistent seasonal pattern (Metcalfe, 2005). Grapsid populations in the two seaward assemblages during 2003-2005 tended to increase more often during the wet season, than they decreased. This pattern was more pronounced in the abundance of grapsid crabs in the landward assemblages. Conditions in the

hinterland margin during the dry season are relatively inhospitable for most crabs and the marked decrease in grapsid abundance during the dry is a clear reflection of this. Furthermore, during the wet season, with its higher tides and freshwater runoff, the hinterland margin is more favourable for crab activity. Indeed, Salgado Kent (2004) found consumption of mangrove litter by grapsid crabs increased during the wet season. In both the one year and three-year Darwin Harbour studies report the lowest density of grapsid crabs from the hinterland margin during the dry (mean of 0.8 m^{-2} ± 0.3 SE in 2001, mean 0.9 m^{-2} ± 0.3 SE during 2003-2005). Consideration of the results of both the one year survey and the three-year study indicated that the only consistent seasonal pattern for grapsid crabs was the dry season decline and wet season increase in abundance in the hinterland margin.

The decline in apparent abundance of crabs in the hinterland margin during the dry season presumably reflects reduced activity during unfavourable periods. Most crabs require a source of water and many intertidal species burrow to the water table (Warner, 1969). Large, strongly built species such as *Neosarmatium meinerti* are well adapted to dig deep burrows through relatively hard ground on the terrestrial edge. Nevertheless, desiccation during the dry season appears to restrict their activity on the surface, such that they are most active only after infrequent high tides (pers. obs.). Overall, the above comparisons emphasise the importance of conducting long term studies to interpret seasonal trends. The seasonal differences observed for crabs—but not for other crustaceans—are most obvious in marginal habitats where environmental fluctuations are greatest. Seasonal variation in edaphic conditions (e.g. desiccation during the dry season) is likely to have a far greater impact on semi-terrestrial crabs, than on other, more marine crustaceans, such as shrimp and isopods.

Diversity and abundance of other crustaceans

After the crabs, palaemonid shrimps were the most diverse and abundant of the other crustacean groups sampled from within the mangal (7 species) but these did not include any species of known commercial importance (e.g. *Penaeis merguiensis*). The most abundant shrimp in the seaward assemblage was *Periclimenes suvadivensis* while in the tidal creek *Leandrites celebensis* was numerically dominant. Palaemonid shrimps also dominate the shrimp fauna of some mangroves in the Philippines (Rönnbäck et al., 1999) comprising 53% of the shrimp catch. In general however, penaied prawns are

most often reported from tidal inlets and channels within mangrove habitats; as in Malaysia where eight of the nine species were penaeid prawns (Chong et al., 1990). The apparent dominance of penaeid prawns in mangrove systems on Australia's east coast may largely be a reflection of the sampling techniques used in previous surveys (e.g.Vance et al., 1996), which have focussed on tidal channels and creeks. Tidal channels were not sampled in the Darwin Harbour surveys, and one penaeid prawn species was abundant in shallow pools (*Metapenaeus insolitus).* The pistol shrimp (*Alphaeus* sp.) was common within unconsolidated mud of the same habitat but the majority of shrimps were tiny palaemonid species that inhabit the surface mud layer or shallow water.

Species richness of shrimps in Darwin Harbour was similar to that found elsewhere. Nine species were recorded in mangrove habitats in Selangor, Malaysia (Chong et al., 1990) and 12 from Alligator Creek in Queensland (Robertson and Duke, 1987). Also like mangrove shrimp populations elsewhere, populations are characterised by low species richness but high standing stock (Chong et al., 1990).

In general, shrimp make extensive use of mangrove habitats, vagile species actively swimming considerable distances (up to 90 m or more) through mangroves at high tide (Vance et al., 1996; Rönnbäck et al., 1999). Small shrimp were recorded in all mangrove assemblages of this survey, although diversity and abundance declined sharply to landward. Shrimp are a very important component of the mangrove food chain (Rönnbäck et al., 1999) as well as adjacent estuarine habitats (Vance et al., 1996; Blaber, 1997). A number of other crustaceans, such as amphipods for instance, are also important components of the food chain; some of which may occur in very high densities in landward assemblages where they play a major role in the breakdown of mangrove leaves to detritus (Lee, 1997).

Tidal elevation or shoreline position strongly influenced crustacean diversity and abundance, which exhibited a marked increase from landward to seaward. A wide range of forms contributed to the diversity of crustaceans in the two seaward zones. These included for example, epifaunal species on the trunks of *Sonneratia alba* trees such as isopods (*Ligia australiensis),* barnacles (*Microeuraphia withersi)* and several species of undescribed amphipods in the families Corophiidae and Talitridae. Amongst the *S. alba* trees, tanaids, upogebiids and isopods were occasionally sampled from the fine surface

layer of unconsolidated sediment. In the tidal creek assemblage sloppy surface sediments were also primary habitat for the pistol shrimp *Alpheus* sp. and other small palaemonid and sergestid shrimps. In landward assemblages, the mud surface is often covered with the mounds of mud excavated from the burrows of the cryptic mud lobster, *Thalassina squamifera.* Although seldom seen, this species is obviously very common and its burrowing activities, which turn over huge amounts of mud (Bennett, 1968; Jones and Morgan, 2002), must have a major impact on sedimentary processes in the landward assemblages. Indeed, the soft mud of the numerous mud lobster mounds is an important microhabitat for other burrowing invertebrates including crabs, polychaetes and molluscs (Hanley, 1993).

Collectively, the crustaceans comprised 65% of all records for marine animals in this survey and were dominant in each of the four assemblages. Crustaceans are often considered the most ecologically important of the mangrove invertebrates mainly due to the feeding and burrowing qualities of crabs (Smith III et al., 1991; Lee, 1998) but other taxa are clearly also important functional components of mangrove ecosystems.

Mollusc diversity and abundance

The mollusc fauna of mangrove habitats in Darwin Harbour was numerically dominated by four families: Potamididae, Neritidae, Ellobiidae and Littorinidae. Combined with the Cerithiidae, these gastropod families, dominate mangrove environments worldwide (Macnae, 1968a). In Darwin Harbour, the most speciose families were found to be the Ellobiidae (8 species), Potamididae (7 species) and Onchiidae (6 species), although the latter comprise six as yet undescribed species. These gastropods form part of a highly diverse, tropical, shallow-water marine faunal assemblage comprising over 754 species of molluscs (Wells, 1990). The mollusc fauna of northern Australia is very closely related to that of the Indo-West Pacific, with over 92% of known species also found in Indonesia and New Guinea, with only 8% endemic to Northern Australia (Wells, 1990).

Previous reviews have tallied the mollusc species from mangrove habitats elsewhere in Australia. Saenger et al. (1978) listed 95 molluscs from within Australian mangroves, but this total was soon revised to 176 by Hutchings and Recher (1982) including 16 species from South Australia, 24 from Victoria, 33 from New South Wales and 57 from Northern

Queensland. Undoubtedly, these totals are now dated, and most certainly underestimates, but nonetheless they indicate the general trend toward increasing species diversity from southern to northern Australia. The molluscan fauna from the two Darwin Harbour surveys, yielded 95 species (see Table 5-7); which exceeds the total recorded for mangroves elsewhere in Australia.

The two data sets examined in this chapter indicate that molluscs were the most diverse faunal group in the mangroves of Darwin Harbour. The molluscan fauna of shallow-water habitats in Northern Australia has a very close affinity with that of Indonesia and New Guinea, and although located further south, is thought to be equally as diverse as the traditional faunistic centre of diversity in the Indo-West Pacific. Indeed, the total of 82 molluscs recorded during this survey of mangrove forests of Darwin Harbour—which increased to 95 species when both data sets are considered, and 112 species in total (R. Willan pers. comm.)—exceeds the species richness documented for mangrove habitats elsewhere, both in the literature and from other studies within Australia.

Gastropods dominate the mangrove fauna, and like bivalves, exhibit a steady increase in species richness from landward to seaward. Peak abundance of gastropods was recorded within the tidal flat assemblage, attributed largely to high densities of potamidid mudwhelks and arboreal littorinids. This pattern of abundance was peculiar to gastropods, however, and consistent with the majority of other taxonomic groups studied, the highest diversity and abundance of bivalves occurred in the seaward assemblage. A relatively diverse range of burrowing and epifaunal bivalves were sampled from amongst *S. alba* forests and to a lesser extent *R. stylosa*. By contrast, the majority of previous studies—typically employing traditional mud sampling and sieving techniques—have reported an almost complete absence of infaunal taxa from mangrove habitats.

A comprehensive checklist of molluscs from the marine and intertidal habitats of Port Darwin lists 112 species from mangrove habitats (R. Willan, pers.com.). This list, however, draws on data from a wider geographical area (i.e. Port Darwin, which includes Shoal Bay) and includes the fauna from mangroves occurring on rocky and sandy substrates. It should be noted that a comprehensive study of molluscs in the diverse and extensive mangroves of North Queensland would likely reveal a mollusc fauna of equivalent or of greater species richness, given the high rainfall and floristic

diversity of this region.

Some of the most comprehensive studies on mangrove molluscs in tropical Australia have been conducted on the north-western coast of Western Australia (Wells, 1981; Wells and Slack-Smith, 1981; Wells, 1983, 1984; Wells, 1986c; Wells, 1990). The majority of work was done in the Bay of Rest, near North West Cape, an area with a more arid climate than Darwin, which is reflected by the pattern of intertidal vegetation. In the absence of substantial seasonal freshwater inflows, the hinterland margin assemblage is absent there; being replaced by a bare, saline backflat. *S. alba* is also absent from the seaward zone in the Bay of Rest and *A. marina* forests occur both on the seaward fringe and on the mid-tidal flat, whereas in Darwin Harbour, the tidal flat is most often dominated by *C. australis*. Within the two main mangrove assemblages, *Avicennia* forests were found to have the highest species richness, density and biomass, with substantially lower values recorded for *Rhizophora* forests. Wells (1984) recorded a total of 21 mollusc species (mean density, 13.9 m^{-2}; biomass 3,012 mg m^{-2}) from *Avicennia* forests, whereas 7 species (density, 1.8 m^{-2}; biomass 324 mg m^{-2}) were found in *Rhizophora*. It is not clear, however, at what tidal elevation Wells placed his *Avicennia* study plots; specifically, if they were situated to landward, or seaward, of the *Rhizophora* zone.

If it is assumed that the *Ceriops*-dominated tidal flat in Darwin Harbour, which also contains *A. marina* is the equivalent assemblage to the *Avicennia* forests sampled by Wells —i.e. located at a similar tidal elevation—a similar pattern in mollusc density was also found in Darwin Harbour. Tidal flat forests (24 species, density 10.8 m^{-2}) in Darwin Harbour had markedly higher mollusc abundance than the *Rhizophora*–dominated tidal creek (27 species, 6.8 m^{-2}). Density values in this study were calculated from quadrat data including epifaunal counts to a height of 2m.

Similar to the findings of the current (Darwin Harbour) study, Wells found the molluscs of the *Rhizophora* assemblage were dominated by the adult *Nerita balteata* which was common on the lower tree trunks and prop roots. Interestingly, both in Darwin Harbour and the Bay of Rest, the juveniles of *N. balteata* were, however, relatively rare in *Rhizophora* forests, but common under the bark of *S. alba* in the seaward assemblage (Wells, 1983). Another similarity was that the high biomass and abundance of molluscs in the mid-tidal flat was due almost entirely to high densities of *Terebralia* species (Wells, 1980, 1983). *Terebralia sulcata* and *T. palustris* co-occur in the Bay of Rest and may reach

densities of up to 100 m $^{-2}$ (Wells, 1980). In the Darwin region, *Terebralia semistriata* occurs in the same niche occupied by *T. sulcata* in Western Australia, where it may be locally abundant in the tidal flat assemblage. Although biomass was not measured during this survey, an estimate of maximum biomass can be inferred just from the extremely high abundance of large, potamidid gastropods in the *Ceriops*-dominated tidal flat (see Table 5-4) and as such, this assemblage represents a rich habitat in terms of secondary production.

In Darwin Harbour, the only taxonomic group in which abundance in the tidal flat exceeded that in the seaward assemblage was the gastropods. This pattern of distribution—with high biomass at a high level in the intertidal zone—has been documented elsewhere, including Malaysia (Ashton et al., 2003) and China (Jiang and Li (1995) as cited in Ashton et al., 2003), and may have some importance ecologically. Mid-tidal habitats in some mangrove systems clearly represent valuable sections of the intertidal zone in terms of the conversion of organic material—presumably detritus, from the breakdown of mangrove leaves and micro-algae from the surface of macrophytes—into secondary productivity. The high abundance of deposit feeding and surface rasping molluscs for example, comprises a rich source of animal tissue for use at higher trophic levels.

The reasons underlying the observed pattern of distribution are complex however, and may involve predation, physiological adaptations and behaviour. Reid (1985) noted that predation by crabs on the ubiquitous, arboreal *Littoraria* species was intense, particularly by *Metapograpsus* species. which are most common in the lower intertidal zone. Such biotic interactions could contribute to reduced numbers of *L. articulata* in the tidal creek, while facilitating the proliferation of *Littoraria filosa* in the tidal flat. Further, pulmonate snails (including the numerous and species-rich Ellobiidae) which dominate the upper intertidal zone, have developed several characteristics which reduce their requirements for frequent tidal inundation including adaptation of the mantle cavity into an air-breathing lung (Ashton et al., 2003) and reproduction without a swimming larval stage (Berry, 1963). Finally, the tree-climbing behaviour of several key species including *Nerita balteata, Littoraria* spp., *Cassidula angulifera* and *Cerithidea obtusa* is well documented (Yipp, 1983; Reid, 1985; McGuinness, 1994) and is considered a successful adaptation for both thermal regulation and predator avoidance. The concentration of numerous

ellobiid and littorinid species that employ such behaviour in the mid-tidal zone may also contribute to the notably high gastropod densities observed in this assemblage.

It should be noted however, that numerous studies have emphasized that the most productive region of the intertidal zone is the extensive mud flats that occur just seaward of the mangroves (Wells and Slack-Smith, 1981; Wells, 1983, 1984; Hanley, 1987; Kumar, 1995; Schrijvers et al., 1995). Indeed, the current findings show a steady increase in mollusc species richness from landward to seaward and presumably the unconsolidated sediments of the extensive mudflats below mean sea level in Darwin Harbour, also represent suitable habitat for a diverse range of molluscs. In this respect, further research on the mudflat habitat in the Darwin region is of key interest. For example, at least one species (*Nassarius fraudator*) is frequent on the mudflat (R. Willan pers. com.) but was not recorded within the mangroves during this survey.

Despite some similarity between the mangrove mollusc populations studied in NW Western Australia and the Darwin region, there are also some striking differences. Almost no infaunal molluscs were sampled from any of the mangrove assemblages in the Bay of Rest. The lack of burrowing species (especially bivalves) within mangrove substrates reported by Wells (1984), has also been noted by previous authors (Berry 1963; Macnae 1967; Sasekumar 1974; Wells and Slack-Smith 1981). By contrast, a relatively diverse bivalve fauna was recorded within the mangrove forests of Darwin Harbour, although infaunal species primarily occurred in the seaward assemblage. Wells (1983; 1984) also found the landward backflat to be impoverished, with only a single species sighted, whereas 14 species (mean density 3.4 m^{-2}) were documented from the hinterland margin of Darwin Harbour. Thus the findings of this study do not concur with those of Wells (1983, 1984) or with several previous studies in which infaunal molluscs were virtually absent in tree zones. More recent research has reported high densities of infaunal molluscs, for example, in Gazi Bay in Kenya (Schrijvers et al., 1995) and Missionary Bay in North Queensland (Dittman, 2001). Both these locations are, however, more tropical than North West Cape.

Although some of these differences may be due to differing efficacy of field sampling techniques, much of the variation can probably be attributed to climatic differences—particularly given the extreme temperatures and the low rainfall at North West Cape. Indeed, Reid (1985) postulated that the landward limits of horizontal distribution for

mangrove gastropods were determined by physiological tolerance. Arboreal littorinids, for instance, are typically absent from the landward mangrove fringe in northern Australia, whereas several species occur in this niche in tropical Malaysia where annual rainfall exceeds 2,000 mm.

Overall, it appears that, unlike some rocky shore habitats, mangrove systems do not necessarily exhibit consistent global patterns in molluscan diversity and density in relation to tidal elevation. One study in the Kimberley found no consistent trend in mollusc diversity and abundance across the intertidal zone but, similar to this study, the highest densities were recorded from *Ceriops* (Wells and Slack-Smith, 1981). Another survey recorded higher mollusc density amongst *Avicennia* on the seaward mangrove fringe than on the adjacent bare mudflat(Wells, 1986c). In addition, the apparent absence of infaunal molluscs noted above (Wells and Slack-Smith, 1981; Wells, 1986b) is not always observed within mangrove forests. Furthermore, the current literature and the findings of this study, tend to indicate wide variation in patterns of diversity and abundance between different mangrove ecosystems, apparently in response to the interplay of a complex set of biotic and abiotic factors. Additionally, much of the variation in results can be attributed to differences in experimental design and sampling techniques.

In Sarawak, Malaysia, for example, a total of 44 mollusc species were recorded in a study in which the quadrats were consistently placed adjacent to tree species characteristic of that assemblage (Ashton et al., 2003). Although apparently less diverse than the Darwin Harbour mangroves, sampling for the Malaysian study was less intense and sampling of infaunal species was not attempted. But there were still some strong similarities in the mangrove molluscan fauna recorded during the Malaysian surveys and that found in this study. For example, as in local mangroves, high mollusc densities in Malaysia mostly consisted of two species of microscopic gastropod of the genus *Assiminea*—one of which had a wide distribution throughout the forest (Ashton et al., 2003). Further, the large predatory gastropod *Chicoreus capucinus* occurred in high numbers amongst *Rhizophora*-dominated forests in both locations, where it feeds exclusively on teredinid bivalves.

As reported for other taxonomic groups studied for this project, there was a high similarity at the generic level between mangrove molluscs found in northern Australia

and those occurring elsewhere in the Indo-Pacific region. The same genera tend to occur at equivalent tidal elevations on mangrove shores throughout the region (Reid, 1985). Indeed, gastropod community structure was found to be correlated with topographic elevation, surface water pH and leaf litter in Malaysia (Ashton et al., 2003). Presumably, a tight relationship exists between species composition, abundance and tidal elevation on mangrove shores elsewhere in the region—as was clearly demonstrated in this study by NMDS ordinations for molluscs and other taxa.

Seasonal variations in mollusc species richness and abundance documented in this study indicated a differing response of bivalves and gastropods to seasonality as well as marked differences amongst the four assemblages. Although the overall results of the one year survey suggested a general elevation in molluscan species richness during the dry season, more detailed examination of patterns, using the results of surveys spanning a three year period, showed more complex seasonal patterns (Metcalfe, 2005).

In the three year study, seasonal variation in bivalve species richness and abundance in the two species-poor, landward assemblages is negligible. Both species richness and abundance in the two seaward assemblages, however, increased during the dry season (Metcalfe, 2005). In contrast, gastropod species richness and abundance varied little in the seaward assemblages during the wet season but showed distinct seasonal variation in the two landward assemblages, where gastropod populations declined during the dry season. It appears that in landward habitats, the increased humidity, high rainfall and more frequent tides during the wet season promote increases in the diversity and abundance of gastropods.

Ants

In general, studies of mangrove ant fauna are very rare and the majority of information has typically derived from broader investigations of insect fauna in these habitats (Nielsen, 1997a) including for example, recent doctoral studies on mangrove insects in Darwin Harbour by Coupland (2002). There is a similar lack of information from overseas except for surveys of mangrove ants for investigations of island biogeography (Cole, 1983, 1983). During the last decade however, Darwin Harbour has been the focus for a number of investigations that deal solely with mangrove ants (Clay and Andersen, 1996; Nielsen, 1997a, 1997b, 2000).

Prior to the current survey, a total of 24 ant species were known from mangrove habitats in Darwin Harbour (Nielsen 2000). Initial surveys, conducted in the landward mangrove assemblages recorded 16 species (Clay and Andersen, 1996), but this investigation did not include the ant fauna of much of the tidal creek and seaward assemblages. Nielsen (2000) reported ten species, only from *S. alba* trees in the seaward assemblage and combined with the earlier findings of Clay and Andersen (1996), this suggested the ant fauna of Darwin Harbour was quite diverse indeed. This survey was perhaps the first to systematically sample ants from each of the major mangrove assemblages. It resulted in a total of 25 species from undisturbed habitats and 32 ant species from both undisturbed and disturbed habitats (see chapter 6) and included several ant species that have unique adaptations for intertidal living. The species tally subsequently increased to 44, with addition of the three years of sampling at monitoring sites (Table 5-7). The ant fauna of the mangroves of Darwin Harbour was surprisingly diverse and abundant for an intertidal habitat largely dominated by marine species.

Most mangrove ant species are also found in other habitats (Clay and Andersen, 1996) and the ant fauna recorded here was comprised largely of savanna species (36%, typically ground dwelling), rainforest species (28%, arboreal) and a number of species that occur exclusively in mangrove environments (28%). Similar to the ant fauna of Northern Territory rainforests, *Polyrhachis* was the richest genus, (Reichel and Andersen, 1996) with six species recorded from mangrove habitats (Clay and Andersen, 1996). Indeed, the three main ant genera recorded in this survey, *Polyhrachis, Camponotus* and *Crematogaster,* represent three of the most common, widespread and diverse groups of ants, comprising 115, 128 and 34 described Australian species respectively, found in most terrestrial habitats across the continent (Shattuck, 1999).

Seven species (*Camponotus anderseni, Camponotus* sp. 3 (*janeti* group), *Crematogaster* sp. 8 (australis group), *Polyhrachis sokolova, Polyrhachis constricta* and *Pheidole* sp. 22) of the total of 44 ants recorded, are considered mangrove specialists (A. Andersen, pers. com.). They include several species that nest either in the mud (e.g. *Polyrachis sokolova*) or in hollow stems in trees (e.g. *Camponotus* sp. 10, *Crematogaster* sp. A and *Camponotus anderseni*). The latter species is phragmotic, using the head of either the queen or worker ant to block the sole nest entrance during high tide (A. Andersen, pers. com.). The genus *Polyrhachis* contains perhaps the only marine ants in the world (Shattuck, 1999) which

have even developed the ability to 'swim' across the surface of the water (Nielsen, 1997a). *P. sokolova* constructs mud nests in the tidal flat and tidal creek assemblages which are inundated by between 13-61% of annual high tides in Darwin Harbour (Nielsen, 1997a). Their nests trap air underground, allowing the ants to survive lengthy periods of inundation.

The only introduced ant species recorded from undisturbed mangroves during this survey (*Paratrechina longicornis*), belongs to a cosmopolitan genus which tends to occur in sites of low ant diversity, including seasonally waterlogged areas and anthropogenic habitats (Andersen, 2000). During this survey *P. longicornis* was found only in the hinterland margin assemblage, which is waterlogged during the wet season. It is an opportunistic species, with an extensive distribution throughout the monsoonal region, where it makes temporary nests under, behind, or inside, any form of shelter (Reichel and Andersen, 1996; Andersen, 2000).

A large proportion of the ant species recorded (32%) were only sampled on a single occasion in the hinterland margin assemblage. This suggests that, aside from a core group of mangrove specialists, and arboreal rainforest species, which are well adapted to mangrove environments, approximately one third of the ant fauna are just intermittent visitors to the landward fringe. Indeed, the majority of these species are savanna species that presumably venture into mangroves only occasionally, to forage and nest. The observed pattern of distribution—in which the hinterland margin fauna is discrete from that found in the other assemblages—reflects the varied but sparse ant fauna on the landward fringe. Ants in the hinterland margin appear to largely consist of unspecialised taxa deriving from surrounding savanna habitats, with the exception of one or two mangrove specialists (*Polyrhachis constricta* and *Pheidole* sp. 22).

The seaward assemblage also has a distinct ant fauna but, in contrast with the hinterland margin, it is comprised of a small number of species, including four of the seven mangrove specialists. The decrease in diversity, from 18 species in the hinterland margin to 8 in the seaward assemblage, is the opposite to that exhibited by most marine groups. It presumably reflects the fact that ants are not a marine group and face increasing levels of biotic and abiotic stress, as well as other challenges associated with living in intertidal habitats, with increasing distance from the high tide mark.

The pattern of zonation of the six *Polyrhachis* species across the intertidal gradient recorded by Clay and Andersen (1996) was broadly similar to that observed in this study, with *P. senilis* and *P. constricta* at the landward fringe and *P. sokolova* further to seaward. By sampling at a finer scale (every 20m along transects) across the intertidal gradient, they observed species replacements, such that only rarely were two species of *Polyrachis* found at the same sampling point. They concluded that the factors determining mangrove ant zonation were complex but may be the outcome of a series of competitive displacements combined with the influence of environmental variation, particularly food availability, across the intertidal zone (Clay and Andersen, 1996).

Of the terrestrial insects inhabiting mangroves, ants have been described as the 'most abundant and influential group of insects in these communities' (De Baar & Hockey (1993) as cited in Nielsen, 2000). Indeed in terrestrial habitats, ants are the dominant invertebrate group, particularly in the Australian environment (Andersen et al., 2004). Their extremely high diversity, abundance (ants constitute 30% of terrestrial animal biomass) and the ecological role of ants has led to their use as bioindicators in environmental assessment programs (Andersen, 1997; Andersen et al., 1998; Andersen et al., 2004). Hence, it was largely for this reason that ants were included in the current research project; to investigate whether the same principles might also apply in intertidal habitats. The effects of anthropogenic disturbance on mangrove ants will be discussed in more detail in Chapter 6 of this thesis.

Fish and other fauna

Mangrove fish

Despite the celebrated role of mangroves in supporting estuarine and near-shore fish populations, few studies have documented the fish that periodically utilise the habitat as a resource (Collette, 1983; Roberston and Duke, 1990; Halliday and Young, 1996). Less is known about the fish that dwell permanently in mangroves—those species that remain in mangrove habitats during low tides. The diverse and abundant ichthyofauna that enters and leaves mangroves with the tide, often comprises species of importance to commercial or recreational fisheries—either directly, or more often as prey items for larger species (Morton, 1990; Halliday and Young, 1996; Martin, 2004). Not surprisingly, these groups have attracted much greater research interest, as outlined below.

Studies in Moreton Bay in south-east Queensland found that at least 42 fish species foraged within mangroves (Morton, 1990) and 14 species occurred exclusively in mangrove habitats (Laegsdsgaard and Johnston, 1995). Further north, a total of 42 species were recorded from within *Rhizophora styosa* forest in Tin Can Bay (Halliday and Young, 1996) and 20 species were recorded from mangroves near Townsville (Roberston and Duke, 1990). Species richness of fish in these subtropical locations is known to be quite low however, whereas tropical estuaries may have two to three times more species (Laegsdsgaard and Johnston, 1995). For instance, 55 fish species were recorded from within mangroves on one creek near Weipa in northern Australia (Vance et al., 1996); 119 species from Selangor in Malaysia (Chong et al., 1990) and surveys at Alligator Creek in tropical North Queensland found 128 species (Robertson and Duke, 1990). Further, inventories of mangrove fish from 12 sites in New Guinea and two in the Northern Territory documented a diverse fauna with over 200 species from 58 families (Collette, 1983). However, as fish species richness is highly dependent on sample size and collection techniques, and varies according to abiotic factors between different systems, comparison of different studies must be done with caution (Robertson and Blaber, 1992).

Overall, although the fish fauna using tropical mangroves is generally diverse, it comprises only a small number of families that occur widely across the Indo-Pacific and the New World; one of which includes the species rich Gobiidae (Collette, 1983). This widespread family is generally represented by numerous species in the fauna of mangrove creeks, but comprises only a small proportion of overall abundance or biomass (Robertson and Blaber, 1992). Indeed, the Gobiidae is the most speciose family (70 species) in Darwin Harbour (Larson, 1987), over half being associated with mangrove forests (Martin, 2004) with all species in the genus *Periopthalmus* obligate mangrove dwellers (Murdy, 1989). All but two of the 12 resident species recorded in this survey were gobies but few gobies were sampled amongst the non-resident mangrove fishes recorded by Martin (2004).

Previous studies have demonstrated that many species of fish utilise mangroves as feeding grounds, often only at a particular stage in their life history, typically as juveniles (Chong et al., 1990; Vance et al., 1996; Martin, 2004). A survey in the mangrove-fringed Trinity Inlet in North Queensland found that the estuary was

dominated by juvenile fish, with 70% of species most abundant as juveniles (Blaber, 1980). These observations and the low numbers of piscivores sampled from within the estuary suggested that such areas are important sanctuaries for juvenile fish. Indeed, studies in Moreton Bay, in eastern subtropical Australia (Laegsdsgaard and Johnston, 1995) and in Alligator Creek, near Townsville (Robertson and Duke, 1987) found that mangrove habitats were preferentially selected (over mudflats and seagrass beds) by juvenile fish. Not only were more species of juvenile fish found in greater abundance in mangroves, but they generally included commercially harvested species. A recent review noted considerable evidence for the hypothesis that mangroves contain a greater supply of food for juvenile fish than other estuarine habitats (Robertson and Blaber, 1992).

Prior to the recent comprehensive survey conducted in Darwin Harbour by Martin (2004), very little was known of the mangrove fish fauna of the Northern Territory. By sampling fish in trammel nets set within different mangrove assemblages, her study documented the fish that enter the mangroves at high tide. Martin (2004) recorded a total of 63 species from three locations in Darwin Harbour but postulated that the number of species that utilise mangroves as a habitat should be closer to 100, due to undersampling of the Gobiidae by her field techniques. Trammel nets recorded only one species of goby, the giant mudskipper *Periopthalmodon freycineti* (Martin, 2004). Pitfall traps and light traps were also used to catch juveniles.

Overall, fish foraged throughout all the four assemblages in Darwin Harbour on high spring tides, moving considerable distances into the forest (Martin 2004). In fact, higher mean capture rates for fish were recorded in the mid-mangrove zone, dominated by *Ceriops australis,* than in the seaward and tidal creek assemblages (Martin, 2004). The extensive use of mangroves by fish is further demonstrated by studies in Pagbilao in the Phillipines, where the highest fish density and biomass was recorded in the most inland habitat studied, dominated by *Avicennia officinalis,* situated some 93 m from the bay (Rönnbäck et al., 1999). These findings suggest that good foraging opportunities are offered within these upper intertidal assemblages, facilitated perhaps, by the temporal refuge from predation afforded by less frequent tidal inundation. For instance, Martin (2004) found a high proportion of the fish sampled in the tidal flat were opportunistic macro-benthic carnivores (feeding mainly on shrimp, crabs and molluscs). Not

surprisingly, surveys of invertebrates showed that mollusc diversity and abundance was also high in the tidal flat assemblage.

These studies have established that a wide range of fish—many of which only use mangroves for part of their life cycle—move into mangroves to feed at high tide, residing elsewhere at low tide, presumably retreating to adjacent creeks. Sampling for each of the above studies was primarily conducted using traps and nets set at high tide, although Collette (1983) used some rotenone. Traditional netting techniques are unlikely to successfully sample the characteristically small (< 150 mm), amphibious or semi-terrestrial fish investigated in the current survey—particularly given that some mudskippers climb trees, or remain in burrows at high tide, possibly to avoid predation. The majority of permanent resident species are sedentary and live either within or on the substrate, in pools of water or in small channels at low tide.

Sampling using pitfall traps by Martin (2004) resulted in 11 species of small fish, all Gobiidae, while this study recorded 12 species, including 9 gobies, Overall, the species richness, species composition and the pattern of distribution of resident fish were highly similar in both studies. This is perhaps not surprising given two of her study sites (E1 and M3) were also surveyed in this project and the projects were of similar duration. Sampling over a longer period (four years) and in anthropogenically disturbed sites, increased the total number of resident fish to 26 species (Table 5-7).

Thus Darwin Harbour appears to have a relatively diverse resident mangrove ichthyofauna. Additional intensive sampling in mangroves elsewhere in the tropics however, is likely to reveal similar results. Further, several species, including *Scartelaos histophorus* and *Boleophthalmus caeruleomaculatus* commonly occur in high densities on mudflats just beyond the mangroves (Anon, 1985), a habitat not sampled in these studies. Although more abundant in seaward assemblages, small resident fish are well adapted to mangrove habitats and occur throughout the four mangrove assemblages where they exploit a wide range of microhabitats. *Periopthalmus* species are extremely hardy, amphibious fish that prefer to remain out of water—to the extent that *P. darwini* nsp. migrates up tree trunks to avoid incoming tides (pers. obs). The tiny *Parioglossus palustris* was recorded from within rotting timber where it remains at low tide and several of the most common gobies inhabit mud burrows (*Amoya gracilis*, *Amoya* sp., *Calamiana* sp. 24).

Seasonal patterns in the species composition of vagrant fish were recorded in mangrove habitats in central Queensland. Although lower densities were also recorded in the dry season and highest recruitment during the wet season, large variances masked significant seasonality in abundance (Roberston and Duke, 1990). These wet season increases in juvenile non-resident fish were thought to be due to higher densities of zooplankton—especially crab larvae—which are particularly abundant in mangroves during the wet season. Martin (2004) also found species richness of fish in Darwin Harbour mangroves was generally higher in the wet season and several common species showed distinct seasonal patterns—typically exhibiting a decline in numbers during the dry season—but overall patterns were again masked by high levels of variability.

In this study, strong seasonal patterns were not observed, but resident fish abundance did vary on some transects from wet to dry seasons. Burrowing species appeared less numerous in the seaward zone during the wet season, when erosion associated with monsoonal conditions may remove the fine sediments in which they live. In contrast, some fish, particularly juvenile mudskippers, appeared to be more abundant during the wet season where they were often observed in the two landward assemblages (pers. obs.). Shallow lenses of freshwater often flow across the hinterland margin assemblage for several months in response to seepage from the hinterland and presumably represent suitable conditions for these immature fish. Analyses also indicated that fish were more abundant in landward assemblages during the wet season, matching the trend exhibited by non-resident fish described above. The pattern may indicate periodic expansion, or migration of resident species from seaward to landward assemblages during the wet season, when regular tides and environmental conditions facilitate the ingress of fish.

In this study the use of pitfall traps, which generally retained water after the tide had ebbed, allowed the sampling of puddle fauna and investigation of the role of mangroves as refuges for juvenile fish. The results suggest that small pools remaining in mangrove forests at low tide do not represent significant habitats for juvenile fish, but are primary habitat for a small number of species, predominantly small gobies that are probably mangrove specialists. It appears that juvenile fish leave the mangroves with the ebbing tide. The results are in accordance with those of Martin (2004) who also trapped only

small mangrove dwelling gobies in pitfalls and suggested that larvae and juveniles of non-resident species do not use this microhabitat as nursery site. However, sampling of tidal channels that contain permanent water at low tide is likely to have revealed very different results (see Robertson and Duke, 1990).

Other invertebrate fauna

Mangrove habitats offer marine invertebrates a diverse array of substrates ranging from soft substrates (with wide variation in grain size); hard substrates (such as tree trunks and roots); and holes, crevices, bark and rotting logs for cryptic fauna (Alongi, 1989a). Occasionally species from other phyla including bryozoa, cnidaria and echinodermata were recorded in mangrove habitats (Table B-1, Appendix B). These marine animals were generally restricted to the most seaward assemblages and presumably comprised only species tolerant of high turbidity. Echinoderms are generally typical of environments with clear water, but the brittlestars (class Ophiuroidea) are one group that has a number of species associated with muddy habitats (Hanley, 1987). Indeed, two undescribed species of brittlestar were recorded during these surveys (T. O'Hara, pers. com.) and represent the first echinoderms recorded from mangrove habitats in Darwin Harbour. In contrast with other marine environments such as coral reefs, these groups exhibit extremely low diversity in mangrove habitats.

Several species of bryozoan are known to occur as encrusting or fouling fauna on mangrove roots in the Caribbean Sea, but only in subtidal habitats (Sutherland, 1980; Diaz et al., 1992). An unusual amphibious species of bryozoan was found in the tidal creek and seaward assemblages of Darwin Harbour mangroves, that mainly encrusts the living leaves of *Rhizophora stylosa.* This organism was first collected during this survey and has been since described as a new genus by Dr Dennis Gordon (National Institute of Water and Atmospheric Research in Wellington, New Zealand). The manuscript is attached to this thesis as Appendix D.

~5.5.3. Seasonality in the wet-dry tropics and effects of monsoons

Darwin's climate is highly seasonal, and 90% of the mean annual rainfall (1,659 mm) falls between November to April, followed by an extremely dry period. It is not surprising therefore, that seasonal patterns in the structure and dynamics of intertidal

faunal communities are also evident. The most pronounced seasonal effects were a decline in invertebrate abundance in seaward habitats during the wet season, and to a lesser extent, the decreased diversity in the hinterland margin assemblage during the dry season (discussed previously for molluscs). The organisms most affected (worms, bivalves and grapsid crabs) were infaunal and benthic taxa inhabiting the seaward assemblage, which suggests that changes in the substrate may be an important factor contributing to the observed faunal response. Furthermore, the fact that organisms with poorer osmoregulatory abilities generally live lower in the shore (Davie, 1993) suggests that seasonal changes in salinity may also be important.

Sedimentary environments are dynamic habitats where the substrate is continually being modified both by biotic forces (eg the burrowing of infaunal animals) and by physical forces, such as displacement and erosion by waves during the wet season (Constable and Fairweather, 1999). Wave action is generally unevenly distributed on the shore and may therefore have a differential impact on infaunal invertebrates at different tidal elevations (Peterson, 1991). In Darwin Harbour, dense mangrove forests rapidly dissipate wave energy (see Mazda et al., 1997; Massel and al, 1999) and wave action is likely to be most concentrated on the mudflats to seaward of the mangroves, and amongst the widely spaced trees of the seaward assemblage. In these habitats, scouring and mobilisation of fine sediments by waves, rainsplash, sheet flow and stormwater runoff associated with the annual monsoon, contributes to the stripping of surface sediments observed at this time of year (pers. obs.). Indeed, wet season conditions appear to erode a substantial proportion of the surface layer of sediment in the seaward assemblage, which may effectively remove the microhabitat of a range of benthic and infaunal invertebrates, helping to explain the observed loss of these taxa. As a consequence, certain faunal groups, particularly those with the greater proportion of infaunal species, may show more temporal variation than others (e.g. worms).

In addition to the physical disturbance of sediment, monsoonal conditions may also alter sediment particle size, a factor known to have a strong impact on the distribution of infaunal invertebrates (Al-Khayat and Jones, 1999), especially polychaetous worms (Sarkar et al., 2005). Alongi (1987) reported that in north-eastern Australia, sediment size changed from coarse silt during the dry season, to coarse sand during the wet season. The impact of seasonality on invertebrate populations appears to vary in response to the

intensity of the annual monsoon. The intense monsoonal and cyclonic activity characteristic of India for example, causes dramatic decreases in density of meiofauna and macroinvertebrates (Nandi and Choudhury, 1983; Kurian, 1984; Kumar, 1995). In contrast, an increase in meiofaunal density was recorded in response to the weaker and shorter monsoonal period in north-eastern Australia (Alongi, 1989a). The increased mortality of tropical intertidal infauna during monsoons is well documented (Nandi and Choudhury, 1983; Kurian, 1984; Kumar, 1995) and thought to be due to fluctuations in salinity and the erosion of sediment (Alongi, 1989b). Heavy rainfall associated with the wet season may cause osmotic shock in invertebrates that have saline body fluids, but are unable to regulate their internal osmotic potential. Consequently, flooding by stormwater runoff may be fatal if it exposes their body membranes to freshwater. Being soft-bodied, and relatively sedentary animals, worms are again likely to be particularly vulnerable to osmotic shock, whereas it may be possible for some crustaceans and molluscs—with their protective exoskeleton and valves respectively—to avoid or escape from harmful changes in salinity and substrate. Such morphological differences may have contributed to the marked response of the worm fauna to seasonality in this study.

Indeed, recent research indicates that major freshwater events can have major impacts on infaunal invertebrates (Chollett and Bone, 2007), to the extent that the majority of mangrove benthos may be lost (Sheaves, 2006). A small remnant fauna generally remains—comprised of a few, previously abundant, 'resident' species—which tend to slowly recover to pre-disturbance levels. It appears that this core group of euryhaline species is slowly replenished, while most of the less tolerant, non-resident benthos does not return. This group is rapidly replaced by a new suite of species (Sheaves, 2006). Indeed, following climatological disturbances, invertebrate populations generally appear to be able to quickly repopulate (Alongi, 1989b) and in the sites examined in this study, fauna in the seaward assemblages appeared to proliferate during the relatively stable, dry season weather conditions (see Appendix C). Despite the reputed ability of invertebrates to recover relatively quickly, post-disturbance, this will however, be dependent on successful recruitment and may vary between locations (Robertson and Duke, 1990), and with environmental conditions. Clearly, an understanding the dynamics of disturbance from natural events such as rainfall and monsoons may be of value in developing our knowledge of the response invertebrate fauna to anthropogenic impacts.

Overall, despite a great deal of scientific research on mangrove invertebrate fauna over the last two decades, there is still a lack of detailed quantitative and ecological information of the faunal communities of mangroves. Disturbingly, expanding our knowledge of these habitats has not diminished the loss of mangrove habitat which has proceeded with unprecented rapidity—such that 17% of Australia's mangroves have been destroyed since European settlement (Duke, 2006) and over 50% of the world's mangroves are now gone (Rönnbäck et al., 1999; Kairo et al., 2001; FAO, 2003). Indeed, there is a growing list of countries in which 50-80% of mangroves have been cleared in the last 15 years alone (Diop, 2003). Further, of the remaining resources in tropical continental Asia, 40% are degraded and at least 90% of the world's largest mangrove area, at the mouth of the Ganges, is either artificial (silviculture) or replanted (Blasco, 2001).

Hence, as the area of the world's mangroves rapidly declines or is modified by anthropogenic activities, our responsibility for the preservation of remaining habitats increases. In 1989 Alongi (1989a) stressed that "with increasing population growth and anthropogenic input to coastlines in tropical countries, accurate information on benthic communities is urgently needed for informed and proper management of these unique ecosystems". To date, this warning remains appropriate and highly relevant, for mangroves in both developed countries (for inventory, environmental assessment, planning and monitoring purposes) and in developing nations for impact assessment and rehabilitation purposes. In particular, sound environmental management of these habitats is often hindered by our poor understanding of the response of mangrove ecosystems to human disturbance. It follows that the subject of the next chapter concerns the impacts of anthropogenic development on the structure and dynamics of mangrove invertebrate assemblages.

5.6. Conclusions

A composite field methodology developed for this study was successfully applied to survey the macro-invertebrate fauna in the four main floristic assemblages of mangroves in Darwin Harbour. The total of 254 taxa recorded in the one year survey, exceeded tallies reported from elsewhere in Australia and placed the mangrove environments of Darwin Harbour as one of the most diverse and productive estuarine

systems in the Indo-West Pacific region. These results however, could reflect lesser sampling efforts elsewhere. Many genera were common to mangrove habitats elsewhere in the region, but represented here by different species.

In general, the fauna increased in diversity and abundance from landward to seaward, though each assemblage had its own distinctive compositional traits. The seaward assemblage, characterised by daily tidal inundation and numerous habitat opportunities potentially offering protection from predation, had particularly high diversity and abundance. By contrast, the less frequent tidal inundation of the tidal flat may have offered a temporal refuge from predation, and this assemblage also supported particularly high densities of invertebrates. Indeed, diversity in the tidal flat was equivalent with that of the tidal creek, and exceeded it in terms of invertebrate abundance. Moreover, the highest densities of predatory fish (Martin, 2004) were recorded in the tidal flat, substantiating trophic links between mangroves and near-shore environments. These findings imply the high conservation and ecological significance of tidal flat and the seaward habitats in Darwin Harbour mangroves.

The likelihood of periodic disturbance from monsoons also increased to seaward, and the strongest temporal patterns in distribution and abundance were shown by infaunal taxa, particularly worms, and to a lesser extent, grapsid crabs and bivalves in the seaward assemblage. Polychaete populations crashed in seaward assemblages during the wet season, reflecting the dynamic nature of sedimentary environments. By contrast, faunal communities on the landward mangrove fringe diminished during the dry season. Rising aridity and increasing soil salinity during the dry season most affected the hinterland margin fauna, apparently contributing to declines in grapsid crabs, gastropods and fish.

Overall, it is apparent that the spatial and temporal variability evident in the primary productivity of these forests, reported previously from mangroves in Darwin Harbour (Woodroffe and Bardsley, 1987; Metcalfe, 1999), is also reflected by patterns in secondary (faunal) productivity. Like the forests, faunal populations tended to increase to seaward across the intertidal gradient, and in some assemblages varied markedly with season. It seems that spatial patterns in the distribution of fauna below mean neap tide level (approx. 2 m AHD) may be strongly regulated by predation, habitat opportunities and periodic disturbance by monsoons. Mangrove faunal assemblages to

landward of this, however, may be constrained more by infrequent tidal inundation, stresses associated with seasonal increases in aridity and salinity, as well as the seasonal influx of freshwater. The seasonal fluctuations evident in invertebrate populations underscore the highly dynamic nature of mangrove environments. Furthermore, the close interdependence of the fauna on these forests is evident from the tight groupings of taxa within each floristic assemblage and the prevalence of species adapted to specific forest microhabitats.

CHAPTER 6. THE IMPACTS OF ANTHROPOGENIC DISTURBANCE ON INVERTEBRATE FAUNA

CHAPTER 6. IMPACTS OF ANTHROPOGENIC DISTURBANCE ON INVERTEBRATE FAUNA

6.1. Introduction

Human settlements, industry and aquaculture have traditionally concentrated around the protected shorelines of estuaries and mangrove environments worldwide have frequently been exposed to anthropogenic disturbance (Constable and Fairweather, 1999; Wolanski, 2006). Estuarine environments are also the primary habitat of mangroves, and globally this coastal resource has been greatly affected by increasing indigenous, commercial and recreational use (Walsh, 1977; Aksornkoae et al., 1985; Ong, 1995; Ellison and Farnsworth, 1996). In the last two decades, 35% of the world's total mangrove area has been lost (Valiela et al., 2001; Wilkie and Fortuna, 2003). Further, a large proportion of remaining mangroves have been subject to anthropogenic modification by increased sedimentation (Ellison, 1998; Ellis et al., 2004), harvesting and silviculture (Kunstadter et al., 1985; Saenger, 2002) and organic and chemical pollution (Dwivedi and Padmakumar, 1983; Jernelov and Linden, 1983; Getter et al., 1985; Bilyard, 1987; Mackey and Hodgkinson, 1995; Raimondi and Reed, 1996; Stark, 1998).

Indeed, despite legislation to protect mangroves from destruction in eastern Australia, their tendency to act as sinks for sediments as well as contaminants (Morissey et al., 1996) has contributed to the pollution of many areas of mangal by industrial waste. Effluent may be discharged directly into mangroves in the form of sewage outfalls (Clough et al., 1983) or indirectly, as leachate from polluted landfills (Clark et al., 1996). Unfortunately, the same attributes that allow mangroves to survive in water-logged, saline environments (pneumatophores, lenticels and salt-excretion, for instance) also increases their vulnerability to water-borne pollutants (Duke et al., 1997), and excessive sedimentation (Ellison, 1998). Due to their tendency to act as geochemical traps for heavy metals and hydrocarbons (Harbison, 1981; Luoma, 1990; Clark et al., 1996; Stark, 1998) mangroves have often been used as 'buffers' between rubbish tips and the ocean. Of some concern, are the results of some studies on the impacts of organic and inorganic pollution, demonstrating that effects on estuarine faunal assemblages are complex,

varying both spatially and temporally, and with changes in tidal and drainage characteristics (Clough et al., 1983). For example, dredging activities may lead to the re-mobilisation of pollutants, while lowering of the water table can release heavy metals previously trapped in mangrove sediments (Clough et al., 1983; Clark et al., 1996). Further, the impact of industrial metal wastes accumulated and transformed in mangrove sediments may be enhanced when redistributed in the marine environment, resulting in insidious and long term effects on estuarine ecology (Harbison, 1981). Oil trapped in anoxic mangrove sediments may become a source of chronic oiling, oozing into the surrounding marine environment for more than a decade (Burns et al., 1993; Duke et al., 1997) and may produce chlorophyll-deficient mutations in *Rhizophora mangle* (Proffitt et al., 1995). Combinations of heated water, chemicals, other wastes and environmental conditions may also act synergistically in marine and intertidal environments resulting in unpredicted and occasionally amplified effects (Jones, 1975; Harbison, 1981; Proffitt et al., 1995).

During the last few decades, awareness of the effects of anthropogenic disturbance on estuarine ecosystems and the ecological connections between habitats has slowly grown. This has been due largely to declines in many coastal fisheries resulting from loss of mangrove habitat (Ellison and Farnsworth, 1996; Roberts et al., 2001). Losses of mangrove habitat in south-eastern Australia have been substantial (Duke, 2006) but with continuing rapid development along coastlines in northern Australia, especially Queensland, reclamation and urbanisation are still significant threats to these environments. In coastal cities around the continent, urban and industrial developments often abut mangrove habitats and the impacts on adjacent mangroves vary widely from minimal disturbance (Moritz-Zimmerman, 1997; Lindegarth and Hoskin, 2001), to minor impacts of urbanisation (Hutchings et al., 1977; Skilleter and Warren, 2000). Extensive areas of tree death have resulted from altered freshwater hydrology (Hegerl and Davie, 1977) and irreversible losses of habitat from changed tidal regimes (Gordon, 1987) and reclamation (Fairweather, 1990; McGuinness, 1992).

Mangrove ecosystems have been relatively poorly studied however, and the majority of mangrove systems in tropical Australia still await basic inventory and biological surveys. Consequently detailed knowledge of the ecological consequences of disturbance to mangrove habitats is lacking. Most previous research on disturbance to

mangroves elsewhere has concerned the impacts of oil spills (Lewis, 1983; Getter et al., 1985; Samiullah, 1985; Dicks, 1986; McGuinness, 1990; Burns et al., 1993; Duke et al., 1997) or the impacts of natural perturbations such as cyclones (Roth, 1992; Smith III et al., 1994; Swiadek, 1997; Sherman et al., 2001; Cahoon and Hensel, 2003). With pressure on remaining mangrove areas steadily growing, study of the impacts of anthropogenic disturbance—particularly the response of biotic assemblages to urbanisation—is becoming an increasingly important area of investigation, especially in terms of management and the conservation of this dwindling resource.

Simplification of ecosystems, and decreases in species diversity, often accompany increasing anthropogenic disturbance, especially pollution (Jernelov and Linden, 1983; Grall and Glémarec, 1997; Carballo and Naranjo, 2002; Sarkar et al., 2005). Unfortunately our knowledge of the consequences of such loss of biological diversity on natural ecosystems is poor (Field et al., 1998c). This is due largely to the complexity of studying such a topic and the shortage of long-term research and monitoring of ecosystems generally. Most studies in this field have been restricted to small-scale experimental situations, which have nevertheless demonstrated that the loss of diversity can have a significant impact on the functioning of ecosystems . Indeed, in one short term experimental study in mangrove habitat near Townsville in north-east Queensland, the removal of grapsid crabs, triggered an increase in toxic soil sulphide and aluminium in mangrove substrates, which in turn, significantly reduced the primary productivity (Smith III et al., 1991). In addition, the replacement of vast areas of previously diverse mangroves with monospecific stands for silviculture in India and South-East Asia is undoubtedly simplifying these habitats, yet the implications of decreased biological diversity on ecosystem function are poorly known. One of the few studies on this topic, found that the species composition of brachyuran crabs in replanted mangroves differed from that in natural mangrove areas, with new species occurring in plantations that were absent from natural mangroves (Al-Khayat and Jones, 1999). In contrast, higher densities of the penaeid shrimp *Penaeus merguiensis* were recorded amongst replanted *Rhizophora apiculata* forests than in natural mangroves in Pagbilao, Phillipines (Rönnbäck et al., 1999).

Chapter five of this thesis described the distribution, diversity and abundance of the major invertebrate groups in mangrove habitats of Darwin Harbour. Anthropogenic

disturbance to mangroves in the harbour has mainly resulted from modifications of coastal landforms, the conversion of mangal for residential and industrial use and from road construction. This chapter investigates the influence of four types of anthropogenic disturbance—urban, industrial, primary production, and small scale clearing—on the distribution, diversity and abundance of mangrove invertebrate fauna. Comparison with undisturbed sites will provide an indication of the response of mangrove invertebrates to differing kinds of disturbance. Although the study is limited, in that it lacks pre-disturbance data, and varying time periods had elapsed since the original disturbance occurred, the dearth of other studies tends to confer considerable value on this type of research. Opportunities to conduct BACI (before and after, control *versus* impact) experiments are rare, and information on the disturbance ecology of natural communities are thus particularly valuable. Without such information, ecologists are limited in their ability to accurately predict the outcomes of various influences on natural systems, particularly anthropogenic disturbance.

One of the impediments to improving our knowledge on the impacts of anthropogenic disturbance to mangrove invertebrate fauna is the increasing cost of identifying large numbers of specimens (Warwick, 1988; Beattie and Oliver, 1994; James et al., 1995; Chapman, 1998). Moreover, the pool of taxonomists specialised to undertake such work is also steadily decreasing (Hutchings, 1999). Consequently the search for taxa that may be specific indicators of disturbance—and thus provide a reliable shortcut for the assessment of environmental health—has become an important area of study (Bilyard, 1987; Reynoldson and Metcalfe-Smith, 1992; Cairns et al., 1993; Grall and Glémarec, 1997). To date, polychaete worms show great potential as bio-indicators of disturbance, being characteristically soft-bodied, relatively sedentary and infaunal (Warwick, 1993; Belan, 2003; Faraco and Lana, 2003; Pagliosa, 2005). Analyses based on functional groups such as feeding guilds, can further simplify ecological investigations, as they may reveal reactions of more general importance than the responses of populations of individual taxa (Bonsdorff and Pearson, 1999). The seminal work by Fauchald and Jumars (1979) and more recently by Pagliosa (2005) on polychaetes provided the foundation for valuable investigations on the faunal response—at the level of feeding guild—to environmental impacts. This chapter therefore makes reference to a preliminary investigation of the role of polychaetes as bio-indicators of disturbance and

the applicability of using worm feeding guilds in ecological and environmental assessment projects in mangrove habitats. This work is included in a manuscript attached to this thesis (Appendix C).

Aim

The aim of this chapter is to test for effects of anthropogenic disturbance on the invertebrate fauna in mangrove forests in Darwin Harbour. The diversity, abundance and distribution of invertebrates within the four main mangrove assemblages (hinterland margin, tidal flat, tidal creek and seaward) was investigated at four sites, each exposed to a different kind of anthropogenic disturbance. The mangrove invertebrate fauna of these disturbed sites will be compared with that of undisturbed sites (described in detail in Chapter 5). The invertebrate groups studied at disturbed sites were worms, ants, crustaceans and molluscs. As for chapter 5, small resident fish were also recorded during invertebrate surveys and are grouped with invertebrate phlya in this study.

6.2. Methods

~6.2.1. Field surveys

One dry season survey of invertebrates was conducted at each of four disturbed study sites selected in the East and Middle Arms of Darwin Harbour—Sites BV (Bayview), DP (Darwin Port), DM (Middle Arm prawn farm) and DE (see Figures 2-7, 2-8, 2-9 and 2-10, Chapter 2). The location, environmental characteristics and the type of anthropogenic disturbance at each of these sites is described in Chapter 2. In all, a total of 26 study plots on eight transects were surveyed in disturbed mangroves during October and November of 2001 (Table 6-1). The methodology used to sample invertebrates in disturbed sites was nearly identical to that employed in undisturbed sites and is described in section 5.2.1 of Chapter 5. The only difference between surveys in disturbed and undisturbed sites was the absence of a wet season survey in disturbed sites, due to time and logistical constraints, and the shape of the study plots, which was adjusted to suit the typically linear form of many disturbed areas. For instance, 33 m × 75 m study plots were aligned parallel to rock walls at Sites BV and DP. As in all sites however, the

rectangular plots had the same total area (0.25 ha) as the standard 50 m × 50 m study plots used elsewhere. In all other respects, the same range of invertebrate fauna was surveyed in disturbed sites using survey methodology the same as that used in undisturbed mangroves.

Due to the patchy nature of disturbance, it was not possible to study all assemblages at every site. At only two sites (BV and DP) did all four assemblages (hinterland margin, tidal flat, tidal creek and seaward) occur in close proximity to anthropogenic disturbance. The seaward assemblage was not sampled at site DM and disturbed (bulldozed) hinterland margin and seaward habitat was not present at site DE (Table 6-1). All invertebrate surveys at disturbed and undisturbed sites examined in this chapter were completed during the dry season months of July to November.

Table 6-1 : Dry season invertebrate fauna surveys in undisturbed and disturbed mangroves in 2001, indicating groups of sites used in statistical analyses.

	UNDISTURBED SITES (Apr-May 2001 & Jul-Aug. 2001)			**DISTURBED SITES (Oct –Nov. 2001)**			
Site	E1	E2	M3	BV	DP	DM	DE
Location	Charles Darwin	Elizabeth River	Jones Creek	Bayview	Darwin Port	Prawn Farm	CDNP Bulldozed
Hint/margin	●	●	●	●	●	●	
Tidal flat	●	●	●	●	●	●	●
Tidal creek	●	●	●	●	●	●	●
Seaward	●	●	●	●	●		

~6.2.2. Analyses

As for chapter 5, unidentified specimens that could be identified to generic level, but not species level, were included in univariate and multivariate analyses and species tallies. Specimens identified only to family or phylum level were deleted from analyses unless they represented the only member of that family, or phylum. Juvenile taxa (e.g. *Perisesarma* immature and Grapsidae immature) were included in analyses of abundance but not species richness. Ants were were omitted from analyses based on abundance but included in univariate and multivariate analyses of species richness.

There are several sets of analyses for this chapter involving (1) comparisons of disturbed sites to look for effects of particular types of disturbance and (2) two comparisons of

disturbed and undisturbed sites to look for effects of disturbance.

Firstly, to examine spatial and temporal trends amongst the four disturbed sites, fully balanced ANOVA's could not be analysed because each of the four assemblages were not present at all the disturbed sites (Table 6-1). Thus for each taxonomic group, analyses comparing four assemblages at two sites (BV and DP) and comparing three assemblages at three sites (DM, BV and DP) were run. These combinations are represented by black and blue outlines in Table 6-1, respectively. Site DE, comprised only the tidal flat and tidal creek assemblages, and ANOVA's including this site involved these two assemblages at the four disturbed sites (pink outline, Table 6-1).

Secondly, to compare disturbed and undisturbed sites, analyses were based on dry season data from (i) all four assemblages at two disturbed sites (black outline) and three undisturbed sites; (ii) the three landward assemblages at three disturbed (blue outline) and three undisturbed sites and (iii) the tidal creek and tidal flat assemblages (pink outline) at all four disturbed sites with three undisturbed sites (Table 6-1).

The procedures described by Winer et al. (1991) and Underwood (1996) were used in preliminary tests on complex ANOVA models to determine if any higher order interactions could be dropped. Following the recommendations of these authors, a conservative approach was adopted and terms were only dropped if the relevant F-ratio was non-significant at $p = 0.25$. In some situations with complex ANOVA models, exact F-ratios could not be calculated. In such situations, the statistical package calculated 'quasi F ratios' (Winer et al. 1991): these particular results were interpreted cautiously as they may be less reliable than exact tests.

6.3. Results

In all, 2,360 records were collected from surveys in both undisturbed and disturbed sites, including species sampled during the pilot and confirmation studies. Of this total, 751 invertebrate fauna records were obtained during the 2001 dry season survey of four disturbed sites (BV, DP, DM and DE).

~6.3.1. All invertebrate taxa

Invertebrate species richness of disturbed mangroves

A total of 171 species from 55 families were recorded from the four disturbed sites (Tables B-1 to B-8 Appendix B). In undisturbed mangroves, 191 species from 81 families were recorded, but sampling effort was greater, spanning both wet and dry seasons. The numbers of plots in assemblages also differed slightly (Table 6-1), but dry season species richness in the 12 study plots in three undisturbed sites (total 163 species; mean 9.9 ± 0.7 SE) was similar to that in 13 study plots in the four disturbed sites (total 171 species; mean 7.7 ± 0.7 per sampling station). Overall, there were 30 species in disturbed sites, not recorded in undisturbed sites. The most speciose invertebrate groups in disturbed mangroves were the molluscs and crustaceans which contained 54 and 48 species respectively, while 33 species of worms, 21 ant species and 12 fish were also recorded (Table 6-2).

Ordination of all invertebrates (171 taxa) based on species richness per study plot, indicated that shoreline position influenced invertebrate diversity at the four disturbed sites (Figure 6-1), but species composition within the four assemblages was more variable than in undisturbed sites (Figure 5-26, Chapter 5). This was particularly evident in the fauna in the tidal flat and hinterland margin assemblages, and in the lower left of the ordination, two tidal flat study plots are clearly distinguishable from the rest of the samples (Figure 6-1).

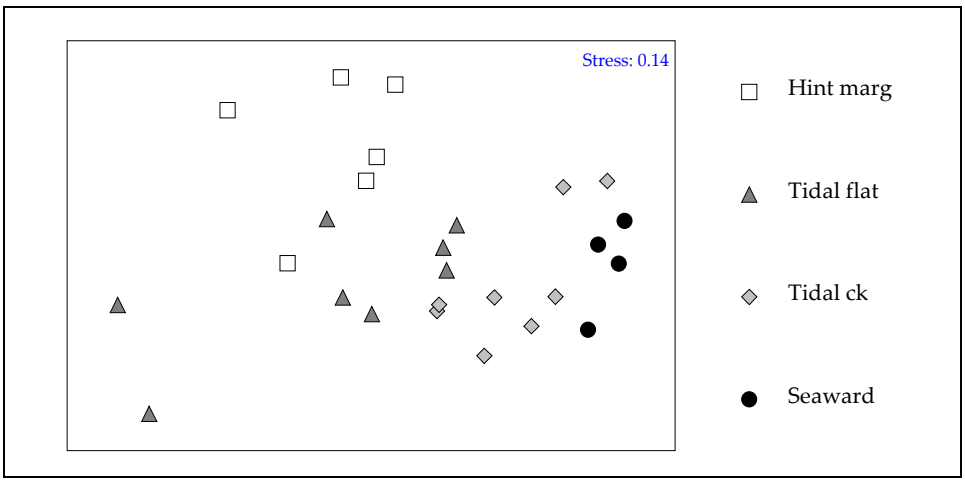


Figure 6-1: Ordination of 26 study plots in four assemblages from disturbed mangroves. based on invertebrate species richness. Data from three replicate sampling stations pooled forone dry season survey.

Table 6-2: Total invertebrate species richness, mean species richness per sampling station (± SE) and mean abundance per station (± SE) averaged across the four disturbed sites.

TAXA	Total species	Mean species richness/ station*	Range	Mean abundance/ station*	Range
ALL ASSEMBLAGES					
Molluscs	54	1.5 ± 0.2	0 – 10	2.7 ± 0.5	0 – 22
Crustaceans	48	3.5 ± 0.3	0 – 15	12.6 ± 1.5	0 – 57
Worms	33	1.1 ± 0.2	0 – 7	1.9 ± 0.4	0 – 20
Fish	12	0.7 ± 0.1	0 – 5	2.1 ± 0.7	0 – 48
Ants	21	1.0 ± 0.1	0 – 3	-	
Other	3	-		-	
TOTAL	**171**	**7.7 ± 0.7**	**1 – 34**	**19.5 ± 2.3**	**0 – 89**
SEAWARD					
Molluscs	30	4.2 ± 0.4	2 – 6	7.6 ± 1.1	3 – 15
Crustaceans	28	7.6 ± 0.9	3 – 15	32.2 ± 3.6	14- 57
Worms	20	2.8 ± 0.8	0 – 7	5.5 ± 2.0.	0 -20
Fish	7	2.1 ± 0.4	1 – 5	9.2 ± 3.9.	1 – 48
Ants	3	0.8 ± 0.2	0 – 2	-	
Other	1	-		-	
Total	**89**	**17.1 ± 1.63**	**14 – 34**	**54.6 ± 5.4**	**26 – 89**
TIDAL CREEK					
Molluscs	30	2.0 ± 0.6	0 – 10	3.9 ± 1.2.	0 – 22
Crustaceans	30	4.5 ± 0.3	1 – 7	14.3 ± 1.2	3 – 27
Worms	18	1.9 ± 0.3	0 – 4	3.0 ± 0.6	0 – 10
Fish	9	0.8 ± 0.2	0 – 3	1.6 ± 0.4	0 5
Ants	4	0.6 ± 0.1	0 – 2	-	
Other	2	-		-	
Total	**93**	**9.5 ± 1.0**	**6 - 24**	**22.9 ± 1.6**	**6 – 40**
TIDAL FLAT					
Molluscs	12	0.7 ± 0.3	0 – 5	0.9 ± 0.3	0 – 5
Crustaceans	15	2.1 ± 0.3	0 – 6	8.8 ± 2.5	0 -46
Worms	6	0.4 ± 0.2	0 – 3	0.6 ± 0.3	0 -6
Fish	4	0.3 ± 0.1	0 – 1	0.5 ± 0.2	0 – 5
Ants	6	0.7 ± 0.2	0 – 3	-	-
Total	**43**	**4.1 ± 0.6**	**1 – 17**	**10.8 ± 2.6**	**0 – 47**
HINTERLAND MARGIN					
Molluscs	4	0.3 ± 0.1	0 – 2	0.3 ± 0.2	0 – 2
Crustaceans	10	1.2 ± 0.2	0 – 3	2.3 ± 0.7	0 – 12
Worms	0	0.0 ± 0.0	0 -0	0.0 ± 0.0	0 -0
Fish	1	0.1 ± 0.1	0 – 1	0.2 ± 0.1	0 – 2
Ants	16	2.1 ± 0.2	0 – 3	-	
Total	**31**	**3.7 ± 0.4**	**2 – 7**	**2.8 ± 0.8**	**0 – 12**

*NB Each station comprised one 1 m^2quadrat, a pitfall trap, a 0.01 m^2 anoxic mat and epifaunal sampling to 2m. Three replicates were sampled per plot.

Comparisons of disturbed sites.

All univariate analyses comparing four disturbed sites (amongst two assemblages), three disturbed sites (amongst three assemblages) and two disturbed sites (two assemblages) revealed that species richness in assemblages varied between sites (Figure 6-2, Tables E-1 to E-3, Appendix E). Diversity in the seaward assemblage at site DP for instance, was substantially higher than that recorded in the seaward assemblage at site BV. Species richness in the tidal flat assemblage at site DP was, however, lower than that recorded at other sites.

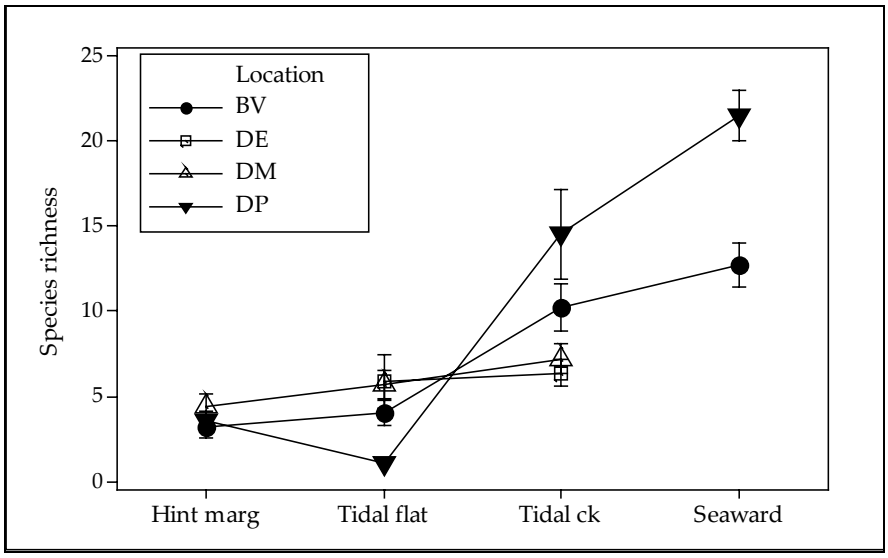


Figure 6-2: Mean species richness (±SE) of all invertebrate taxa at the four disturbed sites studied in assemblages from landward (L) to seaward (R).

Comparisons of disturbed and undisturbed sites

Analyses of invertebrate species richness found no significant differences between disturbed and undisturbed mangroves, nor between study sites (Tables E-4, E-5 Appendix E). There were, however, differences in species richness between assemblages and there was an assemblage × site interaction (Figure 6-3). Species richness was clearly highest in seaward habitats and least in landward habitats. The assemblage × site interaction indicated species richness varied in assemblages amongst sites, with the pattern in the tidal creek and tidal flat less consistent, than for the other two habitats. (Figure 6-3).

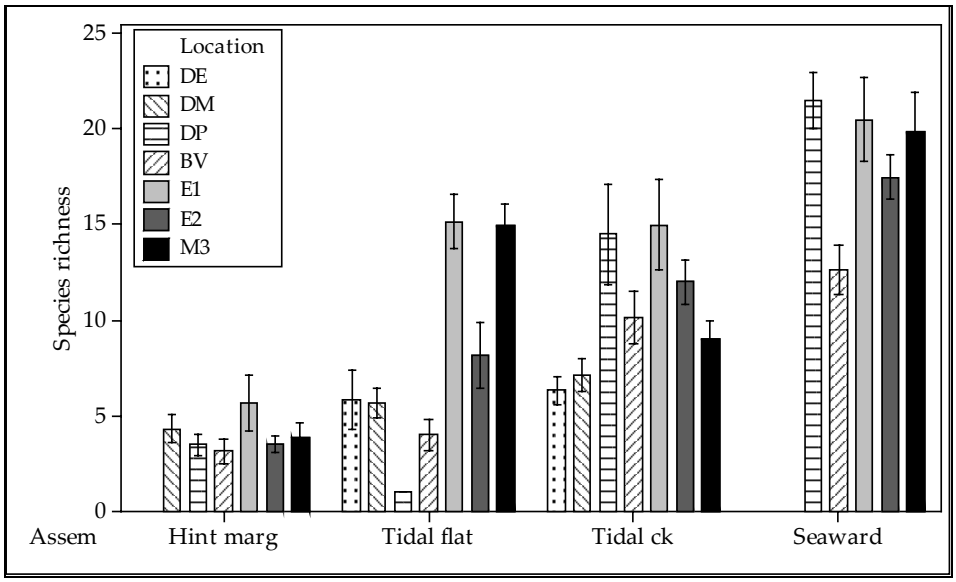


Figure 6-3: Mean species richness (± SE) in four assemblages at disturbed (hatched bars) and undisturbed sites (solid bars).

Comparison of mean species richness between disturbed and undisturbed sites indicates similar diversity in most assemblages except the tidal flat in which richness appeared markedly lower in disturbed sites (Figure 6-4).

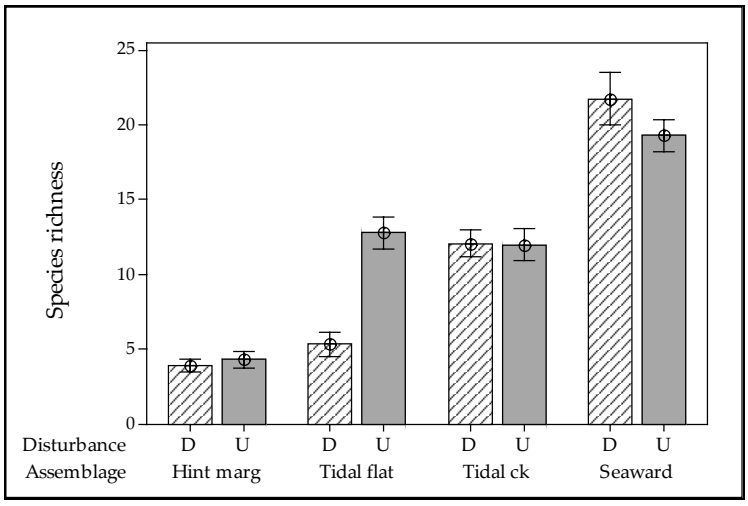


Figure 6-4: Mean species richness (± SE) in disturbed and undisturbed mangroves. Data from dry season surveys pooled from all sites sampled, in the four assemblages from landward (L) to seaward (R).

Although univariate analyses detected little difference in species diversity, multivariate analyses indicated differences in species composition. Ordination of study plots based on the presence/absence of 238 taxa showed that the species composition of undisturbed mangroves differed from that of disturbed mangroves (Figure 6-5). Shoreline position also exerted a strong and overriding influence on invertebrate diversity, shown by

arrangement of study plots in assemblages from the landward to seaward in the same ordination (Figure 6-6).

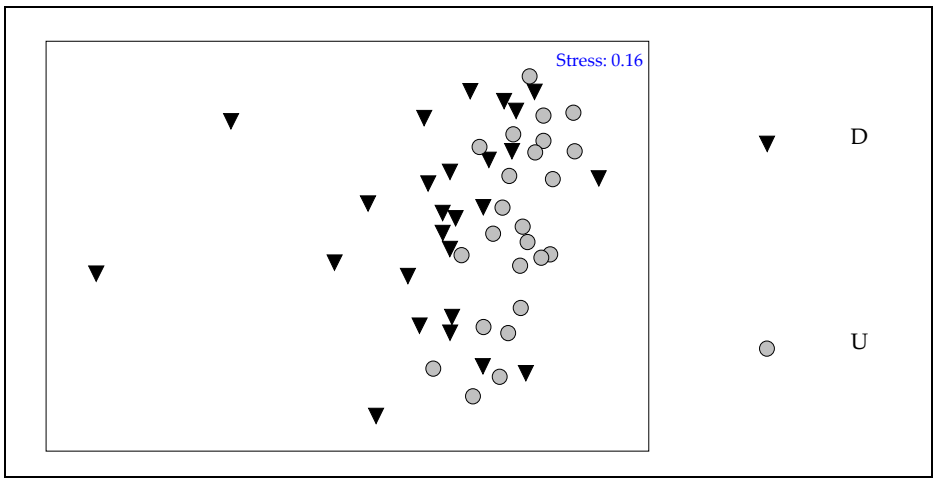


Figure 6-5 : Ordination of 26 disturbed (D) and 24 undisturbed (U) study plots based on invertebrate species richness. Dry season data on the presence or absence of all taxa from three replicate sampling stations pooled for each study plot.

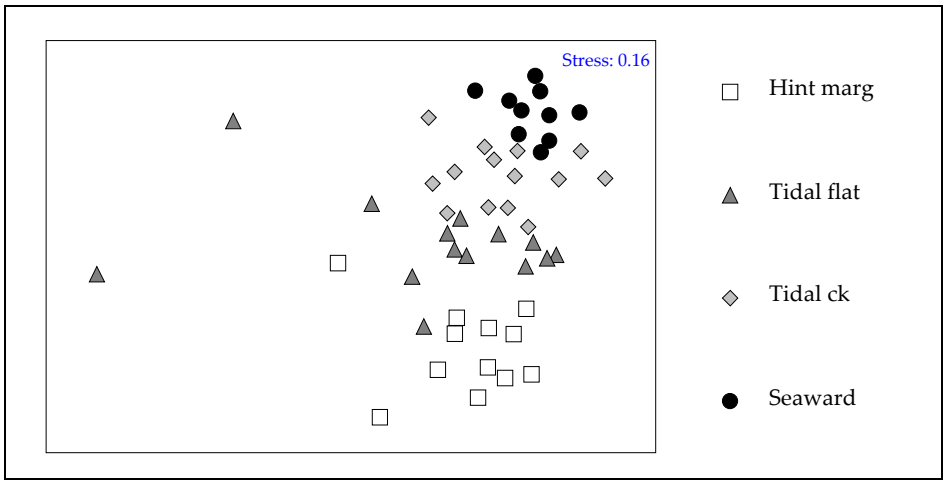


Figure 6-6 : Ordination of 26 disturbed and 24 undisturbed study plots based on invertebrate species richness, indicating zonation. Dry season data on the presence or absence of all taxa (238 species) from three sampling stations was pooled for each plot.

Invertebrate abundance in disturbed mangroves

The mean dry season abundance of invertebrates in disturbed mangroves 19.5 (± 2.3 SE) individuals per sampling station (Table 6-2) was not significantly less than the mean dry season invertebrate abundance for undisturbed sites (24.1 ± 2.6 SE). The highest mean abundance in disturbed mangroves was recorded in the seaward assemblage (54.6 ± 5.4 SE) and the least recorded in the hinterland margin (2.8 ± 0.8 SE).

Comparisons of disturbed sites

ANOVA's revealed no significant differences in mean invertebrate abundance ($\log_{10}(x + 1)$ transformed) between sites or assemblages in disturbed mangroves (Figure 6-7, Tables E-6, E-7 and E-8, Appendix E). A significant main effect for transect was found for analyses involving four disturbed sites (amongst two assemblages), three disturbed sites (three assemblages), and two disturbed sites (four assemblages). The latter two analyses also had a site × assemblage interaction, which indicated that abundance varied between assemblages, amongst sites. Abundance in the seaward assemblage at site DP, for instance, was higher than that recorded in site BV (Figure 6-7).

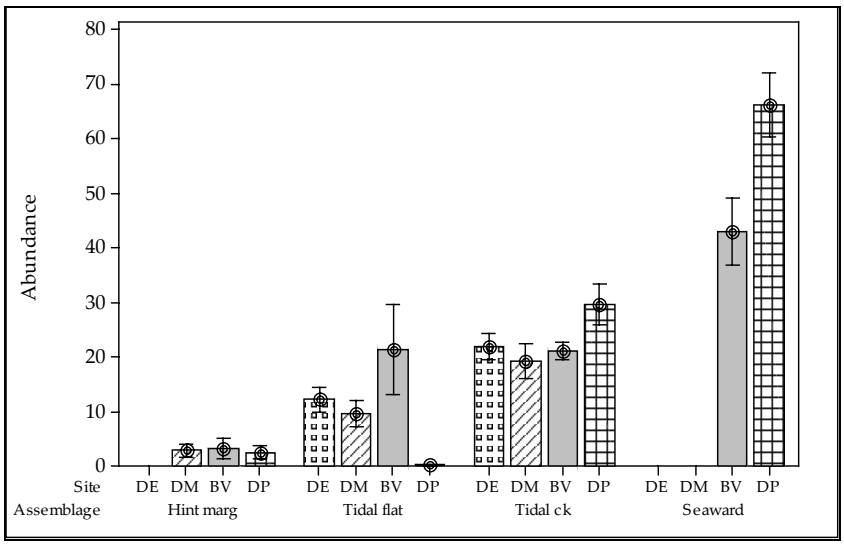


Figure 6-7: Mean abundance of invertebrates in four disturbed sites (± SE). Data pooled for all sampling techniques and averaged for three replicate sampling stations for one dry season survey.

Two of the three analyses comparing abundance in disturbed sites also found a transect × assemblage interaction (Tables E-6 and E-8, Appendix E). This interaction was due to variation between the two transects at each site, in some assemblages. Invertebrate abundance in both the seaward and tidal flat assemblages, differed on Transects 1 and 2 at site BV (Figure 6-8). The higher abundance on transect two in the tidal flat at site BV is presumably due to site specific environmental factors associated with anthropogenic disturbance (see discussion).

Comparisons of disturbed and undisturbed sites

Analyses showed that abundance was not significantly different between disturbed and undisturbed sites and graphs of means show no consistent pattern; abundance in disturbed plots was higher than in undisturbed plots in the seaward assemblage, but

abundance was lower in disturbed sites the tidal flat. Indeed, the most substantial difference between disturbed and undisturbed mangroves appears to be in the tidal flat assemblage (Figure 6-9). Abundance varied significantly between assemblages (Tables E-9 and E-10, Appendix E) and comparison of means indicates that like undisturbed sites, invertebrate abundance in disturbed sites is generally least in the hinterland margin and increases to seaward (Figure 6-9).

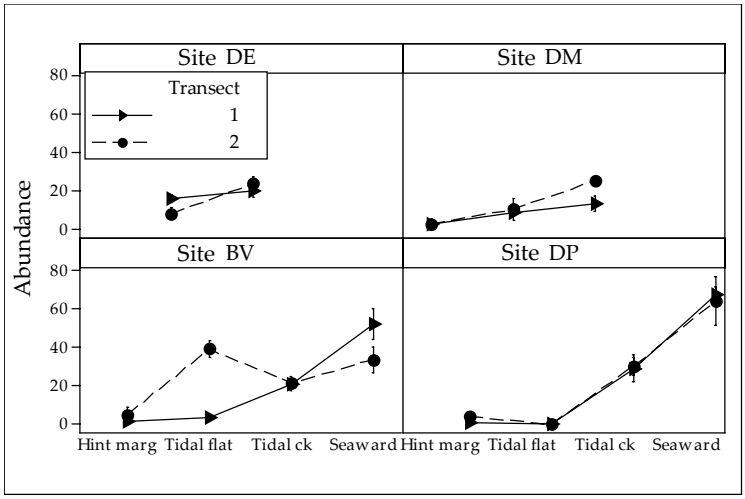


Figure 6-8: Mean abundance of invertebrates recorded on the two transects at each of the four disturbed sites, in assemblages from landward (L) to seaward (R).

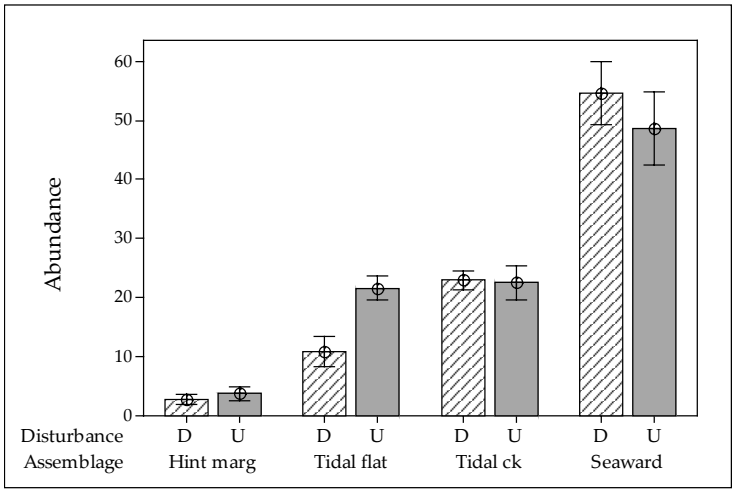


Figure 6-9: Mean abundance (±SE) of invertebrates in disturbed and undisturbed mangroves in assemblages from landward (L) to seaward (R). Data pooled across three undisturbed sites and four disturbed sites sites from one dry season survey.

Significant assemblage × site and assemblage × transect interactions were found for both analyses comparing disturbed and undisturbed sites (Tables E-9 and E-10, Appendix E). These interactions relate primarily to local variations in abundance in assemblages and from one transect to the other, as described above for disturbed sites. The assemblage ×

site interaction is primarily due to markedly low numbers of invertebrates in the heavily impacted tidal flat assemblage at site DP (Figure 6-10).

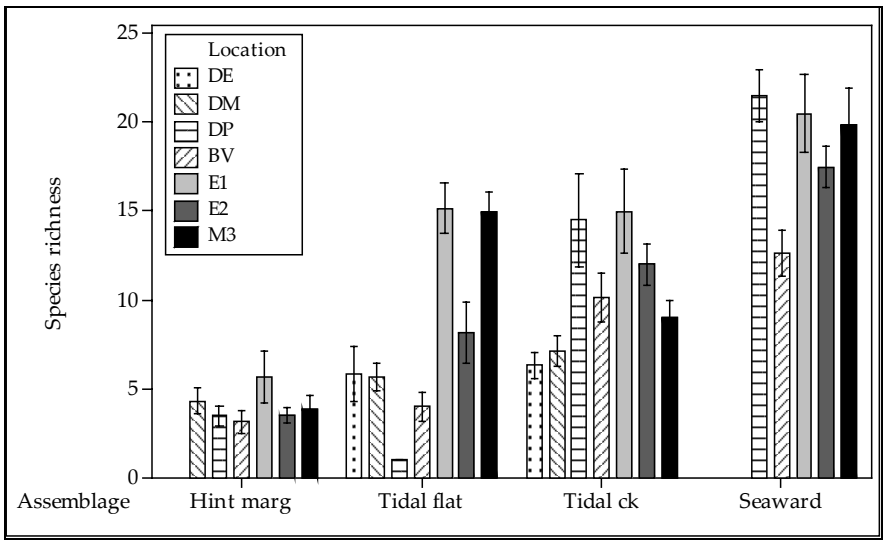


Figure 6-10: Mean abundance (± SE) of all invertebrates in four assemblages at disturbed (solid symbols) and undisturbed sites (hollow symbols).

~6.3.2. Worm species richness in disturbed mangroves

A total of 33 worm species from 21 families were recorded from the four disturbed locations during the single dry season survey (Table B-2, Appendix B). As for undisturbed sites, the majority of species (90.9%) are from the class Polychaeta. Overall species richness of worms recorded at disturbed sites (33 species) was higher than at undisturbed sites (dry season 24 species; 31 species both seasons). Of the grand total of 49 species recorded from disturbed and undisturbed mangroves, 36.7% (18 species) were recorded only from disturbed sites.

Comparisons of disturbed sites

Analyses of species richness in the two disturbed sites (BV and DP), where worms were sampled within all four assemblages, found no significant differences between sites or assemblages (Table E-11, Appendix E). Analyses of worm species richness in three assemblages at three disturbed sites (BV, DM and DP) found differences between assemblages and a site × assemblage interaction (Table E-12, Appendix E). This analysis did not include the more variable data obtained from the seaward assemblage and indicated that worm diversity was significantly different between these assemblages. Indeed, no worms were recorded in the hinterland margin assemblage. Species richness varied in assemblages, between study locations. For example, worms were recorded in

the tidal flat at sites DE and DM, but none were found at sites BV or DP (Figure 6-11). The numbers of worms recorded in the seaward assemblage varied markedly between sites BV and DP

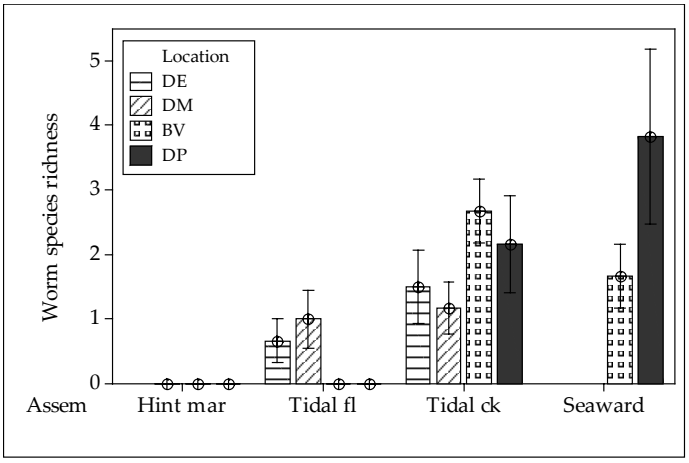


Figure 6-11: Mean species richness (±SE) of worms per sampling station at the four disturbed sites studied in assemblages from landward (L) to seaward (R).

Comparisons between disturbed and undisturbed sites

Univariate analyses found no differences in worm species richness between disturbed and undisturbed mangroves. Worm species richness differed between assemblages however, and species richness in assemblages varied amongst the sites studied. The same pattern was found when comparing the two disturbed sites with three undisturbed sites in the four assemblages (Table E-15, Appendix E) and when comparing three disturbed and three undisturbed sites in the three landward assemblages. Overall, worm species richness varied between sites in most assemblages and was occasionally higher in disturbed sites than in undisturbed (Figure 6-12).

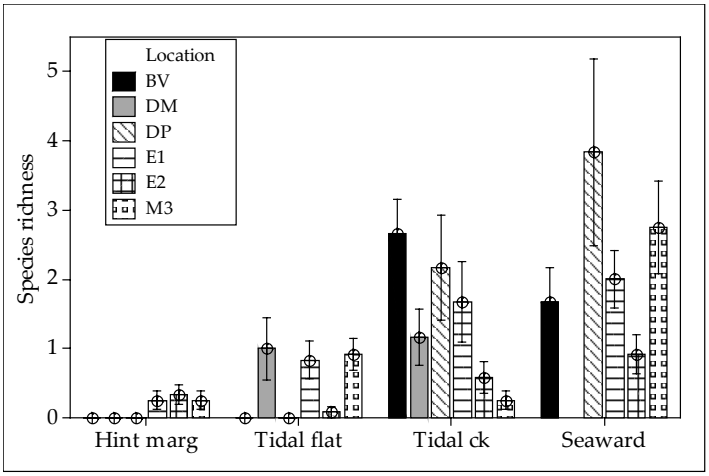


Figure 6-12: Mean worm species richness (±SE) per station in disturbed (solid colour bars) and undisturbed sites (hatched bars) in assemblages from landward (L) to seaward (R).

~6.3.3. Worm abundance in disturbed mangroves

The six most abundant worm species in disturbed sites were *Phascolosoma arcuatum*, *Nereis* sp. 1, *Lepidonotus* sp. 1, *Heteromastis* sp. 1 and *Simplisetia* cf. *erythraensis*.

Comparisons of disturbed sites

Analyses of worm abundance at two disturbed sites (BV and DP) in four assemblages found no significant differences between sites (Table E-13, Appendix E) but as for species richness, worm abundance differed between assemblages. Analyses of abundance in three assemblages at three disturbed sites (BV, DM and DP) found the mean abundance of worms in assemblages varied between sites. This result appears to be due largely to the high abundance of worms in the seaward assemblage at site DP (Figure 6-13,Table E-14, Appendix E).

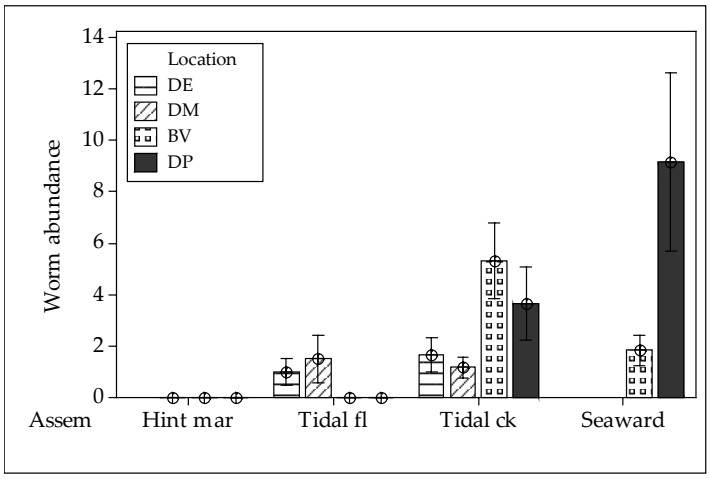


Figure 6-13: Mean abundance of worms (±SE) at the four disturbed sites studied in assemblages from landward (left) to seaward (right).

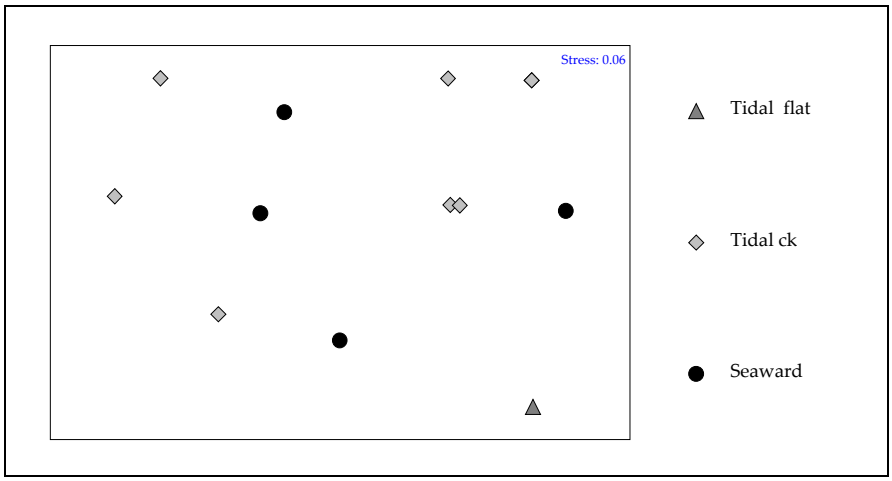


Figure 6-14: Ordination of 14 study plots in three assemblages based on the abundance of 33 worm species in one dry season survey of disturbed mangroves.

The ordination based on the abundance of 33 worm species recorded in 14 study plots indicated no clear pattern of distribution amongst assemblages and suggests that the worm faunas of the tidal creek and the seaward assemblage were similar (Figure 6-14). There were too few worms sampled from the tidal flat and the hinterland margin assemblages to allow any meaningful interpretation.

Comparisons of disturbed and undisturbed sites

Univariate analyses found no difference in worm abundance ($\log_{10}(x + 1)$ transformed) between disturbed and undisturbed mangroves (Tables E-17 and E-18, Appendix E). Analyses comparing disturbed and undisturbed sites indicated variation in the numbers of worms sampled in assemblages, and amongst assemblages between sites (Figure 6-15). This pattern was also found for species richness of worms. Worms were particularly abundant in the tidal creek at site BV, and in the seaward assemblage at site DP.

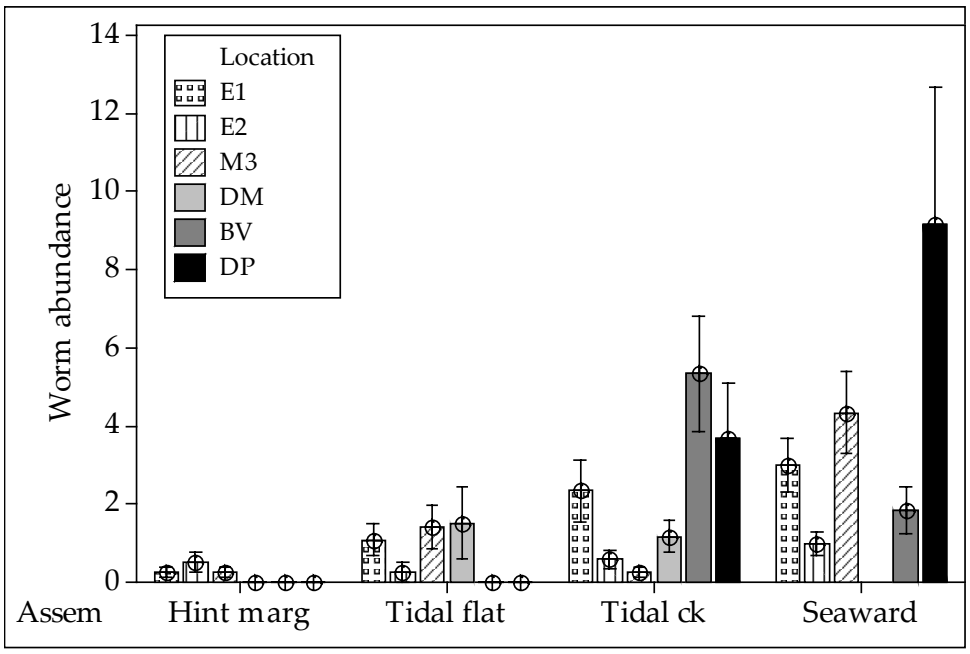


Figure 6-15: Mean abundance (±SE) of worms in disturbed (solid bars) and undisturbed sites (hatched bars) in assemblages from landward (L) to seaward (R).

Comparison of worm abundance in disturbed and undisturbed sites using multivariate analysis clearly showed a distinctive grouping of disturbed sites to the left and undisturbed sites toward the right of the ordination (Figure 6-16). The ordination and the graphs of means indicate increased abundance of worms in the tidal creek and seaward assemblages of the disturbed sites in this study.

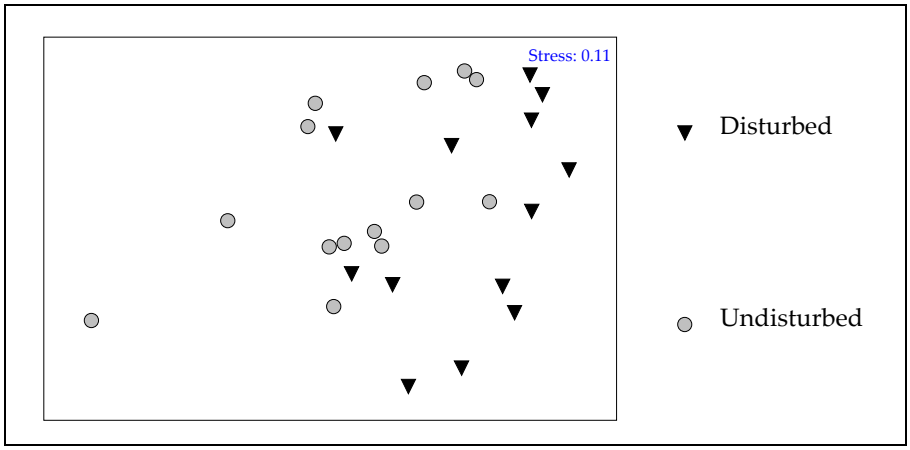


Figure 6-16: Ordination of 27 study plots in four disturbed and three undisturbed locations based on the dry season abundance of 49 worm species. Abundance data was pooled for each sampling method and across three replicates per study plot.

~6.3.4. Worm feeding guilds

Comparisons of disturbed sites

In disturbed mangroves, surface deposit feeders (15 species) and carnivores (8 species) were predominant (Appendix B-2). The abundance of worms in the five main trophic categories were not particularly consistent between assemblages (Figure 6-17) and overall, surface deposit feeders appeared most numerous in the tidal creek, while more carnivores and herbivores were sampled from the seaward assemblage. No worms were sampled from the hinterland margin assemblage and filter feeders were rare.

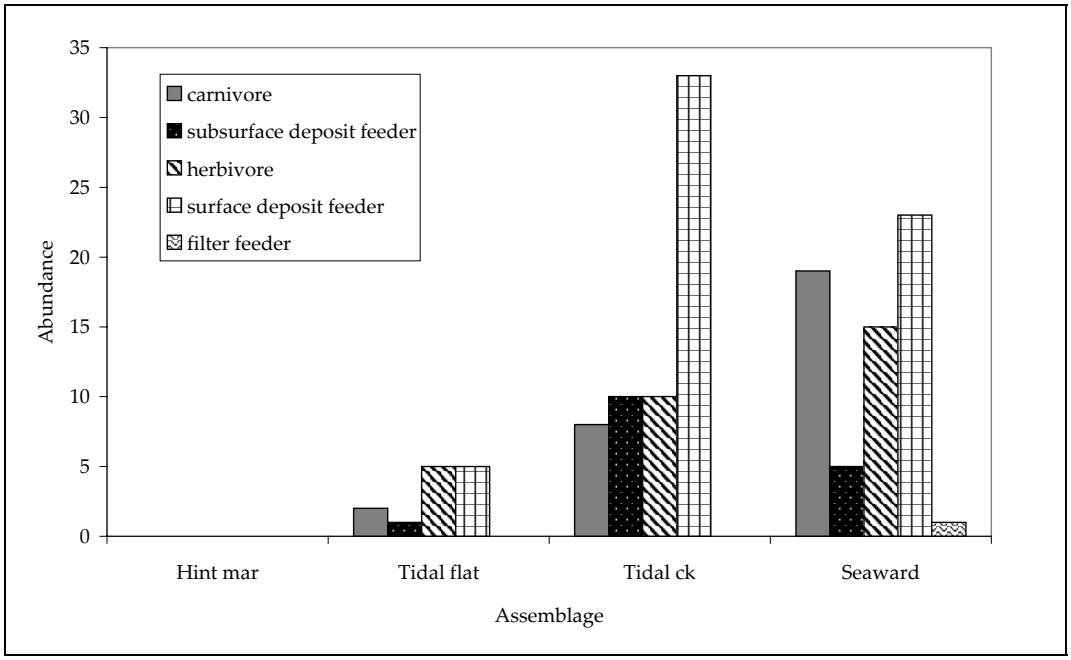


Figure 6-17: Total abundance of worms in trophic groups recorded in the four assemblages, summed for all surveys conducted at four disturbed sites.

Comparisons of disturbed and undisturbed sites

Comparisons of worms in the five trophic groups between disturbed and undisturbed sites indicated differing abundances of species in trophic categories. Analyses of variance found significant differences in abundance of surface deposit feeders; which were more numerous in disturbed sites than in undisturbed sites (Table E-19, Appendix E; Figure 6-18). Although carnivores were apparently less numerous in disturbed sites, the differences were not statistically significant.

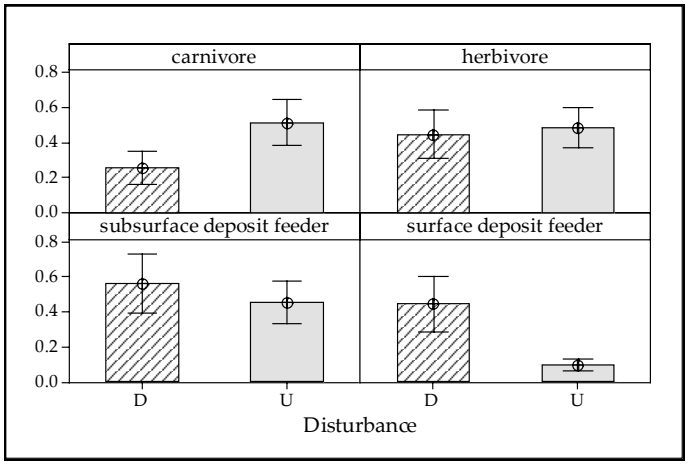


Figure 6-18:Mean abundance of worms in the four main feeding quilds in disturbed (D) and undisturbed (U) mangroves. Means represent average abundance per sampling station, pooled across 78 disturbed and 72 undisturbed replicates.

Abundance of surface deposit feeders differed between assemblages and as for other worms, appeared to be most populous in the seaward assemblage. The abundance of surface deposit feeding worms was significantly greater in assemblages in disturbed sites than in undisturbed sites (Figure 6-19, Table E-19, Appendix E).

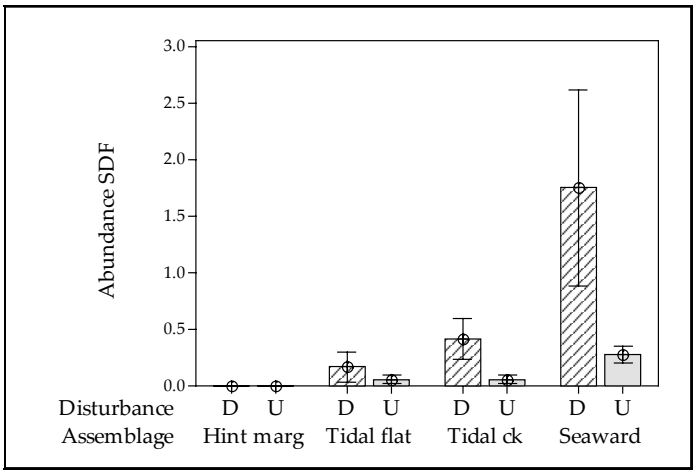


Figure 6-19:Mean abundance ($\log_{10}(x + 1)$ transformed) of surface deposit feeders (±SE) in disturbed (D) and undisturbed sites (U) in the four assemblages from landward (left) to seaward (right). Data pooled for 2 disturbed (BV, DP) and 2 undisturbed sites (E2 , M3).

No differences between disturbed and undisturbed mangroves were detected by analyses for other trophic groups. These results are, however, based on one dry season survey conducted during 2001 and further sampling is required to substantiate these findings.

~6.3.5. The ant fauna of disturbed mangroves

A total of 21 species of ants were recorded from the four disturbed sites (Table B-3, Appendix B). Total species richness was very similar to the dry season tally for undisturbed sites (23 species). Of the grand total of 33 species recorded for disturbed and undisturbed sites, seven species (21.2%) were recorded only from disturbed sites (Table B-3, Appendix B). Across all surveys, three were introduced species, namely *Paratrechina longicornis, Solenopsis geminata* and *Monomorium floricola. P. longicornis* was recorded from undisturbed sites and the other two species from disturbed sites. Several of the ant species represent new records for mangrove habitats (*Crematogaster* sp. 6 (cornigera group); *Polyrhachis* sp. (subgenus Hedomyrma); *Pheidole* sp. A and *Opisthopsis major*).

Comparisons of disturbed sites

Analyses comparing ant diversity (i.e. firstly, comparing the three landward assemblages at three disturbed sites; and secondly, in all four assemblages at two disturbed sites) indicated ant species richness was greatest in the hinterland margin, but lower in the other assemblages (Figure 6-20, Tables E-20 and E-21, Appendix E).

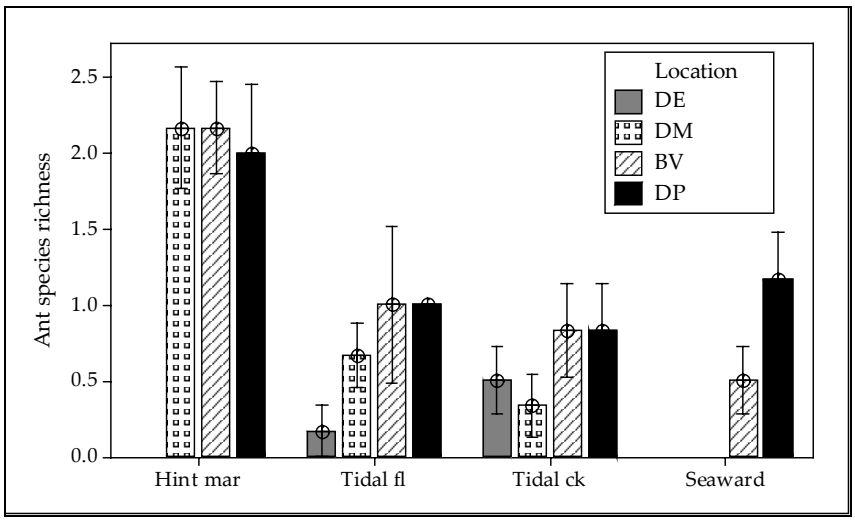


Figure 6-20: Mean ant species richness (± SE) per study plot, in assemblages at the four disturbed sites studied.

Comparisons of disturbed and undisturbed sites

Comparisons of ant diversity between disturbed and undisturbed sites, revealed no significant differences relating to disturbance, but significant differences between assemblages were evident (Table E-23 and E-24 Appendix E). Ant species richness in both disturbed and undisturbed mangroves was higher on the hinterland fringe than in other mangrove habitats (Figure 6-21, Tables E-23, Appendix E).

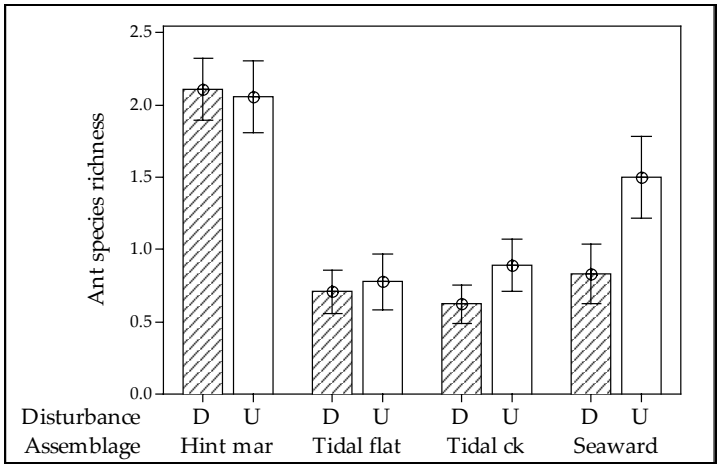


Figure 6-21: Mean species richness of ants in the four assemblages, in disturbed (D) and undisturbed (U) study plots. Means calculated from three replicate sampling stations, for 18 disturbed and 12 undisturbed study plots, during one dry season survey.

NMDS ordination of study plots in disturbed sites indicates that only the ant faunas of the seaward and hinterland margin assemblages were distinct. The ant fauna sampled from the tidal creek and tidal flat assemblages showed no strong affinity to any particular habitat (Figure 6-22).

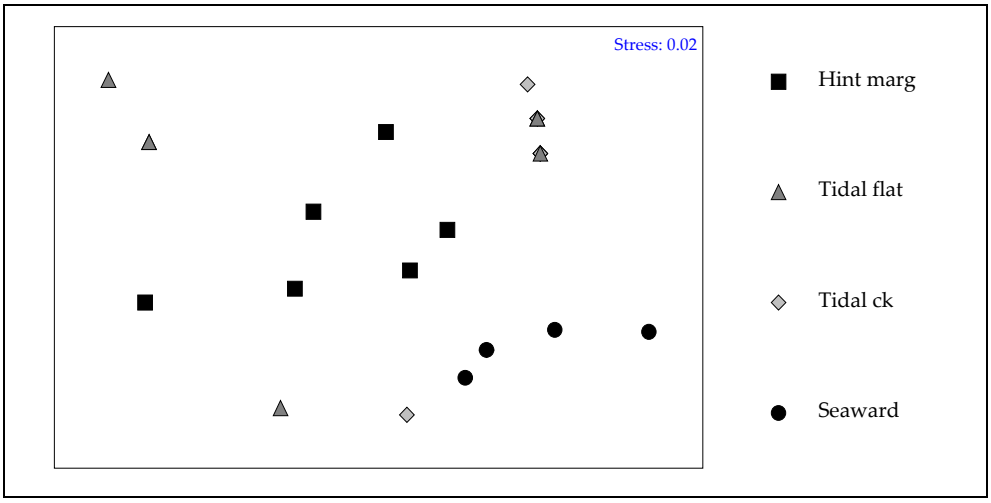


Figure 6-22: Ordination of 25 study plots in disturbed mangroves based on the frequency of 21 species of ants during a single dry season survey. Data pooled for three replicate sampling stations within each subplot, across four sites.

The ordination of all study plots in disturbed and undisturbed sites based on the presence/absence of 32 ant species did not suggest that disturbance strongly affected species composition (Figure 6-23).

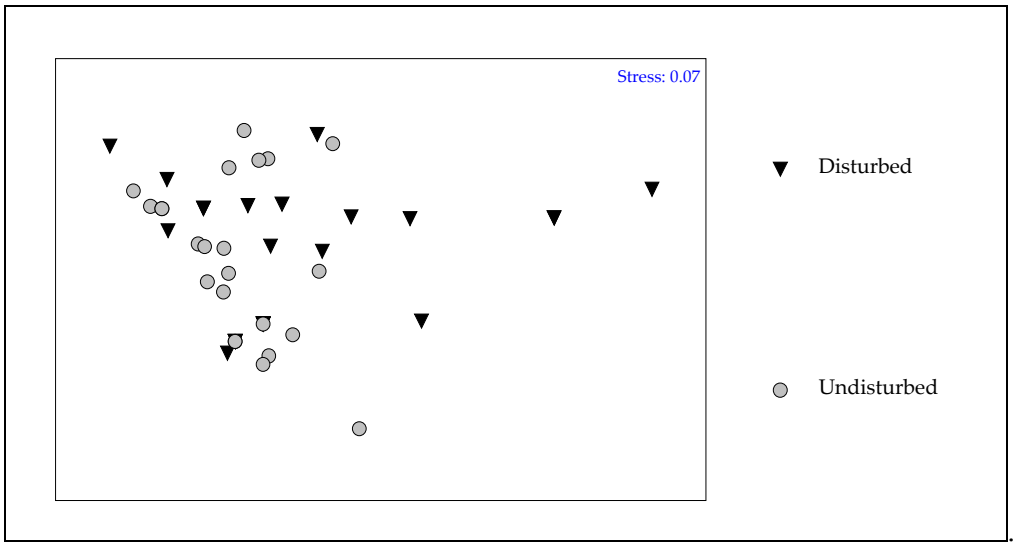


Figure 6-23: Ordination of 48 study plots in disturbed (triangles) and undisturbed (circles) study plots based on frequency of 32 ant species sampled during the dry season. Data pooled from 3 replicate sampling stations per studyplot in each assemblage.

When assemblage is highlighted in the same ordination, shoreline position appears to be the only major factor influencing the diversity of ant species across the intertidal zone (Figure 6-24)

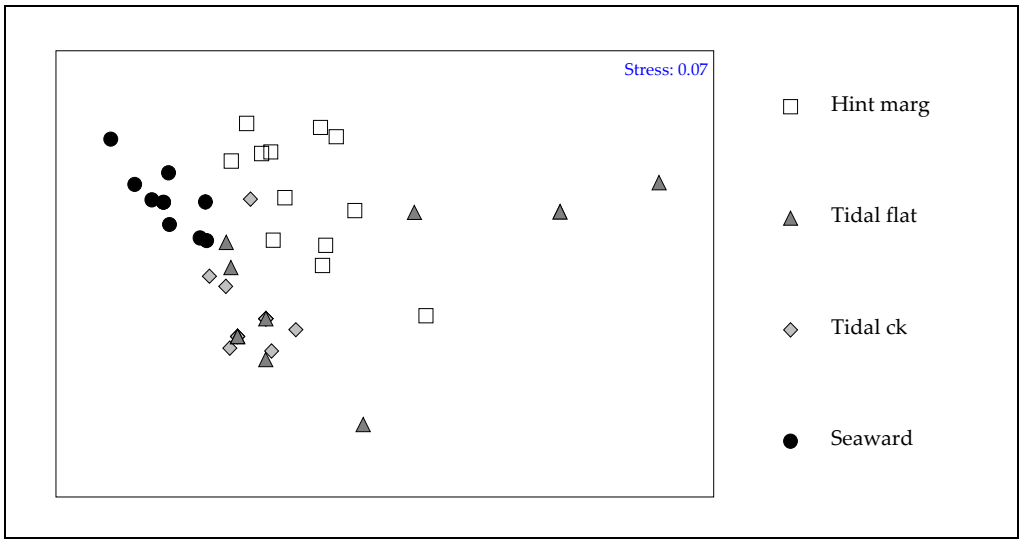


Figure 6-24: Ordination of 48 study plots in assemblages in disturbed and undisturbed study plots based on frequency of 32 ant species sampled during the dry season. Data pooled from 3 replicate sampling stations per studyplot in each assemblage.

Closer examination of ants in the hinterland margin assemblage however, clearly indicated separation of the ant fauna of disturbed and undisturbed mangroves (Figure 6-25). This was the only assemblage in which a pattern related to disturbance was evident for ant species composition. The single disturbed site, amongst the undisturbed plots in Figure 26, was study plot DP62. This plot was one of the least disturbed and the most distant from anthropogenic development.

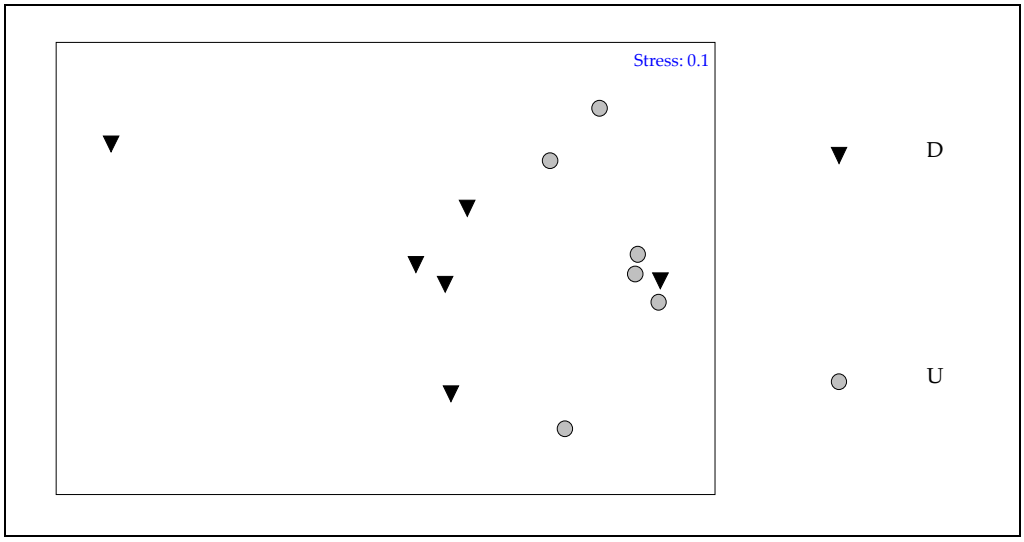


Figure 6-25: Ordination of 12 study plots in the hinterland margin assemblage based on the frequency of 32 ant species, indicating disturbed (D) and undisturbed (U) plots.

~6.3.6. Crustaceans of disturbed mangroves

Crustacean species richness

Forty-eight species of crustaceans were recorded in disturbed mangroves in the dry season of 2001 and of that total, six species were not found in undisturbed sites (Tables B-4 and B-5, Appendix B). Crustaceans other than crabs (particularly amphipods, barnacles) were not found as frequently, and uncommon species, such as tanaids and upogebiids, were not recorded in surveys in disturbed sites (Table 6-3). Consequently, crabs comprised a slightly larger percentage of the crustacean fauna of disturbed mangroves (72.9%) than of that in undisturbed sites (66.7%).

Comparisons of disturbed sites

Crustacean species richness differed between assemblages at disturbed sites, in each of the three ANOVA's comparing two, three and four sites, amongst different combinations of assemblages (Tables E-25 to E-27, Appendix E). Furthermore, analyses

comparing crustacean diversity in the three landward assemblages at three disturbed sites, indicated that species richness on transect two tended to be higher than on transect one. The site × assemblage interaction was mainly attributable to nil species richness of crustaceans in the tidal flat at site DP (Figure 6-26). At this location, the tidal flat had been isolated from tidal inundation by construction of a bund wall.

Table 6-3: Numbers of taxa in different crustacean groups recorded from three undisturbed sites, four disturbed sites and and the tally of species overall.

Crustacean group	Undisturbed wet season	Undisturbed dry season	Disturbed sites dry season	All surveys
Amphipod	5	6	3	7
Barnacle	2	2	-	2
Crab	30	37	35	43
Isopod	2	3	3	4
Mud lobster	1	1	1	1
Shrimp	5	3	6	7
Tanaid	1	1	-	1
Upogebiid	1	1	-	1
Total	60		48	66

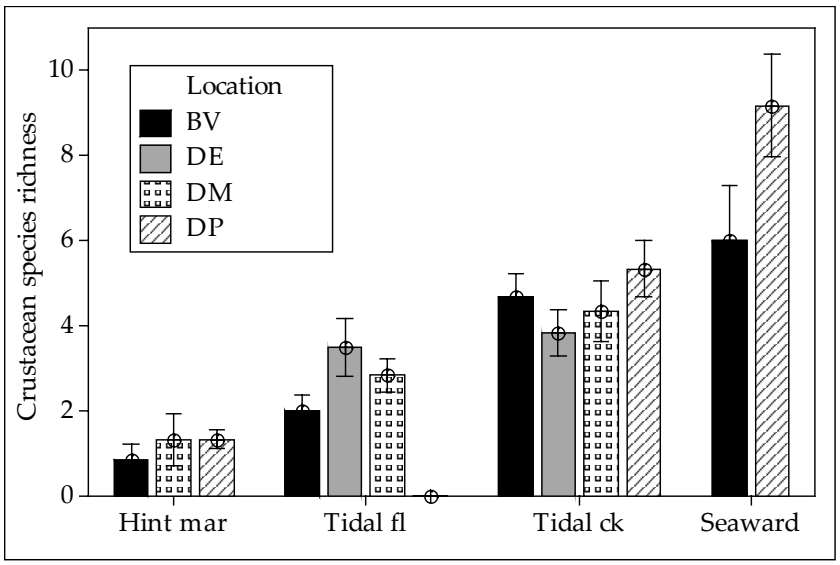


Figure 6-26 : Mean crustacean species richness (± SE) in assemblages at the four disturbed sites studied.

Comparisons of disturbed and undisturbed sites

Mean overall species richness of crustaceans per sampling station in disturbed sites (3.5 ± 0.3 SE) was similar to that recorded in dry season surveys in undisturbed sites (3.9 ± 0.3 SE). Mean crustacean diversity within the four assemblages was also similar between disturbed and undisturbed mangroves (see Table 5-3, Chapter 5 and Table 6-2 of this

chapter). Analyses comparing species richness of crustaceans in disturbed and undisturbed sites found no significant differences between disturbance regimes, nor between sites, but mean crustacean species richness in both disturbed and undisturbed sites increased progressively in assemblages from landward to seaward (Figure 6-27, Tables E-31 and E-32, Appendix E). Significant variation was detected between transects but showed no consistent trends between disturbed and undisturbed sites.

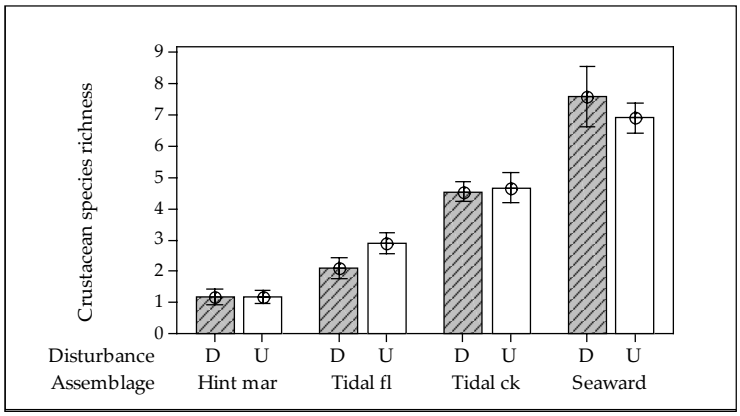


Figure 6-27: Mean crustacean species richness (±SE) in disturbed and undisturbed assemblages. Values are means per study plot, averaged over 3 undisturbed and 4 disturbed sites for all sampling techniques.

Crustacean abundance

Comparisons of disturbed sites

Mean overall abundance per sampling station of crustaceans in disturbed sites (12.6 ± 1.5 SE) was comparable with that recorded in undisturbed sites (14.9 ± 2.0 SE). Analyses of crustacean abundance between the four disturbed sites found only a transect × assemblage interaction for each of the three ANOVAs comparing abundance in different assemblages in two, three and four disturbed sites respectively (Tables E-28 to E-30, Appendix E). The graph of means showed variation between transects in assemblages at the four sites studied, but no consistent trends were evident (Figure 6-28).

Comparisons of disturbed and undisturbed sites

Ordination of the 26 study plots in disturbed sites on the basis of crustacean abundance indicated that, despite the influence of anthropogenic disturbance, crustacean populations within assemblages remained quite discrete. Crustacean diversity and abundance in study plots in the two landward assemblages however, was more variable than that in the two seaward assemblages (Figure 6-29). Comparison of crustacean

abundance between disturbed and undisturbed sites found significant differences between assemblages for ANOVA's comparing crab populations amongst three landward assemblages at three sites, and amongst all four assemblages at two disturbed sites (Tables E-33 and Tables E-34, Appendix E).

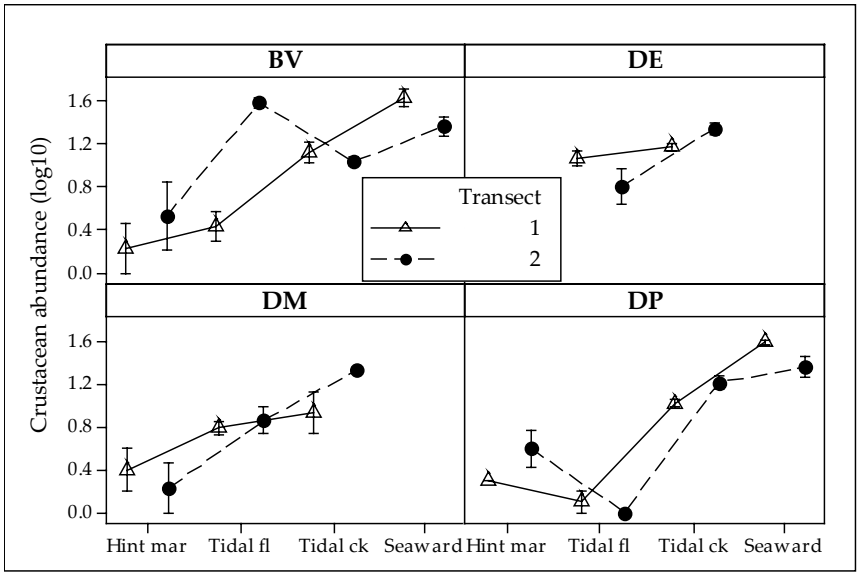


Figure 6-28: Mean crustacean abundance (± SE) in four assemblages from landward (left) to seaward (right) on the two transects at each of the four disturbed sites studied.

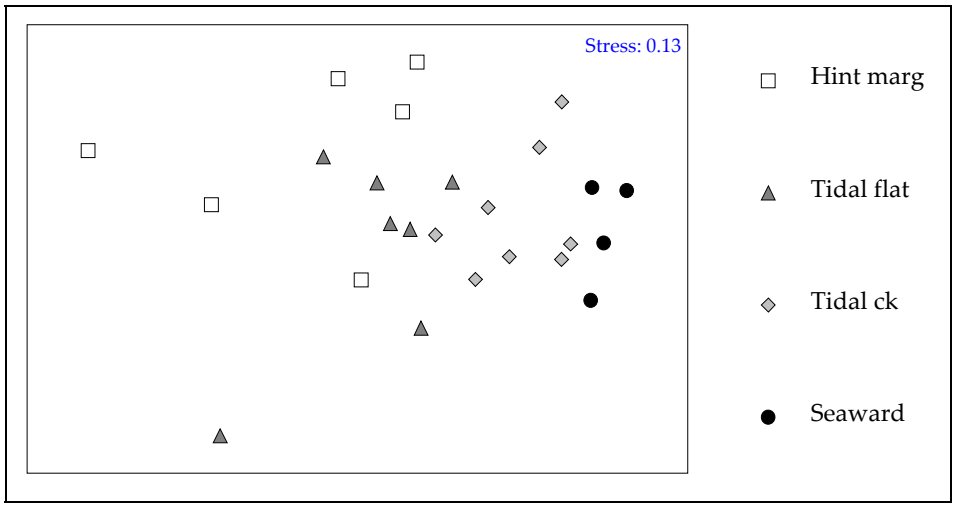


Figure 6-29:Ordination of 26 study plots in disturbed mangroves based on the abundance of 56 crustacean species.

Abundance data displayed the same pattern found for species richness: that is, crustacean abundance was markedly higher in the seaward assemblage and decreased landward, with the lowest numbers of crustaceans in the hinterland margin assemblage. No differences in overall abundance of crustaceans were found between disturbed and undisturbed sites (Figure 6-30).

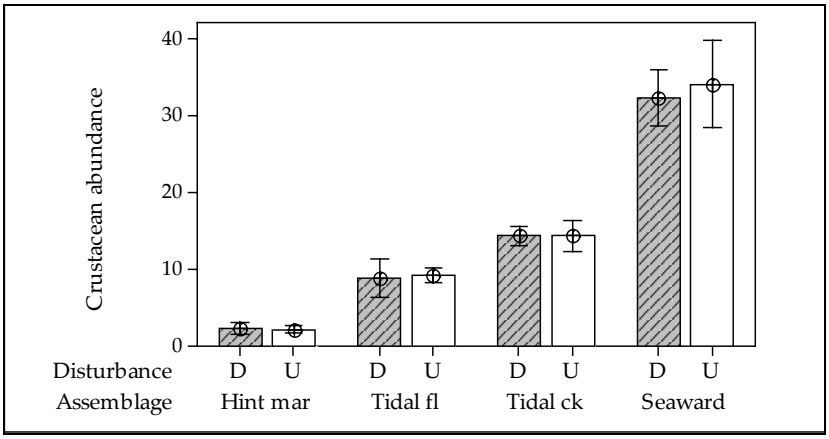


Figure 6-30: Mean crustacean abundance (±SE) in disturbed and undisturbed assemblages. Values are means per study plot, averaged over 3 undisturbed and 4 disturbed sites for all sampling techniques.

An assemblage × transect interaction (graphed for disturbed sites only in Figure 6-29) was also found in analyses comparing disturbed and undisturbed sites, and appeared to represent local, small scale variation in crustacean populations on the two transects studied at each location.

By contrast, NMDS ordination of disturbed and undisturbed study plots on the basis of their species abundance showed differentiation of the crustacean fauna of undisturbed and disturbed sites (Figure 6-31).

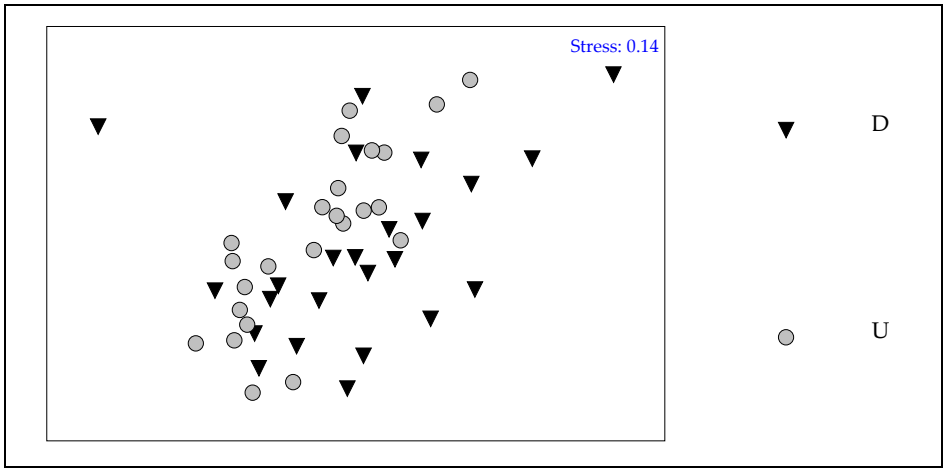


Figure 6-31: Ordination based on the abundance of crustaceans in 26 disturbed and 24 undisturbed study plots sampled during one dry season survey. Data pooled for all sampling techniques and averaged across three sampling stations per study plot.

Most of the disturbed sites scattered amongst the undisturbed sites (to the left of the ordination) were the least impacted of the 'disturbed' sites studied. They include, for instance, several study plots (e.g. DM62, BV22 and BV81, see Chapter 2 for locations)

that, despite being situated immediately adjacent to clearings or man-made structures, showed no major signs of habitat degradation. The influence of assemblage or intertidal position on crab populations was not diminished by disturbance, and crustaceans in assemblages across disturbed and undisturbed mangroves showed close affinity to particular assemblages (Figure 6-32). Crustacean diversity and abundance increased seaward across the intertidal gradient, (i.e. from top right to bottom left in the ordination). The other clear trend evident in this ordination is for disturbance, which decreased from the top left to bottom right of the same ordination (Figure 6-31).

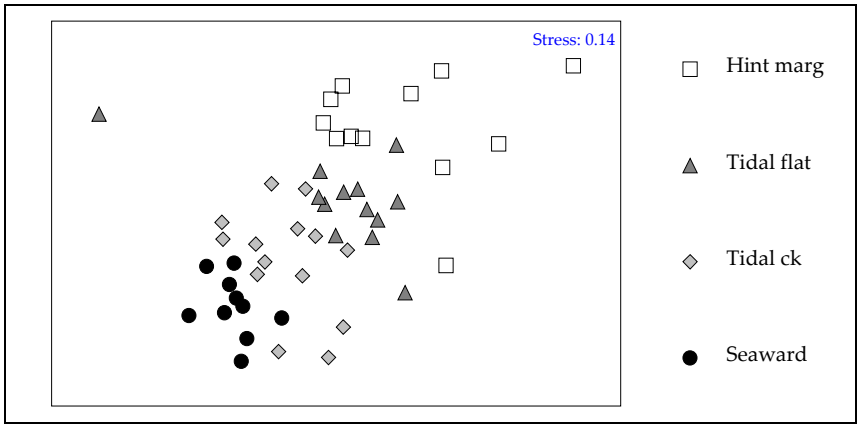


Figure 6-32: Ordination of disturbed and undisturbed sites shown in Fig. 6-31 with the factor, assemblage highlighted.

Although univariate analyses of the mangrove crustacean fauna as a whole detected no significant effects of anthropogenic disturbance, the two main families of mangrove crabs (Grapsidae, 13 species and Ocypodidae, 10 species) differed in their disturbance ecology.

Grapsid crab diversity and abundance

Comparisons of disturbed sites

No significant differences were found between the four disturbed sites in analyses comparing species richness of grapsid crabs (Tables E-35 to E-37, Appendix E). Significant differences between assemblages were found only in analyses that included the seaward assemblage (Figure 6-33, Table E-35, Appendix E). Similarly, the abundance of grapsid crabs varied between assemblages in analyses comparing all four assemblages at two disturbed sites (Table E-38, Appendix E). Significant variations in grapsid abundance were found in comparisons of the three landward assemblages at

the three disturbed sites (Table E-39, Appendix E), related mainly to the absence of crabs in the highly disturbed tidal flat assemblage at Site DP (Figure 6-34). In the two landward assemblages at the four disturbed sites, no differences in grapsid crab abundance were found between sites or assemblages (Table E-40, Appendix E).

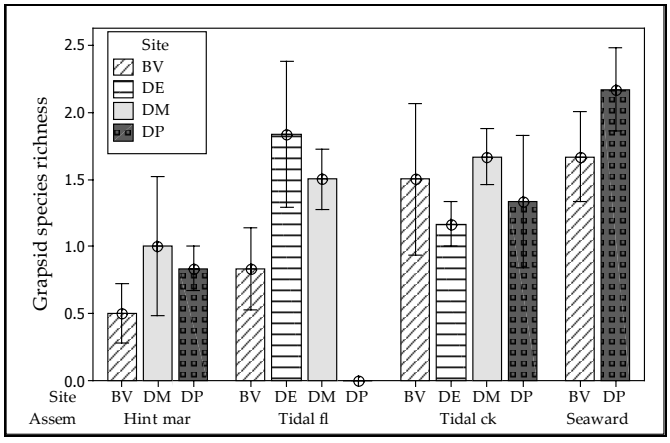


Figure 6-33: Mean grapsid species richness (±SE) in assemblages at the four disturbed sites

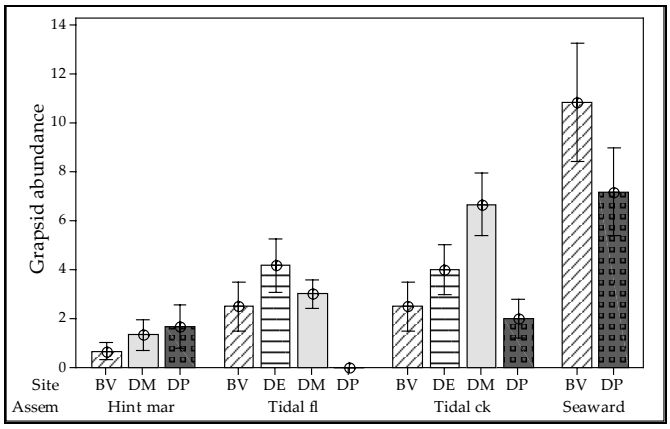


Figure 6-34: Mean grapsid abundance (±SE) in assemblages in the four disturbed sites.

Comparisons of disturbed and undisturbed sites

Analyses comparing the species richness of grapsid crabs between disturbed and undisturbed sites found no significant differences related to disturbance (Tables E-41 and E-42, Appendix E). Grapsid species richness was generally least in the hinterland margin but this varied significantly amongst sites. For example, high grapsid species richness was found on bulldozed tracks in the tidal flat at Site DE and in the seaward assemblage at site BV (Figure 6-33).

A similar pattern (of variation in assemblages between sites) to that observed for grapsid species richness was also observed for grapsid abundance (Figure 6-34, Tables E-43 and E-44, Appendix E). However, the abundance of grapsid crabs was significantly

less in disturbed sites (Figure 6-35, right).

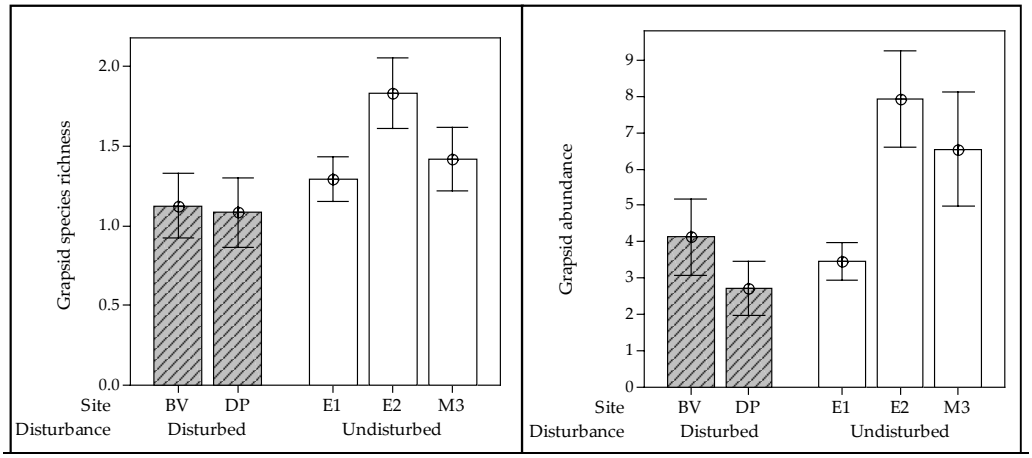


Figure 6-35: Mean species richness± SE (left) and abundance (right) of Grapsid crabs in disturbed and undisturbed sites averaged across the four assemblages.

Ocypodid crab diversity and abundance

Comparisons of disturbed sites

Analyses comparing ocypodid crabs in all four assemblages at sites BV and DP found no significant differences in species richness (Table E-45, Appendix E). Differences in species richness were found between assemblages in comparisons of the three landward assemblages at three disturbed sites (Figure 6-36, Table E-46, Appendix E). Ocypodid diversity also varied between the two transects, amongst assemblages at each site, mainly due to small-scale variation in ocypodid populations. High species richness in the tidal creek assemblage at site DP (Figure 6-37) was, for example, mainly due to the occurrence of several *Macropthalmus* species and *Uca seismella* (Table B-5, Appendix B).

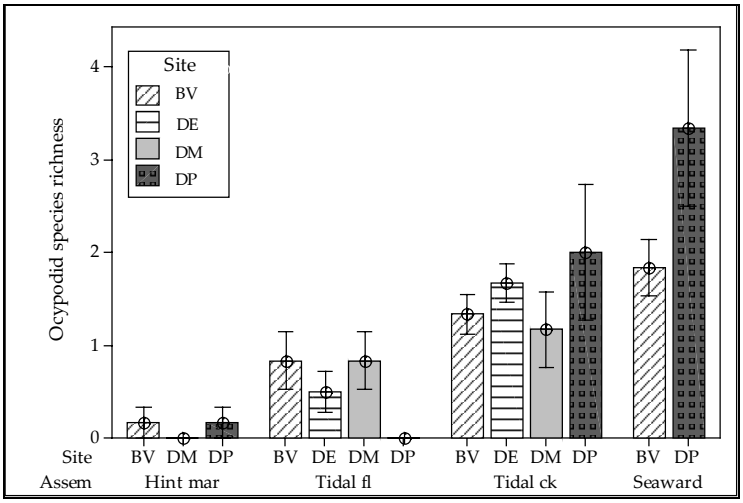


Figure 6-36: Mean Ocypodid species richness (±SE) in assemblages at four disturbed sites.

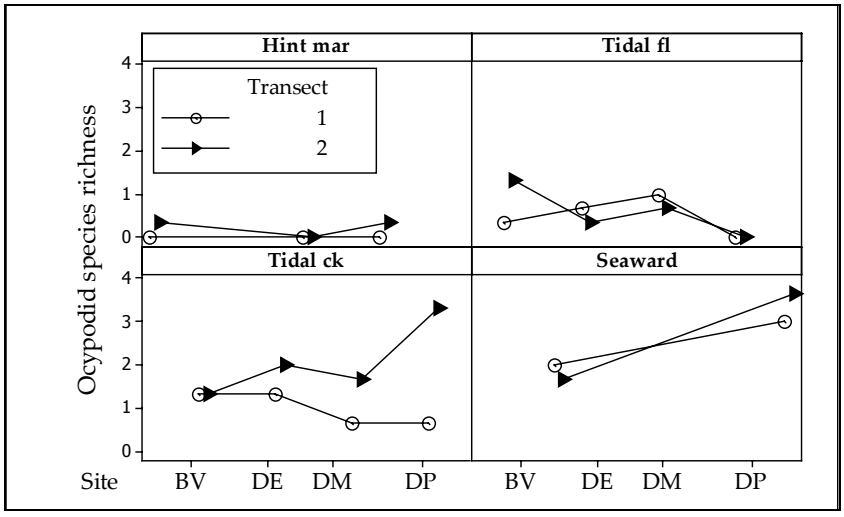


Figure 6-37: Mean Ocypodid species richness (±SE) on two transects at the four disturbed sites.

In each of the three ANOVA's examining the abundance of ocypodid crabs at disturbed sites, significant variation was detected between transects 1 and 2 within the assemblage studied (Tables E-48 to E-50, Appendix E). Overall however, mean abundance of ocypodid crabs in disturbed mangroves did not show consistent patterns between sites or assemblages (Figure 6-38).

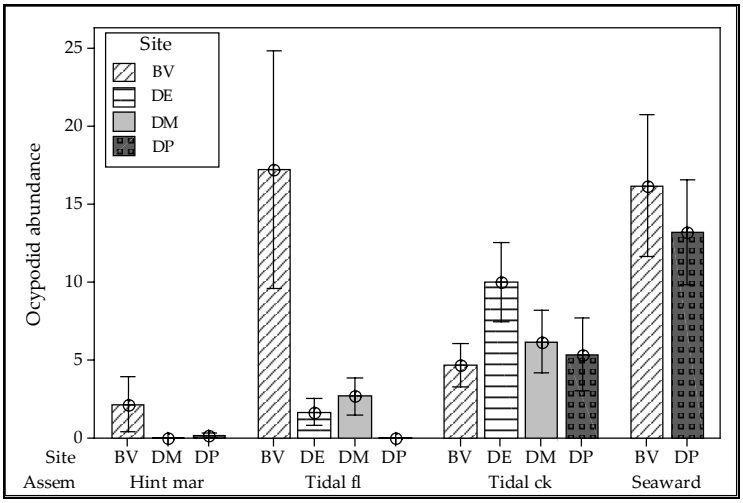


Figure 6-38: Mean abundance of ocypodid crabs (± SE) in assemblages at disturbed sites.

Comparisons of disturbed and undisturbed sites

Analyses comparing the species richness of ocypodid crabs in all four assemblages at 2 disturbed and 3 undisturbed sites found significant differences in relation to disturbance (Tables E-51, Appendix E). Unlike the pattern observed for grapsid crabs which declined in disturbed sites, mean ocypodid crab species richness was significantly higher in disturbed mangroves (Figure 6-39, left). Ocypodid species

richness varied between assemblages in analyses comparing the two combinations of disturbed and undisturbed sites (Tables E-51 and E-52, Appendix E). An assemblage × transect interaction was also found when comparing data from the three landward assemblages at three disturbed sites, with three undisturbed sites. It appears to relate mainly to the high ocypodid diversity in the tidal creek assemblage at site DP, described above.

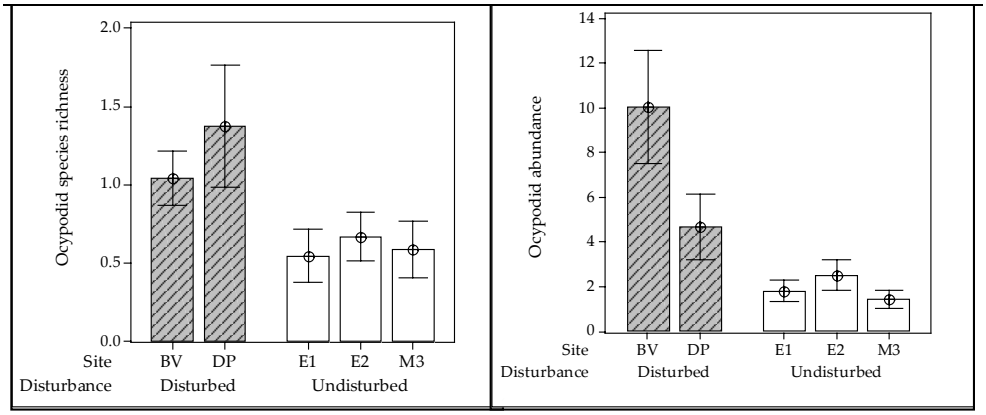


Figure 6-39: Mean species richness ± SE (left) and abundance (right) of Ocypodid crabs in disturbed and undistrubed sites averaged across the four assemblages.

Abundance of ocypodid crabs ($\log_{10}(x + 1)$ transformed) did not vary in relation to disturbance, as did species richness. The graph of means suggests there were differences in ocypodid abundance associated with disturbance (Figure 40, right) but these may not have been detected in analyses because of high variability. The abundance of ocypodids varied amongst assemblages however, and from transect 1 to transect 2 within these assemblages, as was evident in both analyses comparing disturbed and disturbed sites. For example, high densities of ocypodid crabs were recorded on transect 2 in the tidal flat assemblage at Site BV (Figure 6-37).

To investigate the importance of crabs from the genus *Uca* in determining the results gained at the family level for ocypodid crabs, ANOVA's for this genus were also examined. The results were exactly as those found for ocypodid species richness and abundance presented above and were therefore, not reported. *Uca* species richness differed between disturbed and undisturbed sites, and significantly higher abundance was found in some assemblages at disturbed sites. For example local increases in ocypodid diversity (i.e. including *Macropthalmus* spp.) and elevated densities of *Uca capricornis* were recorded in the seaward assemblage at the port (site DP) and unusually high densities of *Uca hirsutimanus* were also recorded in the seaward assemblage at site

BV (Figure 6-40). Clearly ocypodid genera other than the fiddler crabs (*Uca* spp.) are not particularly important in determining the results of these analyses (e.g. *Macropthalmus, Ilyoplax)*.

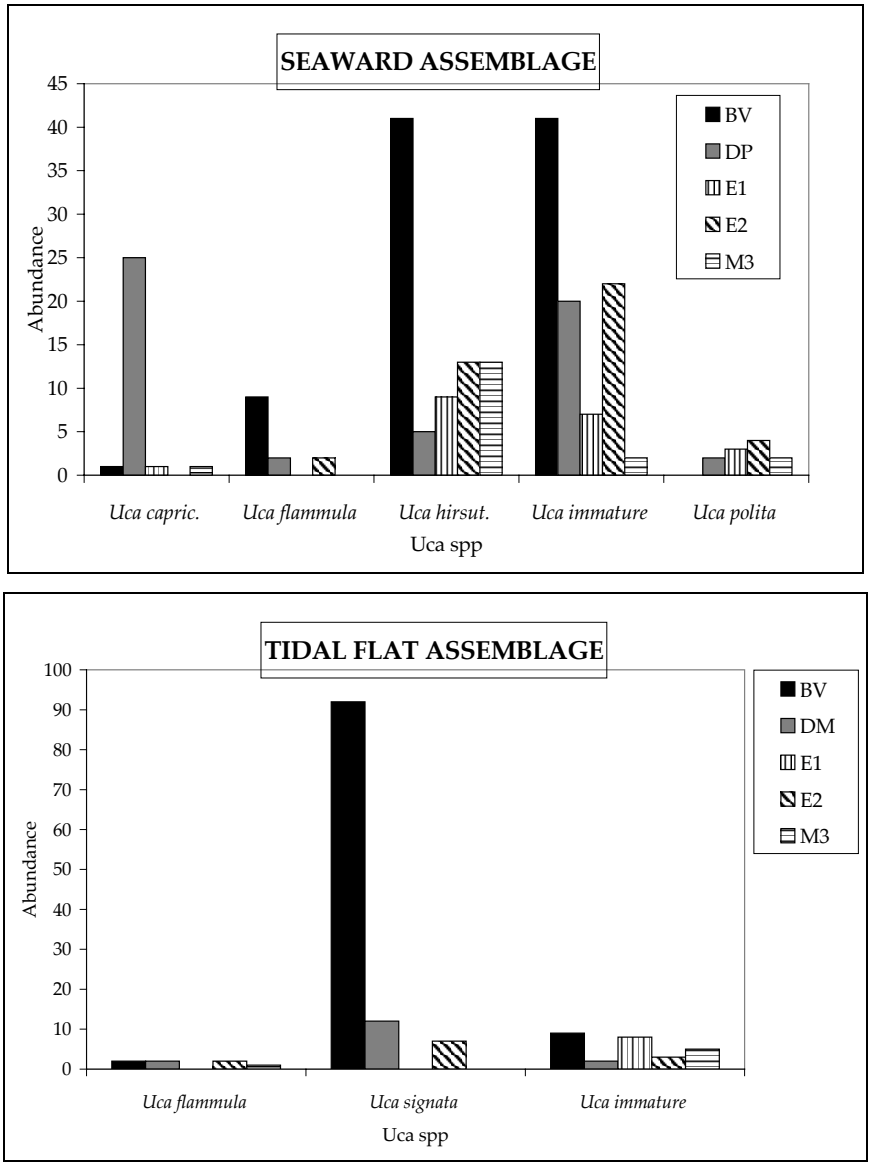


Figure 6-40: Total dry season abundance of species of *Uca* crabs in disturbed (solid bars) and undisturbed (hatched bars) sites in the seaward assemblage (upper) and tidal flat (lower).

~6.3.7. Molluscs of disturbed mangroves

A total of 54 mollusc species (36 gastropods, 18 bivalves) was recorded from disturbed sites during the 2001 dry season survey (Table B-6, Appendix B). The tally for the dry season survey of molluscs in undisturbed sites was similar, with 49 molluscs recorded (31 gastropods, 18 bivalves). As for undisturbed sites, gastropods and bivalves are analysed separately, as follows.

Gastropod diversity and abundance

Gastropods were the dominant class of mollusc, comprising 68% of all records in disturbed mangroves. The most abundant gastropods recorded from disturbed sites included *Nerita balteata, Littoraria articulata* and *Cerithidea obtusa;* these species were also common and abundant in undisturbed mangroves. Two ellobiid species common in undisturbed sites (*Cassidula angulifera* and *Cassidula decussata)* were not recorded from the disturbed sites of this survey and the only introduced marine invertebrate, the gastropod *Melanoides tuberculatus*, was recorded from site BV (Table B-6, Appendix B).

Comparisons of disturbed sites

Gastropod species richness was similar between disturbed sites but significant variation was found between assemblages in analyses for two and three disturbed sites, amongst four and three assemblages respectively (Figure 6-41, Tables E-55 and E-56, Appendix E). Standard error bars on the graphs of means indicate substantial variation in gastropod species richness at the disturbed sites studied. Gastropod abundance did not vary significantly between sites, assemblages or in relation to disturbance, and due to the number of analyses, these results are not presented in Appendix E.

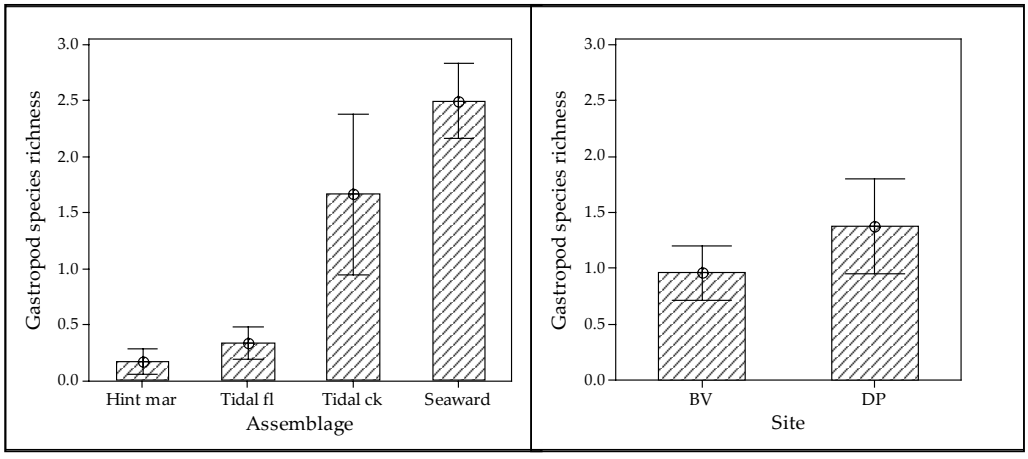


Figure 6-41: Mean species richness (± SE) of gastropods in assemblages at two disturbed sites (BV and DP) during the 2001 dry season survey (left) and in the two disturbed sites, averaged across the four assemblages (right).

Bivalve diversity and abundance

Comparisons of disturbed sites

As in undisturbed mangroves, bivalves were mainly recorded from the two seaward

assemblages and no bivalves were recorded from the tidal flat or the hinterland margin at disturbed sites. The tidal flat at Site DP was, however, heavily disturbed, and devoid of tidal flows. At the two sites in which all four assemblages were surveyed (Site BV and DP) there was substantial variation in bivalve diversity and abundance within assemblages and within sites—indicated by large standard error bars (Figure 6-42).

The species richness of bivalves differed significantly between assemblages and analyses also indicated bivalve abundance varied in assemblages, at the different disturbed sites (Tables E-58 to E-61, Appendix E). For example, mean bivalve abundance was higher in the tidal creek assemblage at site DP than at site BV, but the reverse was found in the seaward assemblage. The results reflected the apparent lack of any consistent pattern between site and assemblages at disturbed sites (Figure 6-43)

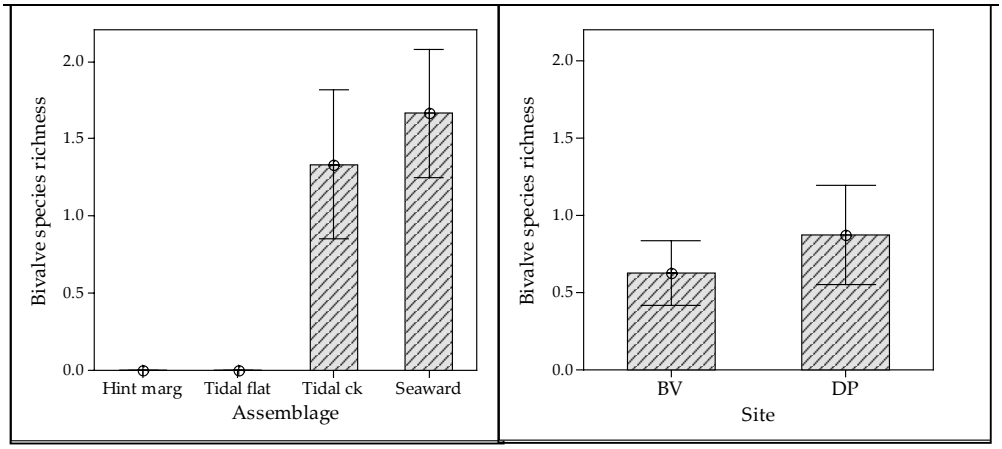


Figure 6-42 : Mean species richness (± SE) of bivalves in assemblages at two disturbed sites (BV and DP) during the 2001 dry season survey (left) and averaged across all assemblages in the two disturbed sites (right).

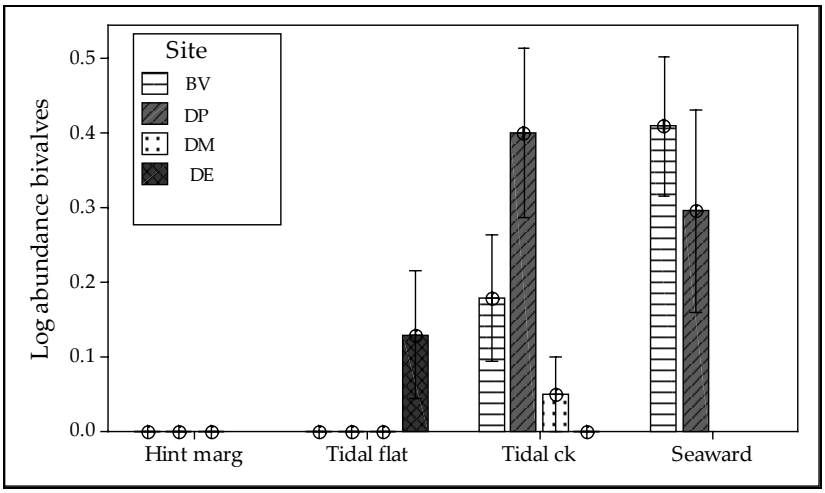


Figure 6-43: Mean abundance ($\log_{10}(x + 1)$ transformed) of bivalves (±SE) in assemblages at the four disturbed sites.

Mollusc species richness and abundance in disturbed and undisturbed sites

Overall species richness for molluscs from both disturbed and undisturbed sites was 75 species from 39 families (Appendix B-1). In total, sixty molluscs were sampled from undisturbed sites and the remaining group of 15 species (20%), were recorded only from disturbed sites (Table B-6 and B-7, Appendix B). The total of 54 molluscs, comprising 36 gastropods and 18 bivalves, recorded in disturbed sites during the 2001 dry season, was actually slightly more than the dry season tally for undisturbed sites (49 species).

Ordination of disturbed and undisturbed study plots based on gastropod abundance, indicated that the fauna of undisturbed sites was fairly uniform. Study plots from disturbed sites show some overlap with undisturbed plots and formed a loose cloud of points around the more cohesive group from undisturbed mangroves (Figure 6-44, upper). The scatter of the disturbed plots indicated a broader range of mollusc species and wider variation in abundance.

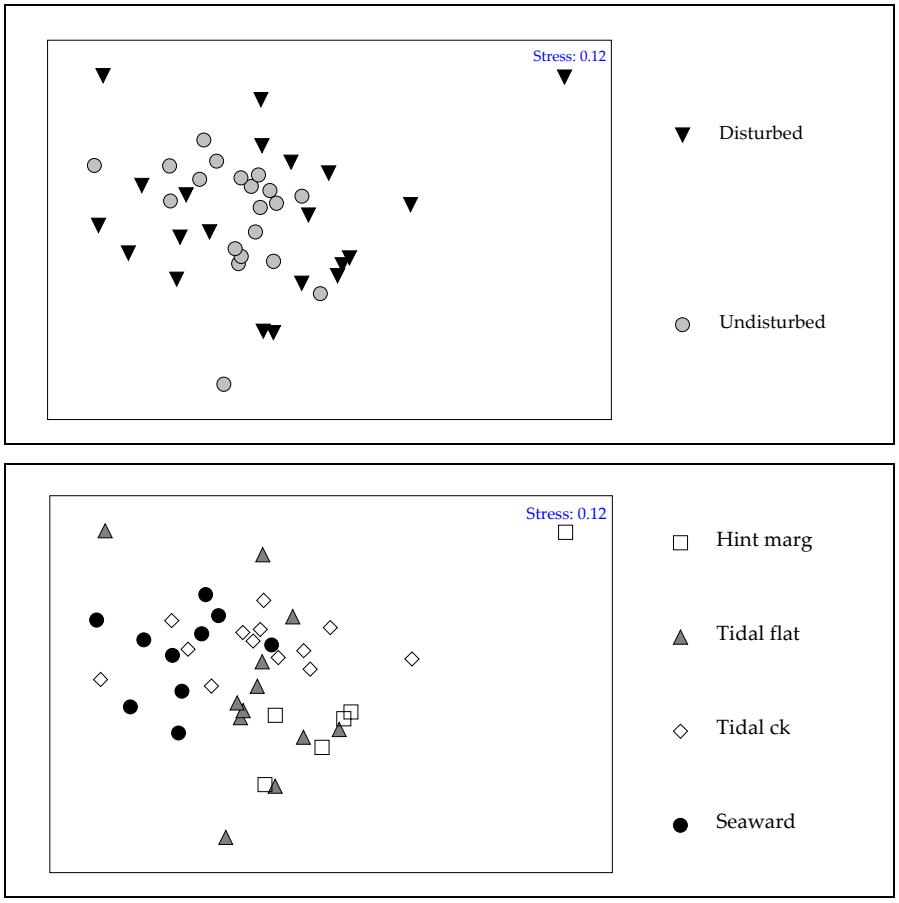


Figure 6-44: Ordination of 41 study plots based on abundance of gastropods indicating disturbed (D) an undisturbed (U) study plots (upper) and assemblage (lower). Points represent study plots surveyed across four locations during one dry season survey, data pooled from three replicate sampling stations.

The same ordination, with assemblage highlighted, showed tight grouping of seaward plots, and separation of these from the two most landward assemblages. The mollusc fauna of the tidal creek was intermediate between the two, and shared many species found amongst plots from the seaward and tidal flat assemblages (Figure 6-44, lower). The overlap of samples from the tidal flat and tidal creek may reflect the distribution of one of the most common gastropods, *Nerita balteata*, which was common throughout both assemblages (see also Figure 6-58, Chapter 5). The division of the gastropod fauna into two groupings, of landward and seaward plots observed in the MDS for undisturbed sites (see Figure 5-65, Chapter 5), was not as well defined in the ordination of disturbed and undisturbed sites.

Comparisons of disturbed and undisturbed sites

Overall mean gastropod species richness per sampling station in undisturbed sites was 2.0 ± 0.2 SE and was 1.0 ± 0.2 SE at disturbed sites. Gastropod species richness in some assemblages was differed significantly between disturbed and undisturbed sites (Table E-63 and E-64, Appendix E). Significant differences were also evident in gastropod species richness between assemblages, as well as variations amongst transects and assemblages at different study sites (Table E-62 to E-64, Appendix E). Diversity was similar in disturbed and undisturbed sites, except in the tidal flat where richness was considerably greater in the disturbed sites (Figure 6-45, upper). Variations in species richness in assemblages on the two transects at each location presumably occurred in response to the patchy nature of disturbance at disturbed sites.

Analyses comparing species richness between the three landward assemblages at three disturbed and three undisturbed sites produced a similar result. Differences between assemblages, a disturbance × assemblage interaction and an assemblage × site interaction were found (Table E-63, Appendix E). The assemblage × site interaction appeared to reflect the unusually low gastropod diversity in the tidal flat assemblage at disturbed site DP, and also at undisturbed site E2 (Figure 6-46).

Analyses comparing gastropod species richness in the two landward assemblages—i.e. those considered most likely to be influenced by urbanisation—did not detect differences associated with disturbance (Table E-64, Appendix E). This result was found when comparing the three disturbed sites (omitting site DP in which the tidal flat was

heavily modified) with three undisturbed sites. A significant main effect for transect, and a site × assemblage interaction were found, relating to the results described for the previous analysis. A high mean square value for disturbance, however, indicates the importance of this factor in the analysis, but the low diversity found at site E2 has influenced this outcome (Figure 6-46). The same analysis (i.e. three disturbed *vs* three undisturbed in two assemblages) for gastropod abundance revealed the same result, but a significant main effect for disturbance was also found (Table E-67, Appendix E). Gastropod abundance in the two landward assemblages at disturbed sites was significantly lower than in undisturbed sites.

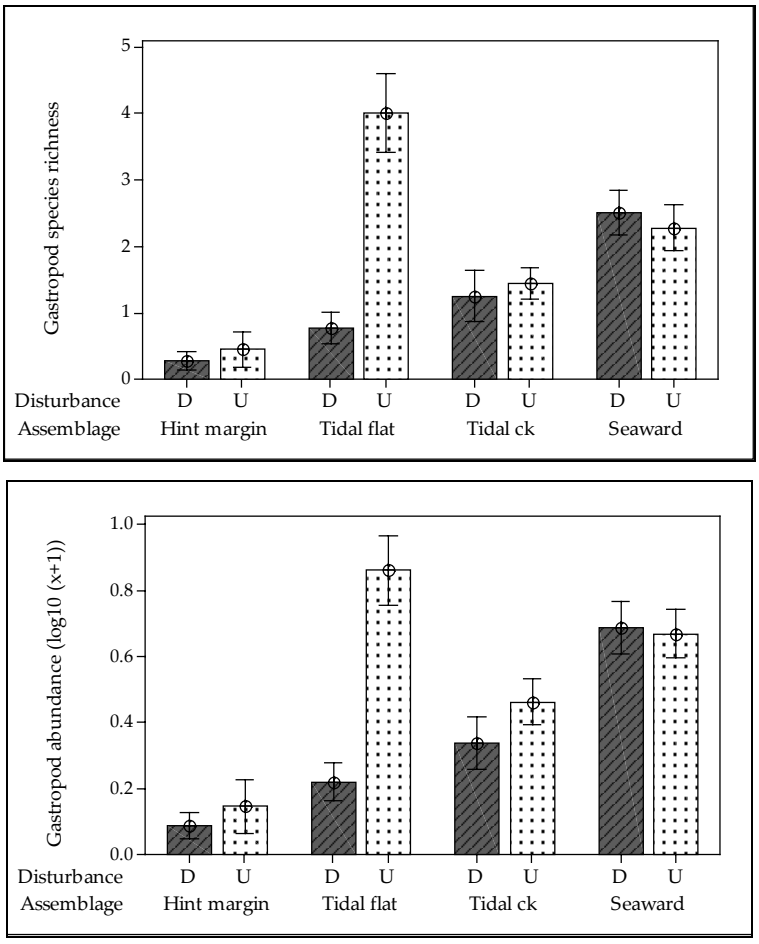


Figure 6-45: Mean gastropod species richness (±SE) in the four assemblages (upper) and $\log_{10}$ abundance (lower) in disturbed (D) and undisturbed (U) sites. Means are from dry season sampling averaged over three undisturbed and four disturbed sites. NB The denuded tidal flat assemblage at site DP was omitted.

The two remaining analyses comparing gastropod abundance in disturbed and undisturbed sites found significant differences between assemblages for both, and a disturbance × assemblage interaction for the comparison of three disturbed with three undisturbed sites, in the three landward assemblages (Tables E-65 and E-66, Appendix

E). The interaction mainly relates to the difference in mean gastropod abundance in the tidal flat at disturbed and undisturbed sites. The difference between disturbed and undisturbed mangroves was significant even when the heavily modified site DP was omitted from the analysis, and site DE included in its place (Table E-67, Appendix E).

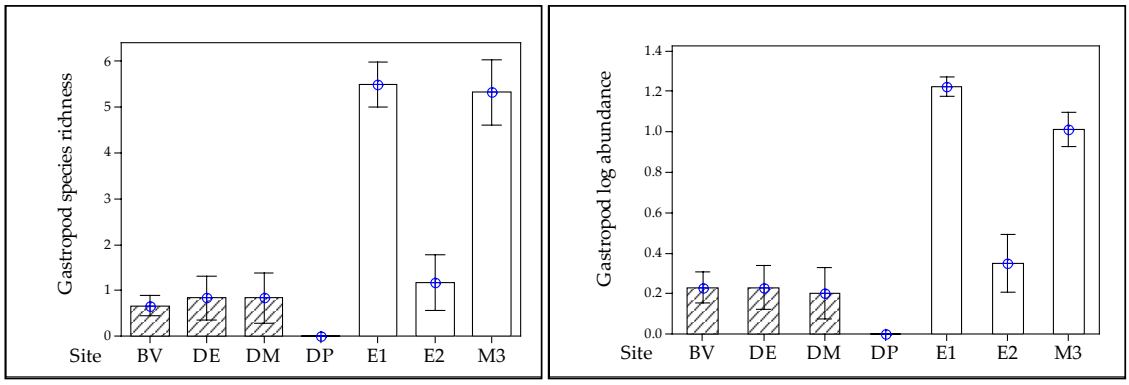


Figure 6-46: Mean gastropod species richness (left) and abundance (right) in the tidal flat assemblage at disturbed sites (hatched) and undisturbed sites (plain).

In contrast, neither bivalve species richness nor abundance varied significantly between disturbed and undisturbed sites (Tables E-68 to E-71, Appendix E). Only differences between assemblages were detected for diversity and abundance. These results have been reported above for disturbed sites and for undisturbed sites in Chapter 5.

~6.3.8. Fish

Twelve species of fish were recorded from disturbed mangroves, including three species not reported from undisturbed sites (*Calamiana* sp. 24, *Periopthalmus kalolo* and *Hemigobius hoevenii).* More species of fish were recorded from disturbed (12) than undisturbed mangroves (9) during the dry season survey, but mean species richness recorded per sampling station was less in disturbed sites (0.7 ± 0.1 SE) than in undisturbed sites (1.0 ± 0.1).

Comparisons of disturbed sites

Analyses of fish species richness comparing two disturbed sites in the four assemblages indicated that fish diversity varied from site to site amongst the different assemblages (Table E-72, Appendix E). This result was mainly due to substantially higher mean species richness of fish in the seaward assemblage at site DP than at site BV (Figure 6-47).

As for species richness, comparison of fish abundance in the four assemblages at site BV and DP reflected the high numbers of fish in the seaward assemblage at the port and revealed variation in fish abundance between transects. A similar result was found in analyses of fish at undisturbed sites (see section 5.4.7) and appeared to reflect both random variation between transects one and two at each site and the sporadic capture of small schools of fish in pitfall traps.

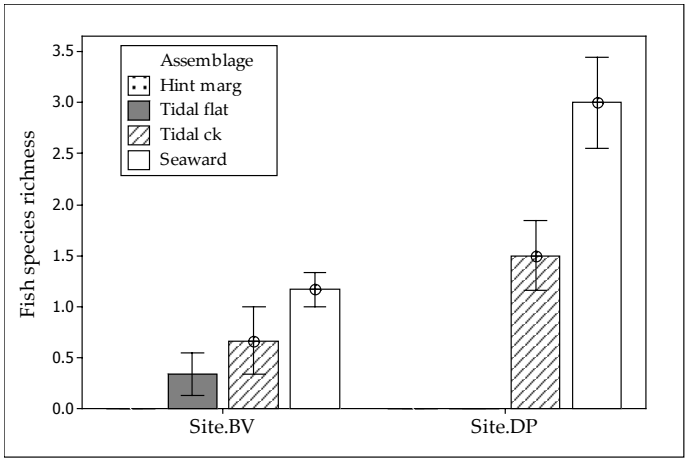


Figure 6-47: Mean species richness of fish in two disturbed sites in assemblages from landward (left) to seaward (right)

Comparisons of disturbed and undisturbed sites

Mean abundance of fish per sampling station, averaged across all assemblages in disturbed sites (2.1 ± 0.7 SE) was more than that recorded in undisturbed sites (1.1 ± 0.2 SE) but univariate analyses found no significant differences between sites or assemblages or in response to disturbance (Tables E-74, E-75 Appendix E). As for species richness, comparison of fish abundance in the four assemblages at site BV and DP found a site × assemblage interaction and a significant assemblage × transect interaction. The site × assemblage interaction mainly relates to the high numbers of fish in the seaward assemblage at the port, described above for species richness. The assemblage × transect interaction also relates to the high abundance of fish at this site but indicates that transect two had much higher abundance than transect one. A similar result was found in analyses of fish in undisturbed sites (section 5.4.7) and appeared to reflect both random variation between transects one and two at each site and the sporadic capture of small schools of fish in pitfall traps.

Analyses comparing the species richness and abundance of fish found no significant differences between disturbed and undisturbed mangroves. Only differences between

assemblages were detected (Tables E-76 to E-79) which again relates to the high fish density in the seaward assemblage at the port (site DP) described above.

6.4. Discussion

~6.4.1. The impacts of disturbance on invertebrate diversity and abundance

Limited differences were found between the invertebrate faunal assemblages of disturbed and undisturbed mangroves in Darwin Harbour. Overall, invertebrate diversity and abundance did not decline in response to moderate levels of anthropogenic disturbance; in fact in some instances, the pool of invertebrate species increased (Table 6-4). Likewise, overall invertebrate abundance was not greatly diminished but localised increases in the populations of some faunal or trophic groups were found (e.g. surface deposit-feeding polychaete worms), while others decreased (e.g. grapsid crabs).

Clearly, the different faunal groups varied in their response to environmental change, and may provide a detailed reflection of the nature and intensity of disturbance associated with urbanisation. Declines in species richness for example, were evident in assemblages where the effects of anthropogenic disturbance were most marked. For example, mean species richness in the tidal flat assemblage which was generally heavily impacted, decreased from (9.2 ± 0.9 SE) in undisturbed sites to (4.1 ± 0.6 SE) in disturbed sites, largely due to significantly reduced gastropod populations. Other authors have noted that benthic invertebrates are very sensitive to habitat disturbance such as organic enrichment of sediments and contamination by toxic substances (Bilyard, 1987), and for a host of reasons make excellent indicators of anthropogenic disturbance (Reynoldson and Metcalfe-Smith, 1992; Grall and Glémarec, 1997).

Environmental heterogeneity, particularly at the level of microhabitat, resulting from anthropogenic disturbance (variations in substrate type, drainage, sediment particle size and canopy cover, for example) may account for much of the observed site-specific variation in invertebrate populations in this study, and in most instances appeared to mediate or negate the effects of shoreline position. In the absence of pre-disturbance data and concomitant data on key environmental variables, however, it was not possible to distinguish disturbance-induced changes from intrinsic differences in faunal

assemblages between sites. Declines in species richness, diversity and abundance are characteristic of highly stressed marine benthic communities (Belan, 2003) but were not evident in the mangrove habitats studied in this thesis.

Table 6-4: Mean dry season total species richness and mean dry season species richness and abundance (± SE) per sampling station for individual faunal groups. Totals and means for all fauna in the four assemblages in undisturbed (U) and disturbed (D) sites.

ASSEMBLAGE	TAXA	Total species		Mean species richness/ station		Mean abundance/ station	
DISTURBANCE		**U**	**D**	**U**	**D**	**U**	**D**
ALL ASSEMBLAGES	Molluscs	49	54	2.9 ± 0.3	1.5 ± 0.2	6.1 ± 0.8	2.7 ± 0.5
	Crustaceans	55	48	3.9 ± 0.3	3.5 ± 0.3	14.9 ± 2.0	12.6 ± 1.5
	Worms	24	33	1.2 ± 0.2	1.1 ± 0.2	1.7 ± 0.3	1.9 ± 0.4
	Fish	9	12	1.0 ± 0.1	0.7 ± 0.1	1.1 ± 0.2	2.1 ± 0.7
	Ants	23	21	1.3 ± 0.1	1.0 ± 0.1	-	-
	Other	3	3	-	-	-	-
	TOTAL	**163**	**171**	**9.9 ± 0.7**	**7.7 ± 0.7**	**24.1 ± 2.6**	**19.5 ± 2.3**
SEAWARD	Total	90	89	16.3 ± 1.0	17.1 ± 1.6	50.1 ± 6.0	54.6 ± 5.4
TIDAL CREEK	Total	75	93	10.2 ± 1.0	9.5 ± 1.0	23.4 ± 2.9	22.9 ± 1.6
TIDAL FLAT	Total	51	43	9.2 ± 0.9	4.1 ± 0.6	22.3 ± 2.1	10.8 ± 2.6
HINT MARG	Total	33	31	3.9 ± 0.5	3.7 ± 0.4	3.8 ± 1.1	2.8 ± 0.8

Multivariate analyses however, based on the species richness of all 238 taxa, showed differences in species composition between disturbed and undisturbed mangroves, a pattern consistent with disturbance effects. Indeed, thirty additional species were recorded from disturbed mangroves during these surveys that were not found in undisturbed sites and species replacements help to explain the lack of significant differences in analyses of invertebrate species richness. Changes in species composition were evident in all the faunal groups studied: multivariate analyses consistently demonstrated the faunal assemblages characteristic of undisturbed habitats were replaced by a different suite of species in disturbed sites.

It is well known that in many coastal and marine communities increased abundance of opportunistic or 'tolerant' species is a typical response to stress (Belan, 2003; Sarkar et al., 2005). It is usually accompanied by a decrease in species richness with the elimination of more 'sensitive' species (Grall and Glémarec, 1997). It is possible that the changes reported here may potentially represent the loss of rare and ecologically sensitive species, but at this stage there is insufficient information on the conservation status (e.g. rare, common, invasive) of invertebrates in Darwin Harbour to verify this.

Moreover, further investigation of the relative abundance of invertebrates in undisturbed and disturbed mangroves would be required in order to detect the proliferation of opportunistic, common taxa and to place the current results in the broader context of the conservation of biological diversity.

Unlike the vertebrate fauna described in Chapters 3 and 4, disturbed sites were not colonised by introduced species. Only two ant species and a single introduced marine species, the gastropod mollusc *Melanoides tuberculatus* were recorded. This ubiquitous snail has an extremely wide distribution in freshwater and estuarine habitats throughout the tropics, in part due to its tolerance of desiccation, salinity fluctuations and the ability to reproduce by parthenogenesis (Healy and Wells, 1998).

One of the limitations of this survey was a lack of temporal replication. Due to time and logistical constraints, only one dry season survey was conducted in disturbed sites and the effects of season were not investigated. As shown in Chapter 5, strong seasonal variation was observed in the diverse mangrove worm fauna of undisturbed mangroves, while the diversity and abundance of crabs and molluscs also varied seasonally, in some assemblages. In the dynamic context of mangrove environments, the effects of anthropogenic disturbances may also vary with season. Indeed, research on mangroves affected by altered tidal exchange resulting from road construction in arid northern Western Australia indicated that season was a major factor involved in widespread vegetation decline and death (Gordon, 1987). Normal annual variation in tidal amplitude combined with the highly seasonal rainfall amplified the impacts of road construction in tidally-restricted mangroves, underscoring the importance of season in exacerbating or mediating the effects of anthropogenic disturbance. Clark et al. (1996) also found that chemical conditions in polluted mangrove soils were modified by seasonal changes, particularly drought, which can lead to the remobilisation of heavy metals down the hydraulic gradient.

Overall, the findings suggest that apart from extreme situations—where tidal inundation had been impeded, restricted or halted completely—disturbance associated with proximity to urban and industrial development in Darwin Harbour did not appear to have a major impact on the invertebrate fauna as a whole. Lindegath and Hoskin (2001) did not detect differences in the benthic fauna of undisturbed and urbanised mangroves, whilst clear differences were found in sandy habitats. Their analyses were

however, based on studies in which fauna was identified to coarser levels of taxonomic resolution (families for polychaetes, classes for molluscs and crustaceans) which may be insufficient to demonstrate differences in ordinations of mangrove fauna.

It should be noted however, that the presence of anthropogenic disturbance does not necessarily mean that the invertebrate fauna will be impacted, as species may resist, or tolerate disturbance, and populations may recover such that persistent impacts do not occur (Lindegarth and Hoskin, 2001). A number of factors may have contributed to the lack of any clear differences when considering the fauna as a whole, including species replacements, relatively low-levels of disturbance and high variation in the nature and severity of anthropogenic impacts within individual study plots. To speculate further, it may reflect a degree of resiliency of the fauna to disturbance, which may in fact be able to cope with high levels of disturbance. Moreover, declines in species richness may not be detected from even quite severe disturbance, if benthic species respond via rapid recolonisation with the same or a different suite of organisms (e.g. Faraco and Lana, 2003) .

In contrast with this study, the impact of severe natural disturbance from Cyclone Tracey was reported to have had a lasting impact on mangrove invertebrate faunal communities in some areas of Darwin Harbour. Cyclone disturbance was evident from lower mean species richness and densities recorded in disturbed sites, seventeen years after the storm (Burke, 1992). Sampling effort at disturbed and undisturbed sites was not equal in Burke's study however, with a total of 61 species recorded from one cyclone-damaged site and 92 species from both control sites (75 species in each of two control sites). Further, the cyclone-damaged mangrove was located in the seaward assemblage at Ludmilla Creek, which has different substrate characteristics and wave climate to the two control sites located at Channel Island within Port Darwin (see Figure 2-3, Chapter 2). Indeed, the lack of replication for disturbed mangroves and the potential for intrinsically different faunal assemblages to naturally occur within the sandy, coastal mangal forest present in the seaward assemblage at Ludmilla Creek may have had a major influence on Burke's findings. These habitat differences were also reported in the results of the confirmation study for this thesis, see section 5.3.2. Nevertheless, similar to current findings, Burke (1992) also found the species richness of some taxonomic groups (e.g. molluscs) was greater in disturbed mangroves and species composition differed

between disturbed and undisturbed mangroves. Other studies investigating less severe impacts on mangroves (Hanley and Couriel, 1992; Skilleter and Warren, 2000) have reported significant changes (both increases and decreases) in the numbers of species and individuals.

~6.4.2. The impacts of disturbance on worm diversity and abundance

Worms were one of three faunal groups, including gastropod molluscs and fish, in which total species richness was higher in disturbed (33 species) than in undisturbed mangroves (24 species) in the same season (Table 6-4). Although totals for four disturbed sites are compared with those for three undisturbed sites, the seaward assemblage (i.e. the primary habitat for worms) was surveyed at only two of the disturbed sites, and site DE comprised only two assemblages.

Worm species composition and abundance clearly differed between disturbed and undisturbed sites. Comparison of species tallies showed 33% of the overall total of 51 worms were recorded only in disturbed sites. This percentage was substantially reduced however, by subsequent sampling spanning three more years, which revealed that many of these species had wider distributions in undisturbed mangroves elsewhere in Darwin Harbour (see Appendix C). Species found only in disturbed mangroves included *Aphelochaeta* sp. 1, *Leonnates stephensoni* and *Simplisetia* cf. *erythraensis.* The sipunculid *Phascolosoma arcuatum* was particularly abundant within substrates of cleared *Rhizophora stylosa* forest (Table B-2, Appendix B). It is not known however whether the changes in taxonomic composition are of rare species, sensitive species or simply reflect the broader changes in environmental characteristics present at disturbed sites.

The increase in the abundance of surface deposit feeding worms recorded in disturbed sites helps to explain observed differences in species composition, and was, perhaps, one of the most important findings of the survey (see Appendix C). Indeed, the major feeding guilds for most polychaetes have been determined, and increased abundance of some of the surface-deposit-feeding species, (e.g. the tubicolous spionids), has been reported in response to organic enrichment (Grall and Glémarec, 1997). Other surface deposit feeding polychaetes are also associated with the most chronic levels of pollution in marine habitats (Phillips, 1990; Rainbow, 1990). Known as first-order opportunistic species, these deposit feeders proliferate in highly reduced sediments and include

widely distributed species such as *Capitella capitata* and *Scolelpis fuliginosa* (Grall and Glémarec, 1997). Yet despite the growing body of information linking changes in the trophic structure of communities to a range of environmental impacts, such functional-group analyses have not been widely used in studies of the effects of disturbance on marine invertebrate communities (Bonsdorff and Pearson, 1999; Pagliosa, 2005). Hence, there is great potential for the application of the results of future research in this area.

Site-specific increases or decreases in local worm populations found in this study appeared to reflect the type and extent of anthropogenic disturbance at each site. Partial clearing of mangroves and the influx of terrigenous sediments, evident at in the tidal creek at site BV and in the seaward assemblage at site DP for example, may have catalysed the observed local increases in worm diversity and abundance. Anthropogenic disturbance to mangroves can affect sediment grain size by altering runoff, currents, tidal flow and the ability of mangrove trees to capture sediments (Kaly et al., 1997). Polychaete diversity and density is particularly affected by sediment properties, especially grain size (Alongi, 1987; Pagliosa, 2005; Sarkar et al., 2005) and silt and clay content (Hsieh, 1995). The increased populations of polychaetes at several sites and increases in the abundance of surface deposit feeders may thus have been related to changes in the sediment. Indeed, benthic communities, in general, including the majority of polychaetes, are particularly useful for identifying sediment-related stress (Reynoldson and Metcalfe-Smith, 1992). By contrast, the absence of any worms in the heavily impacted tidal flat at sites BV and DP reflects the nature and severity of impacts at these locations; the former is characterised by permanent ponding and the latter by the absence of tidal inundation.

Worms as indicators of disturbance

Polychaete worms exhibit wide variation in their biology and are amongst the most diverse and abundant invertebrate groups in intertidal environments (Fauchald and Jumars, 1979). Because they are reliably present in intertidal areas and tend to respond quickly to environmental change (Faraco and Lana, 2003; Chollett and Bone, 2007), and differ widely in feeding ecology, habitat preferences, mobility, reproductive strategies and life span (Glasby et al., 2000) they make ideal indicators of disturbance. Some groups of species will respond positively to disturbance, while other groups may disappear (Morissey et al., 1996). Furthermore, Grall and Glémarec (1997) note that as

due to their differing sensitivity to anthropogenic disturbance, the relative abundances of different groups may allow identification of different stress levels and stages of overload.

Increases or decreases in the specific richness and density of polychaete worms have been linked with human activities in studies conducted elsewhere (Grall and Glémarec, 1997; Belan, 2003; Pagliosa, 2005). The complete dominance of mangrove worm communities by the opportunistic *Capitella* group, for example, may occur in response to organic pollution (Pearson and Rosenberg, 1978; Hernandez-Alcantara and Solis-Weiss, 1991). Other research in heavily polluted mangrove systems in India found that organic pollution caused reduced polychaete species richness, diminished populations and depleted trophic groups (Sarkar et al., 2005). In systems heavily impacted by anthropogenic disturbance, the role of detritus is reduced and the ratio of herbivores to detritivores in mangrove food webs may be altered (Ray et al., 2000). Pagliosa (2005) reported that omnivorous polychaete species were dominant in mangroves heavily impacted by urban pollution in Brazil (i.e. by heavy metals in sediments and dissolved nutrients in the water column).

Due to their potential to simplify ecological studies, many recent investigations of responses of invertebrates to environmental change have focussed on groups of taxa that share similar attributes (functional groups) or that utilise the same resources (guilds). For example, Bonsdorff and Pearson (1999) note that analyses based on feeding guilds may reveal reactions of more general importance than the responses of populations of individual taxa. Further, because these sub-groups may be indicative of the whole community, it has been suggested that functional-groups may be used as cost-effective and time-efficient proxies for the assessment of environmental health.

The relative sensitivity, and rapid response of polychaetes to environmental change (Chollett and Bone, 2007), combined with the high tolerance levels of some taxa to pollution and natural disturbances (Belan, 2003; Faraco and Lana, 2003), suggests that of all the invertebrate groups studied in these surveys, worms may be the most useful as key indicators of anthropogenic disturbances. The findings of this study need to be interpreted with caution however, as the work did not document the direct response of the worm fauna to disturbance. The faunal differences observed in disturbed sites may, to some extent, also be due to intrinsic environmental differences between sites. Pre-

disturbance surveys are required to eliminate such possibilities and to further investigate the response of mangrove polychaetes to anthropogenic disturbance.

~6.4.3. The impacts of disturbance on mangrove ants

The ant fauna of disturbed mangroves was quite speciose and total species richness recorded during the dry season survey (21 species) was similar to that in undisturbed mangroves (23). multivariate techniques indicated that ant species composition differed in mangroves affected by anthropogenic disturbance. Ants recorded only in disturbed sites included three introduced species (*Monomorium floricola*, *Partrechina longicornis* and *Solenopsis geminata)* and several opportunistic native species commonly found in degraded habitats (e.g. *Iridomyrmex sanguineus* (meat ant) and *Iridomyrmex* sp. (anceps group)). The effects of disturbance on the ant fauna was mainly limited to the landward fringe and ordinations of study plots in the hinterland margin assemblage (based on their ant species composition) clearly showed separation of plots in disturbed and undisturbed mangroves. The mangrove assemblages seaward of the hinterland fringe tended to be dominated by just a few mangrove specialists—which appeared less influenced by disturbance. Nevertheless, localised decreases in ant species richness (such as on the bulldozed tracks at DE and in the seaward assemblage at site BV) were detected by site × assemblage interactions, suggesting that the loss of trees at these two sites resulted in diminished arboreal ant fauna.

In terrestrial habitats, much attention has been directed to the role of ants as bio-indicators of disturbance (Andersen, 1997; Andersen et al., 1998; Andersen et al., 2004) and for that reason, ants were included in this study. The ordination comparing the ant species composition in the hinterland margin of disturbed and undisturbed mangroves suggested that ants may in fact, provide an indication of anthropogenic disturbance. Study plots in undisturbed mangroves were quite discrete from those in mangroves adjacent to anthropogenic developments. Furthermore, seven ant species, recorded at disturbed sites but absent from undisturbed sites have been identified (Table B-3, Appendix B), that may be indicative of environmental change associated with urbanisation.

The possible causes of changes in the ant fauna may include such things as habitat modification arising from terrestrial sedimentation; construction of bund walls and other man-made structures; reduced tidal inundation and vegetation clearing. The

incursion of terrestrial and introduced species may result in competition and displacement of native mangrove ant faunas. These influences should not extend far into the mangroves however, as the challenges of increasingly frequent tidal flushing would eliminate many terrestrial ant species not adapted to such unique conditions. With the exception of the mud-nesting *Polyrhachis sokolova,* the loss of forest cover is anticipated to have a severe impact on mangrove ants, as the majority of other species depend on trees for protection during high tides and require hollow twigs for nest chambers. Indeed, diminished ant faunas were recorded at those sites where development had resulted in the loss of forest cover (on bulldozed tracks at site DE for example, and in the seaward assemblage at site BV).

~6.4.4. The impacts of disturbance on crustacean diversity and abundance

In this study, no differences arising from direct or indirect disturbance were found for the crustaceans as a group, but abundance of grapsid crabs declined in disturbed mangroves, and in some assemblages, the species richness of ocypodid crabs was significantly higher. The localised increases in abundance of ocypodid crabs, detected by ANOVA at disturbed sites also suggests that changes in sedimentation, hydrology and forest cover matched the habitat preferences of some *Uca* species. High densities of *Uca signata* were recorded in the tidal flat assemblage at Bayview, where bund wall construction had constricted tidal flows. The consequent loss of canopy cover and localised tree death appeared to suit *U. signata,* which prefers clearings in the mid-tidal flat (Nobbs and McGuinness, 2003).

Hence, in the urbanised mangroves of Darwin Harbour, although significant declines the abundance of grapsid crabs were evident, to some extent their loss may have been balanced by species replacements and local increases in *Uca* abundance. Indeed, analyses of community data suggest this did occur, given the clear separation of study plots in ordinations showing that species composition and abundance of crustaceans in modified habitats differed from that in undisturbed habitats. Examination of species lists (Table B-4 and B-5, Appendix B) however, indicate that very few crustaceans were recorded only from disturbed mangroves.

Icely and Jones (1977) concluded from their detailed study of feeding appendages that each species of *Uca* was adapted to extract organic material and micro-organisms from a

particular sediment type. Frith and Brunenmeister (1980) thus predicted that the degree of mouth part specialisation and the heterogeneity of substrates in an area partly determined *Uca* species composition and/or distribution. Another important factor affecting fiddler crabs is the presence or absence of mangrove vegetation and the associated variations in temperature, humidity and light intensity (Frith and Brunenmeister, 1980). In mangroves of the Darwin region, Nobbs and McGuinness (2003) found that shade was an important factor determining the distribution of individual *Uca* species. Thus, the current findings indicate that the relatively sparse canopy cover at the port site, combined with the substantial inwash of terrestrial sediment from adjacent clearings (pers. obs.) led to the proliferation of ocypodid crabs in this, and other disturbed sites.

The ability of mangrove crabs to withstand environmental change, particularly organic pollution has been reported elsewhere. Machiwa and Hallberg (1995) noted that grapsid crabs were unaffected by deposition of sewage in mangroves in Zanzibar. Indeed, both grapsids and ocypodids may actively benefit from nutrient enrichment due to organic pollution, by exploiting the large quantities of organic matter deposited on the surface of sediments under such conditions (Lee, 1998). Lee ((1995b) as cited in Lee 1998) found that whilst other macrobenthos was impoverished from gross organic pollution, *Uca* spp proliferated. He suggested that grapsid and ocypodid crabs may be more tolerant, or less vulnerable, than other invertebrate groups to organic pollution, and may therefore be better adapted and more able to survive in, urbanised mangroves.

On the other hand, because grapsid crabs are most abundant in the two landward assemblages, they are also the most susceptible to anthropogenic development which often involves the partial or complete clearing of landward mangroves for coastal development projects (Machiwa and Hallberg, 1995; Lee, 1998). Ashton et al. (2003) reported that mangrove crab species richness and community structure was correlated with tree and seedling community structures. Their work indicated the close dependence of this faunal group on the forest for habitat and food and implied that partial or extensive clearing of the forest will have a direct impact on crabs. Furthermore, Lee (1988) noted that the tendency toward habitat loss in landward mangroves may lead to a disproportionate loss of grapsid crab fauna, which in turn may have significant ramifications for mangrove forest productivity. The substantial leaf-

burying activities of grapsid crabs are critical in the processing of accumulated mangrove litter from the upper intertidal (Lee, 1989) and thus a great deal of nutrient recycling occurs in these habitats (Roberston, 1986) such that organic carbon must accumulate in hinterland margin sediments (Machiwa and Hallberg, 1995). It follows that due to the pivotal role played by grapsid crabs in nutrient recycling in the landward mangrove assemblages, anthropogenic disturbance in these habitats may have substantial ecological ramifications.

Moreover, the experimental removal of crabs from *Rhizophora* forests on Hinchinbrook Island resulted in significant reductions in forest primary productivity and significantly reduced reproductive output (Smith III et al., 1991). The lack of aeration from crab burrowing also led to significantly higher concentrations of toxic soil sulphide and ammonium in plots in which crabs were removed. The interdependence of crabs and mangrove forests indicates that if anthropogenic impacts were sufficient to destroy crab populations, it would have serious ecological consequences for forest health, energy flow and productivity.

~6.4.5. The impacts of disturbance on mollusc diversity and abundance

The species richness of molluscs during the dry season in disturbed mangroves (54 species) was slightly higher than that recorded in undisturbed mangroves (49), and of the total of 75 molluscs recorded overall, 15 species (20%) were found only in disturbed sites. Variation in the range of microhabitats available to molluscs at the disturbed locations studied, including for example, areas of sandy and rocky substrate at the port and the localised ponding of water at Bayview, may have contributed to higher numbers of species. Gastropods such as *Clypeomorus batillariaeformis, Neritina violacea* and *Monodonta labio* for instance, which were recorded only from disturbed sites, are more characteristic of rocky rather than muddy intertidal substrates. Further, the bivalves *Circe australis, Gafrarium tumidum, Isognomon legumen* and *Telina iridescens* are indicative of substrates with a coarse to gravelly grain size (R.Willan, pers. com.), rather than the characteristic fine silt and clay of mangrove environments. Due to their specialised feeding structures (Tan and Chou, 2000), molluscs tend to be specifically adapted to particular microhabitats and minor changes in sediment particle size, soil chemistry, hydrology and substratum may be reflected by associated changes in mollusc

populations (see Skilleter and Warren, 2000).

NMDS ordinations based on the presence or absence of mollusc species illustrated differences between the suite of species present in disturbed and undisturbed mangroves but significant differences in mollusc species richness were not, however detected in univariate analyses. The lack of any variation in diversity detected by ANOVA may be due to the replacement of a proportion of molluscs present in undisturbed mangroves by roughly equal numbers of other species better adapted to the altered conditions found in disturbed mangroves. Altered mollusc species composition in disturbed sites appears to be a reflection of environmental changes associated with anthropogenic disturbance; for instance, an increase in the area of rocky substrate associated with rock walls and erosion of fine marine muds to expose coarser sediments. Burke (1992) also found more species of molluscs in mangroves disturbed by cyclone Tracey, than in undisturbed mangroves of Darwin Harbour.

Further evidence of disturbance was shown by significant reductions in the diversity and abundance of gastropod molluscs at disturbed sites. This was particularly evident in the two landward assemblages and was chiefly due to decreased populations of potamidid gastropods (Tables B-1 and B-6, Appendix B). Potamidids are often the dominant invertebrates in muddy intertidal habitats in many regions of the tropics, both in terms of numbers and biomass (Houbrick, 1991; Barnes, 2003). As found in mangroves in tropical north-Western Australia (Wells and Slack-Smith, 1981; Wells, 1984) and elsewhere the Indo-Pacific region (Wells, 1986a; Barnes, 2003) high densities of potamidid gastropods were characteristic of the mid-tidal flat of undisturbed mangroves of this survey (section 5.4.6, Chapter 5). Furthermore, these molluscs are favoured items on the diet of local aboriginals who actively collect and consume large quantities of *Telescopium telescopium, Nerita balteata* and *Terebralia semistriata,* the remains of which were found adjacent to mangroves at Site BV, DM and M3 (pers. obs.). Thus the effect of regular harvesting by humans on these gastropod populations could be substantial.

One factor limiting gastropod abundance at disturbed sites could be reduced canopy cover. Indeed, environmental stress exerts a strong influence on the behaviour of several common mangrove gastropods including littorinids (Yipp, 1983), and locally abundant potamidid species *Cerithidea obtusa* (McGuinness, 1994) and *Telescopium telescopium,*

Terebralia semistriata and *Terebralia palustris* (Crowe, 1997; Crowe and McMahon, 1997). Each of these species retreats to moist, shaded microhabitats during dry periods and would thus avoid the exposed conditions present on bulldozed tracks or amongst patches of dead forest during the dry season. A behavioural response of potamidid mollusc populations in the tidal flat would help account for the pronounced decrease in abundance of gastropods in the landward mangroves of disturbed sites. Lower densities of living trees in disturbed mangroves would also contribute to lower populations of arboreal gastropods including *Littorea filosa* and *Cassidula angulata* (the latter species was absent from disturbed mangroves).

Experimental studies in temperate mangroves revealed gastropods respond rapidly to small-scale changes in microhabitat (Chapman et al., 2005). Reduced gastropod abundance resulted from reductions in the amount of leaf litter, prompting increased dispersal of gastropods (from a lack of detrital based food), and/or increased predation. Skilleter (1996), reported similar results from experimental manipulation, with different suites of gastropods, in response to small scale disturbance to mangrove forests. Studies of *Cerithidea obtusa* in mangroves of the Darwin region demonstrated the importance of physiological stress (from heat and desiccation) in determining gastropod behaviour and survival and the role of dense mangrove forests in moderating the effects of daily and seasonal variation in environmental stress (McGuinness, 1994). Skilleter and Warren (2000) found an 83% reduction in the number of molluscs from experimental removal of pneumatophores and their epiphytic algae. They concluded that even minor disturbances to the physical structure of mangroves may have major effects on the ecological value of these habitats, through potential impacts at higher trophic levels.

It appears that moderate levels of disturbance may occasionally lead to an increase in mollusc abundance over the longer term. Choy and Booth (1994) found that, although mangrove mollusc species suffered high mortality from prolonged (two month) inundation in Brunei Darussalam, nine months later the densities of most mollusc species were significantly higher than prior to flooding. Inundation apparently triggered reproduction in the low numbers of surviving molluscs and high post-disturbance recruitment was observed, resulting in particularly high densities of *Assiminea brevicula, Cerithideopsilla cingulata* and *Terebralia sulcata* in the mid-tidal zone (Choy and Booth, 1994). In the disturbed sites of this survey, however, the levels of

disturbance do not appear to have prompted such a response. Indeed, the most pronounced effect of anthropogenic disturbance was a decline in gastropod abundance in the tidal flat assemblage.

~6.4.6. The impacts of disturbance on fish diversity and abundance

Populations of resident fish appeared resilient to the minor levels of anthropogenic disturbance investigated in this study. In fact, several new species were recorded during surveys of disturbed sites and mean diversity and abundance was particularly high in the seaward assemblage at the port (site DP). Surveys in disturbed and undisturbed mangroves indicate the patchy distribution of resident mangrove fish. For example, the high number of fish recorded in one study plot on transect two at site DP dominated the results of analyses and the significant transect × assemblage and site × assemblage interactions were due mainly to this. No overall differences were detected between disturbed and undisturbed mangroves and the apparent increase in abundance was presumably due to the chance capture of small schools of fish in pitfall traps at this location.

Although this chapter considered only the impacts of anthropogenic disturbance, the impacts of natural disturbance including the long term effects of severe cyclone damage on mangrove forests are considered in the next chapter. This chapter concludes part one of this thesis on the fauna and the impacts of disturbance, whilst part two considers the disturbance of mangrove forests.

6.5. Conclusions

The changes in species composition in disturbed habitats, resulting from the influx of a different suite of species in disturbed sites, suggests substantial areas of undisturbed mangroves within each arm of Darwin Harbour should be retained. Rapid recovery of infauna may be largely dependent on the re-colonisation of species from adjacent, intact mangrove habitats (McGuinness, 1990; Faraco and Lana, 2003) and such action would ensure the resiliency of mangrove faunal assemblages to localised disturbance. Due to the limited water circulation in the harbour, particularly during the dry season (Williams et al., 2006), maintaining high water quality within the harbour is also critical to ensure that larval recruitment is not further diminished.

The diminished populations of gastropod molluscs and grapsid crabs found in disturbed mangroves is of some concern. These groups appear to be especially vulnerable to urban encroachment, which predominantly affects the landward mangrove assemblages. These impacts have potential wider implications for nutrient recycling and forest productivity, as well as for secondary consumers.

Similar to the findings of some other studies, polychaete populations appeared to be potentially the most responsive indicators of environmental change associated with urbanisation (and other anthropogenic impacts) and may thus serve as valuable indicators of degradation by human activities. This possibility is worthy of further study examining a wider range of types of disturbance which also looks more specifically at the kinds of environmental change which occur.

PART 2 – MANGROVE FOREST RECOVERY AND REHABILITATION

CHAPTER 7. THE RECOVERY OF DISTURBED MANGROVE FORESTS

Whilst part one of this thesis examined the fauna of undisturbed and disturbed mangrove ecosystems, this part is primarily concerned with flora and comprises two chapters that investigate factors that influence the reforestation and rehabilitation of disturbed mangroves. The scope of part two and its relationship with part one is summarised in Figure 1-1 (see Chapter 1). In part two, selected aspects of the recovery of mangrove forests are investigated with particular focus on those factors which may limit natural seedling recruitment and survival. Different methods of rehabilitation were investigated and a technique designed to reduce reforestation times was trialed. Underpinning these investigations was the premise that improved knowledge of species characteristics, regenerative strategies and recovery processes is required for proper management—particularly for restoration of disturbed forests—and insight gained in these areas may serve to accelerate the re-establishment of diverse ecosystems.

7.1. Introduction

Global population growth and the demand for land in estuarine areas has led to escalating disturbance to mangrove systems in recent decades. The rapid reduction in

the area of mangroves worldwide has also placed increasing pressure on remaining resources, and on people whose livelihoods depend on mangroves (Hatcher et al., 1989). As levels of disturbance have increased, so has the need for knowledge regarding the process of natural forest recovery (Blanchard and Prado, 1995; McGuinness, 1997a). McGuinness (1992) noted that "a variety of factors are likely to affect the rate and nature of recolonisation" and these factors will vary with the nature and frequency of disturbance, its severity and extent (Sherman et al., 2000). Widespread anthropogenic disturbance and deforestation has also increased the importance of developing sound ecological techniques for restoration and rehabilitation (Field, 1996; Das et al., 1997; Edwards, 1998; Kaly and Jones, 1998; Ellison, 2000a; Lewis, 2005), examined in further detail in Chapter 8.

Because mangroves occur in dynamic coastal environments, one would expect that they are reasonably well adapted to intermittent physical disturbances. Their preference for low-lying coastal habitats with unconsolidated substrates, leaves them particularly vulnerable to destructive waves, storm surges and winds associated with tropical cyclones (Sherman et al., 2001). In order to survive in such dynamic conditions, mangroves have developed a range of successful regenerative strategies (viviparous and water-bouyant propagules, for example), that should enable them to readily colonise and dominate tidal shores (Duke, 2006). Tomlinson (1986) notes that mangrove species possess adaptations and characteristics typical of pioneer plants, which indicates that disturbance has been an important factor in their evolution (Sherman et al., 2001). Yet surprisingly, the recovery of mangrove forests affected by various forms of disturbance often requires long periods of time. In fact it may take several decades for successful revegetation to occur following complete deforestation (McGuinness, 1992; Ellison and Farnsworth, 1996; Imbert et al., 2000).

Macnae (1968b), was one of the first to observe that clear cut forests may fail to re-establish, remaining as non-vegetated tidal flats. Other researchers have reported slow natural regeneration of clearings and clearcut strips more than 20 m wide (Blanchard and Prado, 1995; Kaly and Jones, 1998). Cyclone damaged *Rhizophora stylosa* forests in Darwin Harbour have only partially recovered after three decades and other examples are evident from research elsewhere on the long term effects of both anthropogenic and natural disturbance. One of the most striking examples of delayed recovery is however,

reported from Vietnam, where mangal habitats remained devoid of forest cover, three to four decades after destruction by defoliants during the Second IndoChina war [Hong and San (1993) as cited in Ellison, 2000b)]. By contrast, many terrestrial habitats in the tropics regenerate rapidly following disturbances such as fire and cyclones (Wilson and Bowman, 1987; Unwin et al., 1991) and the effects of localised clearing may be indiscernible after only one or two seasons (pers. obs.)

The long time for mangroves to re-establish after both natural (McGuinness, 1992; Smith III et al., 1994; Cahoon and Hensel, 2003; Hensel and Proffitt, 2003) and anthropogenic (Burns et al., 1993; Duke et al., 1997) disturbance has intrigued a number of authors (e.g. Smith III et al., 1994). The reasons why areas of seemingly suitable habitat do not recolonize may be complex however, and undoubtedly varies between locations and types of disturbance.

Several factors, including rapid soil acidification (McKee, 1993; McKee and Faulkner, 2000), erosion of sediments due to loss of tree cover (Duke et al., 1997; Cahoon and Hensel, 2003; Hensel and Proffitt, 2003; Duke, 2006), shortage of propagules (Elster et al., 1999), insect attack (Duke, 2006) weed invasion (Rubin et al., 1999) and other biotic factors (Ward et al., 1986; Smith III, 1987c; Smith III, 1988; Dahdouh-Guebas et al., 1998), have been linked with inhibited forest recovery. In general, however, the processes delaying the recovery of mangrove forests following deforestation are poorly understood. Although this is an aspect of mangrove ecology that clearly warrants further detailed study, few studies have investigated specific environmental factors that might affect the establishment, growth and survival of particular species (but see Ellison and Farnsworth, 1993; McKee, 1995c; McGuinness, 1997a).

This chapter reports the results of experiments that investigated the role of selected factors in the delayed recovery of mangrove forests in Darwin Harbour, by monitoring the growth and survival of seedlings planted in disturbed areas. Plant growth studies were conducted in forests that had been severely damaged by cyclone Tracey in 1974 and in other areas cleared by bulldozer in 1992. Experimental studies investigated recovery processes in sites affected by natural and anthropogenic disturbance, active over different time scales, and involved four mangrove assemblages (seaward, tidal creek, tidal flat and hinterland margin) at Charles Darwin Park in Darwin Harbour.

Aim

The aim of this study was to test for differences in the survivorship and early growth of seedlings of *Ceriops australis* and *Rhizophora stylosa* planted into clearings created by bulldozer and by cyclone damage, and grown under different treatments. The treatments included:

- Shade
- Protection from above-ground predation and herbivory by fauna > 13 mm in size
- Protection from drift logs (mechanical damage)
- Natural forest
- Control

The study also tested for differences between survival and growth of *C. australis* and *R. stylosa* propagules collected either from the ground, or directly from trees. Another experiment was conducted with the aim of obtaining further information on the size and efficiency of herbivores causing mortality of *Rhizophora stylosa* seedlings in cyclone-damaged areas.

7.2. Methodology

~7.2.1. Experiment 1- The factors delaying recovery of disturbed forests

Two types of disturbance were examined in this experiment – natural damage resulting from Cyclone Tracey in 1974 (25 years ago) and anthropogenic disturbance from bulldozed tracks made in 1992 (7 years ago). Both types of damage were evident in the *Ceriops australis* dominated tidal flat assemblage and in the *Rhizophora stylosa* dominated tidal creek assemblages at Charles Darwin Park (Figure 7-1).

Although 25 years had elapsed since Cyclone Tracey, areas damaged by the cyclone in Charles Darwin Park in 1999 comprised extensive areas of bare mud, just landward of the seaward zone, where there were once tall *Rhizophora stylosa* forests.

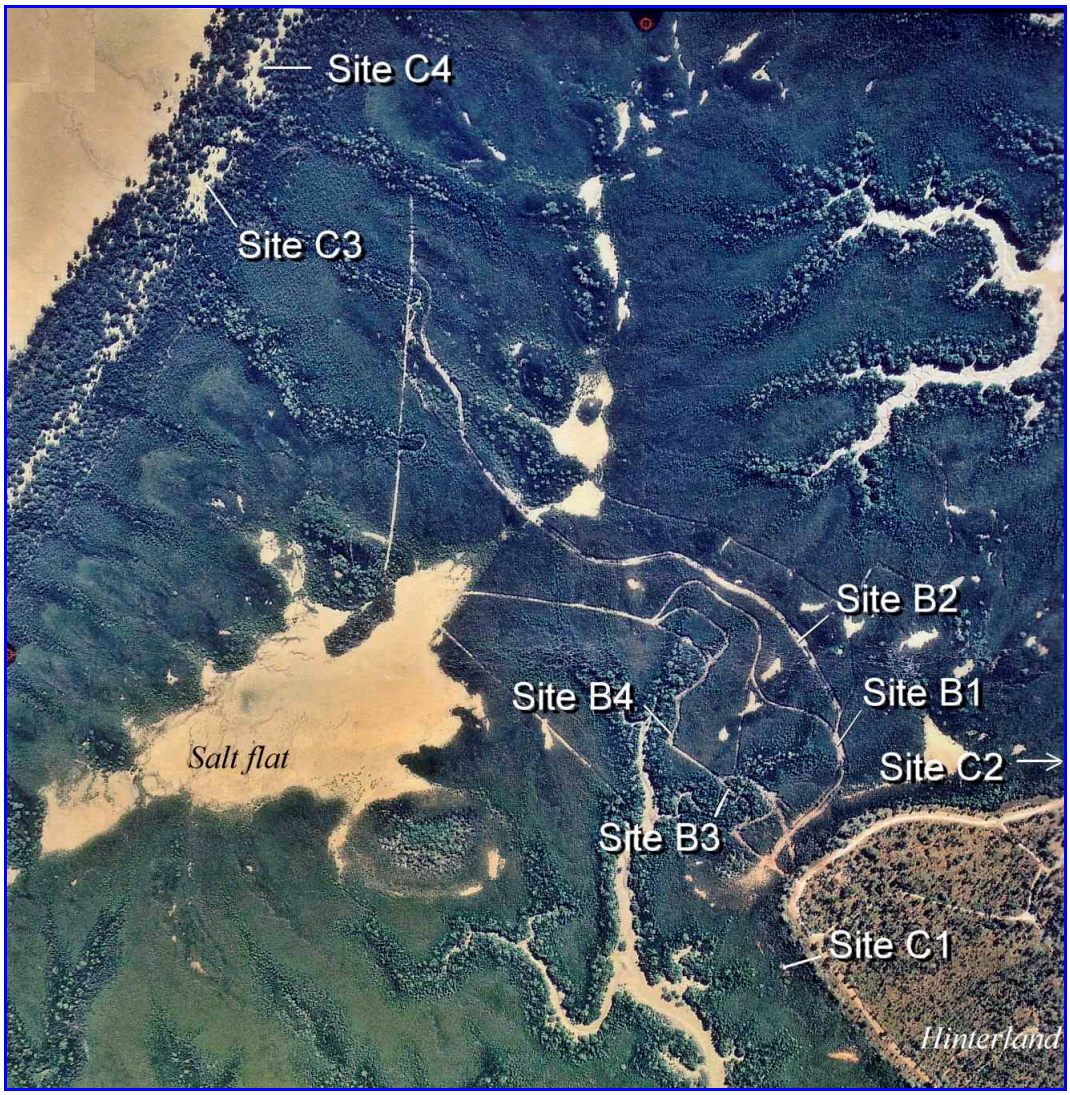


Figure 7-1: Aerial photograph of Charles Darwin Park in 2000 showing clearings created by Cyclone Tracey and bulldozed tracks. Study sites in cyclone-damaged *Ceriops australis* forest (C1 and C2), in *Rhizophora stylosa* forests (C3 and C4), in bulldozed *C. australis* (B1 and B2) and bulldozed *R. stylosa* (B3 and B4) are indicated. Bare areas in the central section of the photo are naturally occurring salt flats

Figure 7-2 : Cyclone damaged *Rhizophora stylosa* forest at site C3, 25 years after the cyclone Tracey (left) and damaged *Ceriops australis* forests in 1995, 21 years after the cyclone (right).

Patches of damaged *Ceriops australis* forest also persisted within the hinterland margin assemblage, approximately 1.3 kilometers to landward. Here, cyclone-damaged bare areas were readily distinguished from salt flats by the abundant windthrown trees that lay in one main direction (Figure 7-2). Delayed recovery of bulldozed areas was also evident, with only sparse regeneration along these extensive tracks in 1999 (Figure 7-3).

Figure 7-3 : Study plots with seedlings planted in four treatments at site B1 in bulldozed *C. australis* forest (left) and at site C3 in cyclone damaged *R. sylosa* forest (right).

Within in each damage type (cyclone or bulldozed), two sampling sites were selected in the tidal flat and tidal creek assemblages (Figure 7-1). Each site comprised three plots, randomly placed within a distance of approximately 100 m, in which five treatments were represented. The treatments were shade, predation/herbivory, mechanical damage, natural forest and control (Table 7-1).

Table 7-1: Five treatments used to investigate seedling growth and survival of *C. australis* seedlings and *R. stylosa* seedlings planted in bulldozed and cyclone-damaged areas.

Symbol	Treatment	Description
S	Shade	Protection from direct sunlight by 50% shadecloth
P	Predation	Protection from seed predators and herbivores >13 mm size provided by hexagonal wire netting
M	Mechanical damage	Protection from drift logs and floating debris provided by steel framework
N	Natural forest	Planted in adjacent undisturbed (same-species) forest - no treatment
C	Control	Seedlings planted in disturbed clearings – no treatment

For three of the five treatments, individual 'propagule pergolas' (117 cm long × 60 cm wide × 100 cm high) that enclosed 10 seedlings were constructed from galvanised steel fence droppers bound together with plastic coated wire. The shade treatment had a roof composed of 50% green shadecloth; the predation treatment was fully enclosed by 13

mm diameter birdwire (0.63 mm thick hexagonal wire netting). The mechanical damage treatment had additional vertical posts to protect enclosed seedlings from damage by floating debris. A control plot comprised corner posts only and was placed adjacent to the other three treatments (Figure 7-3). The natural forest treatment was another control plot, established within adjacent healthy forest (dominated by the same species being planted), generally within forest 5 to 30 m distant from the other four treatments.

Collection of mangrove propagules for the experiment commenced during November 1998. Due to the large number of propagules required for the experiment (600 of each species), some were collected directly from trees, taking care to select mature specimens, while others were collected from the ground (i.e. those fallen within mangrove habitats or washed ashore on nearby beaches). *R. stylosa* propagules picked from trees that still retained the woody calyx, were kept in buckets of seawater until the calyx was shed, prior to planting in containers. Propagules from the two different sources (ground *vs* trees) were cultivated and planted separately, to enable comparison of any effects of propagule collection method on subsequent seedling survival and growth.

Figure 7-4: Nursery culture of *R.stylosa* seedlings prior to planting (left) and planting of *C. australis* using a template to ensure seedlings were evenly placed in plots of 10 (right)

Propagules of both species were placed in 5 litre plastic containers filled with coarse muddy sand (Figure 7-4). Drainage holes were drilled in the bottom of each container and placed in 4 cm high aluminium drip trays. Drip trays were kept full of seawater by watering the seedlings with fresh seawater every few days. To prevent a build up of salt, the containers were fully flushed with seawater approximately once every 2 weeks and occasionally hosed with freshwater. In this way, the sandy growth medium was kept moist and salinity was maintained close to that of seawater.

Seedlings were kept in containers in full sun for approximately 4—6 months. Planting of *Ceriops australis* seedlings was done from 31st May to 8th June 1999 and planting of *Rhizophora stylosa* from 2nd to 6th July 1999. Planted seedlings of both species had 2 (to 4) leaves and well-developed root systems. Seedlings were transported to site in their containers and ten seedlings per treatment were planted within 100 cm × 50 cm subplots using a template to ensure that seedlings were evenly spaced; the minimum linear distance between adjacent seedlings was 20 cm (Figure 7-4). A yabbie pump was used to remove a small mud core of uniform diameter (7 cm) and depth (7-10 cm), creating a hole in which each seedling was planted. The four corners of subplots were marked with a metal post, two of the posts were labelled with an aluminium tag which enabled each plant to be identified by site number, treatment type, collection method and replicate number.

Table 7-2: Sampling regime for plant growth measurements examining recovery from disturbance in cyclone-damaged and bulldozed mangroves in Charles Darwin National Park

RECOVERY FROM DISTURBANCE										
	1999						**2000**			**2001**
	T0	**T1**	**T2**	**T3**	**T4**	**T5**	**T6**	**T7**	**T8**	**T9**
***Ceriops australis*–**	4 Jun	24 Jun	19 Jul	2 Sep	5 Oct	7 Dec	18 Feb	26 May	13 Oct	18 May
Weeks	**0**	**3**	**6**	**13**	**17**	**26**	**36**	**50**	**70**	**101**
	1999					**2000**			**2001**	
***Rhizophora stylosa*–**	5 Jul	27 Jul	3 Sep	11 Oct	6 Dec	24 Feb	20 May	11 Oct	20 Jul	
Weeks	**0**	**3**	**8**	**14**	**22**	**33**	**45**	**66**	**106**	

The first measurements of the 1,200 seedlings were taken at the time of planting and then repeated up to nine times during the next two years (Table 7-2). For both species, seedling height was always measured from the top of the hypocotyl, i.e. from the cotyledonary scar to the tip of the apical shoot. At each sampling time the total number of leaves and leaf scars (i.e. the annular rings on all stems below any living leaves that persist after leaf pairs have been shed) were counted to measure leaf production and turnover respectively. The number of secondary and tertiary shoots and their total length was also recorded. Regular maintenance and replacement of the pergolas was necessary due to rapid corrosion of both the birdwire and the fence droppers. Due to plant growth, it was necessary to increase the height of the *R. stylosa* pergolas after

approximately 33 weeks.

Soil shear strength (indicating soil density) of near surface soil was measured using the 33 mm or 19 mm vane test at each of the eight study sites once during the course of the experiment (on 17 November 2000). The test was carried out in accordance with Australian Standard AS1289.6.2.1 *Soil Strength and Consolidation Tests—Determination of the shear strength of a soil—Field test using a vane*. The shear strength is a measure of the force required to rupture the soil. Three measurements were made at random points within each disturbed site and three readings were also taken within the adjacent natural forest plot. Soil shear strength was calculated using the formula—

$$s = \frac{10^9 \times 6}{\pi} \times \frac{T}{D^2(3H + D)}$$

where s = vane shear strength , in kilopascals; T = torque to shear the soil, in kilo Newton metres; D= diameter of vane, in millimetres; and H = length of vane, in millimetres (Anon, 2000).

Soil salinity was determined by measurement of conductivity of a slurry made from a 1:5 dilution of soil to distilled water using a TPS *AquaCP* meter. Approximately 20 g fresh weight of soil at natural moisture content was sampled from 5—10 cm depth using a yabbie pump and completely mixed with 100 ml water. The conductivity (mS cm^{-1}) was measured after thorough shaking. Three replicate samples were taken at each of the eight disturbed sites and at each of the natural forest treatments.

~7.2.2. Experiment 2: Herbivory in cyclone-damaged *R. stylosa* forests

To further investigate the herbivory of *R. stylosa* seedlings observed during the first experiment in cyclone damaged *Rhizophora stylosa* forests, a second study was commenced in February 2001. Insect herbivory was unlikely given the fact that entire shoots were removed, thus it was assumed that fish or crustaceans might be eating the tips of seedlings during inundation by high tides. Underwater observation at high tide was not an option due to highly turbid water and the possibility of crocodile attack, but a most fortunate sighting was made whilst conducting a fauna survey by canoe at high tide. A sea turtle was observed at site C3 when it surfaced within the cyclone-damaged clearing (pers. obs.). Presumably the turtle was feeding within the mangrove forest,

possibly on algae attached to tree roots or on the leaves of mangrove seedlings. Indeed, judging by the nature of damage incurred by seedlings in experiment 1, the missing shoots appeared to have been sheared off by a turtle beak. To investigate whether sea turtles—or alternatively, other smaller herbivores—were eating the leaves of *R.stylosa* seedlings, a second experiment was initiated to ascertain the size and nature of the herbivore.

Three plots were established, in the same clearings studied in experiment one (Sites C3 and C4), each comprising one exclosure and an adjacent control. The exclosure consisted of a cage, 1.5 m long × 1.0 m wide × 1.5 m high, constructed of 20 cm × 20 cm steel arc mesh supported by star pickets (Figure 7-5). The large mesh was to permit access to medium sized fish, crabs and other invertebrates but to exclude large herbivorous vertebrates, including turtles. Ten *R. stylosa* seedlings were planted in the centre of the cage using the same template described above, such that a 50 cm gap between the plants and the mesh was maintained.

Figure 7-5: Control planting (left) and exclosure (right) constructed of 20 cm × 20 cm steel mesh used to investigate herbivory in cyclone -damaged *Rhizophora stylosa* forests in Experiment 2.

Adjacent to each exclosure, a control plot comprising ten seedlings was planted and marked only by four small corner posts. In all, 120 seedlings (60 in exclosures and 60 in controls) were monitored over a period of 18 months (Table 7-3). The techniques for planting and measurement of seedling growth were the same as those described above for experiment one.

Table 7-3: Sampling regime for plant growth measurements examining recovery from disturbance in cyclone-damaged and bulldozed mangroves in Charles Darwin National Park

HERBIVORE EXCLOSURE EXPERIMENT							
Year	**2001**					**2002**	
Sample	**T0**	**T1**	**T2**	**T3**	**T4**	**T5**	**T6**
Date	8th Feb	1st Mar	30th Mar	27th Apr	5th Jul	6th Dec	20th Jun
Weeks	0	3	7	12	22	44	73

Analyses

All data for experiment 1 was entered into a *Microsoft Access* database from which means for the five treatments were derived for the two collection techniques (n=5). Plant growth and survival data for *Rhizophora stylosa* and *Ceriops australis* was analysed separately. To enable correlations to be performed, samples with zero values (i.e. where there were no results because plants had died) were deleted. A correlation matrix was then generated for the six measures (height, leaf total, leaf scar count, count of secondary shoots, total shoot length and survival) using product moment correlation in *Statistica v5.5.* Correlation matrices were also generated for soil salinity and density, seedling height and survival. Seedling survival data was converted to a proportion prior to analysis. For each species, five factor nested ANOVA's were used to compare seedling survival amongst disturbance type (fixed, 2 levels), site (random, 2 levels, nested in type), treatment (fixed, 5 levels), collection method (random, 2 levels) and plot (random, 3 levels, nested in treatment, site and type). Analyses were run on data from the last two sampling times, i.e. after 66 and 106 weeks for *R. stylosa,* and at 70 weeks and 101 weeks for *C. australis.* These times coincided with the early wet season of 2000 and the following dry season, when seedlings had been monitored for two years. Normality plots and graphs of homogeneity of the variances were examined in *Minitab* before and after transformation to ensure that ANOVA assumptions were satisfactorily met. Where tests indicated transformation was necessary, survival data was transformed using the arcsine squareroot, while heights and leaf scars were transformed using $\log_{10}(x + 1)$.

In analyses of mean height and number of leaf scars, bulldozed and cyclone damaged areas were examined separately due to missing values in data from cyclone-damaged

sites. Mean height and count of leaf scars was analysed in four factor nested ANOVAs comparing site (random, 2 levels), treatment (fixed, four levels), collection method (fixed, 2 levels) and plot (random, 3 levels, nested in treatment and site). For *C. australis* only, the natural forest treatment and the third plot in each treatment was omitted from all analyses due to an unbalanced number of propagules per collection method.

For experiment 2, analyses involved three factor nested ANOVA's comparing mean survival and growth (leaf scar count) in exclosures and control plots. The factors were site (random, 2 levels), treatment (fixed, 2 levels) and plot (random, 3 levels, nested in treatment and site). Analyses were run on data collected during the last two sampling times, i.e. at 44 weeks and at 73 weeks. The effect of different mesh sizes on the cages in experiments 1 and 2 were only compared graphically due to seasonal inconsistency between experiments.

7.3. Results

Experiment 1 – The factors delaying recovery of disturbed forests.

For *R. stylosa*, there was high correlation between the means for total leaf count and leaf scar count, and between leaf count and shoot length. Significant correlation was also found between mean leaf count and number of shoots. The same significant correlations were found for *C. australis* (Tables 7-4 and 7-5). To avoid duplication and to reduce the number of analyses performed, only height, leaf scar and survival data was selected for analysis in experiment 1

Table 7-4 : Correlation matrix for variables measuring growth and survival of *Ceriops australis* seedlings, where n= 170. Significant correlations at $p<0.05$ are marked in red

	Height	Leaf total	Shoot length	Shoot count	Leaf scars
Leaf total	0.94	1.00	-	-	-
Shoot length	0.88	0.90	1.00	-	-
Shoot count	0.90	0.94	0.87	1.00	-
Leaf scars	0.88	0.95	0.85	0.90	1.00
Survival	-0.18	-0.21	0.00	-0.17	-0.20

Table 7-5 : Correlation matrix for variables measuring growth and survival of *Rhizophora stylosa* seedlings, where n= 215. Significant correlations at p<0.05 are marked in red

	Height	Leaf total	Shoot length	Shoot count	Leaf scars
Leaf total	0.60	1.00	-	-	-
Shoot length	0.60	0.94	1.00	-	-
Shoot count	0.57	0.92	0.91	1.00	-
Leaf scars	0.68	0.75	0.72	0.74	1.00
Survival	0.21	0.30	0.31	0.29	0.06

~7.3.1. Disturbed *Rhizophora stylosa* forests

A total of 5,400 measurements of *R. stylosa* seedlings were collected during nine sampling events (T0 to T8) over the two year period from July 1999 to July 2001.

Bulldozed sites

R.stylosa seedlings in each of the five treatments planted in and adjacent to bulldozed tracks grew well over the two-year period. Seedlings in the four treatments on bulldozed tracks attained a mean overall height of 364.4 cm (± 18.8 SE) at 66 weeks and 546.6 cm (± 30.3 SE) at 106 weeks (Figure 7-6). Seedlings in the predation treatment appeared to grow faster than those in other treatments but there was considerable variation among plots and the difference was only significant in the analysis at 106 weeks (Tables F-1 and F-2, Appendix F).

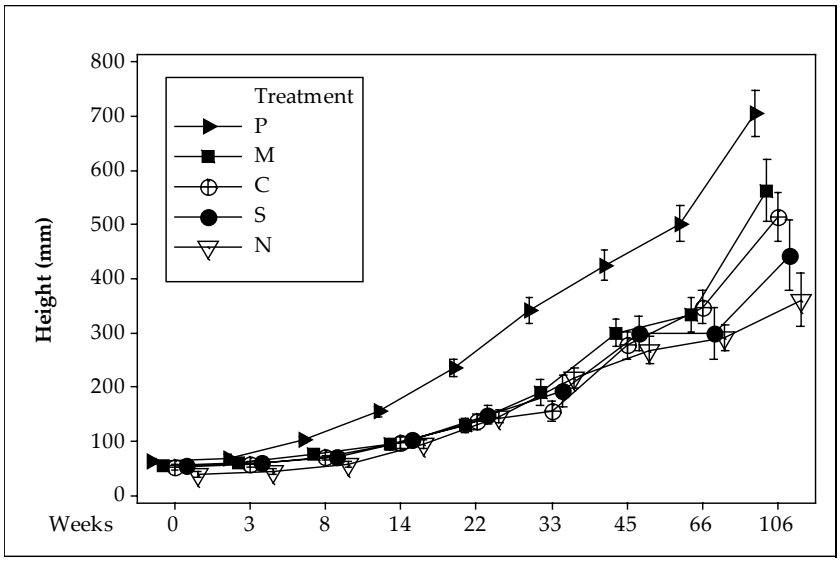


Figure 7-6: Mean height of *R. stylosa* seedlings (± SE) on bulldozed tracks grown under different treatments where P= predation, M= mechanical damage, C=control, S=shade and N= natural forest. Data pooled for two sites (B3 and B4)

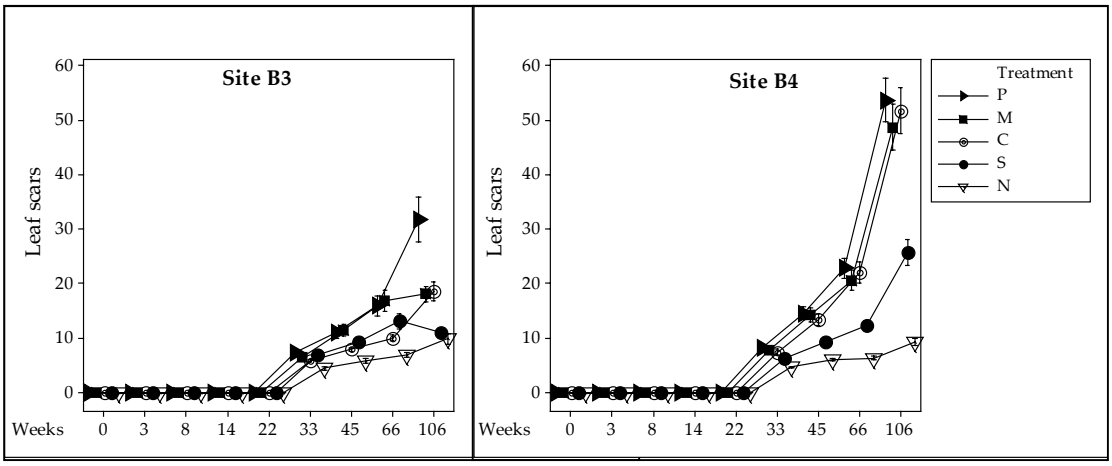


Figure 7-7: Mean numbers of leaf scars (± SE) on *R. stylosa* seedlings planted in different treatments over 106 weeks, at two sites damaged by bulldozer.

Although seedling height was similar at both sites (B3 and B4), mean leaf scar count was higher at site B4 than at site B3. Significant differences in mean leaf scars were also detected between treatments (Tables F3 and F4, Appendix F). Amongst the treatments, seedling growth (as indicated by both leaf scar count and height) was greatest within predation cages and least in the natural forest treatments. Of the three treatments that involved protective structures (P, S and M), the growth of seedlings was least beneath 50% shadecloth (Figures 7-6 and 7-7).

Cyclone-damaged sites

Due to the large numbers of missing plants in cyclone damaged *R. stylosa* forests, analyses were not run on these data. The graph of mean seedling height indicates that from as early as 8 weeks, seedlings not enclosed in predation cages showed diminished growth (Figure 7-8). After 106 weeks, mean seedling height had substantially increased in only two of the five treatments—predation and natural forest—all seedlings in the other treatments had died (see survival graph, Figure 7-10). Surviving seedlings in cyclone damaged clearing grew to a mean height of 577.4 (± 38.7 SE) after 66 weeks and 743.0 (± 57.7 SE) after 106 weeks.

Mean leaf scar count increased steadily over 106 weeks for seedlings protected from predation but this was not found in other treatments (Figure 7-9). Diminished growth in unprotected seedlings was largely due to the removal of leaves and apical shoots of *R. stylosa,* which was evident during the first weeks after planting and occurred repeatedly throughout the experiment. Generally, the entire seedling tip was broken off (pers. obs.),

presumably by an herbivorous animal, typically leaving the propagule in an upright position. After only 8 weeks, apical shoots were missing on 38% of seedlings planted in these treatments. The epicormic growth of secondary shoots generally occurred following leaf removal but repeated grazing appeared to cause the observed high seedling mortality.

Herbivory was also evident in the dense patches of *R. stylosa* seedlings that had regenerated naturally beneath the trees fringing cyclone-damaged clearings. Seedlings and saplings had been 'grazed', with leafless seedlings occurring right up to the edge of existing forests. Seedlings in natural forest plots at the edge of clearings were also affected by herbivory; 23% of seedlings were leafless due to loss of the terminal shoot, eight weeks after planting. Herbivory did not, however, extend far into the dense forest beyond and this type of damage to *R. stylosa* seedlings was not observed in other assemblages.

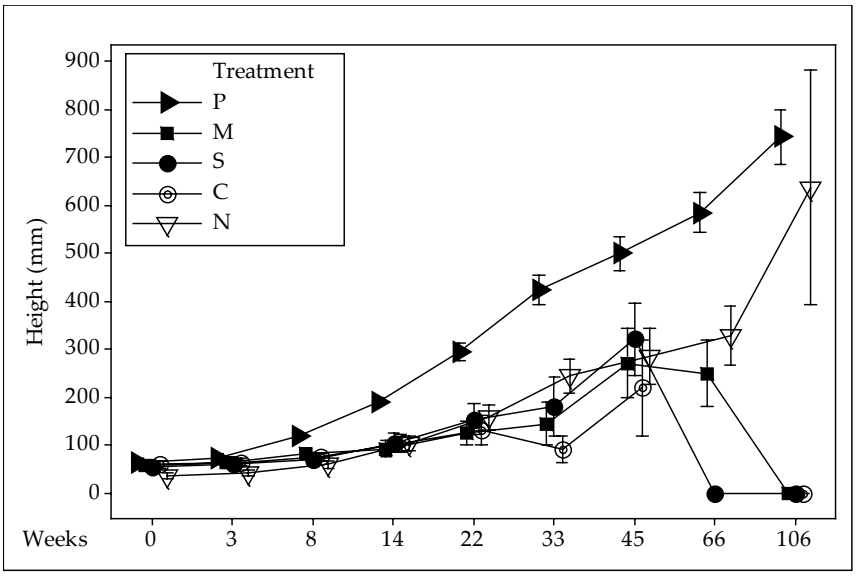


Figure 7-8: Mean height (± SE) of *R. stylosa* seedlings grown under different treatments in cyclone-damaged forests over 106 weeks. Data pooled for two study sites.

Survival of *R. stylosa* seedlings differed between cyclone damaged and bulldozed areas; the difference was evident at both 66 and 106 weeks (Tables F5 and F6, Appendix F). Seedling survival was greater in bulldozed areas where seedlings in the majority of treatments survived. By contrast, survival of seedlings in cyclone damaged areas was poor; most seedlings had died after six months (Figure 7-10).

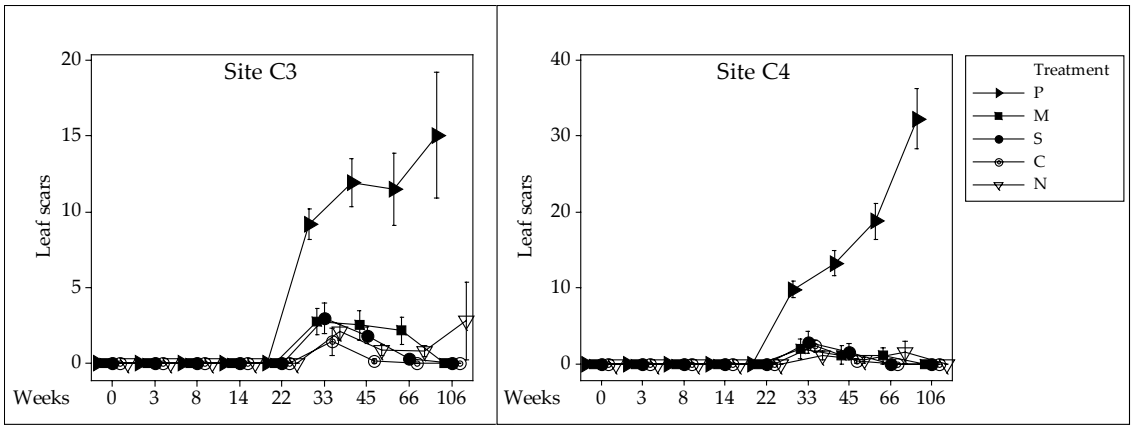


Figure 7-9: Mean numbers of leaf scars (± SE) of *R. stylosa* seedlings grown under different treatments in two cyclone-damaged sites over 106 weeks.

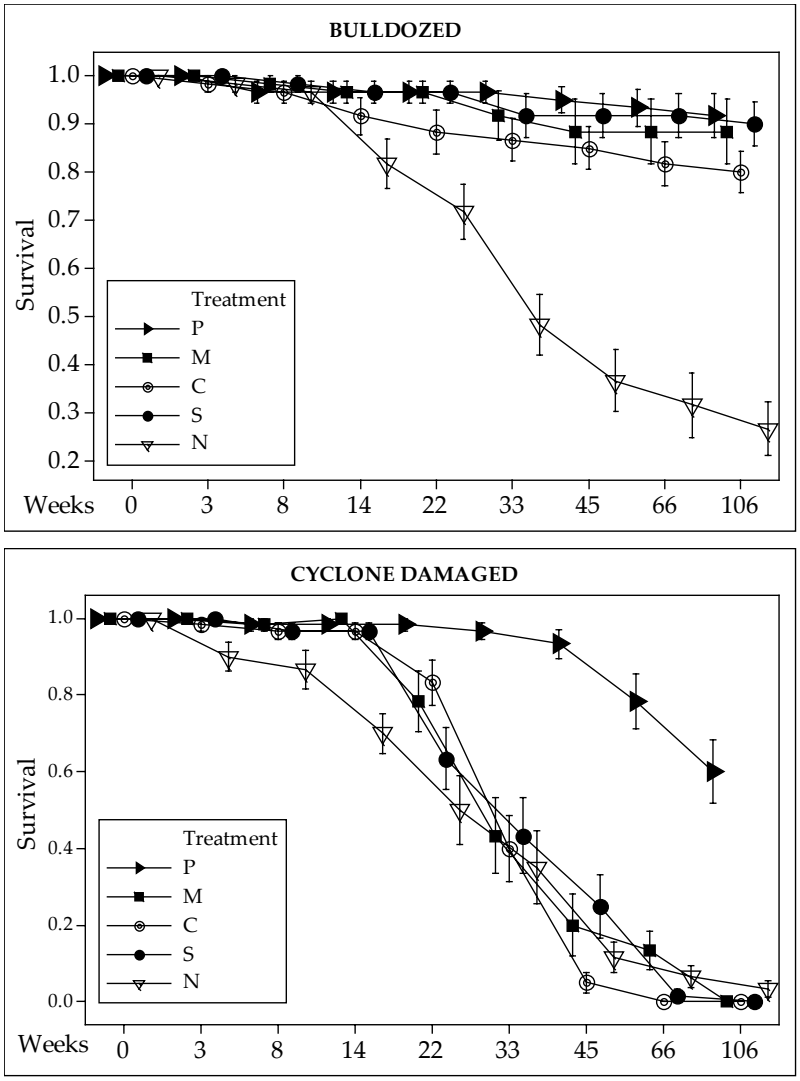


Figure 7-10: Mean survival of *R. stylosa* seedlings (proportion ± SE) grown under different treatments from T0 to T8 in cyclone damaged (lower graph) and bulldozed areas (upper) where P = predation, M = mechanical damage, C =control, S =shade and N = natural forest. Data pooled for the two study sites in each damage type.

Seedling survival differed between treatments and a type × treatment interaction indicated that survival in bulldozed and cyclone damaged areas varied amongst the different treatments. Seedlings within natural forest plots, for example, were the only treatment to show poor survival in bulldozed areas. In cyclone damaged areas seedlings protected in predation treatments were almost the only ones to survive (Figure 7-10). Survival in predation treatments in cyclone damaged areas in the low intertidal zone (61.7 %) was however, substantially lower than in bulldozed areas in the mid-intertidal zone (91.6%) after 106 weeks. Survival of *R.stylosa* seedlings grown from propagules gathered directly from trees was significantly higher than seedlings grown from ground-collected propagules 66 weeks after planting. The difference was only slight however, and no significant difference in survival was evident nine months later, at 106 weeks (Tables F5 and F6, Appendix F). The same pattern was observed in cyclone-damaged sites, with no difference between propagule collection methods evident at the end of the experiment (Figure 7-11).

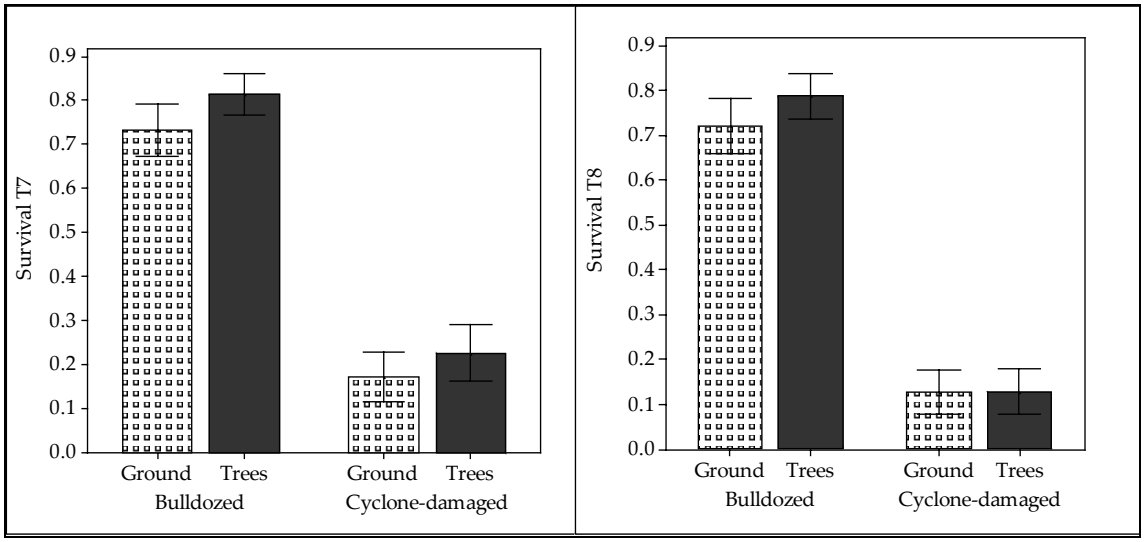


Figure 7-11: Mean survival of *R. stylosa* seedlings (proportion ± SE) grown from propagules collected by different methods in bulldozed and cyclone-damaged forests, 66 weeks (left) and 106 weeks (right) after planting. Data pooled for two sites in each disturbance type.

~7.3.2. Disturbed *Ceriops australis* forests

A total of 6,000 measurments of *C. australis* seedlings were collected during ten sampling events (T0 to T9) over the 23 month period from June 1999 to May 2001.

Bulldozed sites

Over the two-year study period, *C. australis* seedlings planted in the four treatments on bulldozed tracks attained a mean height of 113.8 cm (± 3.3 SE, n=187) at 70 weeks and 228.1 cm (± 6.1 SE, n=183) at 101 weeks (Figure 7-12). By contrast, seedlings planted within natural forest treatments had a mean height of only 23.7 (± 2.1 SE, n=7) after 70 weeks and 29.9 cm (± 3.4 SE, n=7) at 101 weeks. Growth at natural plots seemed markedly lower than in the other treatments (Figure 7-12) but these had to be excluded from analyses because of unbalanced numbers of seedlings collected using different methods (i.e. picked directly from trees or gathered from the ground). There were no significant differences in mean height among the four remaining treatments (Tables F7 and F8, Appendix F).

Mean seedling height at 70 weeks was greater at site B1 (125.9 ± 4.8 SE) than at site B2 (98.9 ± 4.0 SE) but this difference was not evident at 101 weeks (Figure 7-12). Mean number of leaf scars on *C. australis* seedlings 70 weeks after planting was higher at site B1 than that at site B2 (Table F9, Appendix F) but leaf scar counts were similar between the two bulldozed sites at 101 weeks.

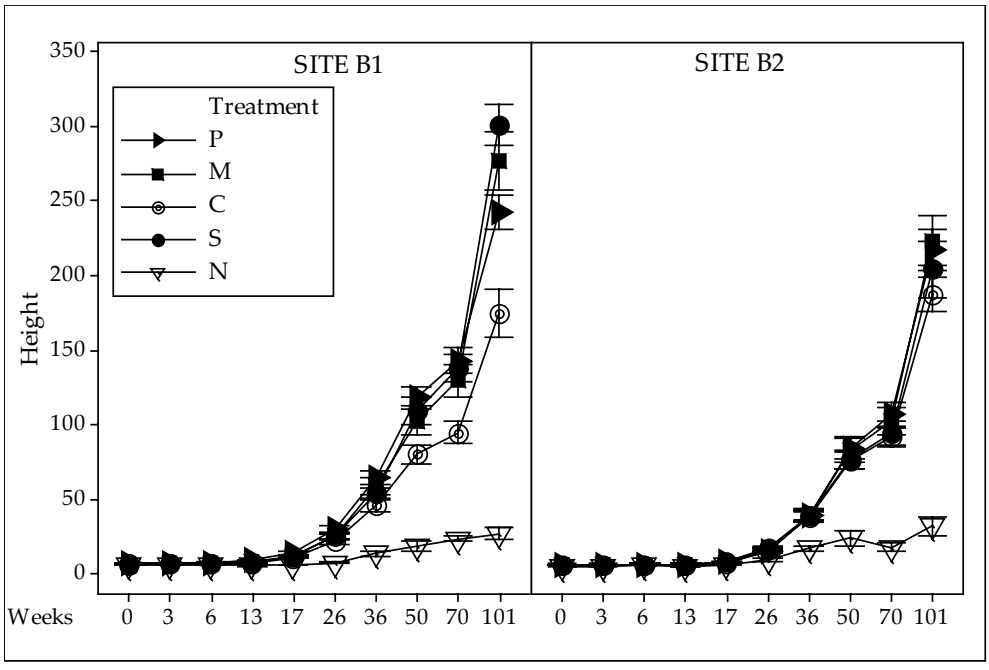


Figure 7-12: Mean height of *C. australis* seedlings (± SE) planted at two sites on bulldozed tracks. Points are means of three study plots in each of five treatments where P = predation, M = mechanical damage, C = control, S = shade and N = natural forest.

Collection method for *C. australis* propagules did not have any significant effect on the

height, growth (leaf scar count) or survival of seedlings planted on bulldozed tracks after two years (Tables F7 to F-12, Appendix F).

Cyclone damaged sites

Over the two-year study period *C. australis* seedlings planted in cyclone damaged clearings attained a mean height of 67.1 cm (± 3.0 SE, n=130) at 70 weeks and 174.5 cm (± 8.3 SE, n=118) at 101 weeks (Figure 7-13). Seedlings planted in adjacent natural forest showed limited growth and survival with a mean height of 21.9 (± 2.2 SE, n=17) after 70 weeks and 32.2 cm (± 2.7 SE, n=10) at 101 weeks

Again, natural forest treatments were excluded and no difference in mean height or leaf scar count was found for seedlings grown in the four remaining treatments at 70 weeks, or at 101 weeks (Tables F7 and F8, Appendix F). Seedling growth in the natural forest plots again seemed substantially lower than in other treatments (Figure 7-13).

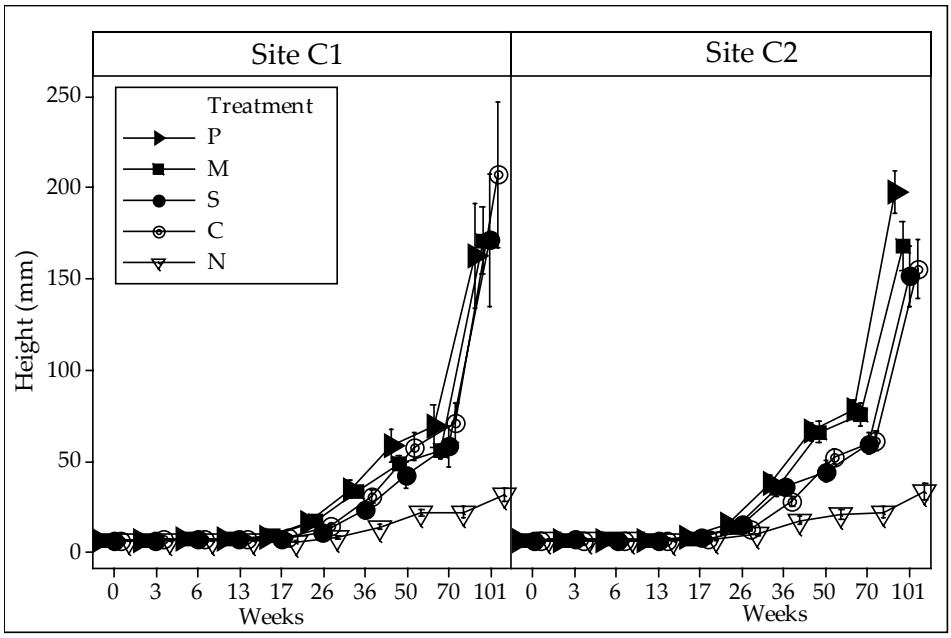


Figure 7-13: Mean height of *C. australis* seedlings (± SE) planted at two sites in cyclone damaged mangroves. Points are means of three study plots in each of five treatments where P = predation, M = mechanical damage, C = control, S = shade and N = natural forest.

Differences in height between the two study sites were evident amongst seedlings grown from propagules collected using different methods. At site C1, the mean height of tree-collected plants was lower than ground-collected plants, whereas seedlings grown from the same stock were slightly taller at site C2 (Figure 7-14). The MS error for that test was, however, unusually small, and the significant effect might just be a chance result (Table F14, Appendix F)

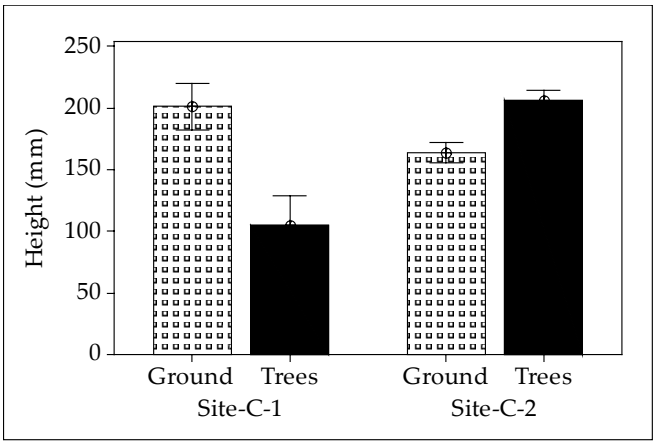


Figure 7-14: Mean height of *C. australis* seedlings (± SE) grown from propagules collected either from the ground or from trees, 101 weeks after planting in cyclone damaged clearings. Data from four treatments pooled for each site, excluding natural forest plots.

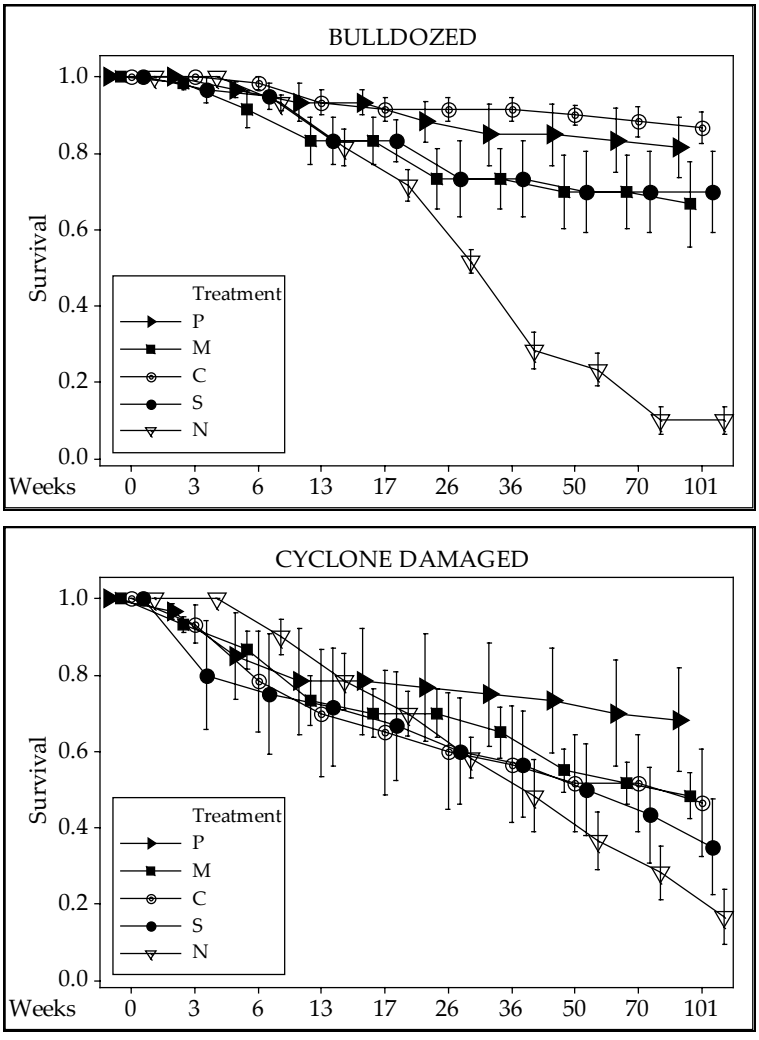


Figure 7-15: Mean survival of *C. australis* seedlings (proportion ± SE) grown under different treatments from T0 to T9 in cyclone damaged (lower graph) and bulldozed areas (upper) where P = predation, M = mechanical damage, C =control, S =shade and N = natural forest. Data pooled for two study sites within each damage type.

Survival of *C. australis* seedlings was higher in bulldozed tracks than in cyclone damaged areas (Tables F11 and F12, Appendix F). Aside from poor survival in natural forest plots, high survival was recorded in the majority of other treatments planted in bulldozed mangroves. By contrast, survival in all treatments planted in cyclone damaged areas was substantially lower, and more variable (Figure 7-15). Survival of seedlings in natural forest plots adjacent to bulldozed tracks appeared lower, however, than that recorded in natural forest plots next to cyclone damaged areas.

Survival of seedlings grown from tree-collected propagules was lower than those originating from the ground, in cyclone-damaged mangroves at 101 weeks. By contrast, this pattern was not observed in bulldozed mangroves where survival of tree-collected and ground-collected material was equivalent (Figure 7-16, Table F12, Appendix F).

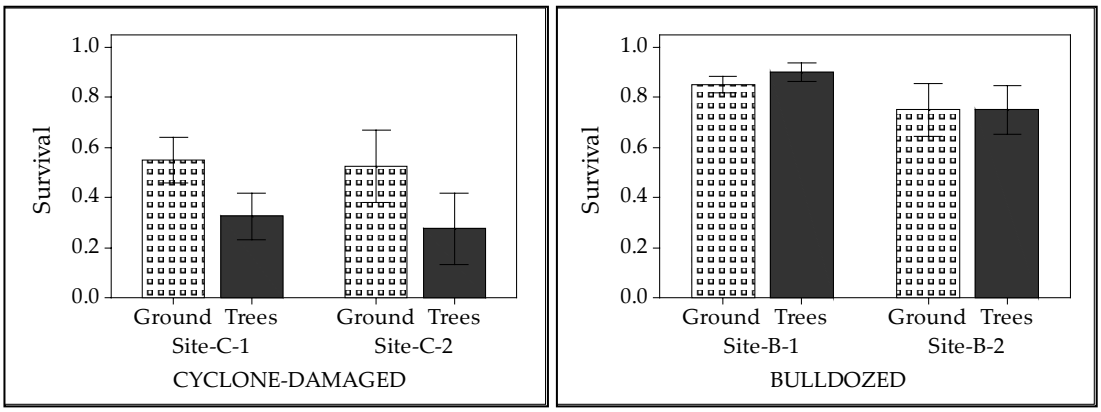


Figure 7-16: Mean survival of *C. australis* seedlings (± SE) grown from propagules collected from the ground or from trees at two study sites in cyclone damaged and bulldozed mangroves, 101 weeks after planting. Data from natural forest treatment excluded.

~7.3.3. Soil density and salinity

Soil density (measured as shear strength) was minimal in the soft marine muds that were characteristic of cyclone-damaged *R. stylosa* forests close to the seaward margin. Measurements at other sites in the mid-intertidal zone revealed intermediate density with very high soil density recorded only at site C1, amongst cyclone-damaged *C. australis* forest at the landward mangrove margin (Figure 7-17). At all the study sites, density was consistently higher in natural forest areas than in clearings created by disturbance.

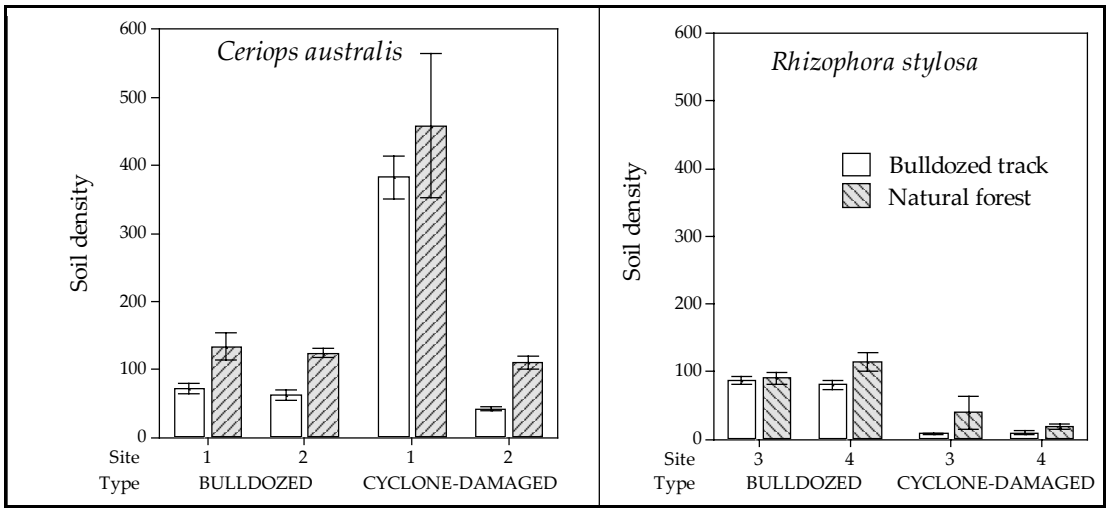


Figure 7-17: Mean soil density or shear strength (kPa) of substrates in bulldozed and cyclone damaged forests (± SE), indicating disturbed (bulldozed track) and undisturbed (natural forest) treatments.

Table 7-6 :Correlation matrix for soil conductivity and density, survival seedling height and leaf scars of *Ceriops australis* in control and natural forest treatments in bulldozed sites and cyclone-damaged sites. Significant correlations at p<0.05 are marked in red, n= 10.

		Conductivity	**Density**	**Survival**	**Height**
BULLDOZED	**Density**	0.63	-	-	-
	Survival	-0.54	-0.82	-	-
	Height	-0.53	-0.84	0.95	-
	Scars	-0.46	-0.70	0.79	0.89
		Conductivity	**Density**	**Survival**	**Height**
CYCLONE-DAMAGED	**Density**	-0.17	-	-	-
	Survival	-0.78	-0.07	-	-
	Height	-0.13	-0.07	0.62	-
	Scars	-0.01	-0.03	0.53	0.95

In and adjacent to bulldozed tracks, seedling growth and survival of *C. australis* was positively correlated with soil density but seedling performance was not correlated with soil density in cyclone-damaged areas (Table 7-6). No correlation was found between soil density and seedling growth and survival of *R. stylosa* in bulldozed tracks.

Soil salinities were uniform in sites located close to the seaward zone (C3 and C4) and increased to landward, with the highest soil conductivity values recorded in the mid and upper tidal zone at sites C2 and B1 (Table 7-7). A simple comparison of means indicates that soil salinity was generally greater in natural forest treatments than in

controls. A significant negative correlation was found between soil salinity and survival of *C. australis* seedlings, in and adjacent to cyclone damaged mangroves (Table 7-6).

Table 7-7: Mean soil density and conductivity at study sites in cyclone damaged and bulldozed mangroves.

Site Type & No	Species	Conductivity (mS cm $^{-1}$)			
CYCLONE-DAMAGED		**DISTURBED**		**NATURAL FOREST**	
		Mean	**SE**	**Mean**	**SE**
C1	*C. australis*	11.1	± 2.1	10.0	± 0.9
C2	*C. australis*	8.2	± 0.3	13.2	± 0.6
C3	*R. stylosa*	9.8	± 0.4	10.9	± 0.4
C4	*R. stylosa*	10.8	± 0.3	11.0	± 0.6
BULLDOZED					
B1	*C. australis*	10.9	± 0.6	13.9	± 0.01
B2	*C. australis*	10.8	± 0.8	11.3	± 0.5
B3	*R. stylosa*	10.9	± 0.7	11.8	± 0.4
B4	*R. stylosa*	11.7	± 0.7	11.6	± 0.7

Experiment 2 – Herbivory of *Rhizophora stylosa* in cyclone damaged clearings

Relatively soon after planting *R. stylosa* seedlings at sites C3 and C4 (see Figure 7-1 for location) the leaves, and often entire terminal shoots, were removed from seedlings in control plots. Seedlings protected by the 20 cm × 20 cm steel mesh exclosures were however, unaffected in this way, indicating that the herbivore responsible was probably a large animal. The impact of herbivory—shown by reduced mean leaf scar counts in control plots—became increasingly evident during the course of the experiment (Figure 7-18, left).

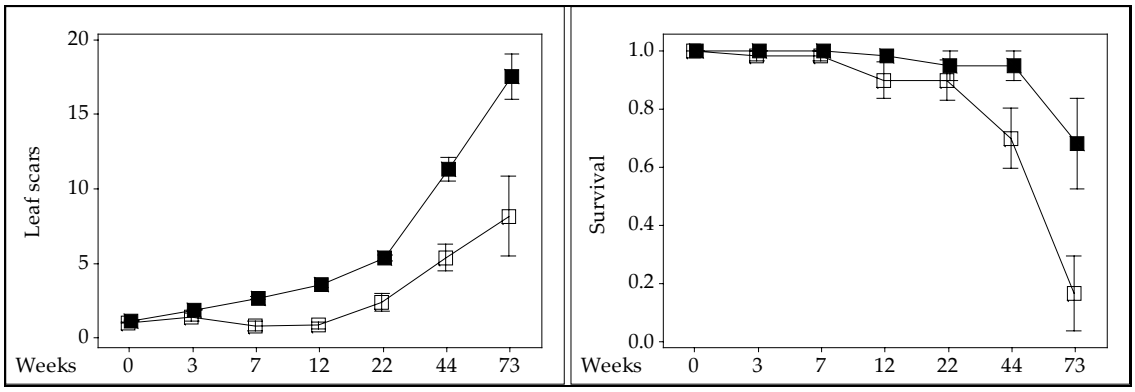


Figure 7-18: Mean leaf scar count (left) and survival (right) of *R. stylosa* seedlings (± SE) planted in exclosures (solid symbols) and controls (open symbols) over 73 weeks. Data for two sites pooled

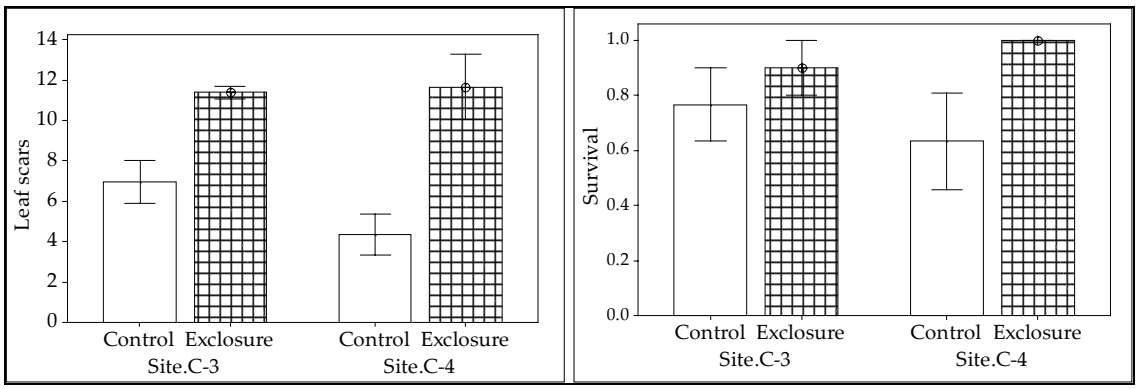


Figure 7-19: Mean leaf scar count and survival (proportion) of *R. stylosa* seedlings planted in control plots and exclosures after 73 weeks. Data for three plots pooled at each site.

Seedlings in the exclosures appeared to grow faster than those in control plots but there was considerable variation among plots and the difference was only significant in the analysis at 73 weeks. (Tables F-17 and F-19, Appendix F). Although the survival of seedlings in controls and exclosures was similar 44 weeks after planting (Figure 7-18 right), survival was significantly lower in control plots at site C4 after 73 weeks (Figure 7-19 right, Tables F-18 and F-20 Appendix F). The difference between treatments (i.e. control *vs* exclosure) for both seedling growth and survival was most pronounced at site C4 (Figure 7-19).

Comparison of the effects of mesh size, i.e. of the 13mm wire netting used in experiment 1 with the 20 cm × 20 cm steel mesh used in experiment 2, showed a similar pattern of high survival within exclosures. Survival in control plots was variable however, with very high mortality for seedlings in experiment 1 during the 11 months prior to May 2000 (Figure 7-20, left) but better survival of controls in the second experiment, spanning the 11 months prior to December 2002 (Figure 7-20, right).

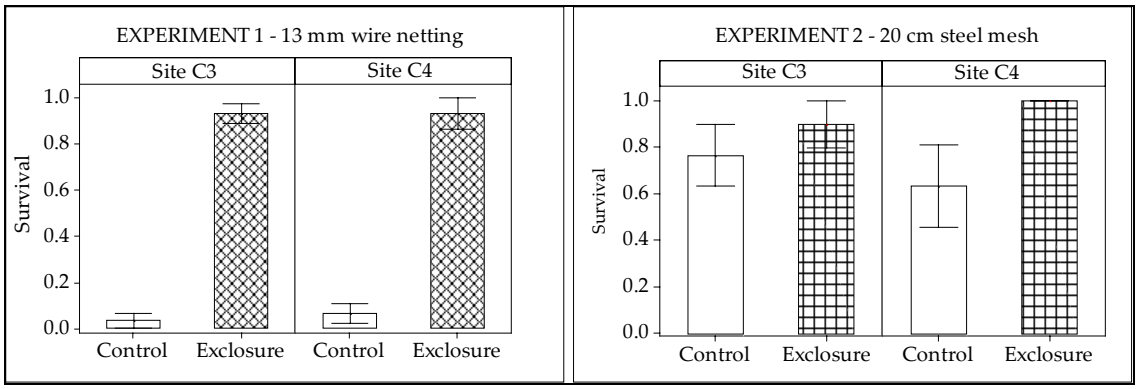


Figure 7-20: Survival of *R. stylosa* seedlings planted in control and exclosure treatments with different mesh size. Left: Exclosures in experiment 1 (45 weeks after planting in May 2000) comprised 13mm wire netting (n = 60 seedlings). Right: Exclosures in experiment 2 (44 weeks after planting in December 2002) comprised 20 cm² steel mesh (n = 60 seedlings). Data from three plots pooled at each site.

Unequivocal evidence that sea turtles eat the leaves of *R. stylosa* was gained in 2006, by examining the contents of a stomach and upper intestine of a green turtle (*Chelonia mydas)* held at the Northern Territory Museum which had been found dead on a Darwin beach. The gut contents included alternating broad bands of plant material recently consumed by the turtle, containing red and yellow algae, seagrass and *R. stylosa* leaves. The mangrove plant material comprised mainly small leaves, stems and shoots easily identified as those of *R. stylosa* (Figure 7-21 right). The mangrove leaves were embedded in red algae (Figure 7-21 left) which appeared very similar to that which thickly covers the lower roots of mature *R. stylosa* trees in Darwin harbour.

Figure 7-21: Left: Gut contents of a green turtle (*Chelonia mydas)* including seagrass leaves in foreground and the leaves and shoots of *R. stylosa* amongst red algae in background. Right: *R. stylosa* leaf fragments and terminal shoots removed from crop and intestine.

Occasionally, leaves from *Aegiceras corniculatum* or *Avicennia marina* were also found amongst the gut contents, but these were more deteriorated and blacker in colour, and may have been ingested accidentally. Overall, it appears that *C. mydas* is the most likely herbivore damaging *R. stylosa* seedlings in cyclone damaged clearings.

7.4. Discussion

A number of similarities and several major differences emerged from these results. On bulldozed tracks, despite minimal natural recovery during the previous seven years, artificially planted seedlings of both *C. australis* and *R. stylosa* had high growth and survival. The high survival of seedlings planted in all treatments on bulldozed tracks indicated that neither shade, predation nor physical damage were limiting the establishment of either species. In particular, the high survival of seedlings in control treatments on bulldozed tracks suggests that natural regeneration has been delayed by other processes acting prior to seedling establishment. Poor dispersal ability and reduced opportunity for propagule establishment are likely to be key factors in this process (see section 7.4.1 below).

Another similarity was that in both bulldozed and cyclone-damaged areas, the performance of seedlings of both species was enhanced within predation exclosures. Moreover, *R. stylosa* and *C. australis* seedlings in both disturbance types, and at all tidal elevations, showed diminished growth in shade treatments. Both species grew best when not beneath the forest canopy, evident by the severely limited survival of seedlings within the forest. In sharp contrast with natural forest treatments, the relatively enhanced growth and high survival of seedlings planted in bulldozed tracks was probably due to factors such as high light and nutrient availability (Smith III, 1987a; Sousa and Mitchell, 1999), and decreased predation by crabs (Osborne and Smith III, 1990). Furthermore, patterns of growth and survival of seedlings were generally similar amongst study sites.

Marked differences in the factors affecting forest recovery were also evident, however, between the two types of disturbance, at different positions on the shoreline and between the two species. Different limiting processes were active at different tidal elevations and this contributed to contrasting experimental results from cyclone-

damaged forests at the landward (*C. australis* dominant) and seaward (*R. stylosa* dominant) margins. A striking difference was evident in the extremely high survival rates of *R.stylosa* seedlings planted in mid–intertidal bulldozed tracks in comparison with the very limited survival of seedlings in cyclone-damaged clearings close to the seaward margin. Furthermore, the survival of *R.stylosa* in seaward cyclone dominated-habitats was strongly regulated by herbivory, whereas this was not a factor limiting survival in landward cyclone-damaged *C. australis* forests. Notwithstanding these differences, recovery of both forest types destroyed by cyclone Tracey remains incomplete, more than two decades after the storm. This and other observations suggested that the processes contributing to the poor recovery of cyclone-damaged forests may have changed over time and may include factors other than recruitment difficulty and predation.

Indeed, the consistently lower performance and survival of seedlings in cyclone damaged areas compared with bulldozed forests underscored the potential importance of abiotic or environmental changes—including a range of secondary impacts caused by deforestation and substrate instability. The survival of *R. stylosa* protected by predation exclosures (61.7%) in low-intertidal cyclone damaged forests was, for example, substantially less than in exclosures in mid-intertidal bulldozed mangroves (91.6%). It appears that the factors delaying recovery may be complex, and may vary spatially and temporally. The potential role of key abiotic factors, including physico-chemical changes in substrate, sediment compaction, substrate collapse and the long-term impacts of vegetation loss, in delaying forest recovery are also considered below.

~7.4.1. Key factors affecting forest recovery

It was evident from the results of these experiments that several factors played a major role in determining natural recovery processes in disturbed and undisturbed mangroves. In this section, the role of competition, dispersal, predation and selected environmental factors in determining the observed patterns of growth and survival of seedlings planted in manipulative experiments is examined. The extent to which each of these factors may contribute to explaining the similarities and differences in recovery of disturbed forests is also discussed.

Competition for light and nutrients

Although competition is clearly not a factor limiting regeneration amongst the bare mud of bulldozed and cyclone-damaged clearings, competition for both light and nutrients appeared crucial to the survival of seedlings within adjacent forests. Both *R. stylosa* and *C. australis* seedlings in natural forest plots showed the lowest growth and survival of any treatment, presumably reflecting the negative effects of low light, competition with established plants for limited resources and predation by herbivorous crabs (Tamai and Iampa, 1988; Osborne and Smith III, 1990; Clarke, 2004). In a recent 5-year study of the survival and growth of six transplanted mangrove species in northern Queensland, no seedlings survived beneath the forest canopy and there was little evidence for shade tolerance (Clarke, 2004). Other authors have noted that recruitment of mangrove seedlings to the sapling stage may be restricted by low light beneath the canopy (Sherman et al., 2000), and by sediment resources (Clarke and Allaway, 1993). Furthermore, mean soil density and conductivity was generally slightly greater in natural forest plots, than in bulldozed clearings of this study. In a similar experiment in Darwin Harbour, O'Grady et al. (1996) also noted that "high salinities in concert with poor light conditions in the forest may account for reduced growth rates and survival of (*R.stylosa)* seedlings in the forest".

Indeed, Kaly and Jones (1998) report "mangrove seedlings often have the best survival and growth rates where adult trees are absent", which accounts for the enhanced survival of seedlings on bulldozed tracks relative to those in natural forest treatments. Similar higher survival of *Ceriops tagal* and *R. stylosa* was reported in light gaps than under the forest canopy in transplant experiments in Queensland (Smith III, 1987a).

It should be noted however, that low light levels may have caused elongation or etiolation in *R. stylosa* seedlings masking differences in height between high and low light conditions. For example, the lack of any differences in height between all five treatments in bulldozed *R. stylosa* forests, whilst significant differences in growth (i.e. leaf scar counts) were detected, may have been due to etiolation of seedlings grown under low light in natural forest and in shade treatments. Despite significantly diminished growth in natural forest and shade treatments there was a lack of any height differences between treatments.

The effects of competition and low light may have contributed to differences in mean leaf scar count amongst the two bulldozed *R. stylosa* sites (B3 and B4). Differences in growth were also discernible in the field, by differences in stature. In two of the three plots at Site B3, seedling habit was a little stunted. The plots affected were situated close to a large *A. marina* tree, which not only cast some shade over the relatively narrow track, but its dense pneumatophores also covered the mud surface. Again, competition and low light may have contributed to the reduced seeling growth at site B3 compared with site B4, where the track was slightly wider and competition unlikely.

Dispersal and recruitment

Previous authors have reported that poor dispersal and limited establishment, as well as propagule availability and proximity to source trees are major factors limiting mangrove seedling recruitment, at least in some species from the Rhizophoraceae family. McGuinness (1997a) noted that although mangrove propagules may travel long distances, in general propagules do not disperse very far. Indeed, in a study of *C. australis* in Darwin mangroves, 91% of propagules dispersed no more than 3m from the parent plant (McGuinness, 1997a). Other studies on natural regeneration within strip clearcuts in *Rhizophora*-dominated forests of Colombia also highlight the importance of proximity to the edge of the forest, and the availability of mature seed trees to provide ample propagules for seedling recruitment (Blanchard and Prado, 1995). They observed that *R. mangle* seedling density was significantly higher within 5 m of parent trees on the borders of clearings, than in the middle of clearings, presumably due to the direct implanting of propagules. Direct implanting occurs when propagules ripen and drop, some like darts, into the mud below, where they take root. At distances greater than 5 m from parent trees however, propagules must be dispersed by tides. Consequently, when clearcuts are too large in area, natural recruitment is often reduced and seedling establishment is delayed (Tamai and Iampa, 1988). It is apparent that with increasing distance from reproductive adults, the vagaries of water dispersal seriously jeopardise the chances of successful recruitment. Moreover, poor dispersal and recruitment ability can be exacerbated by significantly higher mortality of propagules in a prone position than of implanted propagules (McKee, 1995c; Clarke and Kerrigan, 2002).

Furthermore, the clearing of vegetation along the bulldozed tracks of this study in 1992

removed tree trunks, roots, seedlings and saplings, woody debris and other items which present barriers to tidal flows and provide protective sites for young seedlings. Bulldozing effectively removed the primary obstacles against which dispersing propagules might formerly become stranded (see Chapter 8, section 8.4.2). Flattening the mud surface further reduced substrate heterogeneity and the chances of propagules stranding on these bare substrates. In the macrotidal environment of Darwin Harbour, cleared tracks may funnel and amplify tidal currents, sweeping dispersing propagules away. Similarly, after *R. stylosa* forests were destroyed by cyclone Tracey in 1974, it would have taken many years for woody debris to disperse and degrade completely. Once this occurred however, the remaining, extensive bare areas had the same lack of niches for recruitment as bulldozed tracks. Thus in both these areas, it appears likely that forest recovery has been substantially delayed by the interplay of several factors including low dispersal ability and lack of recruitment niches or "dispersal refuges".

Although extensive sections of bulldozed mangroves still remained completely devoid of vegetation in 2006, natural revegetation of tracks—by the incremental establishment of seedlings from the fringe of the forest inwards—has occurred slowly (pers. obs.). Such observations provide further support for the model of limited dispersal, a lack of seed trees and recruitment niches to explain the delayed recovery of the forest. The next chapter investigates the importance of microhabitat in promoting seedling recruitment.

Predation

High rates of post-dispersal predation by crabs on mangrove propagules and seedlings are well known, and often contribute to poor natural establishment (Clarke and Myerscough, 1993; McKee, 1995c; Clarke and Kerrigan, 2002). Indeed, seedlings protected from predation in this study grew and survived better than those in other treatments. In cyclone-damaged areas, exclosures provided crucial protection from intense predation by sea turtles. On bulldozed tracks however, post-dispersal predation—particularly by crabs—was not evident (see also Salgado Kent, 2004). Nevertheless, the wire netting surrounding these treatments not only prevented herbivory by animals larger than 13 mm, but provided protection from physical damage and appeared to provide other, indirect benefits to the enclosed seedlings. Tidal currents typically left abundant leaves and other debris stranded against the wire netting, which

may have enhanced the growth of enclosed seedlings. The debris stimulated faunal activity, particularly leaf-burying crabs such as *Perisesarma darwinensis* (pers. obs) which in turn, increase soil aeration and nutrients (Smith III et al., 1991).

Herbivory by sea turtles

Although the consumption of *Rhizophora stylosa* leaves by sea turtles has not been documented in the literature (C. Limpus, pers. com.), the fruits of *Avicennia marina* are recognised as an important component of the diet of hebivorous green turtles *Chelonia mydas,* (Read, 1991; Limpus, 1998; Limpus and Limpus, 2000). On the east coast of Australia, *C. mydas* actively forage within mangrove habitats when these fruits are available (Limpus and Limpus, 2000). Only rarely however, have *R. stylosa* propagules been reported in the diet of *C. mydas,* and there are few reports of green turtles feeding on mangrove foliage (but see Pritchard (1971) and Bustard (1972) as cited in Read, 1991; Pendoley and Fitzpatrick, 1999). Examination of the gut contents of one *C. mydas* from the Darwin region, however, indicated that amongst a diet largely comprising algae and seagrass, *R. stylosa* was the only mangrove species actively consumed.

Furthermore, two experiments conducted within cyclone-damaged clearings indicated that *C. mydas* has an apparent strong preference for the apical shoots and small, mainly juvenile, leaves of *R. stylosa*. Turtles are surprisingly dextrous feeders (C. Limpus, pers. com.) and it appears that seedlings were selectively eaten—presumably due to differences in chemical composition of older and younger leaves. Indeed, chemical analyses of *A. marina* leaves revealed significantly higher concentrations of nitrogen and phosphorous in seedlings and saplings (i.e. dbh < 2.5 cm) than in older trees (Morissey et al., 2003). Bjorndal (1997) reported that by continually recropping areas they have previously grazed, *C. mydas* can maintain a diet higher in protein and lower in lignin. It is possible that the leaves of mangrove seedlings in cyclone-damaged clearings may also be repeatedly cropped in this fashion.

Of particular interest to the current findings however, is the tendency for *C. mydas* to establish and maintain grazing plots in the areas where they primarily feed (Bjorndal, 1995). As Bjorndal (1997) observed, "grazing by green turtles has significant effects on the structure and nutrient cycling" in the ecosystems in which they feed. If the almost complete mortality of *R. stylosa* seedlings observed in this study was in fact largely due to repeated grazing by turtles over many years, it most likely has substantially delayed

the recovery of forests in cyclone-damaged clearings. Furthermore, it represents a feedback loop linking an unexpected, and rather poorly known, trophic interaction with forest structure. Repeated grazing by turtles of recruiting propagules would continue to impede recovery of the forest, which in turn, would benefit the turtles. Moreover, by selective predation on *R. stylosa* seedlings, *C. mydas* may in fact be a major determinant of forest species composition (Sousa and Mitchell, 1999), clearly evident by recent colonisation of clearings by *Sonneratia alba* (see below). It is well known that predation of mangrove propagules by grapsid crabs can be severe (Smith III, 1987b; Smith III, 1987c; Smith III, 1988; Osborne and Smith III, 1990; McGuinness, 1997c; Dahdouh-Guebas et al., 1998), and may control the distribution of *Avicennia marina* in some forests. Albeit on a far smaller scale, the sustained grazing by turtles in disturbed mangroves in the lower intertidal zone, could have a similar effect to that of grapsid grabs on some species at higher tidal elevations. The phenomenon is also a reminder of the importance of patchiness created by disturbance in maintaining biological diversity.

Propagule collection method

Although no lasting effects of propagule collection method on the growth and survival of *C. australis* seedlings on bulldozed tracks was evident, higher survival of ground collected propagules was found in both cyclone-damaged sites. Ground collected *C. australis* were several months younger than tree-collected seedlings and for this reason may have been able to adapt more readily to the saline soils in cyclone damaged habitats. By contrast, higher mortality of *R. stylosa* seedlings grown from ground-collected propagules, was evident in both cyclone damaged and bulldozed forests. The poor survival of ground-collected stock may have been due to a higher incidence of post-dispersal insect infestation of propagules. A large percentage of mangrove propagules are damaged by insect borers and *R. stylosa* is particularly affected by scolytid beetles (*Poecilips* sp.) (Roberston et al., 1990; Coupland, 2002). Free-floating propagules, and those that have lain on the ground for some time, would be more prone to damage by insects, particularly borers, than tree-collected propagules. Ground-collected propagules in this survey were collected from the strand line in the high intertidal zone, where there is ample opportunity for insect attack (Roberston et al., 1990). Furthermore, mortality from insect borers would have been higher if propagules

had been directly implanted, because many infested seedlings were discarded during several months of nursery culture. Other kinds of physical damage to dispersing propagules, including sunburn, may also leave them more vulnerable to fungal and insect attack, and disease. The viability of ground-collected propagules may also vary with age (due to potential depletion of energy reserves) and origin (O'Grady et al., 1996).

Disturbance-related environmental change

Although severe, grazing by green turtles may be only one of several factors that have inhibited the recovery of cyclone-damaged *R. stylosa* forests. Abiotic factors—including alterations to the structure and physico-chemical conditions of the soil, substrate collapse and erosion—may have contributed to delayed forest recovery. Environmental conditions in these clearings, which had been devoid of forest cover for 25 years, were evidently not as favourable as those amongst *R. stylosa* forests higher in the intertidal zone. The reasons behind the lack of recovery are likely to have varied since the initial disturbance, and may be complex, involving one or more possibly interrelated, factors.

Vegetation loss and destruction by drift logs

It may have taken a decade or more for *R. stylosa* forest shattered by Cyclone Tracey to disintegrate and disperse. During that time, damage from abundant storm wrack and drift logs, rising and falling with every tide, may have precluded any re-establishment of seedlings and saplings in clearings. Similarly, the abundant debris and drift logs present in cyclone damaged clearings in *C. australis* forests is also likely to have reduced seedling growth, and perhaps survival, by damaging shoots and crushing seedlings as logs and debris rose and fell with the tide. McGuinness (1992) also found that in studies of *Ceriops australis* in mangroves of Darwin harbour, that seedlings were indeed smaller in plots with abundant debris. Similarly reduced heights were found in this study, perhaps from structural damage by floating debris.

Nevertheless, protection from drift logs did not confer any advantage to seedlings planted on bulldozed tracks. Growth and survival of seedlings in control plots was not substantially lower than that of seedlings within protective structures. This may have been due in part, to the ineffectiveness of the exclosures. Although the purpose of the

mechanical damage treatment was to exclude logs and floating debris, in practice, the exclosures were not particularly successful. The number of supports and crossbars was insufficient to prevent logs and branches floating inside the exclosures, where they often become trapped. Drift logs occasionally also became trapped amongst seedlings in shade exclosures.

Substrate collapse

Other studies on the impacts of deforestation in *Rhizophora* dominated forests have reported the subsequent collapse of the dense root mat and consequent increases in substrate water levels (Duke et al., 1997; Lugo, 1997; Sherman et al., 2000; Duke, 2001). Described as "the most striking effect of canopy gaps," such changes have been observed at different spatial scales, including lightning gaps averaging only 25 m in diameter (Sherman et al., 2000) up to extensively damaged forests of Florida where soil collapse prevented the re-establishment of *R. mangle* forests (Lugo, 1997). A similar phenomenon was reported in *R. mangle* forests on exposed shores of Panama, where partially recovered forests were lost six years after chronic oil spills, when the protective above- and below-ground roots of the old forest degraded (Duke et al., 1997; Duke, 2001).

Indeed, substrates within the seaward cyclone damaged clearings of this study were extremely soft and deep, almost semi-fluid in places, which contrasted sharply with the root-structured mud of adjacent healthy forests. Further, field notes for both experiments document that many seedlings, planted in both controls and exclosures in this habitat, "fell over" and subsequently died. This could indicate that the substrate may indeed have collapsed and become too soft to support the growth of *R.stylosa* saplings. Without forest cover, and especially after the persistent root mat of the old forest had degraded, the unconsolidated substrates in these clearings were also particularly vulnerable to erosion from wet season storms and dry season winds (pers. obs.). The poor survivorship demonstrated by planted *R. stylosa* seedlings combined with the recent colonisation of these clearings by *S. alba*—dominant at slightly lower tidal elevations—suggests that erosion may also be one of several localised changes to the substratum hindering the re-establishment of *R. stylosa* forests in these areas. In contrast with the tall, heavy propagules of *R. stylosa,* the tiny fruits *S. alba* germinate and

grow extremely rapidly in very soft mud, assisted by the development of a spreading cable root system. This species appears better adapted to colonise the existing soft substrates. Indeed, the combined effects of selective herbivory and adverse substrate conditions suggests that re-establishment of the former *R. stylosa* forests in these clearings is unlikely at this stage.

Soil compaction and bioturbation

Initial clearing by bulldozers may have compacted substrates to the extent that they were impenetrable to propagules or physically unsuitable for survival. Studies in northeast Queensland of the effects of different kinds of anthropogenic disturbance on mangrove soils, report maximum levels of soil compaction associated with bulldozing (Kaly et al., 1997). By contrast, measurement of soil shear strength in this study, showed that nine years after bulldozing, the density of soil was in fact consistently higher in natural forest than in bulldozed clearings—probably due to thick root growth and more consolidated clay substrates. Soil compaction from bulldozing may vary spatially, with local changes in substrate, and temporally, being more severe soon after disturbance. At the time of the experiment however, soil compaction did not appear to be any impediment to seedling recruitment, growth or survival on bulldozed tracks.

Physico-chemical changes in the substrate

When a mature forest dies, such as occurred in *R.stylosa* forests in Darwin Harbour after Cyclone Tracey, a number of other environmental factors including physical and chemical changes in substrates can be initiated which may in turn inhibit seedling recruitment. McKee (1993) found clearing of mangrove forests can result in changes in soil redox potential, associated rapid accumulation of sulphide and subsequent acidification. Such changes have been linked with limited natural regeneration of seedlings in one hectare clearfelled lots (Hamilton and Snedaker (1984) as cited in Ellison and Farnsworth, 1996). The process has reciprocal effects however, because the root systems of adult mangrove trees modify the surrounding soil, reducing redox potential and toxic sulphide levels (McKee, 1993). It follows that if toxic soil conditions actively limits seedling establishment and survival, as suggested by recent research by Youssef and Saenger (1996; 1998), then clearings created by disturbance may remain largely devoid of vegetation until a sufficient level of forest cover alters and improves

sediment structure and chemistry. Such unfavourable substrate conditions in the middle of clearings would provide additional reasons for the incremental recovery of mangrove forests—outward from the edge of the forest—as is often observed in disturbed mangroves. One may speculate further, that once a critical threshold level of mangrove vegetation cover is reached and substrate conditions are suitably ameliorated, subsequent reforestation may be quite rapid. Nevertheless, this whole recovery process may require several decades after the original forest has decayed. It should be noted that during the nine years since this experiment was commenced, seaward cyclone-damaged clearings have recently shown substantial and relatively rapid recovery (pers. obs.). This may indicate that substrate conditions have stabilised and altered sufficiently for this threshold to have been breached. *Sonneratia alba* has, however, effectively replaced *R. styl*osa, which is now virtually absent from these clearings.

Tidal elevation

Seedling performance was strongly affected by tidal elevation or shoreline position, as this primarily determines the frequency and duration of tidal inundation (Pulver, 1976; Lewis, 2005). The effects of tidal elevation were evident by differences in seedling growth and survival between assemblages and small-scale variation amongst sites. *C. australis* planted on bulldozed tracks in the tidal flat for example, were substantially taller (mean 228.1 cm ± 6.1 SE) than seedlings in cyclone damaged clearings in the hinterland margin (mean 174.5 cm ± 8.3 SE) after 101 weeks. Situated close to the tidal limit, cyclone damaged sites were subject to infrequent tidal flushing and elevated dry season soil salinity (particularly adjacent to small salt flats common in this area). By contrast, more frequent tidal inundation in the tidal flat assemblage, provided more favourable conditions for growth.

Tidal elevation also had a strong influence on growth *of R. stylosa*. Seedlings grown in predation cages in the low intertidal zone had a tall, but rather spindly growth form (mean height 743.0 ± 57.7 SE; scar count 23.7 ± 3.8; shoot length 314.6 ± 80.9). By contrast, seedlings within predation cages on bulldozed tracks had lower stature but were more leafy and had numerous branches (mean height 666.5 ± 61.2; scar count 40.1 ± 5.9; shoot length 1,183 ± 215.0 SE). Ellison and Farnsworth (1993) also reported lower survival, but greater height of *Rhizophora mangle* seedlings planted in the low intertidal zone

compared with those in the mid-intertidal in Belizean mangroves.

Without further study however, it is not possible to determine the relative contribution of the above abiotic factors to limiting or delaying forest recovery.

7.5. Conclusions

It is evident from these studies that the factors limiting the recovery of disturbed forests vary substantially with shoreline position, the type of disturbance and amongst mangrove species. In bulldozed forests, biotic factors such as the dispersal and regeneration characteristics of mangrove propagules combined with a lack of recruitment opportunities appeared to be key factors delaying recovery. The reasons underlying poor recruitment and survival appear to be complex however, and in the case of severe cyclone damage, to involve the interplay of several biotic and abiotic factors. In cyclone damaged forests, limited dispersal and a lack of establishment niches again appear to limit recovery but recruitment may also be strongly regulated by predation—surprisingly, by green sea turtles (*Chelonia mydas*). Environmental changes in disturbed mangrove ecosystems have undoubtedly also affected natural recovery processes, particularly altered physico-chemical conditions in exposed substrates and sediment instability associated with vegetation loss. Furthermore, the key processes limiting recovery may vary over time, particularly when natural regeneration occurs over periods of several decades.

Observations made during the studies reported here prompted further investigation of the importance of recruitment refuges for natural seedling establishment and forest recovery. The results of these experiments are examined in the next chapter, which explores a number of rehabilitation methods to enhance recovery of disturbed mangrove ecosystems.

CHAPTER 8. MANGROVE FOREST REHABILITATION

CHAPTER 8. MANGROVE FOREST REHABILITATION

8.1. Introduction

Due to their position at the land-sea interface, mangroves are exposed to a range of different disturbances originating from both realms. As mangroves thrive under such dynamic and challenging circumstances they may be considered robust, but in other respects, they are also relatively fragile. Some of the regeneration characteristics exhibited by mangrove species—including the dispersal properties of water-borne propagules (e.g. buoyancy, anchoring time), vivipary, the lack of a seed bank and seed dispersing animals—may in fact, hamper their re-establishment after disturbance and contribute to extremely long recovery times. Consequently, as described in Chapter Seven, the vulnerability of mangroves to disturbance may, in some circumstances, be exacerbated by poor ability to regenerate. Indeed, the interplay of factors such as limited propagule dispersal, intense predation and adverse physico-chemical substrate conditions in disturbed forests, can lead to recruitment failures (Smith III, 1988; Blanchard and Prado, 1995; McKee, 1995c; McGuinness, 1997a). Furthermore, in the changeable and dynamic context of many intertidal environments, severe disturbances can have unpredictable secondary impacts. Soil erosion, soil acidification and substrate collapse for instance, can occasionally result in forest death and loss of habitat (Kogo et al., 1987; Duke et al., 1997; Rubin et al., 1999; Allen et al., 2001). Recovery times will of course, depend on the severity of the initial disturbance but may also be complicated and delayed further by continuing disturbances (Chapman and Underwood, 1997; Kaly and Jones, 1998).

Despite their vulnerability, mangrove forests generally recover quickly from minor disturbance and rejuvenate naturally from moderate levels of damage. There is, however, clearly also a role for active restoration efforts that speed the natural recovery process, particularly in severely degraded systems (Teas et al., 1975; Komiyama et al., 1996; Saenger, 1996; Ellison, 2000b; Toledo et al., 2001). Indeed, given the implications of "recruitment limitation" on mangrove community structure, Walters (2000) is wise to point out that human dispersal and planting is becoming extremely important in

determining global mangrove floristic diversity. Over the last few decades, the alarming loss of mangrove habitat has concentrated attention not only on conservation of remaining undisturbed mangrove habitat, but on restoration of degraded systems by planting propagules or seedlings, or by facilitating natural recovery (Chapman and Underwood, 1997; Field, 1998b; Ellison, 2000b; Lewis, 2005). In parts of India for example, where the majority of mangroves have been severely overexploited, it has been suggested that mangrove afforestation programs are as important as habitat conservation (Das et al., 1997). Indeed, reforestation or rehabilitation techniques that shorten recovery trajectories represent increasingly valuable tools for mangrove replenishment, management and conservation (Kaly and Jones, 1998; Tri et al., 1998; Saenger, 2002).

There are however, a great variety of motives for mangrove reforestation, ranging from simple replanting of managed forests for timber production, to planting of mangroves purely for aesthetic purposes. In developed countries such as the USA and Australia, the major goals for planting mangroves tend to be the restoration of natural areas and the enhancement of natural regeneration (Field, 1998b). These objectives stem from recognition of the integral value of mangroves as habitats for a rich array of fauna and as highly productive ecosystems (see Kaly and Jones, 1998). Indeed, over the last two decades, the primary goal of the great majority of rehabilitation in the USA has been mitigation, arising from compliance with legislation that only permits clearing of mangroves only if a similar area is restored or created, at another location (Lewis, 1990; Stubbs and Saenger, 2002). Such acknowledgment of the ecological value of mangrove ecosystems, has occurred only relatively recently however, since the pivotal work of Pulver (1976) and Lewis (1982) ushered a major change in attitude. Since then, the primary goal of rehabilitation—at least in developed countries—has gradually shifted from simple afforestation projects, to restoration of ecosystem function (Kaly and Jones, 1998; Ellison, 2000b; Lewis, 2005).

By contrast, in less industrialised nations, mangroves have generally been planted for other reasons including the sustained yield of forest products, coastal protection and stabilisation (Bangladesh); the production of timber and charcoal (Malaysia and Thailand); and restoration of degraded areas (India, Sierra Leone, Indonesia, Phillipines). The widespread conversion of mangroves for agricultural use, and for fish

and shrimp ponds in South East Asia in the 1970's left large areas of reclaimed land derelict (Primavera, 1995; Kairo et al., 2001), providing further impetus for restoration of degraded areas (Field, 1998b).

So mangrove afforestation in these regions is not new. Mangrove forests in Malaysia and the Sundarbans have been actively managed for timber production since the 19th century (Kaly and Jones, 1998; Kairo et al., 2001), with over 80% of the mangrove area in Malaysia under a 40 year rotational harvest program by the early 1950's (Noakes, 1955). Consequently, the basic techniques for propagating, culturing and planting mangrove species of horticultural value are widely practised and well documented (Pulver, 1976; Saenger and Siddiqui, 1993; Youssef, 1997; Stubbs and Saenger, 2002), having changed little during the last century (Ellison, 2000b). Overall, there are two main approaches to mangrove rehabilitation; firstly, *artificial regeneration*, or the planting or transplanting of propagules or seedlings and secondly, *natural regeneration*, which uses naturally occurring propagules or seeds as the source for regeneration (Field, 1998a, 1998b). Where feasible, current trends favour natural regeneration, with artificial plantings used only when necessary to augment natural recruitment (Lewis, 1990; Lewis and Streever, 2000; Saenger, 2002).

Despite the long history of mangrove reforestation worldwide, a scientific approach to rehabilitation, that focuses on the reinstatement of fully functioning ecosystems, is still relatively new (Lewis, 1990), is seldom practiced and poorly monitored (Field, 1998a; 1999). Furthermore, Kaly and Jones (1998) note that due to the complex range of factors influencing mangrove structure and function, ecosystem restoration "will be more sophisticated than simply planting a few trees". Indeed, little is known about the viability and sustainability of replanted forests (Kaly and Jones, 1998; Ellison, 2000b), and the biological diversity of restored ecosystems is undocumented (Field, 1998b; Ellison, 2000b). Consequently much scientific research on restoration ecology still remains to be done (Chapman and Underwood, 1997; Walters, 2000), and it is vital that the results be integrated into future ecosystem management practices (Field, 1998b; Field, 1999; Ellison, 2000b).

As there is already a substantial amount of information on the silviculture of many mangrove species—including the collection, proper handling and culture of propagules and seedlings for planting and transplanting—this should be applied and built upon,

rather than continually repeated (Field, 1998b; Ellison, 2000b). Globally, rehabilitation projects have met with varying success. Many of the early attempts to re-establish mangroves by planting seedlings and propagules in the USA during the 1970's failed completely (Teas, 1977; Lewis, 1990) and most attempts to restore mangroves still fail to achieve the stated goals (Lewis, 2005). These results highlight the need to undertake pilot studies, particularly for projects depending on natural recruitment or in circumstances where artificial regeneration involves nursery culture, requiring considerable time and expenditure.

However, Saenger (2002) notes that several more recent restoration programs have "achieved a degree of ecological functioning similar to natural mangrove systems". For example, McKee and Faulkner (2000) found that 6—13 year old replanted mangroves in Florida had only a few biogeochemical differences from forests undisturbed for 50—60 years. Furthermore, Saenger (1996) reported 80—90% survival of over 50,000 transplants in a channel stabilisation project in Brisbane, Australia, which was self-sustaining after 4—5 years. These projects are dwarfed however, by well established silviculture in Malaysia, Thailand, the Philippines and India—with over 120,000 ha of forests planted in the Sundarbans alone (Saenger and Siddiqui, 1993; Saenger, 2002).

Nevertheless, the success of any reforestation project is defined on the basis of the objectives, which differ for each particular situation. The outcomes of a reforestation project that produces monospecific stands harvested every 20 years are, for instance, unlikely to satisfy the goals of a project attempting to restore ecosystem function. Thus numerous authors have stressed the need to clearly identify the objectives of reforestation well in advance, preferably during the planning phase (Kaly and Jones, 1998; Field, 1998b; Kairo et al., 2001; Stubbs and Saenger, 2002). Is the goal of the project, for example, reforestation? Rehabilitation? Or restoration? Although often used interchangeably, Field (1998b) distinguished different kinds of objectives, and thus outcomes, for each of these terms. Firstly, reforestation generally refers to planting of monospecific, or occasionally mixed species stands of mangroves. Secondly, rehabilitation has been defined as "the act of partially or, more rarely, fully replacing structural or functional characteristics of an ecosystem that have been diminished or lost" (Field, 1998a). Lastly, restoration is defined as "the act of bringing an ecosystem back into, as nearly as possible, its original condition " (Edwards, 1998; Field, 1998b).

In the previous chapter, the role of selected biotic and abiotic factors in delaying the recovery of forests affected by anthropogenic and natural disturbance was investigated (shown by the solid green arrow, Figure 1-1, Chapter 1). In this chapter, the technical feasibility of different rehabilitation methods is investigated. As no comprehensive rehabilitation studies had previously been conducted in Darwin Harbour, these experiments may form the basis on which to build additional knowledge in this area. Several artificial regeneration methods were trialled, utilising planted and transplanted seedlings, and directly sown propagules. In addition, a natural regeneration technique designed to facilitate propagule retention and seedling recruitment was also investigated (pink arrow, Figure 1-1). Both methods attempt to shorten recovery times and hasten the restoration of ecosystem function and natural levels of biological diversity (dashed blue and green arrows respectively, Figure 1-1).

Aims

The purpose of this study was to investigate the technical feasibility of different rehabilitation techniques and to test for differences in the survivorship and early growth of mangrove seedlings grown using these methods.

- The aim of the first experiment was to compare the growth and survival of transplanted and container grown *Ceriops australis* seedlings, at different tidal elevations at one disturbed site.
- The aim of the second experiment was to compare the growth and survival of seedlings and propagules of four mangrove species (*Ceriops australis, Rhizophora stylosa, Avicennia marina* and *Aegialitis annulata*) at three anthropogenically disturbed sites. *A. marina* and *A. annulata* were grown from transplanted seedlings and *C. australis* and *R. stylosa* were grown by directly implanting propagules.
- The aim of the third experiment was to test the feasibility of a passive rehabilitation technique, designed to facilitate propagule retention and the natural recruitment of seedlings.

8.2. Methodology

~8.2.1. Planting and transplanting

The first trials investigating the success of planting *Ceriops australis* in bulldozed clearings at mid- and high tidal elevations were conducted at Charles Darwin Park in 1999–2000. Two sites, located close to the landward margin were selected, site R1 at 7.1 m and site R2 at approximately 6.3 m Darwin Chart Datum; representing roughly the upper and lower limits of the tidal flat assemblage (Figure 8-1).

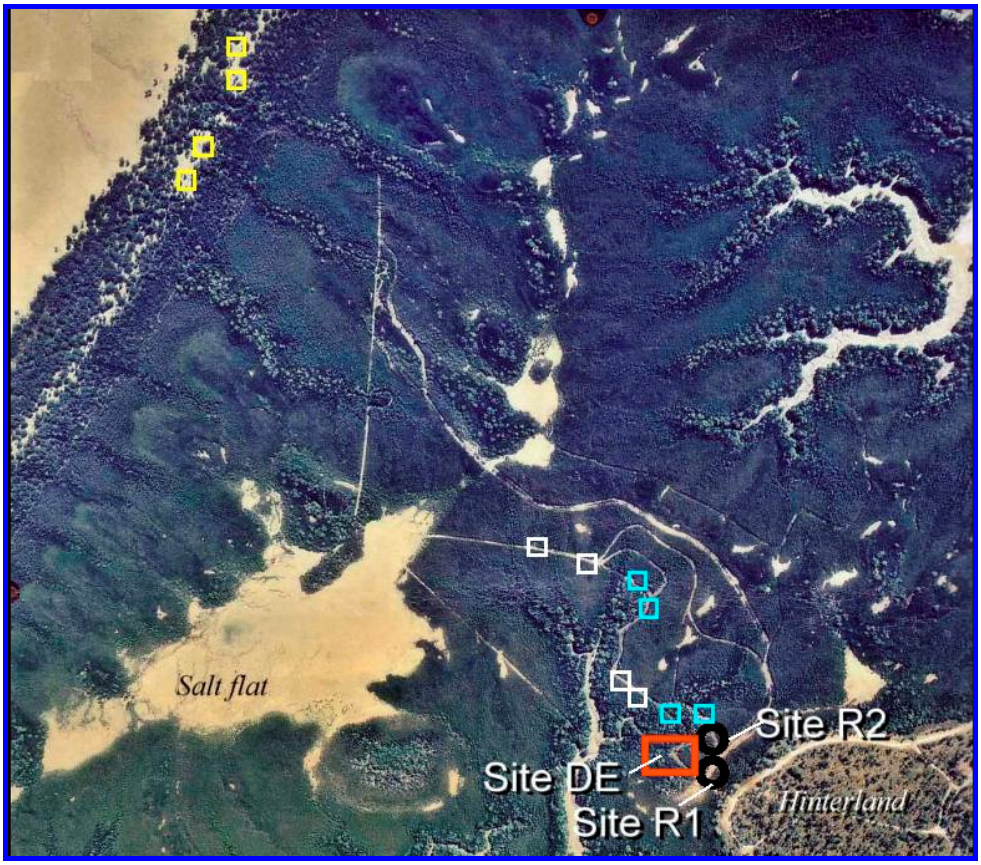


Figure 8-1: Location map showing rehabilitation sites at Charles Darwin Park. *C. australis* was planted at Sites R1 and R2 (black circles) and site DE (red rectangle) was one of the three disturbed sites where multi-species trials were conducted. Squares indicate the location of fence/control plots in tidal flat (white), tidal creek (blue) and seaward (yellow) assemblages.

At each site, 100 container grown seedlings were planted and 100 *C. australis* seedlings were transplanted from nearby forest (total 400 seedlings) in sites approximately 30 m × 100 m in area (Figure 8-1). Container grown seedlings had been raised from propagules gathered from the ground in January 1999, and grown in the nursery prior to planting in June (see methodology, Chapter 7, for details of nursery culture). Seedlings selected for transplanting were carefully dug from undisturbed forest adjacent to sites R1 and R2.

Transplants had 4 to 6 leaves and an intact root ball of approximately 5-10 cm diameter. A template was used during planting to ensure that seedlings were evenly spaced at a minimum linear distance of 20 cm to standardise effects from intraspecific competition. Small mud cores were removed with a yabbie pump (a stainless steel suction coring device) to ensure seedlings were planted in holes of uniform width (7 cm) and depth (7-10 cm). Ten container-grown seedlings were planted in plots of ten, directly adjacent to ten transplanted seedlings (Figure 8-2). Survivorship and growth (indicated by the total number of leaves per seedling) was monitored over the following 23 months (Table 8-1).

Table 8-1 : Sampling regime for initial rehabilitation trials in which 400 *Ceriops australis* seedlings were planted on bulldozed tracks at sites R1 and R2, in Charles Darwin Park.

REHABILITATION TRIAL – CERIOPS AUSTRALIS												
Year	**1999**							**2000**			**2001**	
Sample	T0	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	T11
Date	16 Jun	5 Jul	20 Jul	29 Aug	5 Oct	6 Dec	11 Feb	13 Apr	1 Aug	13 Oct	2 Feb	15 May
Weeks	0	3	5	10	16	25	34	43	58	69	84	98

Figure 8-2: Rehabilitation site R2 on bulldozed tracks in the lower tidal flat assemblage at Charles Darwin Park (left). Paired plots of ten container grown (foreground) and ten transplanted (background)*Ceriops australis* seedlings (right)

In the second experiment, rehabilitation trials involving four mangrove species were established at three disturbed or degraded sites: site DP (East Arm Port), site DM (prawn farm in Middle Arm) and site DE on bulldozed tracks in Charles Darwin park (see Figures 2-8, 2-9, chapter 2, and Figure 8-1). The species studied were *Rhizophora stylosa*, *Ceriops australis*, (both grown from propagules sown directly into the mud), *Avicennia marina* and *Aegialitis annulata* (Figure 8-3). The latter two species were not grown from implanted propagules but were transplanted at the two to four leaf stage.

A. annulata has tiny propagules that might easily be washed away, and even when established are also slow to produce the first pair of leaves (pers. obs.) and *A. marina* propagules are particularly susceptible to predation by crabs (Smith III, 1987b; McGuinness, 1997c). Furthermore, of approximately 800 *A. marina* propagules collected from the strand line for this experiment, only 25% survived fungal and insect attack during temporary storage. It was therefore more practical to use transplanted seedlings of these two species for this experiment. Seedlings and propagules were planted in individual plots comprised of ten seedlings, spaced 20 cm apart, using a template.

Figure 8-3: Four species grown in rehabilitation trials at three disturbed sites (from left) *Aegialitis annulata, Avicennia marina, Ceriops australis, Rhizophora stylosa*

Table 8-2: Schedule of growth measurements at four rehabilitation sites in Darwin Harbour examining the growth and survival of four mangrove species, in 2000–01.

REHABILITATION TRIALS – FOUR MANGROVE SPECIES												
Year	**2000**								**2001**			
Time	**T0**	**T1**	**T2**	**T3**	**T4**	**T5**	**T6**	**T7**	**T8**	**T9**	**T10**	**T11**
DE	8 Mar	20 Mar	3 Apr	13 Apr	17 May	1 Aug	6 Oct	1 Dec	26 Jan	27 Apr	7 Aug	19 Nov
DM	11 Mar	24 Mar	4 Apr	17 Apr	24 May	28 Jul	9 Oct	30 Nov	28 Jan	28 Apr	4 Aug	21 Nov
DP	15 Mar	27 Mar	10 Apr	19 Apr	24 May	27 Jul	9 Oct	4 Dec	27 Jan	29 Apr	6 Aug	28 Nov
Weeks	**0**	**2**	**4**	**5**	**10**	**20**	**30**	**37**	**45**	**58**	**73**	**89**

At each site, ten plots of each of the four species were planted (total 1,200 seedlings) and their growth (leaf total) and survival were monitored over the following two years (Table 8-2). At the conclusion of the experiment, seedling height was also measured. For *R. stylosa* and *C. australis*, height was measured from the cotyledonary scar to the tip of to the plant, for *A. marina* and *A. annulata* the total above ground height of the seedling was measured.

~8.2.2. Assisted seedling recruitment

During field experiments conducted for Chapter Seven, it was observed that leaf litter, propagules and other floating debris collected against the hexagonal wire netting of predation exclosures (Figure 8-4a). Indeed, these wire cages appeared to enhance the natural recruitment of seedlings.

Figure 8-4: Examples of natural seedling recruitment in mangroves of Darwin Harbour. a) propagule establishment amongst abundant leaf litter and organic debris trapped against a predation exclosure; b) to d) stranding and establishment of propagules in natural hollows in intertidal substrates; e) –f) abundant *R. stylosa* seedlings established beneath mature trees and amongst existing seedlings and dense roots.

Furthermore, seedlings were commonly observed collecting in hollows in the substrate as the tide receded (Figure 8-4b—4d) as well as amongst the trunks, tree roots and other seedlings at the edge of the forest (Figure, 8-4e—4f). These observations prompted the third rehabilitation experiment, in which specific structures—comprising low fences made of hexagonal wire netting—were installed in disturbed mangroves to test their effectiveness in assisting natural recruitment. At three disturbed sites (sites DM, DP and DE), the effect of fences and substrate heterogeneity on seedling establishment was investigated over a period of 18 months, commencing during the late wet season of 2000 (Table 8-3).

Table 8-3: Schedule of measurements at three rehabilitation sites investigating the effects of fences in assisting seedling recruitment in the seaward, tidal creek and tidal flat assemblages

ASSISTED SEEDLING RECRUITMENT										
Year	**2000**						**2001**			
Time	**T0**	**T1**	**T2**	**T3**	**T4**	**T5**	**T6**	**T7**	**T8**	**T9**
DE	6 Mar	3 Apr	4 May	22 Jul	10 Oct	1 Dec	26 Jan	15 Mar	28 Apr	12 Aug
DM	14 Mar	17 Apr	24 May	28 Jul	9 Oct	30 Nov	28 Jan	15 Mar	26 Apr	7 Aug
DP	16 Mar	19 Apr	24 May	27 Jul	9 Oct	4 Dec	27 Jan	15 Mar	28 Apr	4 Aug
Months	0	1	2	4	7	9	10	12	13	17

At the three study sites, two plots were randomly established in disturbed, largely bare, mangroves within each of the three assemblages (seaward, tidal creek and tidal flat). A study plot comprised two adjacent 3 m × 3 m patches of ground, that were cleared of any existing plants and the corners marked by posts. One patch functioned as a control for the adjacent fence plot. Each fence plot was divided in half by three star pickets supporting a 3 m long × 900 mm high fence made of 13 mm hexagonal wire netting (Figure 8-5). No attempt was made to prevent making footprints within fence plots while constructing the fence which added to substrate heterogeneity adjacent to fences. By contrast, creating any additional disturbance to the substrate within control plots was strictly avoided.

Where possible, patches were placed side by side, at right angles to the main direction of tidal flow. On bulldozed tracks however, clearings were not sufficiently wide and paired patches were aligned lengthways along the track. Two paired patches (control and fence) were installed at each study plot. Seedling recruitment and species richness

was monitored by periodically counting the number of seedlings of each species that had established within each patch (Table 8-3).

Figure 8-5: Experiment investigating natural recruitment in which seedling establishment in bare 3 m x 3 m control patches (left) was compared with that in fenced patches (right). Three different assemblages were studied including the seaward (pictured).

Analyses

Raw data was entered into either a *Microsoft Access* database or *Microsoft Excel* spreadsheets for analysis using *Statistica v.5.5.* In the first rehabilitation trial involving only *C. australis* at Charles Darwin Park, seedling growth (leaf count) and survival was analysed in three factor nested ANOVA's comparing site (random, 2 levels), treatment (fixed, 2 levels) and plot (random, 9 levels, nested in site). Analyses were run at two times, one midway (58 weeks) and the other just prior to the end of the experiment (84 weeks after planting). Where it was necessary to balance the design of analyses (due to plots in which all ten seedlings were missing), deletions were made using random number tables, until equal numbers of plots were obtained.

In the second rehabilitation trial, involving four species, leaf count and survival were also compared at the mid- and end points of the experiment (58 and 89 weeks after planting). Growth and survival were compared in three factor nested ANOVA's analysing species (fixed, 4 levels), site (random, 3 levels) and plot (random, 7 levels, nested in site and species). Due to interspecific differences in leaf anatomy, counts of leaves, rather than leaf scar counts, were used to document growth. In addition, seedling height, measured from above the cotyledonary scar for Rhizophoraceae, or total above ground height for *A. marina* and *A. annulata,* was recorded at the end of the trial.

Normality plots and graphs of homogeneity of the variances were examined in *Minitab vers. 14* before and after transformation to ensure that ANOVA assumptions were met satisfactorily. Where tests indicated transformation was necessary, survival data was transformed using the arcsine squareroot, while leaf totals and heights were transformed using either the square-root or $\log_{10}(x + 1)$.

For the assisted seedling recruitment experiment, fenced and control patches were compared on the basis of the total number of seedlings and species richness per patch, at intervals of 9, 13 and 17 months after establishment—corresponding to the early wet, late wet and mid-dry season. Analyses comprised five factor nested ANOVA's comparing site (fixed, 3 levels), assemblage (fixed, 3 levels), treatment (fixed, 2 levels), plot (random, 2 levels, nested in site and assemblage) and replicate (random, 2 levels, nested in site, assemblage and plot).

The procedures described by Winer et al. (1991) and Underwood (1996) were used in preliminary tests on complex ANOVA models to determine if any higher order interactions could be dropped. Following the recommendations of these authors, a conservative approach was adopted and terms were only dropped if the relevant F-ratio was non-significant at $p = 0.25$.

8.3. Results

~8.3.1. Mangrove planting and transplanting

Analyses revealed differences in growth and survival of *C. australis* between the two rehabilitation sites at different tidal elevations in Charles Darwin Park. Significantly higher growth (leaf total) and survival was evident at rehabilitation site R2, than at site R1, both 58 weeks and 84 weeks after planting (Figures 8-6 and 8-7, Tables F-21 to F-24, Appendix F).

Seedlings transplanted into the two sites from adjacent forest, had higher numbers of leaves than those outplanted from containers, both 58 and 84 weeks after planting (Figure 8-8, Tables F-21 and F-22, Appendix F). Differences in survival were not detected however, between transplanted and container grown seedlings.

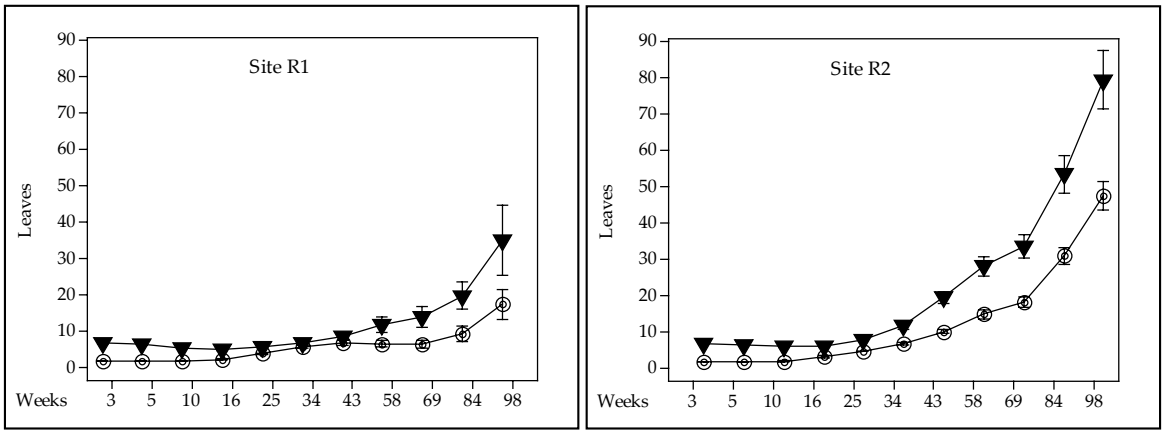


Figure 8-6: Mean number of leaves (± SE) on *C. australis* seedlings either container grown (open circles) or transplanted from nearby forest (closed triangles) at sites R1 and R2 over 98 weeks.

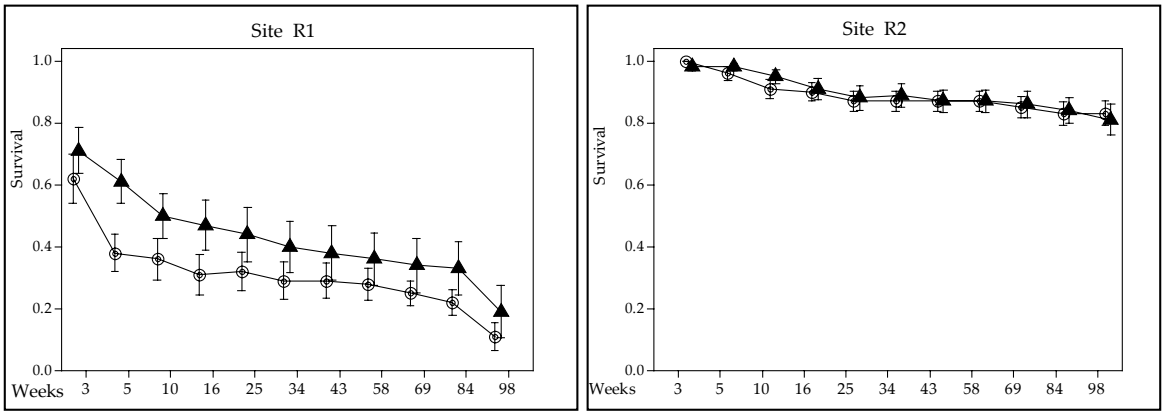


Figure 8-7: Mean survival (± SE) of *C. australis* seedlings that were either container grown (hollow circles) or transplanted from adjacent forest (solid triangles) at sites R1 and R2 over 98 weeks

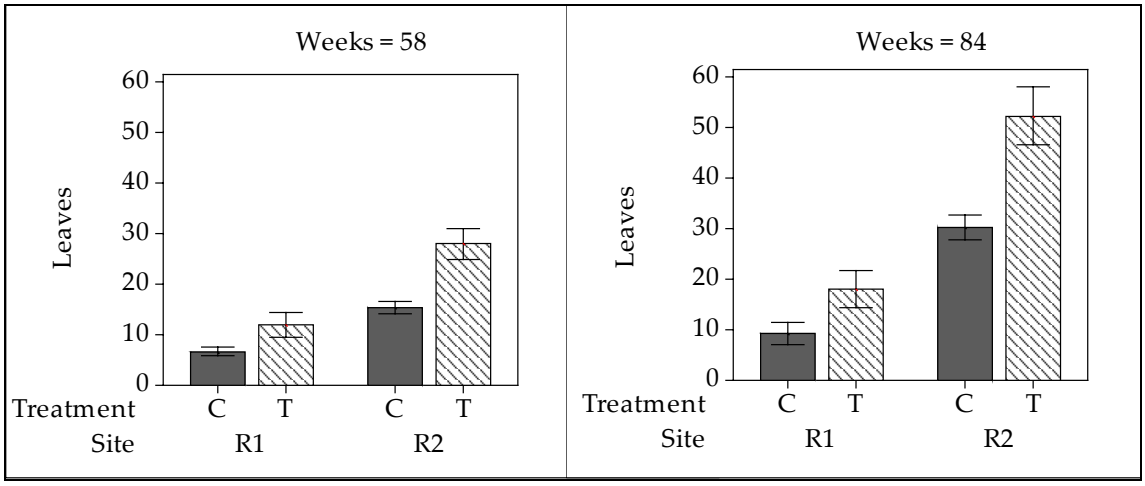


Figure 8-8: Mean number of leaves on container–grown seedlings (C) and transplanted seedlings (T) at rehabilitation sites R1 and R2 at Charles Darwin Park, after 58 weeks (left) and 84 weeks (right).

In trails involving four different species, analyses also revealed significant differences in

leaf total and height of seedlings amongst the three study sites when data for the four species was pooled (Tables F-25, F-27 and F-29, Appendix F). Mean leaf count was higher at site DP than at sites DM and DE (Figure 8-9, left). Mean seedling height was significantly higher at site DM after 89 weeks than at sites DP and DE (Figure 8-9, right).

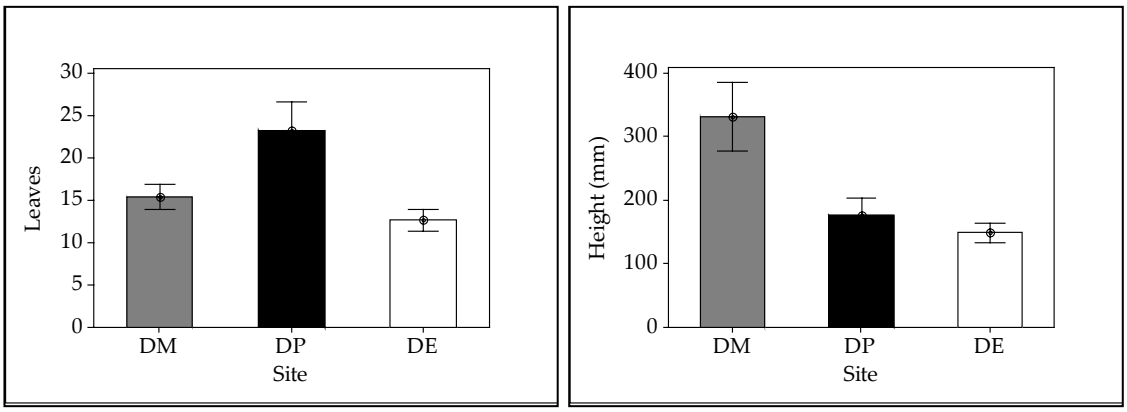


Figure 8-9: Left: Mean number of leaves (left) and mean height (right) of seedlings (± SE) in rehabilitation trials at three disturbed sites 89 weeks after planting. Data pooled for four species at each site.

Marked height differences were found between species, with maximum height recorded for *R. stylosa* (444.7 ± 53.4 SE), intermediate height for *A. marina* (215.1 ± 23.4 SE) and lowest heights for *C. australis* (114.6 ± 9.3 SE) and *A. annulata* (100.7 ± 3.6 SE).

The overall survival of seedlings differed between sites with the lowest mortality recorded at site DP (Tables F-26, F-28, Appendix F). On average, of a possible total of 10 seedlings per plot, 5.7 (± 0.5 SE) seedlings survived at site DP. Mean survival at site DE was similar (5.0 ± 0.3 SE) and lowest at site DM (3.8 ± 0.5 SE).

When data was pooled for the three sites no significant differences in survival were found between the four species after 89 weeks. Survival of *R.stylosa* was 54.3%, and *A. marina* 50.0%, *C. australis* 47.3% and *A. annulata* 41.3%. Although survival of the four species was similar, analyses indicated that after 89 weeks, the survival of particular species varied among sites (Table F-28, Appendix F). This was most evident for *A. marina* which displayed high survival at site DP (86%), intermediate survival at site E1 (53%) and very low survival (11%) at site DM (Figure 8-11).

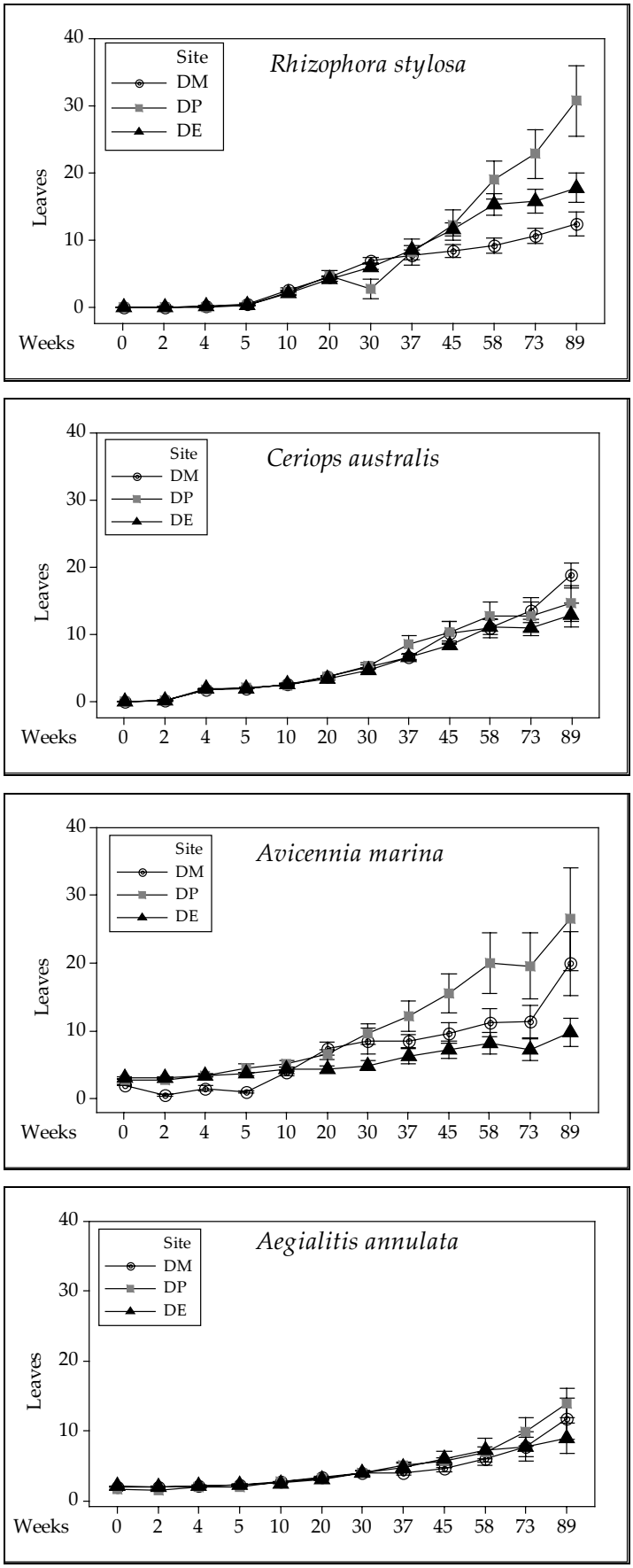


Figure 8-10: Mean number of leaves on seedlings of four species planted in rehabilitation trials in disturbed mangroves at three locations over a period of 89 weeks.

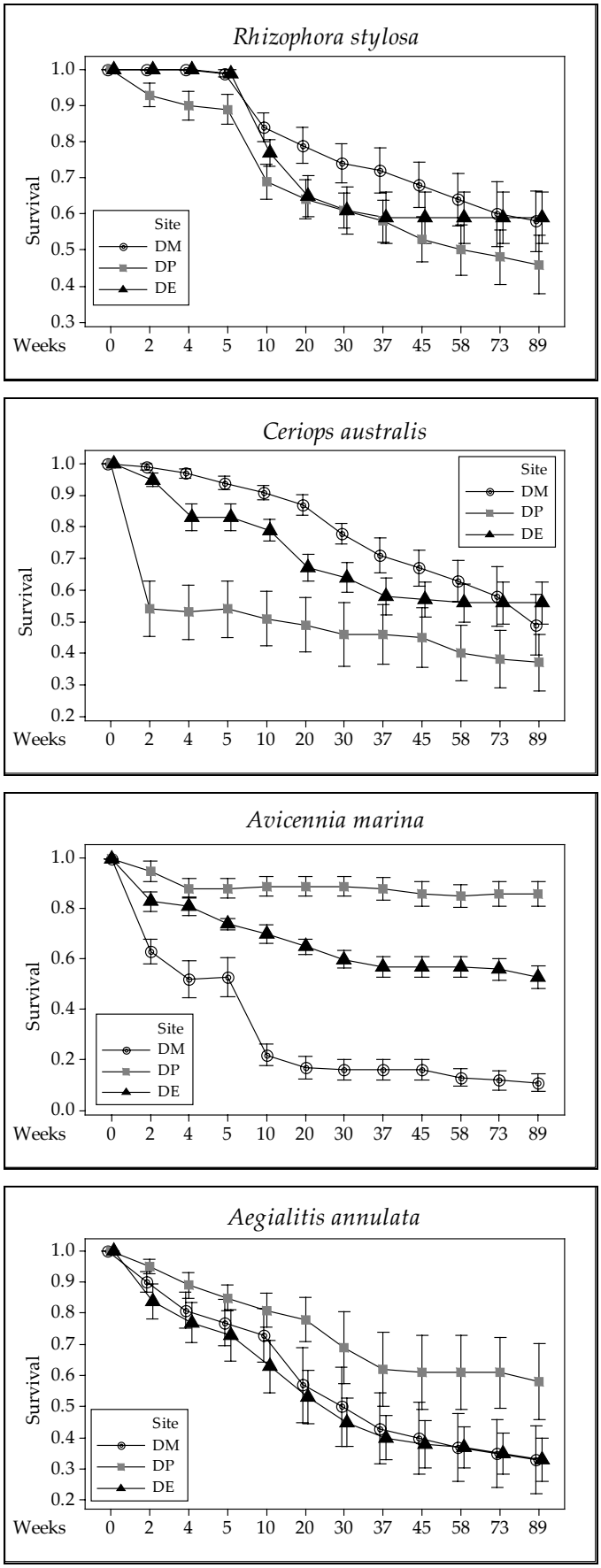


Figure 8-11: Mean survival (proportion) of seedlings of four species planted in rehabilitation trials in disturbed mangroves at three locations over 89 weeks.

~8.3.2. Assisted seedling recruitment

Experiments investigating natural seedling recruitment in fence patches compared with control patches demonstrated that the birdwire barriers were effective in promoting seedling establishment. Analyses of data collected from three locations after 9, 13 and 17 months indicate significantly higher numbers of seedlings and increased species richness occurred in fenced patches than in controls (Tables F-30 to F-35, Appendix F). Mean seedling number and species richness also differed between sites; the highest abundance was recorded at site DE and lowest species richness at site DP (Figure 8-12).

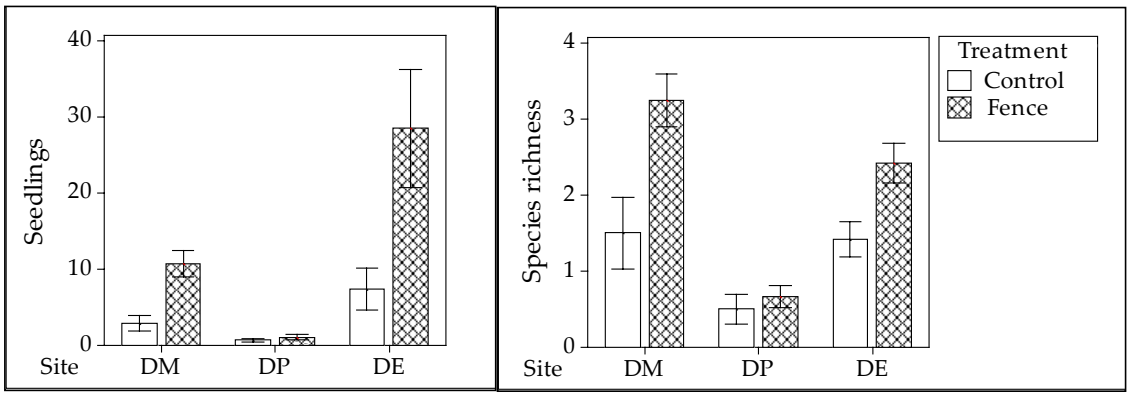


Figure 8-12: Mean number of seedlings ± SE (left) and mean species richness per patch ± SE (right) in fence and control patches at three study sites after 17 months. Data pooled for three assemblages at each site.

Significant differences in recruitment between treatments in different assemblages were found at 9 and 13 months, but were not evident at 17 months. For example, high recruitment was observed in fenced plots in the seaward assemblage at all sites in December 2000 (Figure 8-14). In contrast, the highest recruitment in April 2001 was recorded in the tidal flat assemblage at site DE (Figure 8-14).

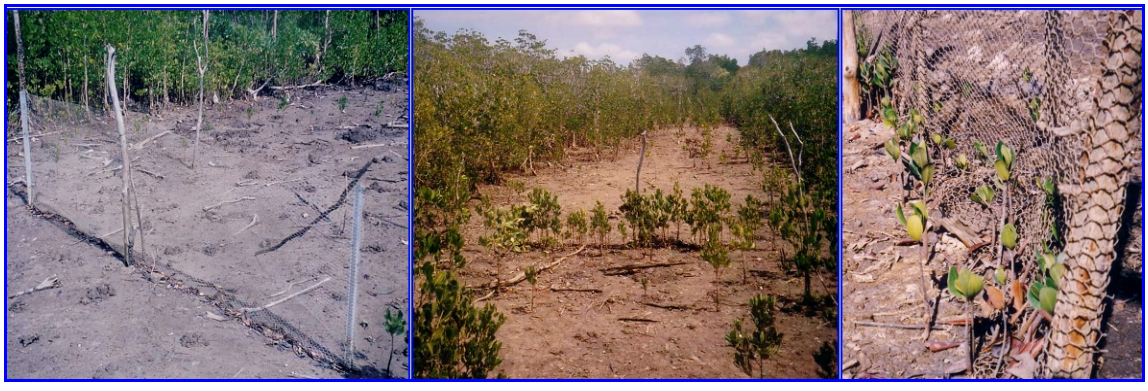


Figure 8-13: Fences were most effective on bulldozed tracks in the tidal flat assemblage at site DE in 2000 (left). The same location in 2004, three years after the end of the experiment (middle). Detail of *C. australis* recruitment along fence in 2001 (right).

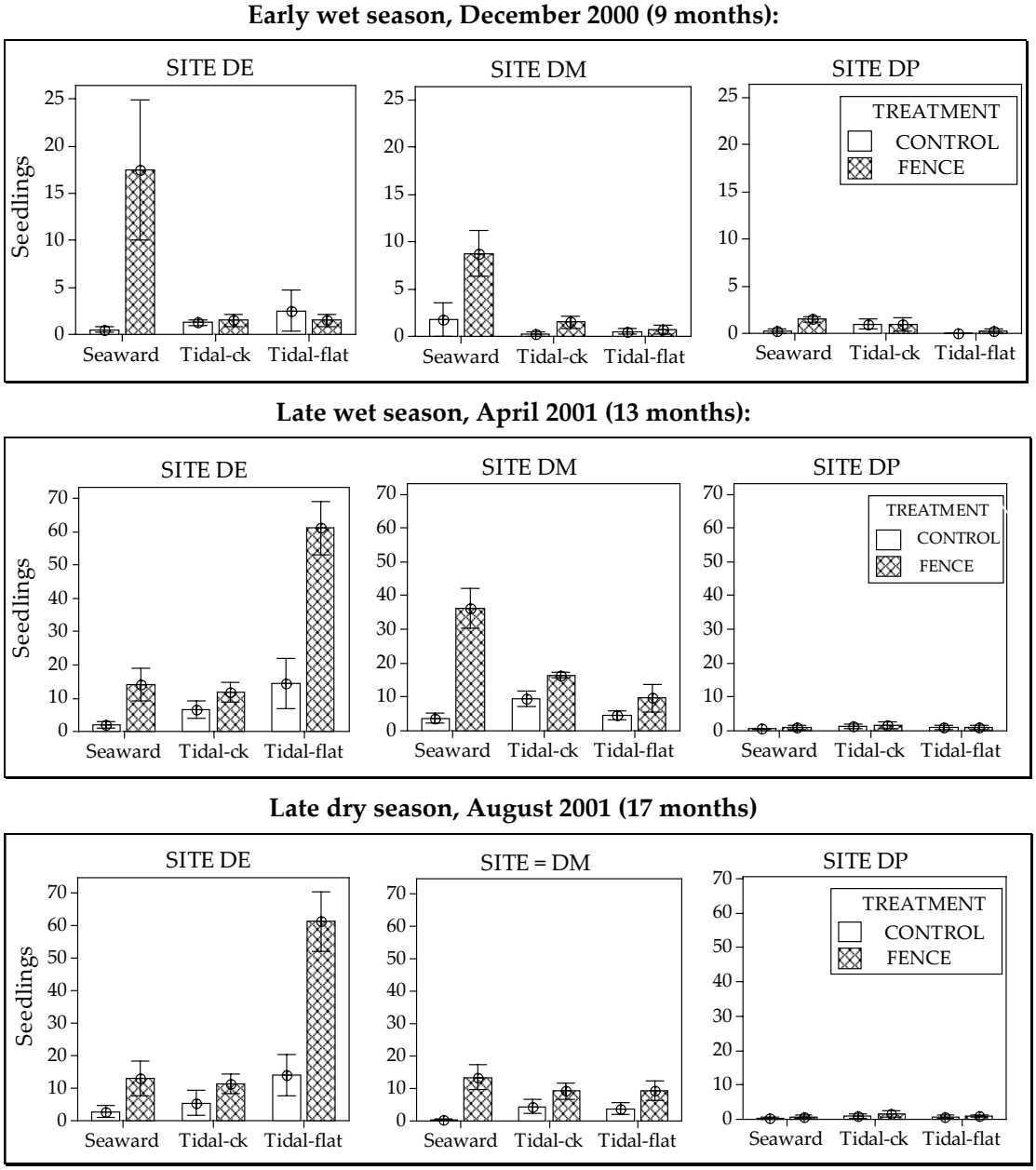


Figure 8-14: Mean number of seedlings in fence and control patches in three assemblages from seaward (left) to landward (right) at three study sites after 9, 13 and 17 months.

After nine months, overall mean species richness was higher in fenced than control patches (Figure 8-12, right) but richness in treatments varied among assemblages. For instance, species richness in fenced plots was greatest in the seaward assemblage and decreased to landward (Figure 8-15). However, no clear pattern amongst assemblages was evident for species richness in control treatments. A significant treatment × site interaction for species richness at 13 months mainly related to the variation between the three sites in the diversity of seedlings within treatments (Figure 8-16). Substantially more species were recorded in fenced than in control patches at site DM compared with

the other two sites. A similar pattern was observed after 17 months, where a wider range of species established in fenced patches at site DM and DE, whilst there was little difference between treatments at site DP (Figure 8-12 right).

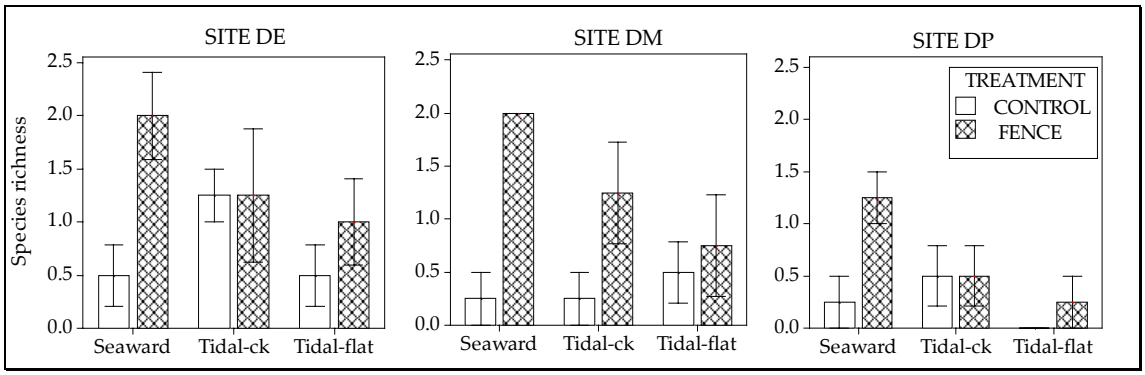


Figure 8-15: Mean species richness per patch (± SE) recorded at three disturbed sites, 9 months after installation of fence and control treatments.

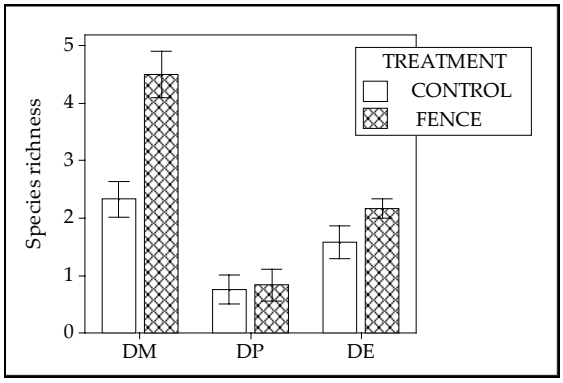


Figure 8-16: Mean species richness (±SE) in fence and control treatments at three disturbed sites after 13 months. Data pooled for three assemblages at each site.

8.4. Discussion

~8.4.1. Rehabilitation trials

Small scale rehabilitation trials with *C. australis* demonstrated that replanting of bulldozed tracks in the tidal flat assemblage of Darwin Harbour was not particularly difficult and overall survival after two years was reasonably high (48.5%). The differential growth and survival observed at the two sites—with high growth and survival (82%) recorded in the lower intertidal range of *C. australis* and poor results (15% survival) reported from higher on the shore—underscored the importance of tidal elevation in mangrove plantings. A number of authors have noted that intertidal position is of primary importance in mangrove rehabilitation (Pulver, 1976; Field, 1998b;

Lewis, 2005), often because the physiological stress associated with duration of tidal inundation is a critical factor determining survival. In this instance however, high soil salinities associated with infrequent tidal inundation in the upper tidal flat (i.e. between 6 and 7 m AHD) appeared to be the primary factor contributing to the observed differences. Many seedlings in site R1 became encrusted with salt prior to withering and dying (pers. obs) whereas seedlings at site R2, which received more frequent tidal inundation, flourished. Indeed, Kaly and Jones (1998) noted that factors such as soil salinity, frequency of tidal inundation, soil chemistry and freshwater availability result in complex patterns—even within small geographic ranges—that substantially affect the success of restoration projects. Toledo et al. (2001) also reported diminished natural regeneration due to elevated soil salinities in clear-cut mangroves in Mexico.

The significantly higher number of leaves on transplanted *C. australis* throughout this study presumably reflected the slightly more advanced status of these seedlings when planted. Although of similar height to container grown plants, which had two to four leaves when planted, transplants had between four and six leaves, and more leaf scars at the start. After one year however, transplanted seedlings had almost double the number of leaves recorded on container grown seedlings. Indeed, transplanting seedlings with larger above and below ground biomass can provide valuable advantages over outplanting of container grown stock (see Saenger, 1996; Stubbs and Saenger, 2002). For *A. marina* and *A. corniculatum*, the best survival rates have been obtained with plants less than 30 cm high, while *Rhizophora* saplings 50 –150 cm high may be successfully transplanted (Saenger, 2002). Transplanting is of particular value in circumstances where available time and resources do not permit nursery culture and the goals of rehabilitation include the rapid stabilisation and establishment of self-sustaining habitats. For example, at a site at Brisbane airport, transplanted *Aegiceras corniculatum* flowered after only four years and *A. marina* after 5 years, at which time natural seedling recruitment numerically dominated the site (Saenger, 1996). Pulver (1976) also noted that transplanting *R. mangle* saplings up to 150 cm in height was a practical option that resulted in faster and more effective shoreline protection than can be achieved by planting seedlings (see also Riley and Salgado Kent, 1999; Salgado Kent and Lin, 1999).

Although the mean number of leaves on transplanted *C. australis* seedlings was higher than on container grown seedlings, no significant difference in survival was found after

23 months—transplants and nursery grown seedlings survived equally well. Transplanting of other mangrove species is often, but not always, as successful. In Florida, Teas (1977) reported that transplanted *R. mangle* generally showed lower survival than nursery grown seedlings which experienced less root damage during transplanting. Initial survival of transplants was however, highly dependent on the size of the plant (transplanting *R. mangle* seedlings taller than 1.5 m was generally less successful) and presumably also on the care taken during the transplanting process. In plantation experiments in Kenya, Kairo [(1995) as cited in (Kairo et al., 2001)] reported similar results, with higher survival of nursery saplings (80–100% after 24 months) compared with transplanted saplings.

By contrast, in a much larger rehabilitation project undertaken at Brisbane airport in Australia, Saenger (1996) found lower survival of nursery grown seedlings (40–60%) compared with the high survival of transplants (80–90%). For that study, nursery seedlings of *A. marina* and *A. corniculatum* were grown in 25% seawater, but it is not stated whether they were acclimatised to 100% seawater prior to planting out. In these Darwin Harbour trials, salinities in the nursery were maintained close to that of seawater, which may have contributed to the lack of any differences in the survival of nursery grown and transplanted seedlings. Furthermore, by selecting small (< 30 cm in height) plants with a root ball of 20–30 cm diameter, Saenger (1996) achieved high (>80%) survival of transplants.

Overall, the survival of *C. australis* seedlings grown using three different techniques at Charles Darwin park was similar. Survival of seedlings grown from propagules in the nursery (47 %) and those transplanted from adjacent forest (50 %) in the first rehabilitation trail was little different to that for implanted propagules recorded in the second trial (56 %). Reduced survival was, however, recorded for *C. australis* propagules on the more exposed shoreline at site DP (37%). Nevertheless, survival was higher than that reported for both implanted and outplanted nursery grown *C. australis* (<20%) in Townsville (Smith III, 1987a). Given that *C. australis* forests comprise over 50% of the mangrove area of Darwin Harbour and are dominant across much of northern Australia (Duke, 2006), information on effective techniques for reforestation of this assemblage may be of value in future.

Rehabilitation trials conducted at two other disturbed locations in Darwin Harbour and

involving three more species, revealed mean survival of 54 % for *R. stylosa,* 50 % for *A. marina* and 41 % for *A. annulata.* Overall, seedling survival recorded in this study was similar to that reported from mixed species rehabilitation projects in the Asia Pacific region (Saenger and Siddiqui, 1993; Das et al., 1997) and Florida (Lewis and Streever, 2000). Survival rates of at least 50% are generally expected for rehabilitation projects using planted seedlings in mangroves. In both rehabilitation trials, most seedling losses occurred within two months of planting, with reduced mortality after 12 months. The same pattern has been reported from other rehabilitation studies, where most losses occurred in the first few weeks after planting (Teas, 1977; McGuinness, 1997a; Lewis and Streever, 2000). Clarke (2004) also noted most mortality (>70%) for six planted mangrove species (including three of the four species in this study) occurred in the first year, and little mortality was recorded after three years.

Survival of the four different species was surprisingly similar, particularly given the differences in planting techniques, susceptibility to predation of the propagules and environmental variation between sites. Survival ranged between 41% (*A. annulata)* and 54% (*R. stylosa*) after two years, but differences between species were non-significant. Clarke (2004) found seedling survival over the first year was correlated with propagule mass—the smallest propagule (*A. corniculatum)* had the lowest survival (0.1%) whilst the largest (*R. stylosa*) had the highest survival (23%) at Townsville in Northern Queensland. Furthermore, seedling height differed between the four species planted in the Darwin Harbour studies—with maximum height recorded for *R. stylosa* and lowest heights for *C. australis* and *A. annulata*—suggesting that propagule size and seedling morphology contribute to height differences in seedlings and saplings.

Planting technique can influence survival, because implanted propagules (which lack any root system) are easily dislodged by tidal currents and floating debris, and are also more vulnerable to predation (Saenger, 2002). Survival of implanted *R. stylosa* (48%, n=300 at 89 weeks) and *C. australis* propagules (44%, n= 300 at 89 weeks) was substantially less than outplanted nursery grown *R. stylosa* (88%, n=240 at 106 weeks) and *C. australis* seedlings (76%, n=240 at 101 weeks) with well developed root systems (see Chapter 7). Saenger (1996) noted that survival of broadcast or implanted *A. marina* and *A. corniculatum* propagules was clearly site specific but ranged between 30-90%. Furthermore, Stubbs and Saenger (2002) in their detailed review of rehabilitation

techniques conclude that the success (survival rates, height increase, number of leaves) of implanted propagules is less than that for nursery raised seedlings in rehabilitation projects.

Predation is likely to have been a major factor contributing to the observed differences in mean leaf total between sites. Intermittent insect predation on *A. marina* for example, was quite severe at sites DE and DM (pers. obs). Furthermore, many *A. marina* seedlings with attached cotyledons disappeared from site DM during the first few weeks, presumably taken by subtidal predators. Predation on *A. marina* did not appear to be so prevalent at site DP, however, which contributed to the high growth and survival of this species at this site. Although insect predation of *R. stylosa* was not observed, intermittent grazing by turtles was evident at site DP. Between 20 and 30 weeks after planting, leaves and shoots were sheared from seedlings in rehabilitation plots at site DP, leading to the noticeable decline in the graph of leaf total recorded for this site (Figure 8-10). The coarse removal of terminal leaves and whole shoots—identical to that observed on the seaward edge of Charles Darwin park—indicated turtles also grazed seedlings at this location, also situated on the seaward edge of the harbour. Subsequent survival of *R. stylosa* did not, however, appear to be greatly affected. In fact the mean leaf count for *R. stylosa* was slightly more at this site than at other sites, perhaps due to prolific epicormic regrowth (pers. obs.).

Even if successful, rehabilitation projects that involve planting and transplanting seedlings or direct implanting of propagules are labour intensive and generally require considerable time and financial input, particularly for nursery culture (Saenger, 1996; Holl and Howarth, 2000; Lewis, 2005). Timing can also be critical, as most species have relatively brief fruiting times. Moreover, propagules cannot be stored for more than a few months and transplants must be replanted quickly to ensure good survival (Saenger, 2002).

Recently, techniques that focus on reinstatement of the substrate, tidal elevations and hydrological regime, and allow natural regeneration to occur have received increasing attention (Lewis and Streever, 2000). Good results have been obtained in Florida by planting a "nurse" plant species such as Cordgrass (*Spartina* spp.) on newly created substrates (e.g. dredge spoil) which stabilises sediments and facilitates the subsequent recruitment of mangroves (Lewis, 1990; Lewis et al., 1999). Given suitable conditions,

systems restored by natural regeneration in tropical regions may develop into dense closed canopy forests within 15 years and may be visually indistinguishable from natural mangrove forests (Lewis and Streever, 2000).

~8.4.2. Natural and assisted seedling recruitment

Of the two main approaches to mangrove restoration—artificial and natural regeneration—methods that rely on natural recruitment are generally considered preferable. Although the costs of restoration programs are not often documented, they are often extremely high (Holl and Howarth, 2000). Indeed, if hydrological conditions are suitable, and the supply of water-borne seeds and propagules is not limited, working with natural recovery processes can provide the most cost-effective and the most efficient results (Lewis, 1990). Lewis and Streever (2000) cite several examples of natural recruitment in restoration projects in Florida far exceeding the densities of planted seedlings. At the Brisbane airport site, Saenger (1996) also achieved self-sustaining habitats after only five years. Due to the unique properties of each rehabilitation site, a pilot study is however, recommended to confirm the utility of such an approach (Lewis, 1990).

Natural recovery processes had been insufficient to revegetate tracks bulldozed through mangroves in Darwin Harbour in 1992, and presented an opportunity—through conducting the fence experiment—to test whether the stranding of propagules could be assisted and recruitment hastened. The experiment indicated that tidal currents and microhabitat (or substrate heterogeneity) had a substantial effect on the anchoring ability of propagules. By arresting propagules for long enough to establish, the fences of this experiment were successful in promoting establishment of a significantly greater diversity and abundance of propagules than recorded in control plots. Although the technique involved some human intervention, it worked with the process of natural regeneration, by assisting natural recruitment rather than by replanting propagules or seedlings.

A number of authors have noted that propagule buoyancy, dispersal ability, floating and anchoring time, and hydrological factors such as currents and tides are primary factors determining the dispersal and establishment of mangroves (Rabinowitz, 1978; McGuinness, 1997a; Clarke et al., 2001; Delgado et al., 2001). In undisturbed habitats,

natural substratum heterogeneity—which includes tree trunks, roots and pneumatophores, logs, debris, other seedlings and saplings, mounds and hollows—provides numerous effective traps where propagules can be retained long enough for the radicle to emerge and anchor the propagule. For example, Minchinton (2001) reported that the establishment of *A. marina* seedlings was more successful on mounds than on flats in mangroves in south Eastern Australia, indicating the importance of this microhabitat for recruitment. Clarke and Allaway (1993) also demonstrated that gross disturbance of the substrate—created by digging to about 20 cm—not only increased establishment, but enhanced post establishment survival of *A. marina*. Similarly, the presence of footprints within fence plots may have temporarily increased substrate heterogeneity and thus assisted seedling recruitment.

By contrast, the clearings created by disturbance in Darwin Harbour, such as the extensive gaps where *R. stylosa* forests grew prior to Cyclone Tracey and on bulldozed tracks at site DE, distinctly lack recruitment refuges (although abundant woody debris must once have littered cyclone damaged sites). Furthermore, in macrotidal environments, microhabitats that provide a refuge from strong and frequent tidal flows may be crucial for propagule establishment. For instance, the fruiting period of the ten most common mangrove species in Darwin harbour is during the wet season months of November to March (Wightman, 1989; Metcalfe, 1999). During this time, copious quantities of floating propagules are dispersed, accumulating in high densities in the upper intertidal zone and along strandlines. The wet season is however, also the time of year when tidal amplitude is greatest (Anon, 2006) and the rapid rise and fall of tides creates strong tidal currents that may scour bare substrates (pers. obs.). In the absence of recruitment refuges, it is not hard to imagine how clearings can remain devoid of regeneration for more than a decade. Indeed, as Ellison (2000) observed "where there is no mechanism for propagule retention, regeneration of any mangrove vegetation in the absence of human intervention may not occur".

As well as creating a small barrage to strong tidal flows, the fences created a mechanism that could retain propagules long enough for them to anchor and establish. Moreover, shortly after fences had been installed, the number of crab burrows in the vicinity increased (pers. obs.). The localised increase in leaf litter trapped by the fences presumably provided a food resource for the ubiquitous herbivorous crab species

Perisesarma darwinensis. Indeed, leaves and propagules were often observed pulled down crab burrows adjacent to fences, where some were consumed by crabs. The negative influence of predation by crabs was, however, presumably balanced by the positive effects of their burrowing on substrate heterogeneity, which facilitates the stranding of propagules. Some propagules pulled into crab burrows also survived (pers. obs.), and thus were effectively 'planted' by crabs.

Although fences may have encouraged propagule establishment in several different assemblages, long-term studies are needed to assess their effectiveness. The relatively short duration of this study did not allow thorough investigation of the long-term viability of established seedlings. Several replanting programmes in Florida for example, sustained reasonable initial survival, but high mortality was reported after several years (Teas, 1977). Nevertheless, in the current experiment, seedlings were still abundant along fence lines in the tidal flat in 2004—three years after the end of the study—despite the birdwire having completely rusted away. Regeneration at fence locations in the tidal creek and seaward assemblages however, appears less persistent.

Fences or similar retention structures may have wider practical application in habitats where the supply of propagules is not limited—the remediation of small clearings for example. Fences could be installed to facilitate post-construction stabilisation of mangrove sediments and the rapid revegetation of clearings created during road construction. Fences could be used in linear clearings made during the installation of transmission lines, pipelines and other disturbances, in the same way hay bales may be used to trap sediment and reduce erosion in upland habitats. If successful, this technique may have implications for forest management at a larger scale, particularly in situations where recruitment failure has occurred, but limited time and resources preclude the use of more intensive rehabilitation techniques. It should be noted however, that the height and length of fences should be such that they do not also function as fish traps. On several occasions during this study, small fish were stranded and died behind the fences, despite their being only 3 m long. Longer fences, and those arranged in series across a clearing could lead to substantial fish kills.

Overall, the current findings suggest that the importance of microhabitat (including hollows, mounds and natural obstacles) for propagule establishment in mangrove ecosystems has perhaps been somewhat overlooked in previous discussions of the

reasons for recruitment failure and poor rehabilitation success. (but see Komiyama et al., 1996; Ellison, 2000b; Minchinton, 2001). Although there are few parallels between rehabilitation in mangrove and terrestrial habitats, the importance of microhabitat in habitat recovery, may be one of the few instances where there is similarity. Soil microtopography is, for example, considered fundamental to the process of restoration in degraded rangelands across Australia (see Tongway and Hindley, 1995, 2004). Microtopography in terrestrial environments determines whether moisture and nutrients are either retained (in localised 'sinks') or lost (with runoff). In upland areas, small patches of vegetation effectively trap litter, debris and seeds, retaining vital resources within the local area in much the same manner that existing vegetation promotes the recruitment of propagules and retention of litter in mangrove environments. Indeed, the basic processes driving the success of the fence technique are not unlike those underpinning landscape function analysis (LFA), a widely used technique for assessing ecosystem health and rehabilitation monitoring in terrestrial habitats (Tongway and Hindley, 1995, 2004).

Traditional planting techniques still have an important role in mangrove rehabilitation projects, particularly in severely degraded systems (where there may be shortages of propagules) and where silviculture remains the primary goal. Natural and assisted rehabilitation techniques based on an understanding of the individual species ecology at a site and removal of impediments to natural recovery (e.g. restoration of the hydrologic pattern) are however, considered current best practice for successful mangrove restoration (Imbert et al., 2000; Lewis and Streever, 2000; Saenger, 2002). Although plantings are often suggested as a 'last resort', should natural recruitment be insufficient to meet the objectives of the restoration project (Lewis, 2005), the current study suggests that a combination of the two methods may prove to be of substantial value in hastening natural recovery. Rows of seedlings (up to 1.0 m in height) could be planted or transplanted for example, rather than installing steel fences that require future removal. Not only would living seedlings/saplings provide the same substrate heterogeneity and barrier to tidal flow as the fences, but they could also rapidly become seed trees and disseminate propagules. This aspect would be of particular benefit to recruitment of Rhizophoraceae species which tend only to establish very close to parent trees (Blanchard and Prado, 1995; McGuinness, 1997a). Using transplanted seedlings from

nearby forest would ensure appropriate stock was used and could be extremely cost effective—completely avoiding the need for nursery culture of seedlings and purchase of materials for fences. Should transplants not survive, dead saplings may still trap and provide refuge for other viable propagules. Plantings may be either linear (perpendicular to the main direction of tidal flow) or clumped, to provide additional support to seedlings in soft substrates and for rehabilitation of more exposed shorelines.

8.5. Conclusions

Edaphic factors can form complex patterns over short distances in intertidal habitats, which may in turn, affect the success of rehabilitation programs. As shown in this study, growth and survival of seedlings planted in single species trials (*C. australis*) varied with topographic elevation, illustrating the importance of the frequency and duration of tidal inundation on concomitant factors such as soil salinity and moisture. Transplanting seedlings from nearby forests was a quick and cost effective option for replanting disturbed *C. australis* forests. Although survival of transplants and container grown seedlings was similar, the growth of transplants was enhanced.

Multi-species rehabilitation trails lasting two years demonstrated that good overall survival rates for four key mangrove species (41—53%) could be expected at other disturbed locations in Darwin Harbour. Directly implanting propagules is a viable alternative to planting nursery-raised seedlings, although propagules show diminished survival. Rehabilitation trails based on traditional techniques confirmed the utility of planting, transplanting and implanting of collected propagules, thereby reducing the need to repeat similar preliminary programs in Darwin Harbour in future.

High natural seedling recruitment was evident in fence experiments testing the effectiveness of retention structures in assisting propagule establishment. Significantly higher seedling abundance and richness in fence plots emphasised the importance of recruitment refuges in natural recovery processes. This technique has potential wider application for small-scale shoreline stabilisation and rehabilitation projects. Overall, the work confirmed the technical feasibility of a range of natural and artificial rehabilitation techniques and suggests that effective reforestation in the mangroves of Darwin Harbour may be achieved in less than five years.

CHAPTER 9. GENERAL DISCUSSION

CHAPTER 9. GENERAL DISCUSSION

The mangrove forests of Northern Australia are remarkable for their floristic diversity, extensive distribution and their largely pristine status (Duke, 2006). These forests are not homogeneous, however, and generally comprise a number of different floristic assemblages ranging from stunted *C. australis* thickets to *S. alba* "parklands" with massive, widely-spaced trees (Brocklehurst and Edmeades, 1996). The intertidal environment in which they flourish is highly dynamic and mangroves on the coastline of the Top End are subject to macrotidal inundation, seasonal aridity, monsoons and periodic natural disturbances such as cyclones. To conserve mangroves in areas like Darwin Harbour, where they are increasingly prone to anthropogenic disturbance, studies in mangrove environments need to account for inherent natural spatial and temporal variation. Understanding natural variability is a necessary step toward detecting and determining the magnitude and significance of anthropogenic changes, prior to taking appropriate action for conservation. It is this goal that has underpinned the major research themes of this study; the documenting of natural spatial and temporal patterns in biological diversity and the effects of disturbance.

9.1. Biological diversity of mangroves in Darwin Harbour

Despite the often acclaimed value of mangroves as habitats for a diverse array of terrestrial and marine fauna—ranked amongst rainforests and coral reefs in terms of biological diversity—there is a distinct lack of quantitative surveys that attempt to cover the entire fauna and do so over reasonable spatial scales. Furthermore, in the face of increasing demand for coastal land, environmental management of mangrove habitats has been hampered by our inability to answer a basic, but important, questions: What is the biological diversity of the fauna of undisturbed mangrove forests? How does this vary amongst different patches and through time? It was to these questions that the first part of this thesis was directed

The survey results reported in Chapters 3 and 5 indicated that undisturbed mangrove habitats of Darwin Harbour may represent one of the most biologically diverse and productive estuarine systems in the Indo-West Pacific region. In all, 366 fauna species

(112 vertebrates, 254 invertebrates) were recorded (Table 9-1).

Table 9-1: Invertebrate species richness recorded in undisturbed and disturbed mangrove habitats during this survey. Data from six sites in Darwin Harbour (including sites E1 and M3) during wet and dry seasons for 3 subsequent years, for a consultancy project included for comparison (Mangrove Monitoring Program). (ns = not sampled).

TAXA	Undisturbed sites	Disturbed sites	Disturbed & undisturbed sites. Pilot & confirmation studies	Mangrove Monitoring Program 2003-05	TOTAL No. SPECIES (all surveys)
VERTEBRATES					
Mammals	13	6	14	ns	ns
Bats	11	ns	11	ns	ns
Birds	70	66	87	ns	ns
Total	94	72	112	ns	ns
INVERTEBRATES					
Molluscs	60	54	82	74	95
Crustaceans	60	48	69	80	85
Worms	31	33	51	68	75
Fish	12	12	16	22	27
Ants	25	21	32	36	44
Other	3	3	4	5	6
TOTAL	**191***	**171****	**254**	**285**	**332**
	1 year (1,690 records)	1 year (753 records)	1 year (2,443 records)	3 years (6,512 records)	4 years (8,754 records)
	(*12 study plots, wet & dry seasons 2001	(**13 study plots, dry season only, 2001))		(24 study plots, wet & dry seasons, 2003-2005)	

The tally of all invertebrate species exceeds totals reported from mangroves elsewhere in Australia (Davie, 1982; Hutchings and Recher, 1982; Jones, 1984) and for many locations in the Indo-Pacific region (Tan and Ng, 1994; Sasekumar and Chong, 1998). It certainly greatly exceeds the tally of 109 and 131 invertebrate taxa (including insects) recorded from the only two previous invertebrate surveys in Darwin Harbour (Burke, 1992; Hanley, 1993). But all these results are still undoubtedly underestimates, strongly influenced by sampling effort and methodology. Invertebrate surveys for this thesis, for example, were only conducted during the wet and dry season of 2001, but results from subsequent sampling in Darwin Harbour using the same methodology over a longer period, and at more sites (Metcalfe, 2004a, 2005), increased the tally of invertebrate species from 254 to 332 (Table 9-1). Furthermore, although comprehensive, these studies

still leave out considerable potential diversity among invertebrates (e.g. spiders, insects and meiofauna.

With the exception of ants, species richness of all faunal groups was significantly different between assemblages. Ants were the only terrestrial invertebrates surveyed and almost one third of the species found occur exclusively in mangrove habitats. Each floristic unit had a distinctive species composition, in which invertebrates and birds, increased in diversity along the gradient from land to sea. The converse was true for terrestrial vertebrates.

The hinterland margin assemblage comprises only 7.5 % of the total mangrove area in Darwin Harbour (Brocklehurst and Edmeades, 1996). On one hand it experiences the harsh effects of infrequent tidal inundation and seasonal aridity during the dry season, but on the other, during the wet season, it receives substantial freshwater runoff and seepage from the adjacent hinterland. Overall, the hinterland margin is highly productive (litter production exceeds 860 g m^{-2} year) and in these terms it rivals the productivity of the two seaward assemblages (Woodroffe and Bardsley, 1987; Metcalfe, 1999).

Mammals were most diverse in the hinterland margin where they most probably emerge from their primary habitat in the terrestrial hinterland to forage opportunistically within mangrove forests at low tide. Insectivorous microbats were also most numerous in this assemblage—foraging along the natural flyway between terrestrial and tidal forests. By contrast, the invertebrate fauna at the landward fringe was depauperate, a reflection of the harsh environmental conditions, and invertebrate species richness and abundance was lowest in this assemblage. However, this assemblage was the sole habitat for *Neosarmatium meinerti*, a grapsid crab of significance throughout the Indo-Pacific region for its role in ecosystem-level nutrient dynamics (Davie, 1994; Lee, 1998). With its proximity to the hinterland and its more consolidated substrates, this assemblage is most prone to being cleared or modified for development and is therefore quite vulnerable to anthropogenic disturbance.

The tidal flat assemblage is extremely extensive in Darwin Harbour, occupying 43% of the total mangrove area (Figure 2-2, Chapter 2). It is characterised by dense, almost monospecific stands of stunted *C. australis,* 2 to 4 m in height with low rates of litter

production (<400 g m^{-1} $year^{-1}$) (Woodroffe and Bardsley, 1987; Woodroffe et al., 1988; Metcalfe, 1999).

The diversity and abundance of most vertebrate groups was least in this assemblage. Birds and bats may have had reduced foraging opportunities in the dense, low stature forest whereas other mammals were possibly limited by the availability of tall trees to shelter in at high tide. In some circumstances, very high densities of mammals appear to reflect a lack of predation pressure in the tidal flat (e.g. at Charles Darwin Park).

In contrast, and despite its low primary productivity, the tidal flat assemblage was very important as a habitat for invertebrate fauna, with diversity and abundance here equivalent to that of the tidal creek. The tidal flats supported the highest recorded densities of gastropod molluscs (e.g. *Terebralia* spp., *Telescopium telescopium* and Ellobiidae species) and grapsid crabs. Receiving less frequent tidal inundation, these forests may offer a temporal refuge from intense predation by subtidal predators, especially during the neap tidal cycle when tides seldom reach this assemblage. Furthermore, the more vulnerable juvenile molluscs and crabs appeared to be very numerous (pers. obs.). High tree densities also create favourable environmental conditions for intertidal species (e.g. reduced temperature and increased humidity levels (see McGuinness, 1997a)); while providing abundant, moist or shaded niches that can be exploited by prolific arboreal and tree-climbing gastropods (Macnae and Kalk, 1962; Cockcroft and Forbes, 1981; McGuinness, 1994). Not surprisingly, the highest abundance of predatory fish in Darwin Harbour mangroves was recorded in the tidal flat assemblage at high tide (Martin, 2004).

Tall *Rhizophora*-dominated forests of the tidal creek assemblage occupy 33% of the total mangrove area of the harbour, and partly due to their high biomass and intertidal position (low on the shoreline on regularly flushed tidal channels), they are also highly productive, with litterfall ranging between 850 to 1,010 g m^{-2} $year^{-1}$ (Metcalfe, 1999). Although a substantial proportion of this material is recycled by organisms within the forest, a large amount is also exported by tides (Woodroffe et al., 1988; Gleason and Ewel, 2002), but the fate of this exported organic material (in this and other mangrove assemblages) is not fully understood.

The tidal creek assemblage supported high densities of mammals (15.7 animals ha^{-1}),

though with few species. Since most of these mammals were herbivorous, their high densities presumably reflect the high primary productivity of the habitat (Metcalfe, 1999). Bird diversity and abundance peaked in these structurally complex forests which were also occasionally used as roost sites for flying fox colonies

Surprisingly, the mass of above-ground roots did not support a diverse or abundant epifauna, which may be retarded by growths of short, thick foliose algae on lower roots. It is possible though, that these algae may be an important component of the diet of green sea turtles (Chapter 7). Although epifauna was sparse in the tidal creek assemblage, a rich and prolific fauna occurs within rotting wood, a characteristic also reported in other studies (e.g. Hegerl and Davie, 1977; Hegerl et al., 1981; Alongi and Sasekumar, 1992). Trapped logs in these forests provided an important microhabitat for highly abundant teredinid molluscs, whose shell-lined burrows created habitat for a varied faunal assemblage including amphipods, polychaetes, turbellarians, crabs, gastropods and occasionally fish. Indeed, the cryptic distribution of epifauna in these forests suggests that these faunal communities are subject to intense predation during high tides. So while regular tidal inundation may facilitate a diverse invertebrate fauna it also allows the regular ingress of sub-tidal predators including a great variety of fish, rays, crustaceans and snakes (Martin, 2004).

Though small in area (just 4.7% of the mangroves in Darwin Harbour), the seaward assemblage is high in productivity. Previous studies in Darwin Harbour have shown that it is by far the most productive, with litter production exceeding 1,250 g (dry weight) m^{-2} $year^{-1}$ (Woodroffe and Bardsley, 1987; Woodroffe et al., 1988; Metcalfe, 1999). The dominant mangrove is *Sonneratia alba*, which is often the sole colonist of the soft, highly bioturbated, unconsolidated muds at the seaward limit of mangrove habitats.

The characteristics of the vertebrate fauna in this assemblage were very similar to those of the tidal creek forest, having a high density, low diversity mammal fauna and a prolific bird fauna. The structural and floral features of *S. alba* that support such a fauna include the availability of hollow limbs above the high water mark and its year round production of large nectar-bearing flowers (Wightman, 1989), and fruits which are particularly favoured by *M. burtoni* (pers. obs.). Nectar foraging by birds involves not just resident species but a range of terrestrial visitors.

The seaward assemblage was the richest habitat for invertebrates with mean species richness (16.3 ± 1.0 SE) and abundance (50.1 ± 6.0 SE per station) substantially higher than in any other (see Table 6-4, Chapter 6). Small tidal channels and pools in the seaward assemblage provided habitat for numerous species of shrimp and fish. *S. alba,* was again of pivotal importance in the life-cycles of numerous invertebrate species, with its old, hollow trunks providing many opportunities for encrusting, boring and epifaunal species. Being flooded for longer and to a greater depth on each tidal cycle than any other assemblage, tree trunks and protected niches beneath flakes of bark were more suitable as habitat for epifauna and cryptofauna. A diverse array of gastropods, bivalves, crustaceans, worms and other less common animals including echinoderms and anthozoans were found on the trunks of these trees. Vast numbers of insects, like birds also visit *S. alba* flowers (Coupland, 2002), including many visitors from terrestrial habitats.

Overall, quite a distinct division between the marine invertebrate species in the two landward mangrove assemblages and those occurring in the two seaward assemblages was evident. A different suite of species, displaying a number of behavioural and physiological adaptations to avoid desiccation and high temperatures, occurred above the mean neap tide level (approximately 2 m AHD). Lower on the shore, environmental conditions are more moderate for marine fauna and a different suite of invertebrates was evident, including epifaunal and filter-feeding species and other organisms.

The strongest temporal patterns in distribution and abundance were shown by infaunal taxa, particularly worms, and to a lesser extent, grapsid crabs and bivalves. The diversity and abundance of these groups declined in seaward assemblages during the wet season. Overall however, the vertebrate and invertebrate fauna did not appear to exhibit pronounced seasonal changes. The seasonal changes shown by populations of infaunal organisms might be a reflection of the dynamic nature of sedimentary environments, where the substrate is continually structured both by the organisms themselves and by physical forces such as wind, waves, salinity and desiccation. Moreover, most invertebrate populations (as well as mudskippers and other small fish) decreased in abundance in landward assemblages during the dry season, probably in response to rising aridity and increasing soil salinity. Patterns of seasonal variation in diversity and abundance were not uniform, however, differing amongst faunal groups

which may, or may not, be influenced by season, and where evident, seasonal effects varied amongst assemblages. Clear seasonal variation was observed in populations of the two most common honeyeaters, however, which were more abundant during the dry season, suggesting a response to increased availability of nectar resources at that time, or perhaps, a lack of these in adjacent terrestrial habitats.

9.2. The impacts of disturbance on mangrove fauna

Overall, there were some similarities and some differences in the response of invertebrate and vertebrate fauna to urbanisation. Whereas the total pool of vertebrate species declined in response to disturbance (from 83 to 72 species, excluding bats), the pool of invertebrate species, sampled in comparable dry season surveys, increased (Table 9-1). Additional habitat opportunities created by anthropogenic disturbance most likely led to a larger total pool of invertebrate species (171) in disturbed mangroves than in undisturbed (163).

In general, in the sites studied for this thesis, there were no detectable impacts from moderate levels of anthropogenic disturbance for all phyla (see Table, 6-4, Chapter 6). Overall mean values for species richness and mean abundance declined in disturbed mangroves, but due to high spatial variability at undisturbed sites and small-scale heterogeneity at disturbed sites, the differences in species richness between disturbed and undisturbed systems were non-significant. This pattern was evident in analyses of both vertebrates (mammals and birds) and invertebrates.

Although no differences were detected by univariate analyses of the invertebrates as a whole, or for any of the individual invertebrate phyla, effects of disturbance were detected in analyses of subsets of the data (eg, faunal groups, feeding guilds or individual genera). Populations of certain invertebrate faunal groups—including ocypodid crabs and surface deposit feeding worms—increased at some locations in disturbed mangroves. Thus studies of invertebrates provided a detailed picture of the response of this community to disturbance. Significant increases in the local abundance of mammals or birds were not found, however, chiefly due to the ingress of other species. In the case of mammals, introduced mice and rats appeared to replace several native species.

Several major similarities were observed in the response of all phyla to urbanisation. The tight partitioning of fauna in assemblages, clearly observed in undisturbed mangroves, disintegrated in response to environmental heterogeneity associated with disturbance. Moreover, the taxonomic composition of fauna in disturbed mangroves differed from that in undisturbed sites, a pattern evident in NMDS ordinations of all faunal groups. Nevertheless, the disturbed sites studied here were still productive habitats for fauna, in which native species remain dominant. Two introduced species were found in undisturbed mangroves (feral cat, introduced ant), whereas six introduced species (black rat, house mouse, a gastropod and three ant species) were recorded in disturbed mangroves. Although the proportion of introduced species increased, their influence was restricted to the fringes of the mangroves. Exotic species were rarely recorded outside the hinterland margin assemblage.

As in natural mangroves, diversity in disturbed systems typically increased from landward to seaward. The effects of urban and industrial development of the adjacent hinterland on mangrove mammals were most pronounced in the hinterland margin assemblage. Several native species that intermittently visited the hinterland margin in undisturbed mangroves disappeared, presumably in response to clearing of hinterland vegetation. Introduced mice and rats were recorded in mangroves immediately adjacent to coastal developments and captures of bandicoots (*Isoodon macrourus*), which tend to favour disturbance, also increased. The predominant faunal group in landward mangrove assemblages—the grapsid crabs—proved quite vulnerable to urban encroachment. The common practice of removing landward habitats not only directly affects populations of grapsid crabs but has a negative effect on juvenile fish populations which feed on the abundant crab larvae at the zooplankton stage (Roberston, 1991).

Anthropogenic disturbance often altered drainage conditions leading to the artificial ponding of water the tidal flat assemblage, and where permanent, areas of forest died due to constant waterlogging. These changes encouraged localised increases in bird diversity and abundance. The ingress of new species adapted to either clearings or waterbodies appeared to balance the loss of forest species, such that overall bird species diversity was not diminished. Birds recorded only at disturbed sites primarily included waders and generalists from terrestrial habitats, and it is recommended that disturbance

effects in relation to the protection of mangrove endemics is investigated further.

Construction activities also caused sedimentation in tidal flat habitats and local increases in the diversity and abundance of ocypodid crabs, especially fiddler crabs (*Uca* spp.) appear to be associated with changed substrate conditions (pers. obs.). One of the most pronounced effects of urbanisation was however, the sharp decline in gastropod abundance in the tidal flat assemblage. Given the tendency for anthropogenic disturbance to mainly affect landward mangrove assemblages (Skilleter, 1996; Lee, 1998) and the apparent susceptibility of mangrove gastropods to a decrease in forest cover (McGuinness, 1994), the results of this survey suggest that gastropods—particularly the large potamidids or mud creepers (e.g. *Telescopium , Terebralia* spp.)—may be significantly affected by anthropogenic disturbance.

Lower densities of vertebrates in disturbed tidal creek assemblages appear to be associated with loss of tall forest trees with crucial refuge hollows for mammals and foraging resources for birds. These small scale variations in modified habitats (e.g. deforestation, ponding) contributed to the varied patterns in faunal diversity and abundance—particularly evident for highly mobile species such as birds—and the consequent lack of clear partitioning of species in different assemblages. The invertebrate fauna of tidal creek assemblages closely reflected such environmental variation, evident by local increases in the abundance of ocypodid crabs and surface deposit feeding polychaetes.

9.3. The recovery and rehabilitation of disturbed mangrove forests

Mangroves in Darwin Harbour are capable of relatively rapid growth: the above-ground height of *R. stylosa* seedlings planted in experiments for this project typically exceeded 800 mm two years after planting, and heights of over 2 m were attained within five years. On average, *C. australis* grew approximately 230 cm during the two-year study period and flowering and fruiting of *C. australis* was observed within four to five years of planting. Thus the reasons why areas of seemingly suitable habitat fail to recover, or require long periods of time to regenerate, are intriguing. Plant growth experiments reported in Chapter 7 eliminated several physical and biotic factors that could potentially limit the recovery of deforested areas and subsequent work focussed

on the pre-establishment phase (i.e. dispersal, recruitment) as being crucial in the recovery of disturbed *C. australis* and *R. stylosa* forests at mid-tidal elevations.

By contrast, *R.stylosa* forests in the seaward fringe were chiefly found to be regulated by biotic factors, operative during the post-establishment phase, but presumably also active within the context of other long-term changes in edaphic factors (e.g. substrate stability, soil toxicity, forest cover). At the time this study was done (i.e. over 25 years after severe cyclone damage), grazing sea turtles and other currently indecipherable factors limited forest recovery on the seaward fringe. In these habitats, forest recovery is clearly complex, and over time, has involved the interplay of a number of biotic and abiotic factors.

Perhaps the most useful outcome of these studies, in terms of understanding natural recovery processes, arose from incidental observations on natural recruitment made during experimental work for Chapter 7. In the absence of natural obstacles to retain bouyant, waterborne propagules for long enough to take root, seedling recruitment can be substantially delayed or fail to occur. Further research, in the context of rehabilitation trials (Chapter 8) highlighted the importance of microhabitat and forest structure in providing adequate recruitment refuges. In natural forests, these may comprise hollows, logs, tree trunks and other seedlings (Figure 9-1).

Collectively, the rehabilitation experiments conducted for this thesis suggest that a combination of artificial and natural techniques promises to be most successful. For example, windrows or clumps of transplanted saplings could perform the same role as steel and birdwire fences. Indeed, transplanted saplings possess valuable advantages over outplanted seedlings, as they provide effective recruitment refuges as well as disseminating their own propagules after only a few years. There is potential for the wider application of these novel techniques, particularly to rehabilitate clearings in mangroves in Darwin Harbour. Although much research on the biodiversity and functioning of rehabilitated mangroves remains to be done, there is clearly great potential for rehabilitation to hasten the processes of natural recovery and ecosystem restoration.

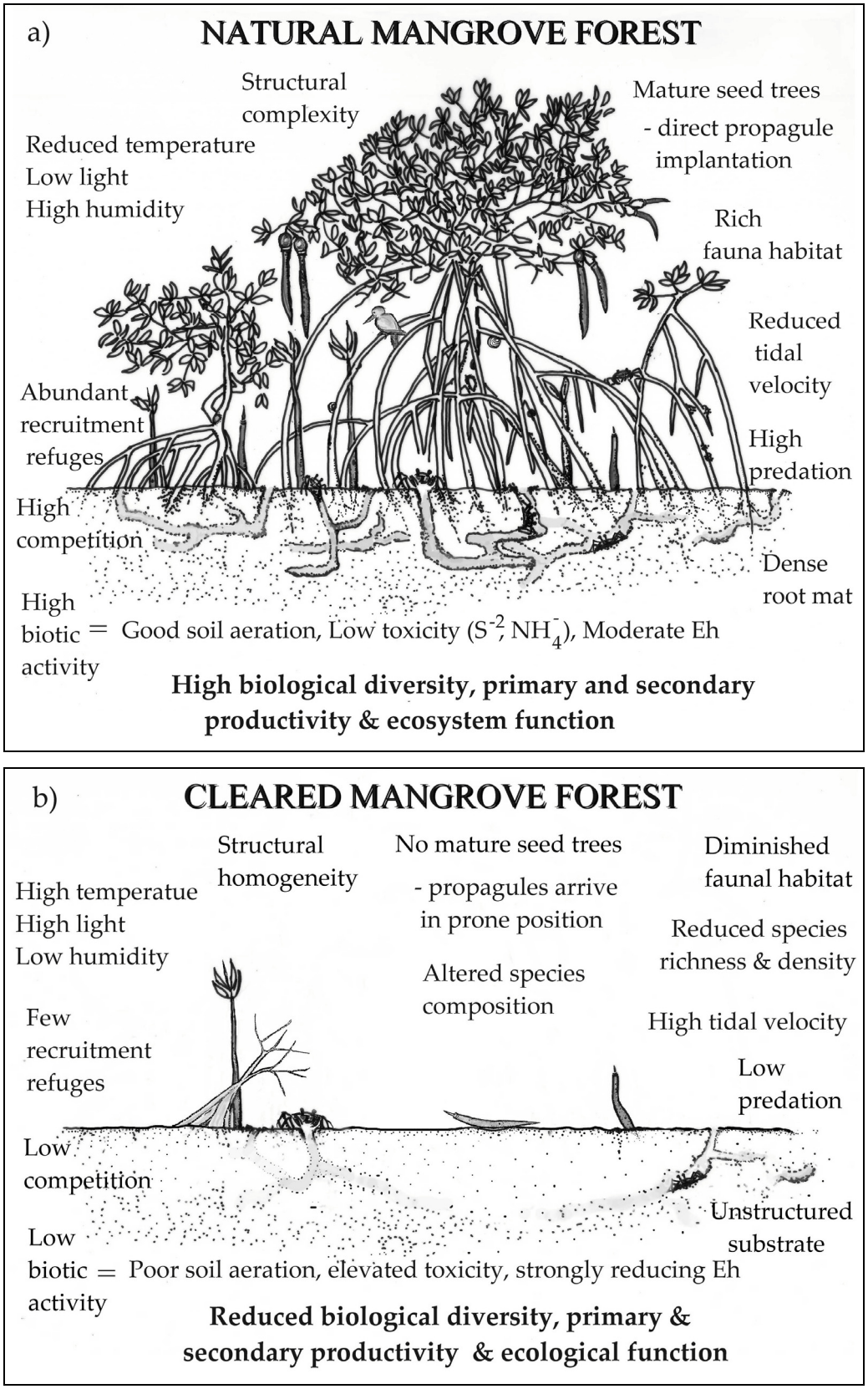


Figure 9-1: A diagrammatic summary of some of the key factors influencing recovery processes in Rhizophoraceae-dominated mangroves of Darwin Harbour. Note that a variety of different alternative scenarios may occur at different locations, or in other regions and the key factors may vary in other forest types and in response to different types and degrees of damage.

Given the long history of mangrove silviculture, most previous work on mangrove rehabilitation and restoration has focussed on the various techniques for growing and planting mangrove trees, with little attention paid to reinstating the original functions of the ecosystem (Kaly and Jones, 1998). Consequently, the success of many of these projects from an ecological perspective is poorly known (Ellison, 2000b). It is not known for example, whether restored systems support a similar range of fauna to undisturbed mangroves and whether similar functional links (including biological and physical) are re-established with other habitats. Furthermore, for an ecosystem to persist over time it must be self-sustaining and able to respond to environmental stresses and changes such as intermittent disturbance, in a similar fashion to natural systems. Research in these areas would provide valuable feedback for future restoration projects whose success should be judged, according to Kaly and Jones (1998), by "the degree to which the functional replacement of the natural ecosystem has been achieved".

9.4. The role of plant-animal interactions in mangrove disturbance ecology

A number of authors have emphasised the importance of the interplay between the flora and fauna of mangrove habitats (Smith III, 1987b; Smith III, 1987c; Smith III, 1988; Roberston, 1991; Lee, 1999; Salgado Kent, 2004) and the studies conducted for this thesis provide several examples of strong plant-animal inter-dependence. Patterns in the diversity and abundance of both vertebrate and invertebrate fauna appeared to respond chiefly to the habitat opportunities and resources provided by the forest. The forests, however, may also be heavily influenced by faunal activity.

The interplay between the decapod crabs, forest health and ecosystem function is an important example of plant-animal interaction (Roberston, 1986; Roberston and Daniel, 1989; Roberston, 1991; Smith III et al., 1991; McGuinness, 1993; Lee, 1998, 1999) with wider implications for the ecology of mangroves affected by disturbance (Machiwa and Hallberg, 1995; Skilleter and Warren, 2000). In this study, 44 species of crabs dominated the invertebrate fauna and constituted 43% of all records. It is not surprising, therefore, that the ecological effects of their burrowing and feeding activities may be very important, particularly as the most abundant grapsid species in Darwin Harbour eat both mangrove leaves and propagules (McGuinness, 1997c; Salgado Kent, 2004). The

leaf-burying crab *Neosarmatium meinerti*, for example, is virtually restricted to upper intertidal habitats where its large burrows, lined with decaying leaves, form an extensive, anastomosing network, which allows water and air to circulate freely around the roots of the trees (pers. obs.). Increased oxygen, nutrients and tidal flushing provided by crab burrowing activities is likely to be of major benefit to the forest. Indeed, the high productivity of this assemblage (Section 9.1) may in part, be attributed to the beneficial effects of these crabs, but is also heavily influenced by the presence of seasonally deciduous species.

Burrowing activities of crabs undoubtedly have a major influence on sedimentary facies, and nutrient chemistry (Roberston, 1991). Furthermore, oxygenation of anaerobic soils by crabs directly affects soil redox potential (Eh) and inhibits an accumulation of soluble phytotoxins (e.g. Fe^{2+}, Mn^{2+}, H_2S, CO_2 and CH_4), which can have profound effects on plant growth (Boto, 1984; Youssef and Saenger, 1996, 1998). The beneficial role that crab bioturbation plays in reducing soil sulphide and ammonium levels was elegantly demonstrated by Smith III et al. (1991), implying that loss of forest cover and attendant crab fauna may increase soil toxicity (Figure 9-1). Plant-animal relationships may thus emerge as important factors in disturbed and deforested mangroves.

Anthropogenic disturbance resulting in the loss of the landward crab fauna for example, could have major ramifications for the sustainability of the forest itself as well as for system-level processes (Lee, 1998). Given the observation of Lee (1988) that "an increasing quantity of data now suggest that the relationship between crabs and mangroves (not only grapsids but ocypodids also) is strongly reciprocal, with each influencing the performance or even survival of the other," the role of fauna in the recovery of disturbed forests gains more significance. In some circumstances, particularly in extensive clearings such as the seaward cyclone-damaged areas of Darwin Harbour, an absence of infaunal species may hamper the growth and survival of seedlings, helping to explain the long recovery times. Replanting and fence installation may trigger faunal recruitment and facilitate the survival of seedlings. Indeed, once recruitment had occurred along the barrier provided by the birdwire fences, colonisation by crabs was rapid (pers. obs.) and this encouraged further establishment through stranding of propagules within the entrances of burrows. It is increasingly evident that the health and sustainability of rehabilitated forests also

depends on their ability to support a range of fauna.

The reciprocal effects of crabs and mangrove forests are one of the most obvious and well-studied examples of important plant-animal relationships in mangroves. Less evident is the interdependence of the vertebrate fauna and the forests of the two seaward assemblages. Tall trees provided not only a food resource but crucial refuges above high tide level for high densities of arboreal mammals and the highest diversity and abundance of birds was also found amongst dense tree cover on the seaward fringe. Over 70% of bird foraging activities involved forest trees and the nectar-rich flowers of *S. alba* represented a particularly rich resource, for which birds and flying foxes presumably compete. In turn, bats and birds are likely to play an important role in the pollination of the majority of mangrove forest trees. These interactions imply that disturbance involving the loss of tree cover will directly affect the biota intrinsically dependent on the vegetation, as was reflected by local variations in faunal populations at the disturbed sites of this study.

This study revealed another plant-animal interaction in the cyclone-damaged clearings close to the seaward margin involving intense predation of *R. stylosa* seedlings by green sea turtles. In this instance, it was evident that the selective predation on *R. stylosa* seedlings by green turtles (*Chelonia mydas)* reduces the recruitment of this species and may thus be a major determinant of forest species composition (e.g. Sousa and Mitchell, 1999). If the almost complete mortality of seedlings observed in this study was sustained over many years by repeated grazing by turtles, it is likely to have substantially delayed the recovery of *R. stylosa* forests in these clearings. Furthermore, it represents a feedback loop linking a rather poorly known trophic interaction with forest structure and is a reminder of the importance of patchiness created by disturbance in maintaining biological diversity. Repeated grazing will continue to impede recovery of the forest, which in turn, benefits the turtles.

9.5. Conclusions and recommendations

Overall, the results of this study indicate that the mangroves of Darwin Harbour may represent one of the most biologically diverse estuarine systems in the Indo-West Pacific region. These surveys have provided insight into the distinctive distribution of fauna

within mangrove forests while increasing our understanding of the spatial and temporal patterns in the richness and abundance of mangrove taxa. Studies of birds, mammals and bats emphasised trophic links between mangroves and adjacent terrestrial habitats. In tandem with concomitant research on the use of mangroves by fish, the work has also substantiated functional and trophic links both within mangroves, and between mangroves and near-shore habitats, and identified priorities for future research (see below).

Furthermore, by highlighting areas with particularly high species richness (e.g. the seaward assemblage) and abundance (e.g. the tidal flat), information of this kind may contribute to the conservation of mangrove and marine biodiversity. For example, due to the relatively small area of the seaward assemblage and its high primary and secondary productivity, this assemblage should be given the highest conservation status. Although providing only limited opportunities for vertebrates, it is evident that the highly extensive, seemingly unproductive tidal flat assemblage, supports high populations of invertebrates of trophic importance to local fisheries (Martin, 2004). The tidal flat should not, therefore, be considered of low conservation value. Furthermore, the work has underscored the importance of the crab fauna in the hinterland margin, for maintaining vital ecosystem function and high productivity. Finally, the quantitative data on the fauna of undisturbed mangrove habitats substantiates claims regarding their rich biological diversity, and may serve as a platform for the management and conservation of this vital, but globally threatened resource.

Mangrove faunal communities appear sensitive to environmental change but also relatively resilient to moderate levels of anthropogenic disturbance. This study indicated that the factors contributing to seedling recruitment failure may be complex and vary with shoreline position. In cyclone damaged seaward forests, recovery has been delayed by sustained seedling predation by green sea turtles while higher on the shore, recruitment failure is perpetuated by limited opportunities for propagules to establish in clearings. The insight gained regarding natural recovery processes inspired the development and trial of new methods for rehabilitation. Given the escalating degradation of this dwindling resource, proven rehabilitation techniques that work with natural processes to accelerate reforestation and ecosystem recovery, represent valuable management tools.

Considerable work is still required to understand mangrove systems, and their interactions with nearby ecosystems, and manage them effectively. Invertebrate diversity and abundance appears to increase downshore, for example, but we do not know if this trend continues beyond the forest. Migratory birds, some of which are listed on international conservation treaties, flock to the mudflats adjacent to the mangroves during the wet season and study of this habitat should be a priority. Further studies on polychaetes in polluted and disturbed mangrove and mudflat environments would test their usefulness as indicators of disturbance. Additional work on the altered species composition in some disturbed assemblages should examine whether rare species or mangrove endemics are being replaced by commoner species, and determine the ecological significance of these changes. Finally, very little is known of the recovery of fauna in rehabilitated mangroves.

In conclusion, the results of this study highlight the potential significance of tropical mangrove forests as habitats for both marine and terrestrial species. They also indicate the potential importance of mangrove resources to vertebrate and invertebrate fauna from other nearby marine and terrestrial communities. The fauna of the forests may be affected by anthropogenic disturbance and, although rehabilitation is feasible, future research should look further into the effects of disturbance and the effectiveness of rehabilitation.

REFERENCES

Aksornkoae S, Priebprom S, Saraya A, Kongsangchai J (1985) Mangrove resources and the socio-ecomomics of dwellers in mangrove forests in Thailand. *In* P Kunstadter, EC Bird, S Sabhasri, eds, Man in the Mangroves. The socio-economic situation of human settlements in mangrove forests. The United Nations University, Tokyo, Japan, pp 11-43

Alfaro AC (2006) Benthic macro-invertebrate community composition within a mangrove/seagrass estuary in northern New Zealand. Estuarine, Coastal and Shelf Science **66:** 97-110

Al-Khayat JA, Jones DA (1999) A comparison of the macrofauna of natural and replanted mangroves in Qatan. Estuarine, Coastal and Shelf Science **49:** 55-63

Allen JA, Ewel KC, Jack J (2001) Patterns of natural and anthropogenic disturbance of the mangroves on the Pacific Island of Kosrae. Wetlands Ecology and Management **9:** 279-289

Alongi DM (1987) Intertidal zonation and seasonality of meiobenthos in tropical mangrove estuaries. Marine Biology **95:** 447-458

Alongi DM (1989a) The role of soft-bottom benthic communities in tropical mangrove and coral reef ecosystems. Review of Aquatic Science **1:** 243-280

Alongi DM (1989b) Ecology of tropical soft-bottom benthos: a review with emphasis on emerging concepts. Revista de Biología Tropical **37:** 85-100

Alongi DM, Ramanathan AL, Kannan L, Tirendi F, Trott LA, Bala Krishna Prasad M (2005) Influence of human induced disturbance on benthic microbial metabolism in the Pichavaram manroves, Vellar-Coleroon estuarine complex, India. Marine Biology **147:** 1033-1044

Alongi DM, Sasekumar A (1992) Benthic communities. *In* AI Robertson, DM Alongi, eds, Tropical Mangrove Ecosystems. American Geophysical Union, Washington, DC, USA, pp 137-172

ANCA (1993) A Directory of Important Wetlands in Australia. Second Edition. Australian Nature Conservation Agency, Canberra. pp.168-170

Andersen AN (1997) Using ants as bioindicators: multiscale issues in ant community ecology. Conservation Ecology [online] **1:** 8

Andersen AN (2000) The Ants of Northern Australia - A Guide to the Monsoonal Fauna. CSIRO Publishing, Melbourne, Australia

Andersen AN, Fisher A, Hoffman BD, Read JL, Richards B (2004) Use of terrestrial invertebrates for biodiversity monitoring in Australian rangelands, with particular reference to ants. Austral Ecology **29:** 87-92

Andersen AN, Morrison S, Belbin L, Ashwath N, Brennan K (1998) The role of ants in minesite restoration in the Kakadu region of Australia's Northern Territory, with particular reference to their use as bioindicators. Supervising Scientist, Canberra

Anon (1985) Mudskippers. Information leaflet, No. 18. Museums and Art Galleries of the Northern Territory

Anon (1994) Paper no. 2, Biodiversity series. Australia's biodiversity - an overview of selected significant components. Biodiversity Unit,Commonwealth Department of the Environment, Sport and Territories, Canberra, Australia

Anon (1996) The national strategy for the conservation of Australia's biological diversity. Commonwealth Department of the Environment, Sport and Territories, Canberra, Australia

Anon (2000) Australian Standard. Methods of testing soil for engineering purposes. Part F - Soil strength and consolidation tests. F2.1-1 to 1-2

Anon (2003) Coastal and marine environment. Year Book Australia. Australian Bureau of Statistics website.

Anon (2006) Darwin Tidal Predictions 2006. Marine Safety Branch. Department of Infrastructure, Palnning and Environment. Transport Division. http://www.nt.gov.au/ipe/dtw/tides/

Anon (2006) EPBC Act List of Threatened Fauna- Endangered mammals. *In*, Vol 2006. Australian Government, Department of the Environment and Heritage website www.deh.gov.au/cgi-bin/sprat/public/publicthreatenedlist

Apel M, Turkay M (1999) Taxonomic composition, distribution and zoogeographic relationships of the grapsid and ocypodid crab fauna of intertidal soft bottoms in the Arabian Gulf. Estuarine, Coastal and Shelf Science **49:** 131-142

Arnold GW (1983) Comparison of numbers of species of birds in wandoo woodland obtained by two census methods. *In* SJJF Davies, ed, Methods of censusing birds in Australia. Royal Australasian Ornithological Union, Melbourne, pp 15-18

Ashton EC, Macintosh DJ (2002) Preliminary assessment of the plant diversity and community ecology of the Sematan mangrove forest, Sarawak, Malaysia. Forest Ecology and Management **166:** 111-129

Ashton EC, Macintosh DJ, Hogarth PJ (2003) A baseline study of the diversity and community ecology of crab and molluscan macrofauna in the Semantan mangrove forest, Sarawak, Malaysia. Journal of Tropical Ecology **19:** 127-142

Audas DM (1992) The effect of disturbance on the fiddler crabs within Darwin Harbour. Honours thesis. Northern Territory University, Darwin, NT

Bailey-Brock JH (1995) Polychaetes of western Pacific islands: a review of their systematics and ecology. *In* J Maragos, MN Peterson, LG Eldredge, JE Bardach, H Takeuchi, eds, Marine and coastal biodiversity in the tropical island pacific region, Vol 1. Program on environment, East-West center, Honolulul, Hawaii, pp 121-134

Bardsley KN (1985) The effects of cyclone Kathy on mangrove vegetation. *In* KN Bardsley, JDS Davie, C Woodroffe, eds, Mangrove Monograph No 1. Coasts and tidal wetlands of the Australian monsoon region. North Australia Research Unit, the Australian National University, Darwin, Northern Territory, pp 167-187

Barnes RSK (2003) Interactions between benthic molluscs in a Sulawesi mangal, Indonesia: the cerithiid mud-creeper *Cerithiium coralium* and potamidid

mud-whelks, *Terebralia* spp. Journal of the Marine Biological Association of the United Kingdom **83:** 483-487

Beardmore J, Mair GC, Lewis RI (1997) Biodiversity in aquatic systems in relation to aquaculture. Aquaculture Research **28:** 829-839

Beattie AJ, Majer JD, Oliver I (1993) Rapid biodiversity assessment: A review. *In* Rapid biodiversity assessment. Proceedings of the biodiversity assessment workshop. Research unit for biodiverstiy and bioresources, Macquarie University, pp 4-14

Beattie AJ, Oliver I (1994) Taxonomic minimalism. Tree **9:** 488-490

Begg R, Walsh B, Woerle F, King S (1983) Ecology of *Melomys burtoni,* the Grassland Melomys (Rodentia: Muridae) at Coburg Peninsula, NT. Australian Journal of Wildlife Research **10:** 259-267

Belan TA (2003) Marine environmental quality assessment using polychaete taxocene characteristics in Vancouver Harbour. Marine Environmental Research **57:** 89-101

Benfield SL, Guzman HM, Mair JM (2005) Temporal mangrove dynamics in relation to coastal development in Pacific Panama. Journal of Environmental Management **76:** 263-276

Bennett I (1968) The mud-lobster. Australian Natural History

Berry AJ (1963) Faunal zonation in mangrove swamps. Singapore National Museum Bulletin **32:** 90-98

Beukema JJ, Flach EC, Dekker R, Starink M (1999) A long-term study of the recovery of the macrozoobenthos on large defuanated plots on a tidal flat in the Wadden Sea. Journal of Sea Research **42:** 235-254

Bilyard GR (1987) The value of benthic infauna in marine pollution monitoring studies. Marine Pollution Bulletin **18:** 581-585

Bird ECF, Barson MM (1982) Stability of mangrove systems. *In* BF Clough, ed, Mangrove Ecosystems in Australia- Structure, Function and Management. Australian Institute of Marine Science, pp 265-274

Bjorndal KA (1995) The consequences of herbivory for the life history pattern of the Caribbean Green Turtle, *Chelonia mydas*. *In* KA Bjorndal, ed, Biology and conservation of sea turtles. Smithsonian Institution Press, Washington, pp 111-116

Bjorndal KA (1997) Foraging ecology and nutrition of sea turtles. *In* PL Lutz, JA Musick, eds, The biology of sea turtles. CRC Press Inc, Boca Raton, Florida, pp 199-232

Blaber SJM (1980) Fish of the Trinity Inlet system of North Queensland with notes on the ecology of fish faunas of tropical Indo-Pacific estuaries. Australian Journal of Marine and Freshwater Research **31:** 137-146

Blaber SJM (1997) Fish and fisheries of tropical estuaries. Chapman and Hall, London

Blanchard J, Prado G (1995) Natural regeneration of *Rhizophora mangle* in strip clearcuts in north western Ecuador. Biotropica **27:** 160-167

Blasco F (2001) Depletion of the mangroves of continental Asia. Wetlands Ecology and Management **9:** 245-256

Blasco F, Saenger P, Janodet E (1996) Mangroves as indicators of coastal change. Catena **27:** 167-178

Bonsdorff E, Pearson TH (1999) Variation in the sublittoral macrozoobenthos of the Baltic Sea along environmental gradients: A functional group approach. Australian Journal of Ecology **24:** 312-326

Boto KG (1984) Waterlogged saline soils. *In* SC Snedaker, JG Snedaker, eds, The mangrove ecosystem: research methods. UNESCO, pp 114-130

Boto KG, Bunt JDS, Wellington JT (1984) Variations in mangrove forest productivity in northern Australia and Papua New Guinea. Estuarine, Coastal and Shelf Science **19:** 321-329

Brennan K, Woinarski JCZ, Hempel C, Cowie I, Dunlop C (2003) Biological inventory of the Arafura Swamp and catchment. Department of Infrastructure, Planning and Environment, Darwin

Brocklehurst PS, Edmeades BF (1996) Mangrove Survey of Darwin Harbour, Northern Territory, Australia. Land Conservation Unit, Conservation Commission of the Northern Territory, Darwin, NT

Bunt JDS (1992) Introduction. *In* AI Roberston, DM Alongi, eds, Tropical Mangrove Ecosystems. American Geophysical Union, Washington, DC, pp 1-5

Bureau of Meteorology (2006) Climate averages for Station 014015 Darwin Airport, NT during the period 1941-2006. *In*, Vol 2006. Commonwealth Bureau of Meteorology Website www.bom.gov.au

Burke MM (1992) Species diversity and abundance of fauna in cyclone disturbed and undisturbed mangrove areas of Darwin Harbour, Northern Territory, 17 years after Cyclone Tracy. Honours thesis,. University of Canberra, Belconnen, Canberra

Burns KA, Garrity SD, Levings SC (1993) How many years until mangrove ecosystems recover from catastrophic oil spills? Marine Pollution Bulletin **26:** 239-248

Byrne AP (1988) Darwin Harbour - Hydrodynamics and coastal processes. *In* HK Larson, MG Michie, JR Hanley, eds, Proceedings of a workshop on research and management held in Darwin, 2-3 September, 1987. Mangrove Monograph No. 4. Australian National University, North Australia Research Unit, Darwin, NT, pp 19-31

Cahoon DR, Hensel P (2003) Hurricane Mitch, a regional perspective on mangrove damage, recovery and sustainability. Open File Report prepared by USGS

Cairns J, McCormick PV, Niederlehner BR (1993) A proposed framework for developing indicators of ecosystem health. Hydrobiologia **263:** 1-44

Cantera JR, Thomassin BA, Arnaud PM (1999) Faunal zonation and assemblages in the Pacific Colombian mangroves. Hydrobiologia **413:** 17-33

Carballo JL, Naranjo S (2002) Environmental assessment of a large industrial marine complex based on a community of benthic filter-feeders. Marine Pollution Bulletin **44:** 605-610

Cawkell EM (1964) The utilization of mangroves by African birds. Ibis **106:** 251-253

Chapman MG (1998) Relationships between spatial patterns of benthic assemblages in a mangrove forest using different levels of taxonomic resolution. Marine Ecology Progress Series **162:** 71-78

Chapman MG, Michie K, Lasiak K (2005) Responses of gastropods to changes in amounts of leaf litter and algae in mangrove forests. Journal of the Marine Biological Association of the United Kingdom **85:** 1481-1488

Chapman MG, Underwood AJ (1997) Concepts and issues in restoration of mangrove forests in urban environments. Chapter 9. *In* P Milliken, ed. gee@bio.usyd.edu.au. Elsevier Science Ltd, p 10p

Chollett I, Bone D (2007) Effects of heavy rainfall on polychaetes: Differential spatial patterns generated by a large-scale disturbance. Journal of Experimental Marine Biology and Ecology **340:** 113-125

Chong VC, Sasekumar AM, Leh UC, D'Cruz R (1990) The fish and prawn communities of a Malaysian coastal mangrove system with comparison to adjacent mud flats and inshore waters. Estuarine, Coastal and Shelf Science **31:** 703-722

Choy SC, Booth WE (1994) Prolonged inundation and ecological changes in an *Avicennia* mangrove: implications for conservation and management. Hydrobiologia **285:** 237-247

Churchill S (1998) Australian Bats. Reed New Holland, Sydney

Clark MW, McConchie D, Saenger P, Pillsworth M (1996) Hydrological controls on copper, cadmium, lead and zinc concentrations in an anthropogenically polluted mangrove ecosystem, Wynnum, Brisbane, Australia. Journal of Coastal Research **13:** 1150-1158

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology **18:** 117-143

Clarke KR, Warwick RM (1994) Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Primer-E Ltd, Plymouth Marine Laboratory

Clarke PJ (2004) Effects of experimental canopy gaps on mangrove recruitment: lack of habitat partitioning may explain stand dominance. Journal of Ecology **92:** 203-213

Clarke PJ, Allaway WG (1993) The regeneration niche of the grey mangrove *Avicennia marina* - effects of salinity, light, and sediment factors on establishment, growth and survival in the field. Oecologia **93:** 548-556

Clarke PJ, Kerrigan RA (2002) The effects of seed predators on the recruitment of mangroves. Journal of Ecology **90:** 728-736

Clarke PJ, Kerrigan RA, Westphal CJ (2001) Dispersal potential and early growth in 14 tropical mangroves: do early life history traits correlate with patterns of adult distribution? Journal of Ecology **89:** 648-659

Clarke PJ, Myerscough PJ (1993) The intertidal distribution of the grey mangrove (Avicennia marina) in southeastern Australia: the effects of physical

conditions, interspecific competition, and predation on propagule establishment and survival. Australian Journal of Ecology **18:** 307-315

Clarke PJ, Ward TJ (1994) The response of southern hemisphere saltmarsh plants and gastropods to experimental contamination by petroleum. Journal of Experimental Marine Biology and Ecology **175:** 43-57

Clay RE, Andersen AN (1996) Ant fauna of a mangrove community in the Australian seasonal tropics, with particular reference to zonation. Australian Journal of Zoology **44:** 521-533

Clough BF, ed (1982) Mangrove ecosystems in Australia- Structure, function and management. Australian Institute of Marine Science

Clough BF (1992) Primary productivity and growth of mangrove forests. *In* AI Robertson, DM Alongi, eds, Tropical mangrove ecosystems. American Geophysical Union, Washington, DC, pp 225-249

Clough BF, Boto KG, Attiwill PM (1983) Mangroves and sewage: a re-evaluation. *In* HJ Teas, ed, Tasks for vegetation science, Vol 8. Dr W Junk Publishers, The Hague, pp 151-161

Cockcroft VG, Forbes AT (1981) Tidal activity rhythyms in the mangrove snail Cerithidea decollata (Linn.) Gastropoda, Prosobranchia: Cerithidae. South African Journal of Zoology **16:** 5-9

Cohen AN, Carlton JT (1998) Accelerating invasion rate in a highly invaded estuary. Science **279:** 555-558

Cole BJ (1983) Assembly of mangrove ant communities: colonization abilities. Journal of Animal Ecology **52:** 349-355

Cole BJ (1983) Assembly of mangrove ant communities: patterns of geographical distribution. Journal of Animal Ecology **52:** 339-347

Cole J, Woinarski JCZ (2002) Field guide to the rodents and Dasyurids of the Northern Territory. Surrey Beatty and Sons, Chipping Norton, NSW

Collette BB (1983) Mangrove fishes of New Guinea. *In* HJ Teas, ed, Biology and ecology of mangroves, Vol 8, The Hague, pp 91-102

Comley BWT (2002) Coastal mangrove wetland productivity and management, Darwin Harbour, Northern Territory, Australia. Master of Science (Research) thesis. Northern Territory University, Darwin, NT

Constable AJ, Fairweather PG (1999) Ecology of estuaries and soft-sediment habitats: Symposium introduction. Australian Journal of Ecology **24:** 289-290

Cosson J-F, Pons J-M, Masson D (1999) Effects of forest fragmentation on frugivorous and nectivorous bats in French Guiana. Journal of Tropical Ecology **15:** 515-534

Coupland GT (2002) Ecological interactions between insects and mangroves in Darwin Harbour, Australia. PhD. Northern Territory University, Darwin, NT

Craighead FC, Gilbert VC (1962) The effects of Hurricane Donna on the vegetation of southern Florida. Quarterly Journal Florida Academy of Science **25:** 1-28

Crowe TP (1997) The distribution of *Terebralia palustris* with respect to microhabitat in mangrove forests of Darwin Harbour**. I: Description of patterns**. *In* JR Hanley, G Caswell, D Megirian, HK Larson, eds, Proceedings of the Sixth International Marine Biological Workshop: the Marine Flora and Fauna of Darwin Harbour, Northern Australia. Northern Territory Museums and Art Gallery of the Northern Territory, Darwin, Darwin, NT, pp 425-433

Crowe TP, McMahon RF (1997) The distribution of *Terebralia palustris* with respect to microhabitat in mangrove forests of Darwin Harbour. **II: Experimental evaluation of behaviour**. *In* JR Hanley, G Caswell, D Megirian, HK Larson, eds, Proceedings of the Sixth International Marine Biological Workshop: The Marine Flora and Fauna of Darwin Harbour, Northern Australia. Museums and Art Galleries of the Northern Territory, Darwin, NT, pp 435-443

Dahdouh-Guebas F, Verneirt M, Tack JF, Van Speybroeck D, Koedam N (1998) Propagule predators in Kenyan mangroves and their possible effect on regeneration. Marine and Freshwater Research **49:** 345-350

Das P, Basak UC, Das AB (1997) Restoration of the mangrove vegetation in the Mahanadi delta, Orissa, India. Mangroves and Salt Marshes **1:** 155-161

Davie PJF (1982) A preliminary checklist of Brachyura (Crustacea: Decapoda) associated with Australian mangrove forests. Operculum **5:** 204-207

Davie PJF (1985) The biogeography of littoral crabs (Crustacea: Decapoda; Brachyura) associated with tidal wetlands in tropical and sub-tropical Australia. *In* KN Bardsley, JDS Davie, C Woodroffe, eds, Coasts and tidal wetlands of the Australian monsoon region. Mangrove Monograph No. 1. North Australia Research Unit, Australian National University, Darwin, Northern Territory

Davie PJF (1992) Revision of *Sarmatium* Dana (Crustacea:Brachyura: Sesarminae) with descriptions of three new species. Memoirs of the Queensland Museum **32:** 79-97

Davie PJF (1993) Grabbed by crabs. Australasian Science **Autumn issue:** 37-40

Davie PJF (1994) Revision of *Neosarmatium* Serene and Soh (Crustacea: Brachyura: Sesarminae) with descriptions of two new species). Memoirs of the Queensland Museum **35:** 35-74

Davie PJF (1994) Variations in diversity of mangrove crabs in tropical Australia. Memoirs of the Queensland Museum **36:** 55-58

Davis S (1985) Aboriginal knowlege and use of the coast and sea in northern Arnhem Land. *In* KN Bardsley, JDS Davie, C Woodroffe, eds, Coasts and tidal wetlands of the Australian monsoon region. Mangrove Monograph No. 1. North Australia Research Unit, the Australian National University, Darwin, Northern Territory, pp 297-312

de Oliveira MC (1998) Anabat system practical guide - survey techniques, collection and characterisation of reference bat echolocation calls, common field problems and problem solving. Department of Natural Resources, Queensland

Delgado P, Hensel PF, Jimenez JW, Day JW (2001) The importance of propagule establishment and physical factors in mangrove distributional patterns in a Costa Rican estuary. Aquatic Botany **71:** 157-178

Dernie K, Kaiser MJ, Richardson EA, Warwick RM (2003) Recovery of soft sedment communities and habitats following physical disturbance. Journal of Experimental Marine Biology and Ecology **285-286:** 415-434

Detwyler TR, Marcus MG (1972) Urbanization and environment. Duxbury Press, Belmont, California

Diaz H, Conde JE, Orihuela B (1992) Estimating the species number and cover of a mangrove root community: a comparison of methods. Australian Journal of Marine and Freshwater Research **43:** 707-715

Dicks B (1986) Oil and the Black Mangrove, *Avicennia marina* in the Northern Red Sea. Marine Pollution Bulletin **17:** 500-503

Diop S (2003) Vulnerability assessment of mangroves to environmental change. Estuarine, Coastal and Shelf Science **58:** 1-2

Dittmann S (2001) Abundance and distribution of small infauna in mangroves of Missionary Bay, North Queensland, Australia. Revista de Biología Tropical **49:** 535-544

Duke NC (2001) Gap creation and regenerative processes driving diversity and structure of mangrove ecosystems. Wetlands ecology and management **9:** 257-269

Duke NC (2006) Australia's Mangroves. University of Queensland and Norman C. Duke, Brisbane, Queensland, Australia

Duke NC, Ball MC, Ellison JC (1998) Factors influencing biodiversity and distributional gradients in mangroves. Global Ecology and Biogeography Letters **7:** 27-47

Duke NC, Pinzón ZS, Prada MC (1997) Large scale damage to mangrove forests following two large oil spills in Panama. Biotropica **29:** 2-14

Dwivedi SN, Padmakumar KG (1983) Ecology of a mangrove swamp near Juhu Beach, Bombay with reference to sewage pollution. *In* HJ Teas, ed, Tasks for vegetation science, Vol 8. Dr W Junk Publishers, The Hague, pp 163-170

EcoSystems (1993) Darwin South Stage 1 Environmental Studies: Flora - The Mangrove Community. Report for the NT Department of Transport and Works, Northern Territory Government, Darwin, NT, Darwin, NT

Edgar GJ (2000) Australian Marine LIfe. Plants and Animals of Temperate Waters. Reed New Holland, Sydney, Australia

Edwards A (1998) Rehabilitation of coastal ecosystems - Editorial. Marine Pollution Bulletin **37:** 371-372

Ellis J, Nicholls P, Craggs R, Hofstra D, Hewitt J (2004) Effects of terriginous sedimentation on mangrove physiology and associated macrobenthic communities. Marine Ecology Progress Series **207:** 71-82

Ellison AM (2000a) Restoration of mangrove ecosystems. Restoration Ecology **8:** 217-218

Ellison AM (2000b) Mangrove restoration: do we know enough? Restoration Ecology **3:** 219-229

Ellison AM, Farnsworth EJ (1993) Seedling survivorship, growth, and response to disturbance in Belizean mangal. American Journal of Botany **80:** 1137-1145

Ellison AM, Farnsworth EJ (1996) Anthropogenic disturbance of Caribbean mangrove ecosystems: past impacts, present trends and future predictions. Biotropica **28:** 549-565

Ellison JC (1995) Systematics and distributions of Pacific Island mangroves. *In* JE Maragos, MN Peterson, LG Eldredge, JE Bardach, H Takeuchi, eds, Marine and coastal biodiversity in the tropical island pacific region. Species systematics and information management priorities, Vol 1. Program on Environment, East-West Center, Hololulu, Hawaii

Ellison JC (1998) Impacts of sediment burial on mangroves. Marine Pollution Bulletin **37:** 420-426

Elster C, Perdomo L, Schnetter M (1999) Impact of ecological factors on the regeneration of mangroves in the Cienaga Grande de Santa Marta, Colombia. Hydrobiologia **413:** 35-46

Ewel KC, Zheng S, Pinzón ZS, Bourgeois JA (1988) Environmental effects of canopy gap formation in high rainfall mangrove swamps. Biotropica **30:** 510-518

Fairweather PG (1990) Ecological changes due to our use of the coast: research needs versus effort. Proceedings of the Ecological Society of Australia **16:** 71-77

FAO (2003) New global mangrove estimate. *In*. Food and Agricultural Organisation website. http://www.fao.org/forestry/foris/webview/forestry2/index.

Faraco LFD, Lana PdC (2003) Response of polychaetes to oil spills in natural and defaunated subtropical mangrove sediments fro Paranagua bay (SE Brazil). Hydrobiologia **496:** 321-328

Farnsworth EJ (1998) Issues of spatial, taxonomic and temporal scale in delineating links between mangrove diversity and ecosystem function. Global Ecology and Biogeography Letters **7:** 15-25

Fauchald K, Jumars PA (1979) The diet of worms: A study of polychaete feeding guilds. Oceanography and Marine Biology Annual Review **17:** 193-284

Fensham RJ, Woinarski JCZ (1992) Yawulama: the ecology and conservation of monsoon forest on the Tiwi Islands, Northern Territory. Report to DASET. Conservation Commission of the Northern Territory, Darwin

Fenton MB (1982) Echolocation calls and patterns of hunting and habitat use of bats (Microchiroptera) from Chillagoe, North Queensland. Australian Journal of Zoology **30:** 417-425

Ferwerda JG (2000) Regeneration of mangroves in the Northern Territory, Australia. Master of Science thesis. Tropical Nature Conservation and Vetebrate Ecology Group, Wageningen University, Wageningen, the Netherlands

Field C, ed (1996) Restoration of mangrove ecosystems. International Society for Mangrove Ecosystems/ITTO, Okinawa, Japan

Field C (1998a) Rehabilitation of mangrove ecosystems: an overview. Marine Pollution Bulletin **37:** 383-392

Field C (1998b) Rationales and practices of mangrove afforestation. Marine and Freshwater Research **49:** 353-358

Field C, Osborn JG, Hoffman LL, Polsenberg JF, Ackerly DD, Berry DA, Bjorkman O, Held Z, Matson PA, Mooney HA (1998) Mangrove biodiversity and ecosystem function. Global Ecology and Biogeography Letters **7:** 3-14

Field CD (1999) Mangrove rehabilitation: choice and necessity. Hydrobiologia **413:** 47-52

Field GD (1968) The utilization of mangroves by birds on the Freetown Peninsula, Sierra Leone. Ibis **110:** 354-357

Fisher A (2001) Biogeography and conservation of Mitchell grasslands in northern Australia. PhD. Northern Territory University, Darwin, Northern Territory, Australia

Fisher A, Woinarski JCZ (2002) Assessment of the vertebrate fauna of the Bradshaw (Juliki) field training area, Northern Territory. *In*. Department of Infrastructure Planning and Environment, Darwin

Ford J (1982) Origin, evolution and speciation of birds specialized to mangroves in Australia. Emu **82:** 12-23

Franklin DC, Noske RA (1988) Local movements of honeyeaters in a sub-coastal vegetation mosaic in the Northern Territory. Corella **22:** 97-103

Franklin DC, Noske RA (2000) Nectar sources used by birds in monsoonal north-western Australia: a regional survey. Australian Journal of Botany **48:** 461-474

Franklin DC, Noske RA (2000) The nesting biology of the brown honeyeater *Lichmera indistincta* in the Darwin region of northern Australia, with notes on tidal flooding of nests. Corella **24:** 38-44

French RP (1966) The utilization of mangroves by birds in Trinidad. Ibis **108:** 423-424

Friend GR, Braithwaite RW (1986) Bat fauna of Kakadu National Park, Northern Territory. Australian Mammalogy **9:** 43-52

Frith DW, Brunenmeister S (1980) Ecological and population studies of fiddler crabs (Ocypodidae, genus Uca) on a mangrove shore at Phuket Island, western peninsular Thailand. Crustaeana **39:** 157-183

Frith DW, Frith CB (1982) An invaluable ecosystem- the mangroves. Hemisphere **27:** 8-13

Frith DW, Tantanasiriwong R, Bhatia O (1976) Zonation of macrofauna on a mangrove shore, Phuket Island. Phuket marine biological center, Research Bulletin **No. 10:** 1-37

Frusher SD, Giddins RL, Smith III TJ (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 RW (1982) Distribution and physiographic patterns of Australian mangroves. *In* BF Clough, ed, Mangrove ecosystems in Australia. Structure, function and management. Australian Institute of Marine Science, Canberra, Australia, pp 31-54

Gautier D, Amador J, Newmark F (2001) The use of mangrove wetland as a biofilter to treat shrimp pond effluents: preliminary results of an experiment on the Caribbean coast of Colombia. Aquaculture Research **32:** 787-799

Getter CD, Ballou TG, Koons CB (1985) Effects of dispersed oil on mangroves. Synthesis of a seven-year study. Marine Pollution Bulletin **16:** 318-324

Gibbs PE (1971) The polychaete fauna of the Solomon Islands. Bulletin of the British Museum of Natural History (Zoology) **21:** 101-211

Gilham MP (1980) Notes on Molluscs in the Mangroves. Certificate of Environmental Biology. Darwin Community College

Gill AM, Tomlinson PB (1971) Studies on the growth of red mangrove (*Rhizophora mangle L.*) 3. Phenology of the shoot. Biotropica **3:** 109-124

Glasby CJ, Hutchings PA, Fauchald K, Paxton H, Rouse GW, Watston Russell C, Wilson RS (2000) Class Polychaeta. *In* PL Beesley, GJB Ross, CJ Glasby, eds, Polychaetes and Allies: The Southern Synthesis. Fauna of Australia. Vol. 4A. Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. CSIRO Publishing, Melbourne, pp 1-296

Gleason SM, Ewel KC (2002) Organic matter dynamics on the forest floor of a micronesian mangrove forest: an investigation of species composition. Biotropica **34:** 190-198

Golley FB, Odum HT, Wilson R (1962) A synoptic study of the structure and metabolism of a red mangrove forest in southern Puerto Rico in May. Ecology **43:** 9-18

Gopal B, Junk WJ (2000) Biodiversity in wetlands: an introduction. *In* B Gopal, WJ Junk, J A, eds, Biodiversity in wetlands: assessment, function and conservation, Vol 1. Bakhuys Publishers, Leiden, pp vii-x

Gordon DM (1987) Disturbance to mangroves in tropical-arid Western Australia. *In*. Environmental Protection Authority, Technical Series No. 12. Centre for water research and botany department, University of Western Australia, Perth, WA, pp 1-35

Gore R (1977) Wild Nursery of the Mangroves. National Geographic Magazine, May 1977**:** 668-689

Grall J, Glémarec M (1997) Using biotic indices to estimate macrobenthic community perturbations in the Bay of Brest. Estuarine, Coastal and Shelf Science **44:** 43-53

Grant DL, Clarke PJ, Allaway WG (1993) The response of grey mangrove (*Avicennia marina*) (Forsk.) Vierh. seedlings to spills of crude oil. Journal of Experimental Marine Biology and Ecology **171:** 273-295

Guinea M (1987) Rapid Creek mangrove regeneration, thirteen years onwards. *In* HK Larson, MG Michie, JR Hanley, eds, Proceedings of a conference on research and managment in Darwin Harbour held 2-3 September, 1987, Vol Mangrove Monograph No. 4. North Australia Research Unit, the Australian National University, Darwin, NT, pp 208-213

Hall JA, Frid CLJ (1997) Estuarine sediment remediation: effects on benthic biodiversity. Estuarine, Coastal and Shelf Science **44:** 53-61

Hall L, Richards G (2000) Flying foxes. Fruit and blossom bats of Australia. UNSW Press, Sydney, NSW

Halliday IA, Young WR (1996) Density, biomass and species composition of fish in a subtropical *Rhizophora sylosa* mangrove forest. Marine and Freshwater Research **47:** 607-615

Hanley JR (1985) Why are there so few Polychaetes (Annelida) in northern Australian mangroves? *In* KN Bardsley, JDS Davie, CD Woodroffe, eds, Coasts and Tidal Wetlands of the Australian Monsoon Region. Mangrove Monograph No. 1. North Australia Research Unit, Australian National University, Darwin, NT, pp 239-250

Hanley JR (1987) Invertebrate fauna of marine habitats in Darwin Harbour. *In* HK Larson, MG Michie, JR Hanley, eds, Workshop on research and management. North Australia Research Unit, Australian National University, Darwin, pp 135-152

Hanley JR (1993) Darwin South Stage 1 Environmental Studies. Mangrove Invertebrate Fauna. Report to the Northern Territory Department of Transport and Works, Darwin, NT

Hanley JR, Couriel D (1992) Discharge of sewage effluent into mangroves at Darwin, NT: is there an impact on the benthic fauna? *In*. Consultancy brief Ref No. 46/4/151 for Power and Water Authority, Darwin, Darwin, Northern Territory

Harbison P (1981) The case for protection of mangrove swamps: geochemical considerations. Search **12:** 273-276

Hatcher BG, Johannes RE, Robertson AI (1989) Review of research relevant to the conservation of shallow tropical marine ecosystems. Oceanography and Marine Biology Annual Review **27:** 337-414

Haverschmidt F (1965) The utilization of mangroves by South American birds. Ibis **107:** 540-542

Healy JM, Wells FE (1998) Superfamily Cerithioidea. *In* BP L, GJB Ross, AE Wells, eds, Mollusca: The Southern Synthesis. Fauna of Australia,, Vol 5, Part B, viii + 565-1234 pp. CSIRO Publishing, Melbourne, pp 707-733

Hegerl EJ, Claridge GF, Davie PJF, Outridge PM, Shanco P, Stock EC (1982) The Kakadu National Park mangrove forests and tidal marshes: Volume 4, preliminary results of field studies. *In*. Australian Littoral Society, Brisbane, p 32

Hegerl EJ, Davie JDS (1977) The mangrove forests of Cairns, Northern Australia. Marine Research in Indonesia **18:** 23-57

Hegerl EJ, Davie JDS, Davie PJF, Outridge PM, Shanco P, Stock EC, Claridge GF (1981) The Kakadu National Park mangrove forests and tidal marshes: Volume 3, the research program for the tidal wetlands survey. Australian Littoral Society, Brisbane

Hegerl EJ, Davie PJF, Claridge GF, Elliot AG (1979) The Kakadu National Park mangrove forests and tidal marshes: Volume 1, a review of the literature and results of a field reconnaissance. Australian Littoral Society, Brisbane

Hensel P, Proffitt CE (2003) Hurricane Mitch: acute impacts on mangrove forest structure and an evaluation of recovery trajectories. USGS Open File Report. 77pp,

Hernandez-Alcantara P, Solis-Weiss V (1991) Ecological aspects of the polychaete populations associated with the Red Mangrove *Rhizophora mangle* at Laguna de Terminos, southern part of the Gulf of Mexico. Ophelia Supplement **5:** 463-466

Hogarth PJ (1999) The Biology of Mangroves. Oxford University Press, North Yorkshire

Holguin G, gonzalez-Zamorano P, de-Bashan LE, Mendoza R, Amador E, Bashan Y (2005) Mangrove health in an arid environment encroached by urban development-a case study. Science of the Total Environment **in press**

Holl KD, Howarth RB (2000) Paying for restoration. Restoration Ecology **8:** 260-167

Houbrick RS (1991) Systematic review and functional morphology of the mangrove snails *Terebralia* and *Telescopium.* Malacologia **33:** 289-338

Hsieh HL (1995) Spatial and temporal patterns of polychaete communties in a subtropical mangrove swamp - influences of sediment and microhabitat. Marine Ecology Progress Series **127:** 157-167

Hutchings P (1997) The Terebellidae (Polychaeta) of northern Australia with a key to all the described species of the region. *In* JR Hanley, G Caswell, D Megirian, HK Larson, eds, Proceedings of the Sixth International Marine Biological Workshop: The Marine Flora and Fauna of Darwin Harbour, Northern Australia. Museums and Art Galleries of the Northern Territory, Darwin, NT, pp 133-161

Hutchings P (1999) Taxonomy of estuarine invertebrates in Australia. Australian Journal of Ecology **24:** 381-394

Hutchings P, Recher HF (1974) The fauna of Careel Bay with comments on the ecology of mangrove and sea-grass communities. Australian Zoologist **18:** 99-128

Hutchings P, Recher HF (1982) The fauna of Australian mangroves. Proceedings of the Linnaean Society of New South Wales **106:** 83-121

Hutchings P, Recher HF (1983) The faunal communities of Australian mangroves. *In* HJ Teas, ed, Biology and ecology of mangroves, Vol 8. Dr W Junk, The Hague, pp 103-110

Hutchings P, Saenger P (1987) Ecology of Mangroves. University of Queensland Press, Brisbane, Queensland

Hutchings PA, Pickard J, Recher HF, Weate PB (1977) A survey of mangroves at Brooklyn, Hawksbury River, NSW. Operculum**:** 105-112

Icely JD, Jones DA (1977) Factors affecting the distribution of the genus *Uca* (Crustacea: Ocypodidae) on an East African Shore. Estuarine, Coastal and Shelf Science **6:** 315-325

Imbert D, Rousteau A, Scherrer P (2000) Ecology of mangrove growth and recovery in the Lesser Antilles: state of knowledge and basis for restoration projects. Restoration Ecology **8:** 230-236

James RJ, Lincoln-Smith MP, Fairweather PG (1995) Sieve mesh size and taxonomic resolution needed to describe natural spatial variation of marine macrofauna. Marine Ecology Progress Series **118:** 187-198

Jernelov A, Linden O (1983) The effects of oil pollution on mangroves and fisheries in Ecuador and Colombia. *In* HJ Teas, ed, Tasks for Vegetation Science, Vol Chapter 20. Dr W Junk, The Hague, Amsterdam, pp 185-188

Johnson RR, Brown BT, Haight LT, Simpson JM (1981) Playback recordings as a special avian censusing technique. *In* JC Ralph, MJ Scott, eds, Estimating numbers of terrestrial birds. Allen Press Inc, Kansas, pp 68-75

Johnstone RE (1990) Mangroves and mangrove birds of Western Australia, Vol Supplement No. 32. Western Australian Museum, Perth, Western Australia

Jones A (1988) In praise of mud. Australian Natural History **22:** 323-327

Jones B (1972) Mangroves. Wildlife **9:** 12-15

Jones DA (1984) Crabs of the mangal ecosystem. *In* FD Por, I Dor, eds, Hydrobiology of the Mangal. W Junk Publishers, The Hague, pp 89-109

Jones DS, Morgan GJ (2002) A field guide to Crustaceans of Australian waters. Reed New Holland, Sydney, Australia

Jones MB (1975) Synergistic effects of salinity, temperature and heavy metals on mortality and osmoregulation in marine and estuarine Isopods (Crustacea). Marine Biology **30:** 13-20

Kairo JG, Dahdouh-Guebas F, Bosire J, Koedam N (2001) Restoration and management of mangrove ecosystems - a lesson for and from the East African region. South African Journal of Botany **67:** 383-389

Kaly UL, Eugelink G, Roberston AI (1997) Soil conditions in damaged north Queensland mangroves. Estuaries **20:** 291-300

Kaly UL, Jones GP (1998) Mangrove restoration: A potential tool for coastal management in tropical developing countries. Ambio **27:** 656-661

Kathiresan K, Bingham BL (2001) Biology of mangroves and mangrove ecosystems. Advances in Marine Biology **40:** 81-251

Kerle JA (1985) Habitat preference and diet of the northern brushtail possum *Trichosurus arnhemensis* in the Alligator Rivers region, NT. Proceedings of the Ecological Society of Australia **13:** 161-176

Kerle JA (1998) The population dynamics of a tropical possum, *Trichosurus vulpecula arnhemensis* Collett. Wildlife Research **25:** 171-181

Kerle JA (2001) Possums. The brushtails, ringtails and greater glider. UNSW Press, Sydney, Australia

Kogo M, Kamimura D, Miyagi T (1987) Research for rehabilitation/reforestation of mangroves in Truk Islands. In Mangroves of Asia and the Pacific: status and management. Technical report of the UNDP/UNESCO Research and Training Pilot Programme on Mangrove Ecosystems in Asia and the Pacific (RAS/79/002). *In*. UNESCO, Quezon City, Phillipines, pp 419-439

Komiyama A, Santiean T, Higo M, Patanaponpaiboon P, Kongsangchai J, Ogino K (1996) Microtopograpy, soil hardness and survival of mangrove (Rhizophora apiculata) seedlings planted in an abandoned tin-mining area. Forest Ecology and Management **81:** 243-248

Kristensen E (2006) Mangrove crabs as potential ecosystem engineers; with emphasis on sediment processes. *In* JSY Lee, NC Duke, R Connolly, PJF Davie, T Meziane, G Skilleter, S Dittman, D Burrows, eds, Mangrove Macrobenthos Meeting II, Conference Program. Abstract only., Cold Coast, Queensland, p 36

Kumar RS (1995) Macrobenthos in the mangrove ecosystem of Cochin backwaters, Kerala (southwest coast of India). Indian Journal of Marine Science **24:** 56-61

Kumar RS (2003) A checklist of polychaete species from some mangroves of Asia. Zoos' Print Journal **18:** 1017-1020

Kunstadter P, Bird ECF, Sabhasri S, eds (1985) Man in the mangroves. The Socio-economic situation of human settlements in mangrove forests. Proceedings of a workshop held at Nong Nuch Village, Pattaya, Thailand, 27-31 May 1985. The United Nations University

Kurian CV (1984) Fauna of the mangrove swamps in Cochin estuary. *In* E Sepadmo, AN Rao, DJ Macintosh, eds, Proceedings of the Asian Symposium on Mangrove Environments: Research and Management. University of Malaya and UNESCO, Kuala Lumpur, pp 226-230

Lacerda LD, ed (2001) Mangrove Ecosystems. Function and management. Springer, Berlin

Lacerda LD, Conde JE, Kjerfve B, Alvarez-Leon R, Alarcaon C, Polania J (2001) American mangroves. *In* LD de Lacerda, ed, Mangrove Ecosystems. Function and management. Springer, Berlin, p 292

Laegdsgaard P, Johnston C (2001) Why do juvenile fish utilise mangrove habitats? Journal of Experimental Marine Biology and Ecology **257:** 229-253

Laegsdsgaard P, Johnston CR (1995) Mangrove habitats as nurseries: unique assemblages of juvenile fish in subtropical mangroves in eastern Australia. Marine Ecology Progress Series **126:** 67-81

Larson HK (1987) The fishes of Darwin Harbour. *In* HK Larson, MG Michie, JR Hanley, eds, Proceedings of a workshop on research and management held in Darwin 2-3 September 1987. North Australia Research Unit, the Australian National University, Darwin, NT, pp 153-164

Larson HK (1988) Proceedings of a workshop on research and management held in Darwin, 2-3 September 1987. *In* HK Larson, MG Michie, JR Hanley, eds,

Mangrove Monograph, Vol No. 4. Australian National University, North Australia Research Unit, Darwin, p 1

Leach GJ, Burgin S (1985) Litter production and seasonality of mangroves in Papua New Guinea. Aquatic botany **23:** 215-224

Lee SY (1989) The importance of sesarminae crabs *Chiromanthes* spp. and inundation frequency on mangrove (*Kandelia candel (*L.) Druce) leaf litter turnover in a Hong Kong tidal shrimp pond. Journal of Experimental Marine Biology and Ecology **131:** 23-43

Lee SY (1997) Potential trophic importance of the faecal material of the mangrove sesarmine crab *Sesarma messa*. Marine Ecology Progress Series **159:** 275-284

Lee SY (1998) Ecological role of grapsid crabs in mangrove ecosystems: a review. Marine and Freshwater Research **49:** 335-343

Lee SY (1999) Tropical mangrove ecology: Physical and biotic factors influencing ecosystem structure and function. Australian Journal of Ecology **24:** 355-366

Lefebvre G, Poulin B (2000) Determinants of avian diversity in neotropical mangrove forests. *In* B Gopal, WJ Junk, JA Davis, eds, Biodiversity in wetlands: assessment, function and conservation, Vol 1. Backhuys, Leiden, pp 161-180

Lewis RR (1982) Mangrove forests. *In* RR Lewis, ed, Creation and restoration of coastal plant communities. CRC Press, Boca Raton, Florida, pp 153-171

Lewis RR (1983) Impact of oil spills on mangrove forests. *In* HJ Teas, ed, Tasks for vegetation science, Vol 8. Dr W Junk Publishers, The Hague, Amsterdam, pp 171-183

Lewis RR (1990) Creation and restoration of coastal plain wetlands in Florida. *In* JA Kusler, ME Kentula eds, Wetland Creation and Restoration : Status of the Science, Washington, DC, pp 73-101

Lewis RR (2005) Ecological engineering for successful management and restorations of mangrove forests. Ecological Engineering **24:** 403-418

Lewis RR, Clark PA, Fehring WK, Greening HS, Johansson RO, Paul RT (1999) The rehabilitation of the Tampa Bay estuary, Florida, USA, as an example of successful integrated coastal management. Marine Pollution Bulletin **37:** 468-473

Lewis RR, Streever B (2000) Restoration of mangrove habitat. *In*. US Army Engineer Research and Development Centre, Vicksburg, MS, p 6p

Lim HC, Navjot SS (2004) Responses of avian guilds to urbanisation in a tropical city. Landscape and Urban Planning **66:** 199-215

Limpus CJ (1998) Overview of marine turtle conservation and management in Australia. *In* R Kennett, A Webb, G Duff, M Guinea, G Hill, eds, Marine turtle conservation and management in Northern Australia. Northern Territory University, Darwin, pp 1-8

Limpus CJ, Limpus DJ (2000) Mangroves in the diet of *Chelonia mydas* in Queensland, Australia. Marine Turtle Newsletter**:** 13-14

Lindegarth M, Hoskin M (2001) Patterns of distribution of macro-fauna in different types of estuarine, soft sediment habitats adjacent to urban and non-urban areas. Estuarine, Coastal and Shelf Science **52:** 237-247

Loughland RA (1988) Mangal roost selection by the flying-fox *Pteropus alecto* (Megachiroptera: Pteropodidae). Marine and Freshwater Research **49:** 351-352

Lugo AE, Snedaker SC (1974) The ecology of mangroves. Annual Review of Ecology and Systematics **5:** 39-64

Lugo AL (1997) Old-growth mangrove forests in the US. Conservation Biology **11:** 11-20

Luoma SN (1990) Processes affecting metal concentrations in estuarine and coastal marine sediments. *In* RW Furness, PS Rainbow, eds, Heavy metals in the marine environment. CRC Press, Inc, Boca Raton, Florida, pp 51-66

Machiwa JF, Hallberg RO (1995) Flora and crabs in a mangrove forest partly distorted by human activities. Ambio **24:** 492-496

Macintosh DJ (1984) Ecology and productivity of Malaysian mangrove crab populations (Decapoda: Brachyura). *In* E Soepadmo, AN Rao, DJ Macintosh, eds, Vol Proceedings of the Asian Symposium on Mangrove Environments: Research and Management. University of Malaysia and UNESCO, Kuala Lumpur, pp 226-230

Macintosh DJ, Ashton EC, Havanond S (2002) Mangrove rehabilitation and intertidal biodiversity: a study in the Ranong mangrove ecosystem, Thailand. Estuarine, Coastal and Shelf Science **55:** 331-345

Mackey AP, Hodgkinson MC (1995) Concentrations and spatial distribution of trace metals in mangrove sediments from the Brisbane River, Australia. Environmental Pollution **90:** 181-186

Macnae W (1963) Mangrove swamps in South Africa. Journal of Ecology **51:** 1-25

Macnae W (1967) Zonation within mangroves associated with estuaries in North Queensland. Estuaries**?:** 432-441

Macnae W (1968a) Mangroves and their fauna. Australian Natural History **16**

Macnae W (1968b) A general account of the fauna and flora of mangrove swamps and forests in the Indo-West Pacific region. Advances in Marine Biology **6:** 73-270

Macnae W, Kalk M (1962) The ecology of the mangrove swamps at Inhaca Island, Mocambique. Journal of Ecology **50:** 19-34

Marion WR, O'Meara TE, Maehr DS (1981) Use of playback recordings in sampling elusive or secretive birds. *In* JC Ralph, MJ Scott, eds, Estimating numbers of terrestrial birds. Allen Press Inc, Kansas, pp 68-75

Martin J (2004) Use of mangroves and their resources by fish in Darwin Harbour. PhD thesis. Faculty of Education, Heath and Science, Charles Darwin University, Darwin, Australia

Masden T, Shine R (1999) Rainfall and rats: Climatically -driven dynamics of a tropical rodent population. Australian Journal of Ecology **24:** 80-89

Massel, al e (1999) Surface wave propagation in mangrove forests. Fluid dynamics research **24:** 219-249

Mazda Y, Magi M, Kogo M, Hong PN (1997) Mangroves as coastal protection from waves in the Tong King delta, Vietnam. Mangroves and Salt Marshes **1:** 127-135

McDonnell MJ, Pickett ST (1990) Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. Ecology **71:** 1232-1237

McGuinness KA (1988) Explaining patterns in abundance of organisms on boulders: the failure of 'natural experiments'. Marine Ecology Progress Series **48:** 199-204

McGuinness KA (1990) Effects of oil spills on macro-invertebrates in mangroves and saltmarshes of Botany Bay, NSW, Australia. Journal of Experimental Marine Biology and Ecology **142:** 121-135

McGuinness KA (1992) Disturbance and the mangrove forests of Darwin Harbour. *In* I Moffatt, A Webb, eds, Conservation and Development Issues in North Australia. North Australia Research Unit, Australian National University, Darwin, pp 55-62

McGuinness KA (1993) Pilot study of mangrove crabs to use in future downstream monitoring. *In*. Faculty of Science, Northern Territory University, Darwin, p 15

McGuinness KA (1994) The climbing behaviour of *Cerithidea anticipata* (Mollusca: Gastropoda): the role of physical versus biological factors. Australian Journal of Ecology **19:** 283-289

McGuinness KA (1997) Dispersal, establishment and survival of *Ceriops tagal* propagules in a north Australian mangrove forest. Oecologia **109:** 80-87

McGuinness KA (1997a) Dispersal, establishment and survival of *Ceriops tagal* propagules in a north Australian mangrove forest. Oecologia **109:** 80-87

McGuinness KA (1997b) Tests for artefacts in some methods used to study herbivory and predation in mangrove forests. Marine Ecology- Progress Series **153:** 37-44

McGuinness KA (1997c) Seed predation in a tropical mangrove forest: a test of the dominance-predation model in northern Australia. Journal of Tropical Ecology **13:** 293-302

McGuinness KA (2002a) The mangrove forests of Darwin Harbour: a review of research on the flora and invertebrate fauna. Unpublished paper presented at the Australian Marine Sciences Association conference in Darwin, November 2002,

McGuinness KA (2002b) Of rowing boats, ocean liners and tests of the ANOVA homogeneity of variance assumption. Austral Ecology **27:** 681-688

McIvor CC, Smith III TJ (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

McKean J (1979) Flying foxes and bats of the Darwin area.

McKee KL (1993) Soil physicochemical patterns and mangrove species distribution - Reciprocal effects? Journal of Ecology **81:** 477-487

McKee KL (1995a) Mangrove species distribution and propagule predation in Belize: an exception to the dominance-predation hypothesis. Biotropica **27:** 334-345

McKee KL (1995c) Seedling recruitment patterns in a Belizean mangrove forest: effects of establishment ability and physico-chemical factors. Oecologia **101:** 448-460

McKee KL, Faulkner PL (2000) Restoration of biogeochemical function in mangrove forests. Restoration Ecology **8:** 247-259

McKenzie NL, Rolfe JK (1986) Structure of bat guilds in the Kimberley mangroves, Australia. Journal of Animal Ecology **55:** 401-420

McKenzie NL, Start AN (1989) Structure of bat guilds in mangroves: environmental disturbances and determinism. *In* DW Morris, Z Abramsky, BJ Fox, MR Willig, eds, Patterns in the structure of mammalian communities. Spec. Publ. Mus., Tech. Univ., No. 28, Lubbock, pp 167-178

Menkhorst KA, Woinarski JCZ (1992) Distribution of mammals in monsoon rainforests of the Northern Territory. Wildlife Research **19:** 295-316

Metcalfe K (1999) Mangrove litter production, Darwin Harbour. A study of litter fall as a measure of primary productivity in the mangrove communities of Darwin Harbour. Master of Tropical Environmental Management thesis. Northern Territory University, Darwin, Australia

Metcalfe K (2004a) Mangrove Invertebrate Fauna. Darwin LNG Project Environmental Monitoring Program. Report 3 in Annual report to URS (Australia). Prepared for ConocoPhillips and URS Australia Pty Ltd, July 2004, Darwin, NT

Metcalfe K (2004b) APPL (Aussie Prawns Project) Environmental Impact Assessment - Intertidal Flora & Fauna. Pre-construction Mangrove Monitoring- Report No. 1. Report prepared for KBR and Tiger International, November 2004

Metcalfe K (2004c) Blacktip Environmental Impact Statement - Intertidal Survey. *In*, pp 1-15

Metcalfe K (2005) Mangrove Invertebrate Fauna. Darwin LNG Project- Mangrove Monitoring Program. Annual Report 2004-2005. 94pp. Prepared for ConocoPhillips and URS Australia, November 2005

Metcalfe K (unpublished report) Variation in the response of *Rhizophora stylosa* forests to cyclone disturbance. Ecological report, Northern Territory University. June,1997, Darwin, NT

Metcalfe KN, Glasby CJ (submitted) Diversity, distribution and abundance of polychaetes and other worm taxa in the mangroves of Darwin Harbour mangroves. Journal of Sea Research

Miles G (2000) Kakadu Wildlife. Australian World Heritage - Kakadu National Park. Barker Souvenirs, Alice Springs, NT

Milne DJ (2002) Key to the Bat Calls of the Top End of the Northern Territory. Technical Report No. 71. Parks and Wildlife Commission of the Northern Territory, Darwin, NT

Milne DJ, Armstrong M, Fisher A, Flores T, Pavey CR (2005) Structure and environmental relationships of insectivorous bat assemblages in tropical Australian savannas. Austral Ecology **30:** 906-919

Milward NE (1982) Mangrove-dependent biota. *In* BF Clough, ed, Mangrove ecosystems in Australia. Australian Institute Marine Science, Canberra, Australia, pp 121-140

Minchinton TE (2001) Canopy and substratum heterogeneity influence recruitment of the mangrove Avicennia marina. Journal of Ecology **89:** 888-902

Morissey DJ, Skilleter GA, Ellis JI, Burns BR, Kemp DE, Burt K (2003) Differences in benthic fauna and sediment among mangrove (*Avicennia marina* var. *australasica*) stands of different ages in New Zealand. Estuarine, Coastal and Shelf Science **56:** 581-592

Morissey DJ, Underwood AJ, Howitt L (1996) Effects of copper on the faunas of marine soft-sediments: an experimental field study. Marine Biology **125:** 199-213

Moritz-Zimmerman A (1997) Impact of urban stormwater drainage channels on the mangrove Ceriops tagal in northern Australia: effects on soils, vegetation and seedlings. Unpublished Thesis, Technical University Darmstadt.

Moritz-Zimmerman A, Comley BWT, Lewis D (2002) Darwin Harbour mangrove monitoring methodology technical manual. Land Monitoring Series No. 3. Report No. 25/2002. Department of Infrastucture, Planning and Environment

Morton (1990) Community structure, density and standing crop of fishes in a subtropical Australian mangrove area. Marine Biology **105:** 385-394

Morton RM (1989) Hydrology and fish fauna of canal developments in an intensively modified Australian estuary. Estuarine, Coastal and Shelf Science **28:** 43-58

Morton SR, Brennan KG (1991) Birds. *In* CD Haynes, MG Ridpath, MAJ Williams, eds, Monsoonal Australia: Landscape ecology and man in the northern lowlands. AA Balkema, Rotterdam, pp 133-149

Murdy EO (1989) A taxonomic revision and cladistic analysis of the Oxudercine Gobies (Gobiidae: Oxudercinae). Records of the Australian Museum **Supplement 11**

Naeem S, Chapin III FS, Costanza R, Ehrlich PR, Golley FB, Hooper DU, Lawton RV, O'Neill RV, Mooney HA, Sala OE, Symsta AJ, Tilman D (1999) Biodiversity and ecosystem functioning: maintaining life support processes. Issues in Ecology No. 4

Naeem S, Thompson LJ, Lawler SP, Lawton JH, Woodfin RM (1994) Declining biodiversity can alter the performance of ecosystems. Nature **368:** 734-737

Nandi S, Choudhury A (1983) Quantitative studies on benthic macrofauna of Sagar Island, intertidal zones, Sunderbans, India. Mahasagar-Bulletin of the National Institute of Oceanography **16:** 409-414

Newell RC, Seiderer LJ, Hitchcock DR (1998) The impact of dredging works in coastal waters: a review of the sensitivity to disturbance and subsequent recovery of biological resources on the sea bed. Oceanography and Marine Biology Annual Review **36:** 127-178

Nielsen MG (1997a) Nesting biology of the mangrove mud-nesting ant *Polyrachis sokolova* Forel (Hymenoptera, Formicidae) in northern Australia. Insectes Sociaux **44:** 15-21

Nielsen MG (1997b) Two Specialised Ant species, *Crematogaster* (*australis* Mayr group) sp. and *Polyrachis sokolova* Forel in Darwin Harbour Mangroves. Northern Territory Naturalist **15:** 1-5

Nielsen MG (2000) Distribution of the ant (Hymenoptera:Formicidae) fauna in the canopy of the mangrove tree *Sonneratia alba* J.Smith in northern Australia. Australian Journal of Entomology **39:** 275-279

Noakes DSP (1955) Methods of increasing growth and obtaining natural regeneration of the mangrove type in Malaya. Malaysian Forester **8:** 23-30

Nobbs M (1999) The behavioural ecology of fiddler crabs (Genus: *Uca*) that live in the mangrove forests of Darwin Harbour. PhD thesis. Northern Territory University, Darwin, NT

Nobbs M, McGuinness KA (1999) Developing methods for quantifying the apparent abundance of fiddler crabs (Ocypodidae: Uca) in mangrove habitats. Australian Journal of Ecology **23:** 43-49

Nobbs M, McGuinness KA (2003) The effect of vegetation on the distribution of fiddler crabs in mangrove habitats in Northern Australia. *Journal of Experimental Marine Biology and Ecology*

Nordhaus I (2006) The trophic role of the mangrove crab *Ucides coratus* in a high intertidal mangrove forest in northern Brazil. *In* JSY Lee, NC Duke, R Connolly, PJF Davie, T Meziane, G Skilleter, S Dittman, D Burrows, eds, Mangrove Macrobenthos Meeting II, Conference Program. Abstract only., Cold Coast, Queensland, p 37

Noske RA (1995) The ecology of mangrove forest birds in Peninsular Malaysia. Ibis **137:** 250-263

Noske RA (1996) Abundance, zonation and foraging ecology of birds in mangroves of Darwin Harbour, Northern Territory. Wildlife Research **23:** 443-474

Noske RA (2001) The breeding biology of the Mangrove Gerygone, *Gerygone laevigaster,* in the Darwin region, with notes on brood parasitism by the Little Bronze-cuckoo, *Chrysococcyx minutillus*. Emu **101:** 129-135

Noske RA (2003) The role of birds in mangroves: pollination and insect predation. *In* The Darwin Harbour Public Presentations - February 2003. Darwin Harbour Regional Plan of Management, Darwin, NT

Odum WE, Heald EJ (1972) Trophic analysis of an estuarine mangrove community. Bulletin of Marine Science **22:** 671-738

O'Grady AP, McGuinness KA, Eamus D (1996) The abundance and growth of *Avicennia marina* and *Rhizophora stylosa* in the low shore zone of Darwin Harbour, Northern Territory. Australian Journal of Ecology **21:** 272-279

Ong J-E (1995) The ecology of mangrove conservation and management. Hydrobiologia **295:** 343-351

Osborne K, Smith III TJ (1990) Differential predation on mangrove propagules in open and closed canopy forest habitats. Vegetatio **89:** 1-6

Othman MA (1994) Value of mangroves in coastal protection. Hydrobiologia **285:** 277-282

Pagliosa PR (2005) Another diet of worms: the applicability of polychaete feeding guilds as a useful conceptual framework and biological variable. Marine Ecology **26:** 246-254

Paine RT, Levin SA (1981) Intertidal landscapes: disturbance and the dynamics of pattern. Ecological Monographs **5:** 145-178

Palmer C, Price O, Bach C (2000) Foraging ecology of the black flying fox (*Pteropus alecto*) in the seasonal tropics of the Northern Territory, Australia. Wildlife Research **27:** 169-178

Palmer C, Woinarski JCZ (1999) Seasonal roosts and foraging movements of the black flying fox *(Pteropus alecto)* in the Northern Territory: resource tracking in a landscape mosaic. Wildlife Research **26:** 823-838

Pearson TH, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology Annual Review **16:** 229-311

Pendoley K, Fitzpatrick J (1999) Browsing of mangroves by Green Turtles in Western Australia. Marine Turtle Newsletter**:** 10

Peterson CH (1991) Intertidal zonation of marine invertebrates in sand and mud. American Scientist **79:** 236-249

Phillips DJH (1990) Use of macroalgae and invertebrates as monitors of metal levels in estuaries and coastal waters. *In* RW Furness, PS Rainbow, eds, Heavy metals in the marine environment. CRC Press, Inc., Boca Raton, Florida, pp 81-99

Pinzón ZS, Ewel KC, Putz F, E (2003) Gap formation and forest regeneration in a Micronesian mangrove forest. Journal of Tropical Ecology **19:** 143-153

Piou C, Feller IC, Berger U, Faustino C (2006) Zonation patterns of Belizean offshore mangrove forests 41 years after a catatrophic hurricane. Biotropica **38:** 365-374

Preuss J (2005) Why 'Tsunami' means wake up call. Planning **71 (8):** 4-7

Primavera JH (1995) Mangroves and brackish water pond culture in the Phillipines. Hydrobiologia **295:** 303-309

Primavera JH (1998) Mangroves as Nurseries: Shrimp populations in mangrove and non-mangrove habitats. Estuarine, Coastal and Shelf Science **46:** 457-464

Proffitt CE, Devlin DJ, Lindsey M (1995) Effects of oil on mangrove seedlings grown under different environmental conditions. Marine Pollution Bulletin **30:** 788-793

Pulver TR (1976) Transplanting techniques for sapling mangrove trees, *Rhizophora mangle, Laguncularia racemosa,* and *Avicennia germinans,* in Florida. *In*. Florida

Department of Natural Resources, Marine Research Laboratory, St Petersburg, Florida, pp 1-14

Rabinowitz D (1978) Dispersal properties of mangrove propagules. Biotropica **10**

Raimondi PT, Reed DC (1996) Determining the spatial extent of ecological impacts caused by local anthropogenic disturbances in coastal marine habitats. *In* RJ Schmitt, CW Osenberg, eds, Detecting ecological impacts: concepts and applications in coastal habitats. Acacemic Press, San Diego, pp 179-198

Rainbow PS (1990) Heavy metal levels in marine invertebrates. *In* RW Furness, PS Rainbow, eds, Heavy metals in the marine environment. CRC Press, Inc., Boca Raton, Florida, pp 67-75

Ravichandran S (2006) Diversity of brachyuran crabs in a mangrove ecosystem of southeast coast of India (Abstract only). *In* JSY Lee, e al., eds, Mangrove macrobenthos meeting II, Conference Program, Gold Coast, Australia

Ray S, Ulanowicz RE, Majee NC, Roy AB (2000) Network analysis of a benthic food web model of a partly reclaimed island in the Sundarban mangrove ecosystem, India. Journal of Biological Systems **8:** 263-278

Read MA (1991) Observations on the feeding ecology of immature Green Turtles, *Chelonia mydas,* in the Moreton Banks region of Moreton Bay, South East Queensland. Honours. University of Queensland

Redhead TD (1979) On the demography of *Rattus sordidus colletti* in monsoonal Australia. Australian Journal of Ecology **4:** 115-136

Reichel H, Andersen AN (1996) The rainforest ant fauna of Australia's Northern Territory. Australian Journal of Zoology **44:** 81-95

Reid DG (1985) Habitat and zonation patterns of *Littoraria* species (Gastropoda: Littorinidae) in Indo-Pacific mangrove forests. Biological Journal of the Linnean Society **26:** 39-68

Reynoldson TB, Metcalfe-Smith JL (1992) An overview of the assessment of aquatic ecosystem health using benthic invertebrates. Journal of Aquatic Ecosystem Health **1:** 295-308

Richardson P (2002) Bats. Smithsonian Institution Press

Ricklefs RE, Latham RE (1993) Global patterns of diversity in mangrove floras. *In* RE Ricklefs, D Schluter, eds, Species Diversity in Ecological Communities: Historical and Geographical Perspectives. University of Chicago Press, Chicago, pp 215-229

Riley R, Salgado Kent CP (1999) Riley encased methodology: principles and processes of mangrove habitat creation and restoration. Mangroves and Salt Marshes **3:** 207-213

Ritchie ME, Olff H (1999) Spatial scaling laws yield a synthetic theory of biodiversity. Letters to Nature **400:** 557-560

Roberston A (1991) Plant-animal interactions and the structure and function of mangrove forest ecosystems. Australian Journal of Ecology **16:** 433-443

Roberston A, Duke NC (1990) Recruitment, growth and residence time of fishes in a tropical Australian mangrove system. Estuarine, Coastal and Shelf Science **31:** 723-743

Roberston AI (1986) Leaf-burying crabs: their influence on energy flow and export from mixed mangrove forests (*Rhizophora* spp.) in northeastern Australia. Journal of Experimental Marine Biology and Ecology **102:** 237-248

Roberston AI, Daniel PA (1989) The influence of crabs on litter processing in high intertidal mangrove forests in tropical Australia. Oecologia **78:** 191-198

Roberston AI, Giddins RL, Smith III TJ (1990) Seed predation by insects in tropical mangrove forests: extent and effects on seed viability and the growth of seedlings. Oecologia **83:** 213-219

Roberston AI, Phillips M (1995) Mangroves as filters of shrimp pond effluent: predictions and biogeochemical reasearch needs. Hydrobiologia **295:** 311-322

Roberts CM, Bohnsack JA, Gell F, Hawkins JP, Goodridge R (2001) Effects of marine reserves on adjacent fisheries. Science **294:** 1920-1923

Robertson AI, Blaber SJM (1992) Plankton, epibenthos and fish communities. *In* A Roberston, DM Alongi, eds, Tropical Mangrove Ecosystems. American Geophysical Union, Washington, DC, pp 173-224

Robertson AI, Duke NC (1987) Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. Marine Biology **96:** 193-205

Robertson AI, Duke NC (1990) Mangrove fish-communities in tropical Queensland, Australia: spatial and temporal patterns in densities, biomass and community structure. Marine Biology **104:** 369-379

Ronnback P, Troell M, Kautsky N, Primavera JH (1999) Distribution pattern of shrimps and fish among *Avicennia* and *Rhizophora* microhabitats in the Pagbilao mangroves, Philippines. Estuarine, Coastal and Shelf Science **48:** 223-234

Roth LC (1992) Hurricanes and mangrove regeneration: effects of hurricane Joan, October 1988, on the vegetation of Isla del Vernado, Bluefields, Nicaragua. Biotropica **24:** 375-384

Rubin JA, Gordon C, Amatekpor JK (1999) Causes and consequences of mangrove deforestation in the Volta Estuary, Ghana: some recommendations for ecosystem rehabilitation. Marine Pollution Bulletin **37:** 441-449

Saenger P (1992) Morphological, anatomical and reproductive adaptations of Australian mangroves. *In* BF Clough, ed, Mangrove ecosystems in Australia. Structure, function and management. Australian Institute Marine Science, Canberra, Australia, pp 153-191

Saenger P (1996) Mangrove restoration in Australia: a case study of Brisbane International Airport. *In* C Field, ed, Restoration of mangrove ecosystems. ISME/ITTO, Okinawa, Japan, pp 36-51

Saenger P (2002) Mangrove Ecology, Silviculture and Conservation. Kluwer Academic Publishers, Dordrecht, Holland

Saenger P, Hegerl EJ, Davie JDS (1983) Global status of mangrove ecosystems. *In* The Environmentalist: Supplement, Vol 3. United Nations Environment Programme and the World Wildlife Fund, p 49p

Saenger P, Rossetto M (2002) The use of DNA molecular techniques for mangrove studies. Mangrove Science **2:** 1-9

Saenger P, Siddiqui NA (1993) Land from the sea: the mangrove afforestation program of Bangladesh. Ocean and Coastal Management **20:** 23-39

Saenger P, Specht MM, Specht RL, Chapman VJ (1977) Mangal and Coastal Salt-Marsh Communities in Australasia. *In* VJ Chapman, ed, Ecosystems of the World Volume I, Wet Coastal Ecosystems. Elsevier, Amsterdam, pp 293-345

Saintilan N, Williams RJ (1999) Mangrove transgression into saltmarsh environments in south-east Australia. Global Ecology and Biogeography **8:** 117-124

Salgado Kent CP (2004) The significance of plant-animal interactions in tropical mangrove forests. PhD thesis. Charles Darwin University, Darwin, Northern Territory

Salgado Kent CP, Lin J (1999) A comparison of Riley encased methodology and traditional techniques for planting red mangroves (*Rhizophora mangle)*. Mangroves and Salt Marshes **3:** 215-225

Salgado Kent CP, McGuinness KA (2006) A comparison of methods for estimating relative abundance of grapsid crabs. Wetlands Ecology and Management **14:** 1-9

Samiullah Y (1985) Biological effects of marine oil pollution. Oil and Petrochemical Pollution **2:** 235-264

Sarkar SK, Bhattacharya SG, Bhattacharya B, Sarkar D, Nayak DC, Chattopadhaya AK (2005) Spatiotemporal variation in benthic polychaetes (Annelida) and relationships with environmental variables in a tropical estuary. Wetands ecology and management **13:** 55-67

Sasekumar A (1974) Distribution of macrofauna on a Malayan mangrove shore. Journal of Animal Ecology **43:** 51-70

Sasekumar A, Chong VC (1998) Faunal diversity in Malaysian mangroves. Global Ecology and Biogeography Letters **7:** 57-60

Schodde R, Mason IJ, Gill HB (1982) The avifauna of the Australian mangroves - A brief review of composition, structure and origin. *In* BF Clough, ed, Mangrove ecosystems in Australia. Australian Institute Marine Science, Canberra, Australia, pp 141-150

Schrijvers J, Van Gansbeke D, Vinex M (1995) Macrobenthic infauna of mangroves and surrounding beaches at Gazi Bay, Kenya. Hydrobiologia **306:** 53-66

Semeniuk V (1983) Mangrove distribution in northwestern Australia in relationship to regional and local freshwater seepage. Vegetatio **53:** 11-31

Semeniuk V (1985) Mangrove environments of Port Darwin, Northern Territory: the physical framework and habitats. Journal of the Royal Society of Western Australia **67:** 81-97

Shattuck SO (1999) Australian Ants, Vol 3. CSIRO Publishing, Melbourne, Victoria

Sheaves J (2006) The response of tropical mangrove benthos to short-term intense freshwater events. *In* e al., ed, Mangrove macrobenthos meeting II, Conference Program. Abstract only., Cold Coast, Queensland

Sheridan PF (1997) Benthos of adjacent mangrove, seagrass and non-vegetated habitats in Rookery Bay, Florida, USA. Estuarine, Coastal and Shelf Science **44:** 455-469

Sherman RE, Fahey TJ, Battles JL (2000) Small-scale disturbance and regeneration dynamics in a neotropical mangrove forest. Journal of Ecology **88:** 165-178

Sherman RE, Fahey TJ, Martinez P (2001) Hurricane impacts on a mangrove forest in the Dominican Republic: damage patterns and early recovery. Biotropica **33:** 393-408

Shivas MA (1999) The larval biology of *Culicoides ornatus* Taylor in mangroves near Darwin, Northern Territory. PhD thesis, Northern Territory University, Darwin, Australia

Simpson K, Day N (1996) Field Guide to the Birds of Australia, Ed Sixth Edition. Penguin Books Australia, Ringwood, Victoria

Skilleter G (1996) Validation of rapid assessment of damage in urban mangrove forests and relationships with molluscan assemblages. Journal of the Marine Biological Association of the United Kingdom **76:** 701-716

Skilleter G, 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

Skilleter GA (2000) Environmental disturbances. *In* AJ Underwood, MG Chapman, eds, Coastal Marine Ecology. UNSW Press, Sydney, pp 121-135

Smith AN, Hanley JR, Love B (1997) Comparisons of different quadrat sizes for measuring the densities of crabs and macromolluscs of the mangrove forest floor. *In* JR Hanley, G Caswell, D Megirian, HK Larson, eds, Proceedings of the Sixth International Marine Biological Workshop - the Marine Flora and Fauna of Darwin Harbour. Northern Territory Museum of Arts and Sciences, Darwin, Australia, pp 461-466

Smith III TJ (1987a) Effects of light and intertidal position on seedling survival and growth in tropical tidal forests. Journal of Experimental Marine Biology and Ecology **110:** 133-146

Smith III TJ (1987b) Effects of seed predators and light level on the distribution of *Avicennia marina* (Forsk.) Vierh. in tropical, tidal forests. Estuarine, Coastal and Shelf Science **25:** 43-51

Smith III TJ (1987c) Seed predation in relation to tree dominance and distribution in mangrove forests. Ecology **68:** 266-273

Smith III TJ (1988) The influence of seed predators on structure and succession in tropical, tidal forests. Proceedings of the Ecological Society of Australia **15:** 203-211

Smith III TJ, Boto KG, Frusher SD, Giddins RL (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

Smith III TJ, Robblee MB, Wanless HR, Doyle TW (1994) Mangroves, hurricanes and lightning strikes. BioScience **44:** 256-257

Snedaker SC, Brown Ms, Lahmann EJ, Araujo RJ (1992) Recovery of a mixed-species mangrove forest in south Florida following canopy removal. Journal of Coastal Research **8:** 919-925

Sousa WP (1984) The role of disturbance in natural communities. Annual Review of Ecology and Systematics **15:** 353-391

Sousa WP, Mitchell BJ (1999) The effect of seed predators on plant distributions: is there a general pattern in mangroves? Oikos **86:** 55-66

Staples DJ (1980a) Ecology of juvenile and adolescent Banana Prawns, *Penaeus merguiensis*, in a mangrove estuary and adjacent off-shore area of the Gulf of Carpentaria. I. Immigration and settlement of postlarvae. Australian Journal of Marine and Freshwater Research **31:** 635-652

Staples DJ (1980b) Ecology of juvenile and adolescent Banana Prawns, *Penaeus merguiensis*, in a mangrove estuary and adjacent off-shore area of the Gulf of Carpentaria. II. Emigration, population structure and growth of juveniles. Australian Journal of Marine and Freshwater Research **31:** 653-665

Stark JS (1998) Heavy metal pollution and macrobenthic assemblages in soft sediments in two Sydney estuaries, Australia. Marine and Freshwater Research **49:** 533-540

Stocker GC (1976) Report on cyclone damage to natural vegetation in the Darwin area after cyclone Tracy, 25 December 1974. AGPS, Canberra

Stubbs BJ, Saenger P (2002) The application of forestry principles to the design, execution and evaluation of mangrove restoration projects. Bois et forets des tropiques **273:** 1-22

Sutherland JP (1980) Dynamics of the epibenthic community of roots of the mangrove *Rhizophora mangle* at Bahía de Buche, Venezuela. Marine Biology **58:** 75-84

Swiadek JW (1997) The impacts of Hurricane Andrew on mangrove coasts in southern Florida - a review. Journal of Coastal Research **13:** 242-245

Tam NFY, Wong YS (1995) Mangrove soils as sinks for waste water-borne pollutants. Hydrobiologia **295:** 231-241

Tamai S, Iampa P (1988) Establishment and growth of mangrove seedlings in mangrove forests of southern Thailand. Ecological Research **3:** 227-238

Tan CGS, Ng PKL (1994) An annotated checklist of mangrove brachyuran crabs from Malaysia and Singapore. Hydrobiologia **285:** 75-84

Tan KS, Chou LM (2000) A guide to common seashells of Singapore. Singapore Science Centre, Singapore

Taylor JA, Tulloch D (1985) Rainfall in the wet-dry tropics: Extreme events at Darwin and similarities between years during the period 1870-1983. Australian Journal of Ecology **10:** 281-295

Teas HJ (1977) Ecology and restoration of mangrove shorelines in Florida. Environmental Conservation **4:** 51-58

Teas HJ, Jurgens W, Kimball MC (1975) Plantings of red mangrove (*Rhizophora mangle* L.) in Charlotte and St Lucie counties, Florida. *In* RR Lewis, ed, Proceedings of the Second Annual Conference on Restoration of Coastal Vegetation in Florida. Hillsborough Community College, Tampa Audubon Society and Florida Audubon Society, Tampa, Florida, pp 132-161

Thayer GW, Colby DR, Hettler WF (1987) Utilization of the red mangrove prop root habitat by fishes in south Florida. Marine Ecology Progress Series **35:** 25-38

Thom BG (1982) Mangrove ecology - a geomorphological perspective. *In* BF Clough, ed, Mangrove ecosystems in Australia. Structure, function and management. Australian Institute of Marine Science, Canberra, ACT, pp 3-30

Thomson BG (1989) A field guide to bats of the Northern Territory. Conservation commission of the Northern Territory, Darwin, NT

Thrush SF, Whitlatch RB, Pridmore RD, Hewitt JE, Cummings VJ, Wilkinson MR (1996) Scale-dependent recolonization: the role of sediment stability in a dynamic sandflat habitat. Journal of ? **77:** 2472-2487

Toledo G, Rojas A, Bashan Y (2001) Monitoring of black mangrove restoration with nursery-reared seedlings on an arid coastal lagoon. Hydrobiologia **444:** 101-109

Tomlinson PB (1986) The Botany of Mangroves. Cambridge University Press, Cambridge

Tongway DJ, Hindley NL (1995) Manual for assessment of soil condition of tropical grasslands. *In*. Division of Wildlife and Ecology, CSIRO, Canberra, p 59pp

Tongway DJ, Hindley NL (2004) Landscape function analysis. Procedures for monitoring and assessing landscapes. CSIRO, Sustainable Ecosystems, Canberra

Tri NH, Adger WN, M KP (1998) Natural resource management in mitigating climate impacts: the example of mangrove restoration in Vietnam. Global Environmental Change **8:** 49-61

Underwood AJ (1996) Experiments in Ecology: Their Logical Design and Interpretation using Analysis of Variance. Cambridge University Press, Cambridge

Underwood AJ (2000) Detection and measurement of environmental impacts. *In* AJ Underwood, MG Chapman, eds, Coastal marine ecology of temperate Australia. UNSW Press, Sydney, pp 311-322

Unwin GL, Applegate GB, Stocker GC, Nicholson DI (1991) Initial effects of Tropical Cyclone 'Winifred' on forests in north Queensland. Proceedings of the Ecological Society of Australia **15:** 283-296

URS Pty Ltd (2004) Darwin LNG Plant Mangrove Monitoring Programme. 2003-2004 Annual Report. Report prepared for ConocoPhillips Australia Pty Ltd, October 2004, Darwin, Australia

Valiela I, Bowen JL, York JK (2001) Mangrove forests: one of the world's threatened major tropical environments. BioScience **51:** 807-815

Van Dyck S (1996) *Xeromys myoides* Thomas, 1889 (Rodentia: Muridae) in mangrove communities of north Stradbroke Island, Southeast Queensland. Memoirs of the Queensland Museum **42:** 337-366

Vance DJ, Haywood MDE, Heales DS, Kenyon RA, Loneragan NR, Pendrey RC (1996) How far do prawns and fish move into mangroves? Distribution of juvenile banana prawns *Penaeus merguiensis* and fish in a tropical mangrove forest in Northern Australia. Marine Ecology Progress Series **131:** 115-124

Vance DJ, Haywood MDE, Staples DJ (1990) Use of a mangrove estuary as a nursery area by postlarval and juvenile banana prawns, *Penaeus merguiensis* de Man, in northern Australia. Estuarine, Coastal and Shelf Science **31:** 689-710

Vardon MJ, Tidemann CR (1999) Flying-foxes (*Pteropus alecto* and *P. scapulatus*) in the Darwin region, north Australia: patterns in camp size and structure. Australian Journal of Zoology **47:** 411-423

Vermeij GJ (1973) Molluscs in mangrove swamps: physiognomy, diversity and regional differences. Systematic Zoology **22:** 609-624

Von Hagen HO, Jones DS (1989) The Fiddler Crabs (Ocypodidae: *Uca*) of Darwin, Northern Territory, Australia. The Beagle **6:** 55-68

Walsh GE (1977) Chapter 16 - Exploitation of mangal. *In* VJ Chapman, ed, Ecosystems of the World - Wet Coastal Ecosystems, Vol 1. Elsevier Scientific, Amsterdam, pp 347-358

Walters BB (2000) Local mangrove planting in the Philippines: are fisherfolk and fishpond owners effective restorationists? Restoration Ecology **8:** 237-246

Ward CJ, Steinke TD, Ward MC (1986) Mangroves of the Kosi System, South Africa: their re-establishment since mass mortality in 1965/66. South African Journal of Botany **52:** 501-512

Warner GF (1969) The occurrence and distribution of crabs in a Jamaican mangrove swamp. Journal of Animal Ecology **38:** 379-389

Warwick RM (1988) The level of taxonomic discrimination required to detect pollution effects on marine benthic communities. Marine Pollution Bulletin **19:** 259-268

Warwick RM (1993) Environmental impact studies on marine communities: Pragmatical considerations. Australian Journal of Ecology **18:** 63-80

Wells AE (1983) Distribution of mangrove species in Australia. *In* HJ Teas, ed, Tasks for Vegetation Science, Vol 8. Dr W Junk Publishers, The Hague, pp 57-76

Wells FE (1980) Comparative distributions of the mudwhelks *Terebralia sulcata*and *T. palustris* in a mangrove swamp in northwestern Australia. Malacological Review **13:** 1-5

Wells FE (1983) An analysis of marine invertebrate distributions in a mangrove swamp in northwestern Australia. Bulletin of Marine Science **33:** 736-744

Wells FE (1984) Comparative distributions of macromolluscs and macrocrustaceans in a north-western Australian mangrove system. Australian Journal of Marine and Freshwater Research **35:** 591-596

Wells FE (1986a) The Potamididae (Mollusca: Gastropoda) of Hong Kong, with an examination of habitat segregation in a small mangrove system. *In* B Morton, D Dudgeon, eds, Proceedings of the Second International Workshop on the Malacofauna of Hong Kong and Southern China. Hong Kong University Press, Hong Kong, pp 139-154

Wells FE (1986b) Distribution of marine invertebrates in a Hong Kong mangrove with emphasis on molluscs. *In* Proceedings of the Second International Marine Biological Workshop: the Marine Flora and Fauna of Hong Kong and Southern China. Hong Kong University Press, Kong Kong, pp 783-793

Wells FE (1986c) Distribution of molluscs across a pneumatophore boundary in a small bay in northwestern Australia. Journal of Molluscan Studies **52:** 83-90

Wells FE (1990) Comparative zoogeography of marine mollusks from northern Australia, New Guinea and Indonesia. The Veliger **32:** 140-144

Wells FE, Slack-Smith SM (1981) Zonation of molluscs in a mangrove swamp in the Kimberley, Western Australia. *In* Biological survey of Mitchell Plateau and Admiralty Gulf, Kimberley, Western Australia. Western Australian Museum, Perth, pp 265-274

Wightman GM (1989) Mangroves of the Northern Territory. Northern Territory Botanical Bulletin No. 7. Conservation Commission of the Northern Territory, Palmerston, Northern Territory, Australia.

Wilkie ML, Fortuna S (2003) Status and trends in mangrove area extent worldwide. *In*. Working paper FRA 63. Forest Resources Division, Forestry Department, UN-Food and Agriculture Organisation, pp 0-292

Willan R (in prep) Checklist of marine and freshwater Mollusca from Darwin Harbour, Northern Territory. Northern Territory Museum of Arts and Sciences, Darwin, Australia

Williams D, Wolanski E, Spagnol S (2006) The hydrodynamics of Darwin Harbour. Chapter 26. *In* E Wolanski, ed, The Environment in Asia Pacific Harbours. Springer, Dordrecht, the Netherlands, pp 461-476

Wilson BA, Bowman DMJS (1987) Fire, storm, flood and drought: the vegetation ecology of Howards Peninsula, Northern Territory, Australia. Australian Journal of Ecology **12:** 165-174

Wilson EO (1988) The current state of biological diversity. *In* EO Wilson, ed, Biodiversity. National Academy Press, Washington, D C, pp Chapter 1, 3-17

Wilson KA (1989) Ecology of mangrove crabs: predation, physical factors and refuges. Bulletin of Marine Science **44:** 263-273

Winer BJ, Brown DR, Michels K (1991) Statistical principles in experimental design (3rd edition). McGraw-Hill Inc, New York

Woinarski JCZ, ed (1998) Wildlife of the English Company (and Wessel) Islands, north-east Arnhem Land. Report to the Australian Heritage Commission

Woinarski JCZ (2000) The conservation status of rodents in the monsoonal tropics of the Northern Territory. Wildlife Research **27:** 421-435

Woinarski JCZ (2003) Threatened Species of the Northern Territory - Northern Quoll, Dasyurus hallucatus. *In*, Vol 2006. Northern Territory Government, Department of Natural Resources, Environment and the Arts website. www.nt.gov.au/nreta/wildlife/threatened/specieslist.html

Woinarski JCZ, Braithwaite RW (1990) The terrestrial vertebrate fauna and vegetation of the Kakadu Conservation Zone. *In*. CSIRO, Darwin

Woinarski JCZ, Brennan K, Hempel C, Armstrong M, Milne AK, Chatto R (2003) Biodiversity conservation on the Tiwi Islands, Northern Territory: Part 2. Fauna. *In*. Department of Infrastructure Planning and Environment, Darwin, Northern Territory, p 127

Woinarski JCZ, Fisher A, Brennan K, Morris I, Chatto R (2001) Patterns of bird species richness on islands off Arnhem Land, Northern Territory, Australia. Australian Journal of Ecology **26:** 1-13

Woinarski JCZ, Milne AK, Wanganeen G (2001) Changes in mammal populations in relatively intact landscapes of Kakadu National Park, Northern Territory. Austral Ecology **26:** 360-370

Woinarski JCZ, Tidemann SC, Kerin S (1988) Birds in a tropical mozaic: the distribution of bird species in relation to vegetation patterns. Australian Journal of Wildlife Research **15:** 171-196

Wolanski E, ed (2006) The Environment in Asia Pacific Harbours. Springer, Dortrecht, the Netherlands

Woodroffe CD (1985) Variability in detrital production and tidal flushing in mangrove swamps. *In* KN Bardsley, JDS Davie, CD Woodroffe, eds, Coasts and tidal wetlands of the Australian Monsoon Region. Mangrove Monograph No. 1. North Australia Research Unit, Australian National University, Darwin, NT, Australia, pp 201-212

Woodroffe CD (1992) Mangrove sediments and geomorphology. *In* AI Roberston, DM Alongi, eds, Tropical Mangrove Ecosystems. American Geophysical Society, Washington, DC

Woodroffe CD (1995) Response of tide-dominated mangrove shorelines in northern Australia to anticipated sea-level rise. Earth surface processes and landforms **20:** 65-85

Woodroffe CD, Bardsley KN (1987) The distribution and productivity of mangroves in Creek H, Darwin Harbour. *In* HK Larson, MG Michie, JR Hanley, eds, Proceedings of a workshop on research and management held in Darwin, 2-3 September 1987, Vol Mangrove Monograph No. 4. North Australia Research Unit, the Australian National University, Darwin, pp 82-122

Woodroffe CD, Bardsley KN, Ward PJ, Hanley JR (1988) Production of mangrove litter in a macrotidal embayment, Darwin Harbour, Northern Territory, Australia. Estuarine, Coastal and Shelf Science **26:** 581-598

Woodroffe CD, Mulrennan ME, Chappell J (1993) Estuarine infill and coastal progradation, southern van Diemen Gulf, northern Australia. Sedimentary Geology **83:** 257-275

Woodroffe CD, Thom BG, Chappell J (1985) Development of widespread mangrove swamps in mid-Holocene times in northern Australia. Nature **317:** 711-713

Yipp MW (1983) Tidal rhythyms of *Littorina melanostoma* and *L. scabra* in a Hong Kong mangal. Proceedings of the Second International Workshop on the Malacofauna of Hong Kong and Southern China**:** 613-621

Youssef T (1997) Approaches in mangrove planting: some options for Darwin mangroves. *In* JR Hanley, G Caswell, D Megirian, HK Larson, eds, Proceedings of the sixth International Marine Biological Workshop - the marine flora and fauna of Darwin Harbour. Northern Territory Museum of Arts and Sciences, Darwin, Australia, pp 451-460

Youssef T, Saenger P (1996) Anatomical adaptive strategies to flooding and rhizosphere oxidation in mangrove seedlings. Australian Journal of Botany **44:** 297-313

Youssef T, Saenger P (1998) Photosynthetic gas exchange and accumulation of phytotoxins in mangrove seedlings in response to soil physico-chemical characteristics associated with waterlogging. Tree physiology **18:** 317-324

APPENDICES

APPENDIX A

Table A-1: Mean abundance of mammals (per hectare) occurring in different assemblages in Darwin Harbour mangroves during 1999-2001 including incidental records (denoted by *). Undisturbed sites were sampled during the dry season only for 2 years (1999-2001) and disturbed sites sampled once during the dry season (2001), n= no of study plots. Species recorded only in disturbed mangroves are indicated (**).

NB. This table includes data from Chapters 3 and 4.

FAMILY	Species	Common Name	Disturbed sites only	Hint marg	Tidal flat	Tidal ck	Seaw-ard	**Undisturbed – all assem.**	Hint marg	Tidal flat	Rhizo ph	Seawa rd	**Disturbed - all assemblages**
Species trapped during surveys:				n=12	n=12	n=12	n=12	n=48	n=8	n=8	n=8	n=8	n=32
DASYURIDAE	*Dasyurus hallucatus*	Northern Quoll		0.67	0.17	0.00	0.00	**0.21**	0.00	0.00	0.00	0.00	**0.00**
DASYURIDAE	*Antechinus bellus*	Fawn Antechinus		0.08	0.00	0.00	0.00	**0.02**	0.00	0.00	0.00	0.00	**0.00**
PHALANGERIDAE	*Trichosurus vulpecula*	Common Brushtail Possum		2.58	4.58	5.50	2.08	**3.69**	1.00	0.00	0.25	0.25	**0.38**
PERAMELIDAE	*Isoodon macrourus*	Northern Brown Bandicoot		2.50	0.92	0.00	0.00	**0.85**	2.25	0.75	0.00	0.00	**0.75**
MURIDAE	*Melomys burtoni*	Grassland Melomys		2.25	6.08	10.08	8.33	**6.69**	2.50	7.00	6.00	4.25	**4.94**
MURIDAE	*Mesembriomys gouldii*	Black-footed Tree-rat		0.17	0.00	0.00	0.00	**0.04**	0.00	0.00	0.00	0.00	**0.00**
MURIDAE	*Rattus tunneyi*	Pale Field -rat		0.00	0.25	0.08	0.00	**0.08**	0.00	0.00	0.00	0.00	**0.00**
MURIDAE	*Hydromys chrysogaster*	Water-rat	**	0.00	0.00	0.00	0.00	**0.00**	0.25	0.00	0.00	0.50	**0.19**
FELIDAE	*Felis catus*	★ Cat		0.00	0.08	0.00	0.00	**0.02**	0.00	0.00	0.00	0.00	**0.00**
MURIDAE	*Mus musculus*	★House Mouse	**	0.00	0.00	0.00	0.00	**0.00**	0.50	0.50	0.00	0.00	**0.25**
MURIDAE	*Rattus rattus*	★Black Rat		0.08	0.00	0.00	0.00	**0.02**	0.00	1.25	1.25	0.00	**0.63**
		Mean density ha^{-1} :		**8.33**	**12.08**	**15.67**	**10.42**	**11.63**	**6.50**	**9.50**	**7.50**	**5.00**	**7.13**
Species recorded from incidental observations, tracks and traces:													
MACROPODIDAE	*Macropus agilis*	Agile Wallaby		*	*			*					
CANIDAE	*Canis familiaris*	★Dog/Dingo		*	*			*					
SUIDAE	*Sus scrofa*	★Pig		*				*					
★ Denotes an introduced species							TOTAL :	**13 species**				TOTAL :	**6 species**

ANALYSES FOR CHAPTERS 3 & 4.

Significant main effects or interactions at $p<0.05$ are denoted by an asterisk (*) in the P column and highlighted with grey shading.

** indicates post-hoc modification of the model (see Winer et al., 1991).

VERTEBRATE FAUNA OF UNDISTURBED MANGROVES

Table A-2: Three factor nested ANOVA comparing **mammal species richness** (pooled over 4 night survey per 0.25 ha study plot) among years (fixed), sites (random), and assemblages (fixed).

	df effect	Ms effect	df error	MS error	F	P
Year	1	1.333	2	0.583	2.29	0.270
Site	2	0.583	24	0.583	1.00	0.383
Assemblage	3	3.667	6	0.750	4.89	0.047*
Year*Site	2	0.583	24	0.583	1.00	0.383
Year*Assemblage	3	0.667	6	0.750	0.89	0.499
Site*Assemblage	6	0.750	24	0.583	1.29	0.301
Year*Site*Assemblage	6	0.750	24	0.583	1.29	0.301

Table A-3: Three factor nested ANOVA comparing **mammal abundance** ha^{-1} ($\log_{10}(x + 1)$ transformed sum of total captures per 0.25 ha study plot over 4 night survey) among years (fixed), sites (random), and assemblages (fixed).

	df effect	Ms effect	df error	MS error	F	P
Year	1	0.434	2	0.147	2.94	0.228
Site	2	0.868	24	0.043	20.31	0.000*
Assemblage	3	0.175	6	0.158	1.11	0.416
Year*Site	2	0.147	24	0.043	3.45	0.048*
Year*Assemblage	3	0.087	6	0.092	0.95	0.474
Site*Assemblage	6	0.158	24	0.043	3.69	0.010*
Year*Site*Assemblage	6	0.092	24	0.043	2.14	0.085

Table A-4: Bat species associated with mangroves communities in Darwin Harbour recorded at sites E1, E2 and M3 during three surveys (wet season, dry season and early wet season) in 2000-01.

FAMILY	Species	Species code	Common Name	Hint marg	Tidal flat	Rhizoph	Seaward
PTEROPODIDAE	*Pteropus alecto*	Pter al	Black flying-fox			+	+
PTEROPODIDAE	*Macroglossus minimus*	Mac min	Northern blossom bat			+	+
EMBALLONURIDAE	‡ *Saccolaimus flaviventris*	Sac fla	Yellow-bellied sheathtail bat	+			
MOLOSSIDAE	‡ *Chaerephon jobensis*	Cha job	Northern freetail bat				+
MOLOSSIDAE	*Mormopterus beccarii*	Mor bec	Beccari's freetail bat	+	+	+	+
MOLOSSIDAE	‡ *Mormopterus loriae*	Mor lor	Little northern freetail bat		+		+
VESPERTILIONIDAE	*Nyctophilus* sp.	Nyct sp	Longeared bat	+			
VESPERTILIONIDAE	‡ *Miniopterus schreibersii*	Min sch	Large bentwing bat	+			
VESPERTILIONIDAE	‡ *Myotis moluccarum (adversus)*	Myo mol	Large-footed myotis	+			
VESPERTILIONIDAE	‡ *Pipistrellus westralis*	Pip wes	Northern pipistrelle	+	+	+	
VESPERTILIONIDAE	Pipisrellus westralis/Miniopterus schreibersii	Pip/Min	Undet 1			(+)	
VESPERTILIONIDAE	‡ Scotorepens greyii/Chalinolobus nigrogriseus	Sco/Cha	Undet 2	(+)	(+)	(+)	
	‡ denotes species also recorded in Kimberley survey by McKenzie and Rolfe (1986)		**Species richness in assemblages**:	**6**	**3**	**4**	**5**

Table A-5: Four factor nested ANOVA comparing **bat species richness** (untransformed data) between seasons (fixed), sites (random), transects (random, nested in site) and assemblages (fixed). Data from 10-minute censuses were pooled for each study plot

	df effect	MS effect	df error	MS error	F	P
Season	2	0.847	4	0.243	3.49	0.133
Site	2	0.597	3	0.792	0.75	0.543
Transect	3	0.792	0	0.000	-	-
Assemblage	3	0.606	6	0.523	1.16	0.400
Season*Site	4	0.243	6	0.333	0.73	0.604
Season*Transect	6	0.333	0	0.000	-	-
Season*Assemblage	6	0.718	12	0.447	1.61	0.228
Site*Assemblage	6	0.523	9	1.088	0.48	0.807
Transect*Assemblage	9	1.088	0	0.000	-	-
Season*Site*Assemblage	12	0.447	18	0.463	0.96	0.512
Season*Transect*Assemblage	18	0.463	0	0.000	-	-

Table A-6: Four factor nested ANOVA comparing **microbat species richness** between seasons (fixed), sites (random), transects (random, nested in site) and assemblages (fixed). Data from 10 minute censuses was pooled for each study plot (megachiropterean bats excluded).

	df effect	MS effect	df error	MS error	F	P
Season	2	0.014	4	0.451	0.03	0.970
Site	2	0.264	3	0.569	0.46	0.668
Transect	3	0.569	0	0.000	-	-
Assemblage	3	2.347	6	0.431	5.45	0.038*
Season*Site	4	0.451	6	0.444	1.02	0.469
Season*Transect	6	0.444	0	0.000	-	-
Season*Assemblage	6	0.181	12	0.201	0.90	0.528
Site*Assemblage	6	0.431	9	0.903	0.48	0.810
Transect*Assemblage	9	0.903	0	0.000	-	-
Season*Site*Assemblage	12	0.201	18	0.333	0.60	0.812
Season*Transect*Assemblage	18	0.333	0	0.000	-	-

Table A-7 : Mean abundance of birds (per hectare) recorded during 96 ten minute censuses in each assemblage is listed for both disturbed and undisturbed sites. Species recorded only in disturbed mangroves are indicated (**), n= total no of birds, including incidental records (denoted by *). Undisturbed sites were sampled during wet and dry seasons for 2 years (1999-2001) and undisturbed sites, were sampled once during the dry season (2001). **N**= nesting

Family	Species	Common Name	Dist sites only	Hint marg	Tidal flat	Tidal ck	Seaward	**Undisturbed - all assemblages (birds ha^{-1})**	Hint margin	Tidal flat	Rhizophora	Seaward	**Disturbed - all assemblages (birds ha^{-1})**
				n=96	n=70	n=96	n=102	**n=364**	n=44	n=37	n=45	n=33	**n=159**
ACCIPITRIDAE	*Haliastur indus*	Brahminy Kite		0.04	0.11		0.08	**0.05**				0.09	**0.02**
ACCIPITRIDAE	*Pandion haliaetus*	Osprey		0.04				**0.01**					
ACCIPITRIDAE	*Accipiter novaehollandiae*	Grey Goshawk	**						0.09				**0.02**
ACCIPITRIDAE	*Accipiter cirrhocephalus*	Collared Sparrowhawk					0.04	**0.01**					
ACCIPITRIDAE	*Haliaeetus leucogaster*	White-bellied Sea-eagle		0.04	0.06			**0.02**				0.12	**0.03**
ACCIPITRIDAE	*Milvus migrans*	Black Kite		0.13	0.06	0.04		**0.05**			0.09		**0.02**
ACCIPITRIDAE	*Haliastur sphenurus*	Whistling Kite				0.08	0.12	**0.05**					
ALCEDINIDAE	*Alcedo pusilla*	Little Kingfisher					0.04	**0.01**					
ALCEDINIDAE	*Alcedo azurea*	Azure Kingfisher				0.08	0.04	**0.03**					
ANATIDAE	*Tadorna radjah*	Radjah Shelduck	**							0.09			**0.02**
ARDEIDAE	*Ardea intermedia*	Intermediate Egret					0.04	**0.01**		0.09		0.09	**0.05**
ARDEIDAE	*Ardea alba*	Great Egret					*			0.09			**0.02**
ARDEIDAE	*Ardea sumatrana*	Great-billed Heron					*						
ARDEIDAE	*Ardea picata*	Pied Heron	**								0.09	0.09	**0.05**

Family	Species	Common Name	Dist only	Hint marg	Tidal flat	Rhizo phora	Seaw ard	**Undisturbed - all assemblages**	Hint marg	Tidal flat	Rhizo phora	Seaw ard	**Disturbed - all assemblages**
ARDEIDAE	*Ardea pacifica*	White-necked Heron					0.04	**0.01**					
ARDEIDAE	*Egretta sacra*	Eastern Reef Egret	**							0.09		0.27	**0.09**
ARDEIDAE	*Butorides striatus*	Striated Heron					0.12	**0.03**		0.09		0.36	**0.11**
ARDEIDAE	*Egretta garzetta*	Little Egret	**							0.27			**0.07**
ARDEIDAE	*Egretta novaehollandiae*	White-faced Heron					*						
ARTAMIDAE	*Cracticus quoyi*	Black Butcherbird		0.29		0.50		**0.20**	0.27	0.18	0.18		**0.16**
ARTAMIDAE	*Artamus leucorynchus*	White-breasted Woodswallow		0.25	0.25	0.17	0.21	**0.22**			0.55	1.73 **N**	**0.57**
BURHINIDAE	*Esacus neglectus*	Beach Stone-curlew	**									0.09	**0.02**
CAMPEPHAGIDAE	*Coracina novaehollandiae*	Black-faced Cuckoo-shrike	**							*			
CAMPEPHAGIDAE	*Lalage leucomela*	Varied Triller		0.33		0.04	0.12	**0.13**				0.36	**0.08**
CAMPEPHAGIDAE	*Coracina tenuirostris*	Cicadabird		0.08				**0.02**					
CAMPEPHAGIDAE	*Coracina papuensis*	White-bellied Cuckoo-shrike		0.29		0.13	0.16	**0.15**	0.09		0.09	0.18	**0.09**
CAMPEPHAGIDAE	*Lalage sueurii*	White-winged Triller	**									0.27	**0.07**
CAPRIMULGIDAE	*Caprimulgus macrurus*	Large-tailed Nightjar		*					0.18				**0.05**
CICONIIDAE	*Ephippiorhynchus asiaticus*	Black-necked Stork	**									*	
COLUMBIDAE	*Geopelia placida*	Peaceful Dove				0.08		**0.02**	0.55	1.09	0.09	0.73	**0.61**

Family	Species	Common Name	Dist only	Hint marg	Tidal flat	Rhizo ph	Seaw ard	**Undisturbed - all assemblages**	Hint marg	Tidal flat	Rhizo phora	Seaw ard	**Disturbed - all assemblages**
COLUMBIDAE	*Ducula bicolor*	Pied Imperial Pigeon	**									0.18	**0.05**
COLUMBIDAE	*Geopelia humeralis*	Bar-shouldered Dove		0.29	0.04	0.38 **N**	0.08	**0.20**	0.82		0.09	0.18	**0.27**
CORACIIDAE	*Eurystomus orientalis*	Dollarbird			0.06			**0.01**					
CORVIDAE	*Corvus orru*	Torresian Crow				0.04		**0.01**					
CUCULIDAE	*Chalcites minutillus*	Little Bronze-Cuckoo				0.04	0.21	**0.06**					
DICAEIDAE	*Dicaeum hirundinaceum*	Mistletoebird		0.04		0.13	0.04	**0.05**					
DICRURIDAE	*Myiagra rubecula*	Leaden Flycatcher		0.17				**0.04**					
DICRURIDAE	*Myiagra ruficollis*	Broad-billed Flycatcher				0.63	1.18	**0.49**				0.55	**0.14**
DICRURIDAE	*Grallina cyanoleuca*	Magpie-lark	**						0.09			0.18	**0.07**
DICRURIDAE	*Rhipidura rufifrons*	Rufous Fantail		0.08				**0.02**	0.36				**0.09**
DICRURIDAE	*Rhipidura phasiana*	Mangrove Grey Fantail		0.42	0.04	0.13	0.16	**0.19**	0.09				**0.03**
DICRURIDAE	*Rhipidura rufiventris*	Northern Fantail		0.92	0.04	0.83	0.25	**0.51**	0.09		0.18		**0.08**
DICRURIDAE	*Dicrurus bracteatus*	Spangled Drongo				0.17	0.04	**0.05**		0.11		0.12	**0.05**
DICRURIDAE	*Myiagra alecto*	Shining Flycatcher		0.21	0.50	1.38	0.29	**0.59**	0.55	0.11	0.18		**0.23**
HAEMATOPODIDAE	*Haematopus longirostris*	Pied Oystercatcher	**									*	
HALCYONIDAE	*Todiramphus sanctus*	Sacred Kingfisher		0.08				**0.02**		0.18			**0.05**
HALCYONIDAE	*Todiramphus chloris*	Collared Kingfisher				0.25	1.88	**0.53**			0.64	3.00	**0.91**
HALCYONIDAE	*Todiramphus macleayii*	Forest Kingfisher		*					0.18 **N**				**0.05**

Family	Species	Common Name	Dist only	Hint marg	Tidal flat	Rhizo ph	Seaw ard	**Undisturbed - all assemblages**	Hint marg	Tidal flat	Rhizo phora	Seaw ard	**Disturbed - all assemblages**
HIRUNDINIDAE	*Hirundo nigricans*	Tree Martin		1.00	1.03	0.42	0.04	**0.63**	0.09		0.55	0.09	**0.18**
LARIDAE	*Sterna bergii*	Crested Tern	**									0.09	**0.02**
MELIPHAGIDAE	*Philemon argenticeps*	Silver-crowned Friarbird		0.04				**0.01**					
MELIPHAGIDAE	*Philemon citreogularis*	Little Friarbird				0.08		**0.02**	0.36				**0.09**
MELIPHAGIDAE	*Lichenostomus unicolor*	White-gaped Honeyeater		0.21	0.08	0.38	0.08	**0.19**	0.18		0.36	0.18	**0.18**
MELIPHAGIDAE	*Melithreptus albogularis*	White-throated Honeyeater					0.29	**0.07**	0.18				**0.05**
MELIPHAGIDAE	*Philemon buceroides*	Helmeted Friarbird		0.13	0.13	1.38	0.71	**0.58**			0.09		**0.02**
MELIPHAGIDAE	*Conopophila albogularis*	Rufous-banded Honeyeater				0.08	0.43	**0.14**		0.09	0.91	2.64 **N**	**0.91**
MELIPHAGIDAE	*Myzomela erythrocephala*	Red-headed Honeyeater		1.08	1.50	3.67	2.46	**2.18**	3.00	0.82	3.09		**1.73**
MELIPHAGIDAE	*Myzomela obscura*	Dusky Honeyeater				0.04		**0.01**					
MELIPHAGIDAE	*Lichmera indistincta*	Brown Honeyeater		3.83	3.00	1.08	2.83	**2.69**	2.91	2.45	1.64	1.45	**2.11**
MEROPIDAE	*Merops ornatus*	Rainbow Bee-eater		0.08	0.17	0.13	0.42	**0.20**			0.09	0.09	**0.05**
ORIOLIDAE	*Oriolus flavocinctus*	Yellow Oriole		0.04			0.12	**0.04**				0.18	**0.05**
ORIOLIDAE	*Sphecotheres viridis*	Figbird					0.08	**0.02**				0.18	**0.05**
PACHYCEPHALIDAE	*Pachycephala melanura*	Mangrove Golden Whistler			0.29	0.42	0.08	**0.20**					
PACHYCEPHALIDAE	*Colluricincla megarhyncha*	Little Shrike-thrush		0.04		0.71	0.16	**0.23**					

Family	Species	Common Name	Dist only	Hint marg	Tidal flat	Rhizo phora	Seaw ard	**Undisturbed - all assemblages**	Hint marg	Tidal flat	Rhizo phora	Seaw ard	**Disturbed - all assemblages**
PACHYCEPHALIDAE	*Pachycephala simplex*	Grey Whistler		0.88	0.08	0.17	0.04	**0.29**	0.09				**0.02**
PARDALOTIDAE	*Gerygone levigaster*	Mangrove Gerygone		0.29	0.75	0.25	0.13	**0.35**		0.91	0.27		**0.30**
PARDALOTIDAE	*Gerygone magnirostris*	Large-billed Gerygone			0.04	1.25 **N**	0.21	**0.38**					
PARDALOTIDAE	*Gerygone chloronotus*	Green-backed Gerygone		0.92	0.08			**0.25**	1.36 **N**				**0.34**
PASSERIDAE	*Taeniopygia bichenovii*	Double-barred Finch		0.29				**0.07**	2.18 **N**	0.82		0.12	**0.77**
PASSERIDAE	*Neochmia phaeton*	Crimson Finch	**							0.18			**0.05**
PELECANIDAE	*Pelecanus conspicillatus*	Australian Pelican					*						
PETROICIDAE	*Microeca flavigaster*	Lemon-bellied Flycatcher				0.67 **N**	2.71	**0.84**	0.45		0.45	0.73	**0.41**
PETROICIDAE	*Peneoenanthe pulverulenta*	Mangrove Robin		0.29	0.46	0.08		**0.21**	0.09	0.36 **N**			**0.11**
PHALACROCORACI-DAE	*Phalacrocorax melanoleucos*	Little Pied Cormorant	**							0.09			**0.02**
PHASIANIDAE	*Coturniz ypsilophora*	Brown Quail	**						0.09		0.18		**0.07**
PODARGIDAE	*Podargus strigoides*	Tawny Frogmouth		0.04				**0.01**					
PSITTACIDAE	*Platycercus venustus*	Northern Rosella	**						0.09				**0.02**
PSITTACIDAE	*Aprosmictus erythropterus*	Red-winged Parrot	**						0.36				**0.09**

Family	Species	Common Name	Dist only	Hint marg	Tidal flat	Rhizo phora	Seaw ard	**Undisturbed - all assemblages**	Hint marg	Tidal flat	Rhizo phora	Seaw ard	**Disturbed - all assemblages**
PSITTACIDAE	*Trichoglossus rubritorquis*	Red-collared Lorikeet		0.13			0.29	**0.10**					
PTILONORHYNCHI-DAE	*Chlamydera nuchalis*	Great Bowerbird		0.04				**0.01**					
RALLIDAE	*Gallirallus philippensis*	Buff-banded Rail	**						0.09	0.18		0.09	**0.09**
RALLIDAE	*Eulabeornis castaneoventris*	Chestnut Rail			0.08	0.79	0.08	**0.24**		0.22			**0.05**
SCOLOPACIDAE	*Numenius madagascariensis*	Eastern Curlew			*					0.09			**0.02**
SCOLOPACIDAE	*Actitis hypoleucos*	Common Sandpiper					0.08	**0.02**		1.09	0.71	1.09	**0.73**
SYLVIIDAE	*Cisticola exilis*	Golden-headed Cisticola		0.04	0.08			**0.03**					
THRESKIORNITHID-AE	*Threskiornis molucca*	Australian White Ibis			0.04	0.08		**0.03**	0.09	0.18			**0.07**
ZOSTEROPIDAE	*Zosterops luteus*	Yellow White-eye		0.25	1.21	1.92	4.67	**2.01**	1.00	0.73	1.09	0.36	**0.80**
	MEAN ABUNDANCE (birds ha^{-1}):			**13.33**	**10.13**	**18.67**	**21.21**	**15.83**	**16.00**	**10.55**	**11.64**	**15.55**	**13.43**

Table A-8: Five factor nested ANOVA comparing **bird species richness** among years (fixed), seasons (fixed), sites (random), transects (random, nested in site) and assemblages (fixed). Data from 10 minute censuses was pooled for each study plot.

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Year	1	0.375	2	1.906	0.20	0.701
Season	1	37.500	2	4.031	9.30	0.093
Site	2	19.198	3	1.313	14.63	0.028*
Transect	3	1.313	0	0.000	-	-
Assemblage	3	67.125	6	6.198	10.83	0.008*
Year*Season	1	8.167	2	8.823	0.93	0.438
Year*Site	2	1.906	3	5.646	0.34	0.737
Season*Site	2	4.031	3	1.604	2.51	0.229
Year*Transect	3	5.646	0	0.000	-	-
Season*Transect	3	1.604	0	0.000	-	-
Year*Assemblage	3	7.069	6	1.434	4.93	0.047*
Season*Assemblage	3	4.750	6	1.531	3.10	0.111
Site*Assemblage	6	6.198	9	5.618	1.10	0.429
Transect*Assemblage	9	5.618	0	0.000	-	-
Year*Season*Site	2	8.823	3	6.271	1.41	0.371
Year*Season*Transect	3	6.271	0	0.000	-	-
Year*Season*Assemblage	3	1.361	6	6.684	0.20	0.890
Year*Site*Assemblage	6	1.434	9	3.396	0.42	0.847
Season*Site*Assemblage	6	1.531	9	3.188	0.48	0.808
Year*Transect*Assemblage	9	3.396	0	0.000	-	-
Season*Transect*Assemblage	9	3.188	0	0.000	-	-
Year*Season*Site*Assemblage	6	6.684	9	1.299	5.15	0.015*
Year*Season*Transect*Assemblage	9	1.299	0	0.000	-	-

Table A-9: Five factor nested ANOVA comparing **bird species abundance** ($\log_{10}(x+1)$ transformed) among years (fixed), seasons (fixed), sites (random), transects (random, nested in site) and assemblages (fixed). Data from 10 minute censuses was pooled for each study plot.

‡ NB A significant effect for season is obtained by post-hoc modification of the model involving the deletion of Season*Site which is not significant at p<0.25 (Winer 1977)

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Year	1	0.002	2	0.002	1.42	0.356
Season ‡	1	1.326	2	0.073	18.25	0.051
Site	2	0.586	3	0.001	477.95	0.000*
Transect	3	0.001	0	0.000	-	-
Assemblage	3	0.745	6	0.047	15.79	0.003*
Year*Season	1	0.164	2	0.073	2.24	0.273
Year*Site	2	0.002	3	0.042	0.04	0.962
Season*Site	2	0.073	3	0.118	0.62	0.596
Year*Transect	3	0.042	0	0.000	-	-
Season*Transect	3	0.118	0	0.000	-	-
Year*Assemblage	3	0.036	6	0.021	1.67	0.271
Season*Assemblage	3	0.063	6	0.017	3.63	0.084
Site*Assemblage	6	0.047	9	0.041	1.14	0.413
Transect*Assemblage	9	0.041	0	0.000	-	-
Year*Season*Site	2	0.073	3	0.034	2.18	0.260
Year*Season*Transect	3	0.034	0	0.000	-	-
Year*Season*Assemblage	3	0.009	6	0.054	0.16	0.917
Year*Site*Assemblage	6	0.021	9	0.053	0.40	0.862
Season*Site*Assemblage	6	0.017	9	0.062	0.28	0.931
Year*Transect*Assemblage	9	0.053	0	0.000	-	-
Season*Transect*Assemblage	9	0.062	0	0.000	-	-
Year*Season*Site*Assemblage	6	0.054	9	0.032	1.71	0.226
Year*Season*Transect*Assemblage	9	0.032	0	0.000	-	-

Table A-10: Five factor nested ANOVA comparing **abundance** ($\log_{10}(x + 1)$ transformed) of the **brown honeyeater** (*Lichmera indistincta***)** among years (fixed), seasons (fixed), sites (random), transects (random, nested in site) and assemblages (fixed).

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Year	1	0.018	2	0.076	0.23	0.676
Season	1	5.441	2	0.154	35.30	0.027*
Site	2	1.264	3	0.055	23.06	0.0158
Transect	3	0.055	0	0.000		
Assemblage	3	0.398	6	0.188	2.12	0.199
Year*Season	1	0.005	2	0.069	0.07	0.820
Year*Site	2	0.076	3	0.087	0.88	0.500
Season*Site	2	0.154	3	0.112	1.38	0.376
Year*Transect	3	0.087	0	0.000	-	-
Season*Transect	3	0.112	0	0.000	-	-
Year*Assemblage	3	0.098	6	0.038	2.60	0.148
Season*Assemblage	3	0.085	6	0.084	1.00	0.453
Site*Assemblage	6	0.188	9	0.022	8.39	0.003*
Transect*Assemblage	9	0.022	0	0.000	-	-
Year*Season*Site	2	0.069	3	0.055	1.24	0.406
Year*Season*Transect	3	0.055	0	0.000	-	-
Year*Season*Assemblage	3	0.032	6	0.021	1.50	0.307
Year*Site*Assemblage	6	0.038	9	0.042	0.90	0.532
Season*Site*Assem	6	0.084	9	0.044	1.92	0.182
Year*Transect*Assem	9	0.042	0	0.000	-	-
Season*Transect*Assem	9	0.044	0	0.000	-	-
Year*Season*Site*Assem	6	0.021	9	0.032	0.67	0.680
Year*Season*Transect*Assem	9	0.032	0	0.000	-	-

Table A-11: Five factor nested ANOVA comparing **abundance** ($\log_{10}(x+1)$ transformed) of **red-headed honeyeaters** (*Myzomela erythrocephala)* among years (fixed), seasons (fixed), sites (random), transects (random, nested in site) and assemblages (fixed).

	df effect	MS effect	df error	MS error	F	P
Year	1	0.001	2	0.068	0.01	0.933
Season	1	3.289	2	0.009	355.87	0.003*
Site	2	0.150	3	0.126	1.19	0.416
Transect	3	0.126	0	0.000	-	-
Assemblage	3	0.434	6	0.073	5.96	0.031*
Year*Season	1	0.324	2	0.072	4.52	0.168
Year*Site	2	0.068	3	0.016	4.18	0.136
Season*Site	2	0.009	3	0.080	0.12	0.894
Year*Transect	3	0.016	0	0.000	-	-
Season*Transect	3	0.080	0	0.000	-	-
Year*Assemblage	3	0.071	6	0.040	1.77	0.253
Season*Assemblage	3	0.239	6	0.073	3.27	0.101
Site*Assemblage	6	0.073	9	0.051	1.44	0.300
Transect*Assemblage	9	0.051	0	0.000	-	-
Year*Season*Site	2	0.072	3	0.074	0.97	0.472
Year*Season*Transect	3	0.074	0	0.000	-	-
Year*Season*Assemblage	3	0.020	6	0.015	1.34	0.347
Year*Site*Assemblage	6	0.040	9	0.032	1.28	0.356
Season*Site*Assemblage	6	0.073	9	0.064	1.14	0.413
Year*Transect*Assemblage	9	0.032	0	0.000	-	-
Season*Transect*Assemblage	9	0.064	0	0.000	-	-
Year*Season*Site*Assem	6	0.015	9	0.088	0.17	0.977
Year*Season*Transect*Assem	9	0.088	0	0.000	-	-

VERTEBRATE FAUNA OF DISTURBED MANGROVES

Table A-12: Three factor nested ANOVA comparing **mammal species richness** (pooled over 4 night survey per 0.25 ha study plot) at two disturbed sites in 2001 among sites (random), transects (random, nested in site) and assemblages (fixed).

	df effect	Ms effect	df error	MS error	F	P
Site	1	0.063	2	0.063	1.00	0.423
Transect	2	0.063	0	0.000	-	-
Assemblage	3	1.729	3	1.563	1.11	0.468
Site*Assemblage	3	1.563	6	0.396	3.95	0.072
Transect*Assemblage	6	0.396	0	0.000	-	-

Table A-13: Three factor nested ANOVA comparing **mammal abundance** ($\log_{10}(x + 1)$ transformed) at two disturbed sites in 2001 among sites (random), transects (random, nested in site) and assemblages (fixed).

	df effect	Ms effect	df error	MS error	F	P
Site	1	0.004	2	0.079	0.05	0.837
Transect	2	0.079	0	0.000	-	-
Assemblage	3	0.088	3	0.079	1.12	0.467
Site*Assemblage	3	0.079	6	0.127	0.62	0.627
Transect*Assemblage	6	0.127	0	0.000	-	-

Table A-14: Four factor nested ANOVA comparing **species richness of mammals** among disturbed and undisturbed locations (fixed), sites (random, nested in disturbed), transects (random, nested in site) and assemblages (fixed). Mammal data from two disturbed sites collected in 2001 and three undisturbed sites in 1999.

**Note: Post hoc modification of the model gives a new test for assemblage—$F_{3,15}$, $p<0.05$

Year 1 : 1999	df effect	Ms effect	df error	MS error	F	P
Disturbed	1	0.104	3.00	0.215	0.48	0.537
Site	3	0.215	1.67	0.463	0.46	0.742
Transect	5	0.275	15.00	0.675	0.41	0.836
Assemblage	3	2.560	9.00	0.863	2.96	0.090**
Disturbed*Assemblage	3	0.360	9.00	0.863	0.42	0.745
Assemblage*Site	9	0.863	15.00	0.675	1.28	0.323

Table A-15: Four factor nested ANOVA comparing **species richness of mammals** among disturbed and undisturbed locations (fixed), sites (random, nested in disturbed), transects (random, nested in site) and assemblages (fixed). Mammal data from two disturbed sites collected in 2001 and three undisturbed sites in 2000.

Year 2 : 2000	df effect	Ms effect	df error	MS error	F	P
Disturbed	1	1.838	3.00	0.604	3.04	0.180
Site	3	0.604	3.55	0.778	0.78	0.571
Transect	5	0.075	15.00	0.475	0.16	0.974
Assemblage	3	4.649	9.00	1.178	3.95	0.048*
Disturbed*Assemblage	3	0.049	9.00	1.178	0.04	0.988
Assemblage*Site	9	1.178	15.00	0.475	2.48	0.058

Table A-16: Four factor nested ANOVA comparing **abundance** ($\log_{10}(x + 1)$ transformed) of **mammals** among disturbed and undisturbed locations (fixed), sites (random, nested in disturbed), transects (random, nested in site) and assemblages (fixed). Mammal data from disturbed sites collected in 2001 and undisturbed sites in 1999

Year 1: 1999	df effect	Ms effect	df error	MS error	F	P
Disturbed	1	0.047	3.00	0.391	0.12	0.753
Site	3	0.391	0.73	0.035	11.15	0.295
Transect	5	0.069	15.00	0.083	0.84	0.543
Assemblage	3	0.177	9.00	0.048	3.66	0.057
Disturbed*Assemblage	3	0.043	9.00	0.048	0.88	0.487
Assemblage*Site	9	0.049	15.00	0.083	0.58	0.791

Table A-17: Four factor nested ANOVA comparing **abundance** ($\log_{10}(x + 1)$ transformed) of **mammals** among disturbed and undisturbed sites (fixed), transects (random, nested in site) and assemblages (fixed). Mammal data from disturbed sites collected in 2001 and undisturbed sites in 2000

Year 2: 2000	df effect	Ms effect	df error	MS error	F	P
Disturbed	1	0.647	3.00	0.288	2.24	0.231
Site	3	0.288	6.29	0.162	1.78	0.247
Transect	5	0.058	15.00	0.066	0.88	0.520
Assemblage	3	0.068	9.00	0.170	0.40	0.756
Disturbed*Assemblage	3	0.132	9.00	0.170	0.77	0.539
Assemblage*Site	9	0.170	15.00	0.066	2.58	0.050*

Table A-18: Three factor nested ANOVA comparing **bird species richness** between three disturbed sites (random), transects (random, nested in site) and three assemblages (fixed).

	df effect	**Ms effect**	**df error**	**MS error**	**F**	**P**
Site	2	66.722	3	5.667	11.77	0.038*
Transect	3	5.667	0	0.000	-	-
Assemblage	2	4.056	4	12.056	0.34	0.733
Site*Assemblage	4	12.056	6	7.500	1.61	0.287
Transect*Assemblage	6	7.500	0	0.000	-	-

Table A-19: Three factor nested ANOVA comparing **bird species richness** between two disturbed sites (random), transects (random, nested in site) and four assemblages (fixed).

	df effect	**Ms effect**	**df error**	**MS error**	**F**	**P**
Site	1	9.000	2	0.00	-	-
Transect	2	0.000	0	0.00	-	-
Assemblage	3	4.833	3	25.50	0.19	0.897
Site*Assemblage	3	25.500	6	10.67	2.39	0.167
Transect*Assemblage	6	10.667	0	0.00	-	-

Table A-20: Three factor nested ANOVA comparing **abundance of birds** between three disturbed sites (random), transects (random, nested in site) and three assemblages (fixed).

	df effect	**Ms effect**	**df error**	**MS error**	**F**	**P**
Site	2	966.500	3	132.78	7.28	0.07
Transect	3	132.778	0	0.00	-	-
Assemblage	2	168.000	4	105.00	1.60	0.309
Site*Assemblage	4	105.00	6	96.11	1.09	0.439
Transect*Assemblage	6	96.11	0	0.00	-	-

Table A-21: Three factor nested ANOVA comparing **abundance** of birds between two disturbed sites (random), transects (random, nested in site) and four assemblages (fixed).

	df effect	**Ms effect**	**df error**	**MS error**	**F**	**P**
Site	1	390.06	2	13.813	28.24	0.034*
Transect	2	13.81	0	0.00	-	-
Assemblage	3	323.73	3	386.06	0.84	0.556
Site*Assemblage	3	386.06	6	203.98	1.89	0.232
Transect*Assemblage	6	203.98	0	0.00	-	-

Table A-22: Four factor nested ANOVA comparing **species richness of birds** among disturbed and undisturbed locations (fixed), sites (random, nested in disturbed), transects (random, nested in site) and assemblages (fixed). Bird data from disturbed sites collected in 2001 and undisturbed sites in 1999 and 2000.

	df effect	Ms effect	df error	MS error	F	P
Disturbed	1	0.150	3.00	13.750	0.01	0.923
Site	3	13.750	3.59	8.791	1.56	0.341
Transect	5	1.625	15.00	5.825	0.28	0.917
Assemblage	3	25.761	9.00	12.991	1.98	0.187
Disturbed*Assemblage	3	13.228	9.00	12.991	1.02	0.429
Assemblage*Site	9	12.991	15	5.825	2.23	0.082

Table A-23: Four factor nested ANOVA comparing **abundance** (data not transformed) of **birds** among disturbed and undisturbed locations (fixed), sites (random, nested in disturbed), transects (random, nested in site) and assemblages (fixed). Bird data was collected from two disturbed sites in 2001 and three undisturbed sites in 1999 and 2000.

	df effect	MS effect	df error	MS error	F	P
Disturbed	1	656.7	3.00	1500.8	0.44	0.556
Site	3	1500.8	0.04	0.00	-	-
Transect	5	32.4	15.00	212.5	0.15	0.976
Assemblage	3	674.3	9.00	163.7	4.12	0.043*
Disturbed*Assemblage	3	232.0	9.00	163.7	1.42	0.300
Assemblage*Site	9	163.7	15.00	212.5	0.77	0.645

Table A-24: Four factor nested ANOVA comparing **abundance** (data not transformed) of **carnivorous bird species** among disturbed and undisturbed locations (fixed), sites (random, nested in disturbed), transects (random, nested in site) and assemblages (fixed). Bird data was collected from two disturbed sites in 2001 and three undisturbed sites in 1999 and 2000.

	df effect	MS effect	df error	MS error	F	P
Disturbed	1	156.817	3	16.361	9.58	0.053
Site	3	16.361	6.26	21.120	0.77	0.548
Transect	5	2.025	15	5.692	0.36	0.871
Assemblage	3	145.139	9	24.787	5.86	0.017*
Disturbed*Assemblage	3	51.139	9	24.787	2.06	0.176
Assemblage*Site	9	24.787	15	5.692	4.35	0.006*

Table A-25: Four factor nested ANOVA comparing **abundance** (data not transformed) of **insectivorous bird species** among disturbed and undisturbed locations (fixed), sites (random, nested in disturbed), transects (random, nested in site) and assemblages (fixed). Bird data was collected from two disturbed sites in 2001 and three undisturbed sites in 1999 and 2000.

	df effect	MS effect	df error	MS error	F	P
Disturbed	1	264.60	3.00	115.67	2.29	0.228
Site	3	115.67	2.55	-	-	-
Assemblage	3	51.14	9.00	7.69	6.65	0.012*
Transect	5	7.00	15.00	27.87	0.25	0.933
Disturbed*Assemblage	3	19.68	9.00	7.69	2.56	0.120
Assemblage*Site	9	7.69	15.00	27.87	0.28	0.972

Table A-26: Four factor nested ANOVA comparing **abundance** (data not transformed) of **nectivorous\insectivorous bird species** among disturbed and undisturbed locations (fixed), sites (random, nested in disturbed), transects (random, nested in site) and assemblages (fixed). Bird data was collected from two disturbed sites in 2001 and three undisturbed sites in 1999 and 2000.

	df effect	MS effect	df error	MS error	F	P
Disturbed	1	555.10	3.00	663.97	0.84	0.428
Site	3	663.97	0.14	-	-	-
Assemblage	3	83.96	9.00	34.72	2.42	0.133
Transect	5	44.83	15.00	92.02	0.49	0.781
Disturbed*Assemblage	3	101.49	9.00	34.72	2.92	0.093
Assemblage*Site	9	312.52	15.00	92.02	0.38	0.928

APPENDIX B

Table B-1 : List of fauna recorded during surveys in four disturbed and three undisturbed mangroves, Darwin Harbour. Species are listed in phylogenetic order according to recent reviews (Shattuck, 1999; Martin and Davis, 2001; Jones and Morgan, 2002) and taxonomic catalogues (Anon, 2006) and includes invertebrates recorded during wet and dry seasons of 2001. Also included are species sampled during the pilot study in Charles Darwin National Park (1999) and a confirmation study in Ludmilla Bay (2000). ***** denotes introduced (non-native) species

KINGDOM ANIMALIA

PHYLUM CNIDARIA (cnidarians)

Class Anthozoa (sea anemones, corals, sea pens)

Order Actiniaria (anemones)

Unidentified sea anemone

Order Ceriantharia

Unidentified tube anemone

PHYLUM PLATYHELMINTHES (flatworms, platyhelminthes)

Class Turbellaria

?Turbellaria spp.

PHYLUM NEMERTEA (nemerteans, proboscis worms, ribbon worms)

Nemertea spp.

Order Heteronemertea

Cerebratulus sp.

PHYLUM ANNELIDA (segmented worms)

Class Polychaeta (polychaete worms)

Clade Scolecida

Family Capitellidae

Heteromastides sp.
Heteromastus sp. 1
Mediomastus sp. 1
Notomastus sp.

Family Orbiniidae

Leitoscoloplos latibranchus
Scoloplos normalis

Clade Phyllodocida

Family Glyceridae
Glycera nicobarica
Family Nephtyidae
Nephtys mesobranchia

Family Nereididae
Ceratonereis NTMW6742
Dendronereides heteropoda
Leonnates stephensoni
Namalycastis nicoleae
Namalycastis abiuma
Namanereis malaitae
Neanthes cf. *biseriata*
Nereis sp. 1
Paraleonnates bolus
Perinereis aibuhitensis
Perinereis singaporiensis
Simplisetia cf. *erythraensis*

Family Phyllodocidae
Eteone sp. 1
Phyllodoce sp. 1

Family Polynoidae
Lepidonotus sp. 1
Olgalepidonotus kumari

Family Syllidae

Syllis sp. 1

Clade Eunicida

Family Eunicidae
Marphysa mossambica

Family Lumbrineridae

Arabelloneris broomensis
Scoletoma sp. 1

Clade Sabellida

Family Sabellidae
Branchiomma sp.1
Demonax sp. 1

Clade Terebellida

Family Ampharetidae

Isolda pulchella

Family Cirratulidae

Aphelochaeta sp. 1

Cirriformia sp. 1

Family Terebellidae
Terebella tantabiddycreekensis

Family Trichobranchidae
Terebellides kowinka

Clade Spionida

Family Magelonidae
Magelona sp. 1

Family Spionidae
Aonides oxycephala
Polydora sp.
Polydora sp. 2
Polydora sp. 3
Prionospio sp. 1
Scolelepis sp. 1

PHYLUM SIPUNCULA (peanut worms, sipunculans)

Sipuncula sp. 2
Sipuncula sp. 3

Family Phascolomatidae
Phascolosoma arcuata

PHYLUM ECHIURA (echiurans, spoon worms)

Family Thalassematidae
Listriolobus bulbocaudatus

PHYLUM ARTHROPODA (arthropods)

SUBPHYLUM UNIRAMIA

Class Insecta (Insects)
Order Hymenoptera

Family Formicidae
Camponotus anderseni
Camponotus mackayensis
Camponotus sp. 3 (janeti group)
Camponotus sp. 9 (novaehollandiae group)
Camponotus sp. 10 (novaehollandiae group)
Crematogaster sp. 2 (australis group)
Crematogaster sp. 3 (group A)
Crematogaster sp. 6 (cornigera group)
Crematogaster sp. 8 (australis group)
Crematogaster sp. 9

Iridomyrmex sp. (anceps group)
Iridomyrmex sanguineus
**Monomorium floricola*
Odontomachis aff. *turneri*
Oecophylla smaragdina
Opisthopsis major
**Paratrechina longicornis*
Paratrechina sp. 3 (obscura group)
Paratrechina sp. 4 (vaga group)
Pheidole sp. 22
Pheidole sp. A
Podomyrma basalis
Polyrhachis constricta
Polyrhachis senilis
Polyrhachis sokolova
Polyrachis sp. 18
Polyrachis sp. (subgenus *Chariomyrma*)
Polyrachis sp.(subgenus *Hedomyrma*)
Polyrhachis terpsichore
**Solenopsis geminata*
Solenopsis sp. A
Tapinoma sp. 1
Tetraponera punctulata

SUBPHYLUM CRUSTACEA (crustaceans)

Class Maxillopoda

Subclass Cirripedia (barnacles)
Order Sessilia
Family Chthamalidae
Microeuraphia withersi
Family Balanidae
Balanus cf *rhizophorae*

Class Malacostraca (malacostracans, higher crustaceans)

Order Amphipoda (amphipods, beach hoppers)

Family Corophiidae
Corophiidae sp. 1
Corophiidae sp. 2
Corophiidae sp. 4

Family Hyalidae
?*Parhyale* sp.

Family Talitridae
Talitridae sp. 1
Talitridae sp. 2
Talitridae sp. 3

Order Isopoda (isopods)

Family Cirolanidae
Limicolana dinjerra

Family Sphaeromatidae
Sphaeromatidae unident sp.
Sphaeromatidae unident sp.3

Family Ligiidae
Ligia australiensis

Family Oniscidae
Oniscidae unident sp.

Order Tanaidacea (tanaids)

Family Apseudidae
Apseudes sp.

Order Decapoda (prawns, shrimps, lobsters, crabs)

Family Penaeidea
Metapenaeus insolitus

Family Sergestidae
Acetes sp.

Family Palaemonidae
Leandrites celebensis
Metapenaeus insolitus
Metapenaeus sp.
Palaemon serrifer
Periclimenes suvadivensis
Potomalpheops hanleyi

Family Alpheidae
Alpheus sp.

Family Thalassinidae
Thalassina squamifera

Family Upogebiidae
Wolffogebia inermis

Family Porcellanidae
Petrolisthes limicola
Petrolisthes haplodactylus
Petrolisthes krangiensis

Family Diogenidae
Clibanarius longitarsus
Diogenes sp.

Family Paguridae
Pagurus sp.

Family Hymenosomatidae
Elamenopsis lineata
Neorhynchoplax torrensica

Family Portunidae
Scylla serrata

Family Eriphiidae
Myomenippe fornasinii
Epixanthus dentatus

Family Pilumnidae
Heteropanope longipedes
Heteropanope glabra

Family Camptandriidae
Baruna trigranulum
Camptandrium sp. nov. 1
Camptandrium sp. nov. 2
Camptandrium sp. nov. *(*cf. *mcneilli)*
Cleistostoma sp. nov
Paracleistostoma sp. nov.
Paracleistostoma sp. nov. (cf. *wardi*)

Family Ocypodidae
Ilyoplax strigicarpus
Macropthalmus darwinensis
Macropthalmus sp. nov.
Uca capricornis
Uca dampieri
Uca flammula
Uca hirsutimanus
Uca polita
Uca seismella
Uca signata

Family Grapsidae

Subfamily Grapsinae
Metapograpsus latifrons
Metapograpsus frontalis

Subfamily Sesarminae
Clistocoeloma merguiensis
Episesarma sp. nov.
Nanosesarma batavicum
Neosarmatium meinerti
Parasesarma moluccensis
Perisesarma darwinensis
Perisesarma semperi
Sarmatium germaini
Sarmatium hegerli
Selatium brockii
Sesarmoides borneensis

Subfamily Varuninae
Ilyograpsus paludicola

PHYLUM MOLLUSCA (molluscs)

Class Polyplacophora (chitons)

Family Acanthochitonidae
Craspedoplax sp. nov.

Family Chitonidae
Acanthopleura curisiana

Class Gastropoda (gastropods, univalves)

Family Lottiidae
Patelloida cryptalirata

Family Trochidae
Monodonta labio

Family Cerithiidae
Cerithium coralium

Family Neritidae
Dostia violacea
Nerita balteata

Family Potamididae
Cerithidea obtusa
Cerithidea largillierti
Cerithideopsilla cingulata
Terebralia palustris
Terebralia semistriata
Terebralia sulcata
Telescopium telescopium

Family Thiaridae
**Melanoides tuberculatus*

Family Littorinidae
Littoraria articulata
Littoraria filosa
Peasiella tantilla

Family Iravadiidae
Iravadia australis

Family Assimineidae
Assiminea sp. 1
Assiminea sp. 2

Family Stenothyridae
Stenothyra sp.

Family Muricidae
Chicoreus capucinus

Thais trigonus

Family Columbellidae
Pseudanchis duclosianus
Zafra troglodytes

Family Nassariidae
Hebra oberwimmeri
Nassarius melanoides

Family Melongenidae
Pugilina cochlidium

Family Pyramidellidae
Odostomia sp. 1
Odostomia sp. 2
Turbonilla sp.

Family Retusidae
Retusa sp.

Family Haminoeidae
Atys sp. (cf. *ooiformis*)
Haminoea sp.

Family Onchidiidae
Onchidium sp. 1
Onchidium sp. 2
Onchidium sp. 3
Onchidium sp. 4
Onchidium sp. 5
Onchidium sp. 6

Family Amphibolidae
Salinator cf. *fragilis*

Family Ellobiidae
Auriculastra subula
Auriculastra sp. 1
Cassidula angulifera
Cassidula decussata
Cassidula aff. *doliolum*
Cylindrotis quadrasi
Ellobium aurisjudae
Melampus sp.

Class Bivalvia (bivalves, lamellibranchs)

Family Mytilidae
Brachidontes maritimus
Modiolus sp. 2
Musculista cf. *japonica*
Xenostrobus sp.

Family Arcidae
Arcopsis afra

Family Isognomonidae
Isognomon ephippium
Isognomon legumen

Family Ostreidae
Booneostrea cuculina
Saccostrea cucullata

Family Anomiidae
Enigmonia aenigmatica

Family Lucinidae
Austriella corrugata
Myrtea sp.

Family Galeommatidae
Scintilla cf. *borneensis*

Family Pharidae
Siliqua sp.

Family Tellinidae
Macoma sp.
Tellina australis
Tellina iridescens

Family Corbiculidae
Polymesoda erosa

Family Veneridae
Circe australis
Gafrarium tumidum
Pitar inconstans
Placamen calophyllum
Family Glauconomidae
Glauconome plankta

Family Lyonsiidae
Entodesma sp.

Family Pholadidae
Martesia striata

Family Teredinidae
Bactronophorus thoracites
Dicyathifer manii

Family Thraciicae
Thracia sp.

Family Laternulidae
Laternula faba
Laternula sp.

PHLYUM BRYOZOA (bryozoans, moss animals, lace corals)

Order Cheilostomata

Superfamily Buguloidae

Family Beaniidae
Amphibiobeania epiphylla (nsp)

PHYLUM ECHINODERMATA (echinoderms)

Class Ophiuroidea (brittle stars)

Family Amphiuridae
Amphioplus sp.
Amphiodia sp

PHYLUM CHORDATA (chordates)

Class Osteichthyes (bony fishes)

Family Syngnathidae (pipefishes, seahorses, seadragons)
Hippichthys parvicarinatus

Family Gobiidae
Amoya gracilis
Amoya sp.
Boleophthalmus birdsongii
Boleophthalmus caeromaculatus
Hemigobius hoevenii
Parioglossus palustris
Pandaka lidwilli
Periophthalmus argentilineatus
Periophthalmus kalolo
Periophthalmus novaeguineaensis
Pseudogobius poicilosomus
Pseudogobius sp. 3
Periopthalmodon freycineti
Gobiopterus sp.
Calamiana sp. 24
Mugilogobius filifer
Mugilogobius mertoni

Family Eleotridae
Bostrychus sinensis

Table B-2 : List of 51 **worm** species recorded in undisturbed and disturbed mangroves indicating frequency (count of abundance) and sampling season.

Species name	Wet season	Dry season	Dry season	Trophic category	Feeding guild code (after Pagliosa 2005)
	Undistur-bed	Undistur-bed	Distur-bed		
Aonides oxycephala			1	surface deposit	SDT
Aphelochaeta sp. 1			3	surface deposit	SMT
Arabelloneris broomensis		1		subsurface	BMJ
Branchiomma sp.1			1	filter feeder	FST
Ceratonereis NTMW6742		2		herbivore	HMJ
Cerebratulus sp.		1		carnivore	CMX
Cirriformia sp. 1		2	2	surface deposit	SMT
Demonax sp. 1		1		filter feeder	FST
Dendronereides heteropoda		1		surface deposit	SDJ
Eteone sp. 1			1	carnivore	CMX
Glycera nicobarica	2	7	4	carnivore	CDJ
Heteromastus sp. 1	3		5	subsurface	BMX
Heteromastus sp. 2		**		subsurface	BMX
Isolda pulchella		1		surface deposit	SST
Leitoscoloplos latibranchus	1	1	2	subsurface	BMX
Leonnates stephensoni			2	surface deposit	SDJ
Lepidonotus sp. 1		2	1	carnivore	CMJ
Listriolobus bulbocaudatus			1	surface deposit	SDX
Magelona sp. 1	1		4	surface deposit	SDT
Marphysa mossambica			2	carnivore	CMJ
Mediomastus sp. 1	1	3		subsurface	BMX
Namalycastis abiuma	1			herbivore	HMJ
Namalycastis nicoleae	1			herbivore	HMJ
Namanereis malaitae	1	1		herbivore	HMJ
Neanthes cf. *biseriata*			2	herbivore	HMJ
Nemertea spp.	2	8	3	carnivore	CMX
Nephtys mesobranchia	2	2	1	carnivore	CMJ
Nereis sp. 1	1	9	4	herbivore	HMJ
Notomastus sp.	2			subsurface	BMX
Olgalepidonotus kumari			1	carnivore	CMJ
Onuphidae unident.	1			herbivore	HDJ
Paraleonnates bolus	3	1	1	surface deposit	SDJ
Paraonidae unident.			1	surface deposit	SMX
Perinereis aibuhitensis	1	5	2	herbivore	HMJ
Perinereis singaporiensis	2	9	2	herbivore	HMJ
Phascolosoma arcuatum	1	4	12	surface deposit	SDT
Phyllodoce sp. 1		5		carnivore	CMX

Polydora sp. 1	1			surface deposit	SDT
Polydora sp. 2			1	surface deposit	SDT
Polydora sp. 3		**		surface deposit	SDT
Prionospio sp. 1		2	2	surface deposit	SDT
Scolelepis sp. 1			1	surface deposit	SDT
Scoletoma sp. 1	4	7	3	subsurface	BMJ
Scoloplos normalis			1	subsurface	BMX
Simplisetia cf. *erythraensis*			3	herbivore	HMJ
Sipuncula sp. 2		2		surface deposit	SDT
Sipuncula sp. 3		1		surface deposit	SDT
Syllis sp. 1			1	carnivore	CMJ
Terebella tantabiddycreekensis			1	surface deposit feeder	SST
Terebellides kowinka			1	surface deposit	SST
Turbellaria spp.			2	surface deposit	SMX
** Denotes species recorded only during the pilot or confirmation studies.					

Table B-3 : List of 33 **ant** species recorded in undisturbed and disturbed mangroves indicating frequency (number of records per survey) and season. * Denotes introduced species and *Inc* – incidental record

	Wet season	Dry season	Dry season	
Species name	Undisturb.	Undisturb.	Disturbed	Arboreal/ Ground
Camponotus anderseni	1	2		Arboreal
Camponotus mackayensis		1		Arboreal
Camponotus sp. 10 (novaehollandiae group)	4	1	1	Arboreal
Camponotus sp. 3 (janeti group)	2	2		Arboreal
Camponotus sp. 9 (novaehollandiae group)			1	Ground
Crematogaster sp. 2 (australis group)	1			Arboreal
Crematogaster sp. 3 (group A)	1	2	1	Arboreal
Crematogaster sp. 6 (cornigera group)			1	Arboreal
Crematogaster sp. 8 (australis group)	18	21	11	Arboreal
Crematogaster sp. 9	4	3	3	Arboreal
Iridomyrmex sanguineus			4	Ground
Iridomyrmex sp. (anceps group)			7	Ground
* *Monomorium floricola*			1	Ground
Odontomachis aff. *turneri*		1	1	Ground
Oecophylla smaragdina	3	2	2	Arboreal
Opisthopsis major	2	1		Ground
* *Paratrechina longicornis*	2	3		Ground
Paratrechina sp. 4 (vaga group)		2	2	Ground
Paratrechina sp.3 (obscura group)			2	Ground
Pheidole sp. A	2			Ground

Pheidole sp.22	3	3	4	Ground
Podomyrma basalis		1		Arboreal
Polyrachis sp.18	3	1	3	Arboreal
Polyrhachis constricta	1		7	Ground
Polyrhachis senilis		1		Ground
Polyrhachis sokolova	16	19	16	Ground
Polyrhachis sp. (subgenus *Chariomyrma)*		1		Ground
Polyrhachis sp. (subgenus *Hedomyrma)*		*Inc*		Unknown
Polyrhachis terpsichore	10	12	6	Arboreal
* *Solenopsis geminata*			1	Ground
Solenopsis sp. A		1		Ground
Tapinoma sp.1	2	7	2	Arboreal
Tetraponera punctulata	8	7	4	Arboreal

Table B-4 : List of 23 **crustacean** species recorded in undisturbed and disturbed mangroves indicating frequency (number of records per survey) and season. See Table B-4 for crabs. (*** denotes taxon not included in species tally)

	Wet season	Dry season	Dry season
Species name	Undisturbed	Undisturbed	Disturbed
Acetes sp.			1
Alpheus sp.	5		2
Apseudes sp.	2	6	
Balanus cf. *rhizophorae*	2	4	
Corophiidae sp. 1		1	
Corophiidae sp. 2	1	2	
Corophiidae sp. 4		1	
Hyalidae unident. *(?Parhyale sp.)*	9	7	2
Leandrites celebensis	7	1	2
Ligia australiensis	10	3	3
Limicolana dinjerra	3	2	1
Metapenaeus insolitus	7	1	1
Microeuraphia withersi	3	5	
Oniscidae unident.			1
Palaemon serrifer			1
Periclimenes suvadivensis	4	5	5
Potamalpheops hanleyi	1		
Sphaeromatidae sp.3		1	
Talitridae sp. 1	3	4	2
Talitridae sp. 2	3	7	2
Talitridae sp. 3	1		
Talitridae unident.***	5	3	
Thalassina anomala	2	1	2
Wolffogebia inermis	1	2	

Table B-5 : List of 44 **crab** species recorded in undisturbed and disturbed mangroves indicating frequency (count of abundance) and season. (*** denotes taxon not included in species tally)

	Wet season	Dry season	Dry season
Species name	Undisturbed	Undisturbed	Disturbed
Baruna trigranulum	1	7	2
Camptandrium cf. *mcneilli*	14	9	20
Camptandrium sp. 2		2	1
Camptandrium sp. nov. 1	3	6	10
Cleistostoma sp. nov.	1	9	12
Clibanarius longitarsus	17	16	7
Clistocoeloma merguiensis	9	10	9
Diogenes sp.		1	1
Elamenopsis lineata			1
Episesarma sp. nov.	2	2	4
Epixanthus dentatus		1	
Eriphidae unident.		1	1
Heteranope longipedes	5	6	4
Ilyograpsus paludicola	3	1	8
Ilyoplax strigicarpus		7	5
Macropthalmus darwinensis	3		5
Macropthalmus sp. nov.	2		6
Metopograpsis frontalis	27	18	14
Myomenippe fornasinii		1	
Nanosesarma batavicum	1	8	10
Neorhynchoplax torrensica	1	4	
Neosarmatium meinerti	5	1	2
Pagurus sp.		4	
Paracleistostoma sp. nov.	5	3	8
Paracleistostoma sp. nov. (cf. *wardi)*	7	4	9
Parasesarma moluccensis	3	2	4
Perisesarma darwinensis	58	41	30
Perisesarma immature ***	7	33	7
Perisesarma semperi longicristatum	43	50	36
Petrolisthes haplodactylus			1
Petrolisthes kranjiensis	1	3	
Petrolisthes limicola	2	6	2
Sarmatium germaini	1	1	
Sarmatium hegerli	1	1	1
Scylla serrata	3		
Selatium brockii		1	1
Sesarmoides borneensis	5	2	
Uca capricornis	7	4	10

Uca dampieri		1	1
Uca flammula	13	11	21
Uca hirsutimanus	24	18	27
Uca immature ***	7	27	39
Uca polita		5	3
Uca seismella			1
Uca signata	1	5	28

Table B-6 : List of 49 **gastropod** molluscs recorded in undisturbed and disturbed mangroves indicating frequency (count of abundance) and season. New species records for mangrove habitats and new records for Australia also shown.

Species name	Wet season	Dry season	Dry season	New mang-rove record	New record NT/ Australia
	Undisturbed	Undisturbed	Disturbed		
Acanthopleura curtisiana			1	**	
Assiminea sp. 1	2	5	1	*	
Assiminea sp. 2	1	1		*	
Atys sp.		1	2	*	
Auriculastra sp. 1			1		
Auriculastra subula		1	2		
Cassidula aff. *doliolum*	1	5	1		
Cassidula angulifera	5	8			
Cassidula decussata	9	6			
Cerithidea largillierti	4	2	1		
Cerithidea obtusa	21	20	8		
Cerithideopsilla cingulata	1	1	1		
Cerithium coralium		1			
Chicoreus capucinus	9	2	2		
Clypeomorus batillariaeformis			3		
Craspedoplax sp. nov.	1			*	New species
Cylindrotis quadrasi	1	1			
Ellobium aurisjudae	1				
Haminoea sp.		5	1		
Hebra oberwimmeri	1	2	1	*	
Littoraria articulata	4	5	8		
Littoraria filosa	4	4	3		
Melampus sp.			2		
Melanoides tuberculatus			1		
Monodonta labio			1		
Nassarius melanoides	4	1	2		
Nerita balteata	33	32	9		

Neritina violacea	1		1		
Odostomia sp. 1	1		1		
Odostomia sp. 2			1		
Onchidium sp. 1	1		1		
Onchidium sp. 2	1				
Onchidium sp. 3	3	5	3		
Onchidium sp. 4		3	1		
Onchidium sp. 5		1	1		
Onchidium sp. 6		1			
Patelloida cryptalirata			3		
Peasiella tantilla			6	*	
Pugilina cochlidium	1				
Retusa sp.	1	1	1	*	
Salinator fragilis	6	15	4		
Stenothyra sp.	1			*	
Telescopium telescopium	11	8	5		
Terebralia palustris	5	3	1		
Terebralia semistriata	6	13	2		
Terebralia sulcata	3	4	1		
Thais trigonus	1	1			
Turbonilla sp.	3	2			
Zafra troglodites			1		

Table B-7 : List of 26 **bivalve** molluscs recorded in undisturbed and disturbed mangroves indicating frequency (count of abundance) and season. New species records for mangrove habitats and new records for Australia also shown.

Species name	Wet season Undisturbed	Dry season Undisturbed	Dry season Disturbed	New mang-rove record	New record NT/ Australia
Arcopsis afra	1	1	2	*	
Austriella corrugata	1		1		
Bactrinophorus thoracites		2			
Booneostrea cuculina	1				
Brachidontes maritimus	1	6	4	*	
Circe australis			2		
Dicyathifer manii		1	5		
Enigmonia aenigmatica	4	6	3		
Entodesma sp.	1	1			
Gafrarium tumidum			1		
Glauconome plankta	9	1	2		
Isognomon ephippium	2	4	2		
Isognomon legumen			2	*	Aus

Laternula sp.	2	7			
Macoma sp.	1	2	3		
Martesia striata		1	2	*	
Modioulus sp. 2	2	1			
Musculista cf. *japonica*		2			
Pitar inconstans	1	6	1		
Placamen calophyllum			2		
Polymesoda erosa	1	1			
Saccostrea cucullata	1	10	3		
Siliqua sp.	1			*	
Telina irridescens			1		
Thracia sp.		6	3		
Xenostrobus sp.	3	6	1		

Table B-8 : List of 14 **fish** species recorded in undisturbed and disturbed mangroves indicating frequency (count of abundance) and season. (*** denotes taxon not included in species tally)

	Wet season	Dry season	Dry season
Species name	Undisturbed	Undisturbed	Disturbed
Amoya gracilis	4	12	10
Amoya sp.	3		1
Bostrychus sinensis	1	1	1
Calamiana sp. 24			1
Gobiopterus sp.	1	2	1
Hemigobius hoevenii			2
Hippichthys parvicarinatus	1		
Mugilogobius filifer	13	11	4
Pandaka lidwilli	3	5	8
Parioglossus palustris		2	
Periophthalmus argentilineatus	2	3	7
Periophthalmus kalolo			1
Periophthalmus novaeguineaensis		6	8
Periophthalmus unident.***	20	10	2
Pseudogobius sp. 3	2	1	12

ANALYSES FOR CHAPTER 5.

Significant main effects or interactions at $p<0.05$ are denoted by an asterisk (*) in the P column and highlighted with grey shading.

‡ indicates post-hoc modification of the model (see Winer et al., 1991).

Table B-9: Four factor nested ANOVA comparing **invertebrate species richness** (untransformed data) between seasons (fixed), sites (random), transects (random, nested in site) and assemblages (fixed). Data from the four sampling techniques pooled and means calculated for each study plot from three replicate sampling stations.

	df effect	MS effect	df error	MS error	F	P
Season	1	91.840	2	5.299	17.33	0.053
Site	2	110.465	3	28.757	3.84	0.149
Transect	3	28.757	96	6.736	4.27	0.007*
Assemblage	3	557.229	6	34.826	16.00	0.003*
Season*site	2	5.299	3	17.313	0.31	0.757
Season*transect	3	17.313	96	6.736	2.57	0.059
Season*assembalge	3	57.729	6	5.160	11.19	0.007*
Site*transect	6	34.826	9	15.887	2.19	0.140
Transect*assemblage	9	15.887	96	6.736	2.36	0.019*
Season*site*assemblage	6	5.160	9	11.220	0.46	0.822
Season*transect*assemblage	9	11.220	96	6.736	1.67	0.108

Table B-10: Four factor nested ANOVA comparing **invertebrate species abundance** ($\log_{10}(x + 1)$ transformed total abundance) between seasons (fixed), sites (random), transects (random, nested in site) and assemblage (fixed). Data from the four sampling techniques pooled and means calculated for each study plot from three replicate sampling stations

	df effect	MS effect	df error	MS error	F	P
Season	1	0.002	2	0.001	1.37	0.363
Site	2	0.410	3	0.139	2.96	0.195
Transect	3	0.139	96	0.042	3.33	0.023*
Assemblage	3	3.639	6	0.090	40.21	0.000*
Season*site	2	0.001	3	0.039	0.03	0.968
Season*transect	3	0.039	96	0.042	0.95	0.420
Season*assemblage	3	0.104	6	0.049	2.11	0.201
Site*assemblage	6	0.090	9	0.057	1.58	0.258
Transect*assemblage	9	0.057	96	0.042	1.38	0.209
Season*site*assemblage	6	0.049	9	0.069	0.71	0.649
Season*transect*assemblage	9	0.069	96	0.042	1.66	0.110

Table B-11: Four factor nested ANOVA comparing **worm species richness** (untransformed data) between seasons (fixed), sites (random), transects (random, nested in site) and assemblages (fixed). Data from the four sampling techniques pooled and means calculated for each sampling station from three replicates.

	df effect	MS effect	df error	MS error	F	P
Season	1	13.444	2	0.507	26.52	0.036*
Site	2	6.715	3	2.264	2.97	0.195
Transect	3	2.264	96	0.924	2.45	0.068
Assemblage	3	17.435	6	4.206	4.15	0.066
Season*site	2	0.507	3	0.153	3.32	0.174
Season*transect	3	0.153	96	0.924	0.17	0.919
Season*assemblage	3	7.593	6	1.627	4.67	0.052
Site*assemblage	6	4.206	9	2.319	1.81	0.203
Transect*assemblage	9	2.319	96	0.924	2.51	0.013*
Season*site*assemblage	6	1.627	9	0.653	2.49	0.105
Season*transect*assemblage	9	0.653	96	0.924	0.71	0.701

Table B-12: Four factor nested ANOVA comparing **worm species abundance** ($\log_{10}(x + 1)$ transformed total abundance) between seasons (fixed), sites (random), transects (random, nested in site) and assemblage (fixed). Data from the four sampling techniques pooled and means calculated per sampling station from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Season	1	0.428	2	0.010	41.51	0.023*
Site	2	0.356	3	0.093	3.85	0.149
Transect	3	0.093	96	0.041	2.26	0.086
Assemblage	3	0.892	6	0.212	4.20	0.064
Season*site	2	0.010	3	0.015	0.71	0.561
Season*transect	3	0.015	96	0.041	0.36	0.784
Season*assemblage	3	0.285	6	0.122	2.34	0.173
Site*assemblage	6	0.212	9	0.098	2.17	0.142
Transect*assemblage	9	0.098	96	0.041	2.39	0.017*
Season*site*assemblage	6	0.122	9	0.039	3.13	0.061
Season*transect*assemblage	9	0.039	96	0.041	0.95	0.485

Table B-13: Four factor nested ANOVA comparing abundance ($\log_{10}(x + 1)$ transformed total abundance) of **carnivorous worms** between seasons (fixed), sites (random), transects (random, nested in site) and assemblage (fixed). Data from the four sampling techniques pooled and means calculated per sampling station from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Season ‡	1	0.310	96	0.024	12.92	0.001*
Site ‡	2	0.101	96	0.024	4.21	0.018*
Transect	3	0.015	96	0.024	0.63	0.596
Assemblage ‡	3	0.131	96	0.024	5.46	0.001*
Season*site	2	0.040	3	0.010	4.00	0.143
Season*transect	3	0.010	96	0.024	0.41	0.744
Season*assemblage	3	0.039	6	0.016	2.35	0.172
Site*assemblage	6	0.034	9	0.033	1.05	0.454
Transect*assemblage	9	0.033	96	0.024	1.36	0.216
Season*site*assemblage	6	0.016	9	0.010	1.67	0.235
Season*transect*assemblage	9	0.010	96	0.024	0.41	0.927

Table B-14: Four factor nested ANOVA comparing abundance ($\log_{10}(x + 1)$ transformed total abundance) of **herbivorous worms** between seasons (fixed), sites (random), transects (random, nested in site) and assemblage (fixed). Data from the four sampling techniques pooled and means calculated per sampling station from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Season	1	0.174	2	0.054	3.20	0.215
Site	2	0.068	3	0.037	1.81	0.305
Transect	3	0.037	96	0.012	3.01	0.034*
Assemblage	3	0.348	6	0.091	3.81	0.077
Season*site	2	0.054	96	0.012	4.50	0.014*
Season*transect	3	0.011	96	0.012	0.88	0.454
Season*assemblage	3	0.082	6	0.033	2.44	0.162
Site*assemblage	6	0.091	9	0.046	1.98	0.172
Transect*assemblage	9	0.046	96	0.012	3.70	0.001*
Season*site*assemblage	6	0.033	9	0.021	1.61	0.251
Season*transect*assemblage	9	0.021	96	0.012	1.67	0.106

Table B-15: Four factor nested ANOVA comparing abundance ($\log_{10}(x + 1)$ transformed total abundance) of **surface deposit feeding worms** between seasons (fixed), sites (random), transects (random, nested in site) and assemblage (fixed). Data from the four sampling techniques pooled and means calculated per sampling station from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Season	1	0.044	2	0.003	12.85	0.070
Site ‡	2	0.057	96	0.015	3.80	0.026*
Transect	3	0.008	96	0.015	0.56	0.645
Assemblage	3	0.025	6	0.020	1.25	0.371
Season*site	2	0.003	3	0.001	4.06	0.140
Season*transect	3	0.001	96	0.015	0.06	0.983
Season*assemblage	3	0.012	6	0.011	1.16	0.399
Site*assemblage	6	0.020	9	0.014	1.42	0.306
Transect*assemblage	9	0.014	96	0.015	0.92	0.508
Season*site*assemblage	6	0.011	9	0.004	2.70	0.087
Season*transect*assemblage	9	0.004	96	0.015	0.26	0.984

Table B-16: Four factor nested ANOVA comparing abundance ($\log_{10}(x + 1)$ transformed total abundance) of **sub-surface deposit feeding worms** between seasons (fixed), sites (random), transects (random, nested in site) and assemblage (fixed). Data from the four sampling techniques pooled and means calculated per sampling station from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Season	1	0.008	2	0.001	14.73	0.062
Site	2	0.126	3	0.070	1.81	0.305
Transect	3	0.070	96	0.021	3.24	0.026*
Assemblage	3	0.184	6	0.018	10.30	0.009*
Season*site	2	0.001	3	0.012	0.05	0.956
Season*transect	3	0.012	96	0.021	0.57	0.633
Season*assemblage	3	0.022	6	0.010	2.26	0.182
Site*assemblage	6	0.018	9	0.019	0.94	0.513
Transect*assemblage	9	0.019	96	0.021	0.89	0.540
Season*site*assemblage	6	0.010	9	0.041	0.24	0.951
Season*transect*assemblage	9	0.041	96	0.021	1.90	0.061

Table B-17: Four factor nested ANOVA comparing **ant species richness** (untransformed data) between seasons (fixed), sites (random), transects (random, nested in site) and assemblages (fixed) in **undisturbed** mangroves. Means calculated for each sampling station from three replicates.

	df effect	MS effect	df error	MS error	F	P
Season	1	0.840	2	5.674	0.15	0.737
Site	2	1.021	3	0.701	1.46	0.362
Transect	3	0.701	96	0.722	0.97	0.410
Assemblage	3	6.525	6	1.817	3.59	0.086
Season*site ‡	2	5.674	96	0.722	9.18	0.000*
Season*transect	3	0.618	96	0.722	0.86	0.467
Season*assemblage	3	1.137	6	0.914	1.24	0.374
Site*assemblage	6	1.817	9	0.924	1.97	0.174
Transect*assemblage	9	0.924	96	0.722	1.28	0.258
Season*site*assemblage	6	0.914	9	0.914	1.00	0.480
Season*transect*assemblage	9	0.914	96	0.722	1.27	0.265

Table B-18: Four factor nested ANOVA comparing **crustacean species richness** (untransformed data) between seasons (fixed), sites (random), transects (random, nested in site) and assemblages (fixed) in **undisturbed** mangroves. Means calculated for each sampling station from three replicates.

	df effect	MS effect	df error	MS error	F	P
Season	1	0.444	2	1.444	0.31	0.635
Site	2	4.111	3	15.056	0.27	0.778
Transect	3	15.056	96	2.222	6.78	0.000*
Assemblage	3	142.417	6	3.778	37.70	0.000*
Season*site	2	1.444	3	0.694	2.08	0.271
Season*transect	3	0.694	96	2.222	0.31	0.816
Season*assemblage ‡	3	8.278	96	2.222	4.52	0.005*
Site*assemblage	6	3.778	9	3.444	1.10	0.432
Transect*assemblage	9	3.444	96	2.222	1.55	0.142
Season*site*assemblage	6	1.833	9	1.972	0.93	0.518
Season*transect*assemblage	9	1.972	96	2.222	0.89	0.539

Table B-19: Four factor nested ANOVA comparing **crustacean species abundance** ($\log_{10}(x + 1)$ transformed total abundance) between seasons (fixed), sites (random), transects (random, nested in site) and assemblage (fixed). Data from the four sampling techniques pooled and means calculated per sampling station for all sampling techniques from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Season	1	0.067	2	0.068	0.98	0.426
Site	2	0.235	3	0.374	0.63	0.592
Transect	3	0.374	96	0.074	5.07	0.003*
Assemblage	3	4.833	6	0.050	97.22	0.000*
Season*site	2	0.068	3	0.038	1.79	0.308
Season*transect	3	0.038	96	0.074	0.52	0.672
Season*assemblage	3	0.186	6	0.065	2.87	0.126
Site*assemblage	6	0.050	9	0.102	0.49	0.802
Transect*assemblage	9	0.102	96	0.074	1.38	0.208
Season*site*assemblage	6	0.065	9	0.065	1.00	0.478
Season*transect*assemblage	9	0.065	96	0.074	0.88	0.547

Table B-20: Four factor nested ANOVA comparing **crab species richness** (untransformed data) between seasons (fixed), sites (random), transects (random, nested in site) and assemblages (fixed) in **undisturbed** mangroves. Means calculated for each sampling station for all sampling techniques from three replicates.

	df effect	MS effect	df error	MS error	F	P
Season	1	2.007	2	1.03	1.95	0.297
Site	2	5.028	3	4.30	1.17	0.421
Transect	3	4.299	96	1.72	2.50	0.064
Assemblage	3	91.877	6	3.04	30.25	0.001*
Season*site	2	1.028	3	0.41	2.51	0.229
Season*transect	3	0.410	96	1.72	0.24	0.870
Season*assemblage	3	6.451	6	1.33	4.84	0.048*
Site*assemblage	6	3.037	9	1.58	1.93	0.181
Transect*assemblage	9	1.576	96	1.72	0.92	0.515
Season*site*assemblage	6	1.333	9	1.91	0.70	0.659
Season*transect*assemblage	9	1.910	96	1.72	1.11	0.364

Table B-21: Four factor nested ANOVA comparing **crab species abundance** ($\log_{10}(x + 1)$ transformed total abundance) between seasons (fixed), sites (random), transects (random, nested in site) and assemblage (fixed). Data from the four sampling techniques pooled and means calculated per sampling station for all sampling techniques from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Season	1	0.033	2	0.016	2.08	0.286
Site ‡	2	0.236	96	0.053	3.93	0.023*
Transect	3	0.060	96	0.053	1.12	0.346
Assemblage	3	3.847	6	0.110	34.85	0.000*
Season*site	2	0.016	3	0.022	0.74	0.547
Season*transect	3	0.022	96	0.053	0.41	0.749
Season*assemblage	3	0.299	6	0.044	6.75	0.024*
Site*assemblage	6	0.110	9	0.037	2.95	0.071
Transect*assemblage	9	0.037	96	0.053	0.70	0.705
Season*site*assemblage	6	0.044	9	0.104	0.43	0.844
Season*transect*assemblage	9	0.104	96	0.053	1.95	0.054

Table B-22: Four factor nested ANOVA comparing **grapsid crab species richness** (untransformed data) between seasons (fixed), sites (random), transects (random, nested in site) and assemblages (fixed) in **undisturbed** mangroves. Means calculated for each sampling station for all sampling techniques from three replicates.

	df effect	MS effect	df error	MS error	F	P
Season	1	0.340	2	0.34	1.00	0.423
Site	2	1.938	3	1.03	1.87	0.297
Transect	3	1.035	96	0.76	1.35	0.261
Assemblage ‡	3	3.766	96	0.76	4.96	0.003*
Season*site	2	0.340	3	0.95	0.36	0.726
Season*transect	3	0.951	96	0.76	1.25	0.298
Season*assemblage ‡	3	2.359	6	0.22	10.73	0.008*
Site*assemblage	6	0.947	96	0.48	1.98	0.172
Transect*assemblage	9	0.479	96	0.76	0.63	0.771
Season*site*assemblage	6	0.220	9	0.40	0.56	0.756
Season*transect*assemblage	9	0.396	96	0.76	0.52	0.858

Table B-23: Four factor nested ANOVA comparing **grapsid crab species abundance** ($\log_{10}(x + 1)$ transformed total abundance) between seasons (fixed), sites (random), transects (random, nested in site) and assemblage (fixed). Data from the four sampling techniques pooled and means calculated per sampling station for all sampling techniques from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Season	1	0.005	2	0.047	0.11	0.776
Site ‡	2	0.403	96	0.077	5.23	0.007*
Transect	3	0.086	96	0.077	1.11	0.348
Assemblage	3	1.566	6	0.165	9.49	0.011*
Season*site	2	0.047	3	0.064	0.73	0.553
Season*transect	3	0.064	96	0.077	0.83	0.478
Season*assemblage	3	0.311	6	0.051	6.06	0.030*
Site*assemblage	6	0.165	9	0.065	2.52	0.103
Transect*assemblage	9	0.065	96	0.077	0.85	0.573
Season*site*assemblage	6	0.051	9	0.089	0.57	0.743
Season*transect*assemblage	9	0.089	96	0.077	1.16	0.328

Table B-24: Four factor nested ANOVA comparing **ocypodid crab species richness** (untransformed data) between seasons (fixed), sites (random), transects (random, nested in site) and assemblages (fixed) in **undisturbed** mangroves. Means calculated for each sampling station for all sampling techniques from three replicates.

	df effect	MS effect	df error	MS error	F	P
Season	1	0.007	2	0.05	0.14	0.742
Site	2	0.049	3	0.53	0.09	0.916
Transect	3	0.535	96	0.30	1.79	0.154
Assemblage	3	14.674	6	1.72	8.55	0.014*
Season*site	2	0.049	3	0.42	0.11	0.895
Season*transect	3	0.424	96	0.30	1.42	0.242
Season*assemblage	3	0.100	6	0.36	0.27	0.842
Site*assemblage	6	1.715	9	0.55	3.10	0.062
Transect*assemblage	9	0.553	96	0.30	1.85	0.069
Season*site*assemblage	6	0.363	9	0.37	0.99	0.486
Season*transect*assemblage	9	0.368	96	0.30	1.23	0.284

Table B-25: Four factor nested ANOVA comparing **ocypodid crab species abundance** ($\log_{10}(x + 1)$ transformed total abundance) between seasons (fixed), sites (random), transects (random, nested in site) and assemblage (fixed). Data from the four sampling techniques pooled and means calculated per sampling station for all sampling techniques from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Season	1	0.094	2	0.009	10.50	0.084
Site	2	0.063	3	0.013	4.80	0.116
Transect	3	0.013	96	0.048	0.27	0.844
Assemblage	3	3.099	6	0.158	19.60	0.002*
Season*site	2	0.009	3	0.063	0.14	0.873
Season*transect	3	0.063	96	0.048	1.33	0.270
Season*assemblage	3	0.221	6	0.025	8.74	0.013*
Site*assemblage ‡	6	0.158	96	0.048	3.29	0.005*
Transect*assemblage	9	0.057	96	0.048	1.20	0.302
Season*site*assemblage	6	0.025	9	0.041	0.62	0.709
Season*transect*assemblage	9	0.041	96	0.048	0.85	0.571

Table B-26: Four factor nested ANOVA comparing **abundance of *Perisesarma darwinensis*** ($\log_{10}(x + 1)$ transformed total abundance) between seasons (fixed), sites (random), transects (random, nested in site) and assemblage (fixed). Data from the four sampling techniques pooled and means calculated per sampling station for all sampling techniques from three replicate samples. Two assemblages were analysed (tidal flat and hinterland margin).

	df effect	MS effect	df error	MS error	F	P
Season ‡	1	0.408	48	0.055	7.42	0.009*
Site	2	0.018	3	0.092	0.20	0.831
Transect	3	0.092	48	0.055	1.68	0.185
Assemblage	1	2.013	2	0.244	8.26	0.103
Season*site	2	0.035	3	0.028	1.27	0.398
Season*transect	3	0.028	48	0.055	0.51	0.678
Season*assemblage	1	0.022	2	0.053	0.42	0.584
Site*assemblage	2	0.244	3	0.032	7.59	0.067
Transect*assemblage	3	0.032	48	0.055	0.59	0.626
Season*site*assemblage	2	0.053	3	0.107	0.50	0.650
Season*transect*assemblage	3	0.107	48	0.055	1.95	0.134

Table B-27: Four factor nested ANOVA comparing **abundance of *Perisesarma semperi*** ($\log_{10}(x + 1)$ transformed total abundance) between seasons (fixed), sites (random), transects (random, nested in site) and assemblage (fixed). Data from the four sampling techniques pooled and means calculated per sampling station for all sampling techniques from three replicate samples. Two assemblages were analysed (tidal creek and seaward).

	df effect	MS effect	df error	MS error	F	P
Season	1	0.344	2	0.070	4.94	0.156
Site	2	0.103	3	0.215	0.48	0.659
Transect	3	0.215	48	0.095	2.26	0.094
Assemblage	1	1.322	2	0.066	19.88	0.047*
Season*site	2	0.070	3	0.131	0.53	0.635
Season*transect	3	0.131	48	0.095	1.38	0.260
Season*assemblage	1	0.000	2	0.021	0.02	0.899
Site*assemblage	2	0.066	3	0.248	0.27	0.781
Transect*assemblage	3	0.248	48	0.095	2.61	0.063
Season*site*assemblage	2	0.021	3	0.110	0.19	0.838
Season*transect*assemblage	3	0.110	48	0.095	1.16	0.335

Table B-28: Four factor nested ANOVA comparing **abundance of *Uca hirsutimanus*** ($\log_{10}(x + 1)$ transformed total abundance) between seasons (fixed), sites (random), transects (random, nested in site) and assemblage (fixed). Data from the four sampling techniques pooled and means calculated per sampling station for all sampling techniques from three replicate samples. Two assemblages were analysed (tidal creek and seaward).

	df effect	MS effect	df error	MS error	F	P
Season	1	0.121	2	0.007	17.79	0.052
Site	2	0.010	3	0.062	0.17	0.853
Transect	3	0.062	48	0.065	0.96	0.418
Assemblage	1	2.665	2	0.256	10.42	0.084
Season*site	2	0.007	3	0.050	0.14	0.878
Season*transect	3	0.050	48	0.065	0.78	0.513
Season*assemblage	1	0.043	2	0.040	1.07	0.410
Site*assemblage	2	0.256	3	0.150	1.70	0.321
Transect*assemblage	3	0.150	48	0.065	2.33	0.086
Season*site*assemblage	2	0.040	3	0.086	0.46	0.668
Season*transect*assemblage	3	0.086	48	0.065	1.33	0.274

Table B-29: Four factor nested ANOVA comparing **gastropod species richness** (untransformed data) between seasons (fixed), sites (random), transects (random, nested in site) and assemblages (fixed) in **undisturbed** mangroves. Means calculated for each sampling station for all sampling techniques from three replicates.

	df effect	MS effect	df error	MS error	F	P
Season	1	1.563	2	0.333	4.69	0.163
Site	2	27.250	3	1.910	14.27	0.029*
Transect	3	1.910	96	1.188	1.61	0.193
Assemblage	3	57.340	6	11.639	4.93	0.047*
Season*site	2	0.333	3	5.910	0.06	0.946
Season*transect	3	5.910	96	1.188	4.98	0.003*
Season*assemblage	3	5.488	6	0.981	5.59	0.036*
Site*assemblage	6	11.639	9	1.613	7.21	0.005*
Transect*assemblage	9	1.613	96	1.188	1.36	0.218
Season*site*assemblage	6	0.981	9	3.058	0.32	0.910
Season*transect*assemblage	9	3.058	96	1.188	2.58	0.011*

Table B-30: Four factor nested ANOVA comparing **gastropod species abundance**($\log_{10}(x + 1)$ transformed total abundance) between seasons (fixed), sites (random), transects (random, nested in site) and assemblage (fixed). Data from the four sampling techniques pooled and means calculated per sampling station for all sampling techniques from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Season	1	0.006	2	0.090	0.07	0.817
Site	2	1.219	3	0.105	11.60	0.039*
Transect	3	0.105	96	0.072	1.46	0.230
Assemblage	3	2.639	6	0.419	6.30	0.028*
Season*site	2	0.090	3	0.075	1.20	0.415
Season*transect	3	0.075	96	0.072	1.04	0.379
Season*assemblage ‡	3	0.308	96	0.072	4.28	0.007*
Site*assemblage	6	0.419	9	0.057	7.41	0.004*
Transect*assemblage	9	0.057	96	0.072	0.79	0.630
Season*site*assemblage	6	0.081	9	0.107	0.75	0.623
Season*transect*assemblage	9	0.107	96	0.072	1.49	0.161

Table B-31: Four factor nested ANOVA comparing **bivalve species richness** (untransformed data) between seasons (fixed), sites (random), transects (random, nested in site) and assemblages (fixed) in **undisturbed** mangroves. Means calculated for each sampling station for all sampling techniques from three replicates.

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Season	1	6.250	2	0.521	12.00	0.074
Site	2	3.521	3	1.208	2.91	0.198
Transect	3	1.208	96	0.632	1.91	0.133
Assemblage	3	13.852	6	0.956	14.49	0.004*
Season*site	2	0.521	3	1.458	0.36	0.726
Season*transect	3	1.458	96	0.632	2.31	0.081
Season*assemblage	3	3.583	6	0.271	13.23	0.005*
Site*assemblage	6	0.956	9	1.264	0.76	0.621
Transect*assemblage	9	1.264	96	0.632	2.00	0.047*
Season*site*assemblage	6	0.271	9	0.662	0.41	0.856
Season*transect*assemblage	9	0.662	96	0.632	1.05	0.409

Table B-32: Four factor nested ANOVA comparing **bivalve species abundance** ($\log_{10}(x + 1)$ transformed total abundance) between seasons (fixed), sites (random), transects (random, nested in site) and assemblage (fixed) in undisturbed mangroves. Data from the four sampling techniques pooled and means calculated per sampling station for all sampling techniques from three replicate samples

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Season	1	0.387	2	0.027	14.61	0.062
Site ‡	2	0.213	96	0.054	3.94	0.023*
Transect	3	0.053	96	0.054	0.97	0.412
Assemblage	3	1.061	6	0.067	15.84	0.003*
Season*site	2	0.027	3	0.164	0.16	0.857
Season*transect	3	0.164	96	0.054	3.00	0.034*
Season*assemblage	3	0.321	6	0.026	12.28	0.006*
Site*assemblage	6	0.067	9	0.088	0.76	0.617
Transect*assemblage	9	0.088	96	0.054	1.61	0.122
Season*site*assemblage	6	0.026	9	0.063	0.41	0.852
Season*transect*assemblage	9	0.063	96	0.054	1.16	0.331

Table B-33: Four factor nested ANOVA comparing **fish species richness** (untransformed data) between seasons (fixed), sites (random), transects (random, nested in site) and assemblages (fixed) in **undisturbed** mangroves. Means calculated for each sampling station for all sampling techniques from three replicates.

	df effect	MS effect	df error	MS error	F	P
Season	1	0.563	2	1.521	0.37	0.605
Site	2	1.688	3	3.618	0.47	0.666
Transect	3	3.618	96	0.729	4.96	0.003*
Assemblage	3	12.544	6	1.558	8.05	0.016*
Season*site	2	1.521	3	0.285	5.34	0.103
Season*transect	3	0.285	96	0.729	0.39	0.760
Season*assemblage	3	0.785	6	0.688	1.14	0.405
Site*assemblage	6	1.558	9	2.396	0.65	0.691
Transect*assemblage	9	2.396	96	0.729	3.29	0.002*
Season*site*assemblage	6	0.688	9	1.025	0.67	0.677
Season*transect*assemblage	9	1.025	96	0.729	1.41	0.196

Table B-34: Four factor nested ANOVA comparing **fish species abundance** ($\log_{10}(x + 1)$ transformed total abundance) between seasons (fixed), sites (random), transects (random, nested in site) and assemblage (fixed) in undisturbed mangroves. Data from the four sampling techniques pooled and means calculated per sampling station for all sampling techniques from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Season	1	0.020	2	0.072	0.28	0.651
Site	2	0.150	3	0.103	1.46	0.360
Transect	3	0.103	96	0.045	2.26	0.086
Assemblage	3	0.590	6	0.185	3.18	0.106
Season*site	2	0.072	3	0.068	1.06	0.448
Season*transect	3	0.068	96	0.045	1.49	0.223
Season*assemblage	3	0.041	6	0.078	0.53	0.676
Site*assemblage	6	0.185	9	0.161	1.15	0.406
Transect*assemblage	9	0.161	96	0.045	3.54	0.001*
Season*site*assemblage	6	0.078	9	0.096	0.81	0.586
Season*transect*assemblage	9	0.096	96	0.045	2.11	0.036*

REFERENCES – Appendix B

Anon (2006) Australian Faunal Directory. Australian Biological Resources Study. In. Australian Government. Department of the Environment and Heritage website. http://www.deh.gov.au/biodiversity/abrs

Jones DS, Morgan GJ (2002) A field guide to Crustaceans of Australian waters. Reed New Holland, Sydney, Australia

Martin JW, Davis GE (2001) An updated classification of the recent Crustacea. Natural History Museum of Los Angeles County

Shattuck SO (1999) Australian Ants, Vol 3. CSIRO Publishing, Melbourne, Victoria

APPENDIX C

Manuscript submitted on 29 September 2006 for publication in a special issue of *Journal of Sea Research* amongst a selection of papers presented at the Mangrove Macrobenthos Meeting II, held at the Gold Coast, Australia 26th—30th June 2006.

Manuscript accepted for publication in June 2007.

Diversity of Polychaeta (Annelida) and other worm taxa in mangrove habitats of Darwin Harbour, northern Australia

K. N. Metcalfe[1], C. J. Glasby[2]

[1]*School of Science, Faculty of Education, Health and Science, Charles Darwin University, Darwin, NT, 0909, Australia*

[2]*Museum and Art Gallery of the Northern Territory, GPO Box 4646, Darwin, NT 0801, Australia*

Abstract

In this paper the diversity, distribution and abundance of polychaetes and other worm taxa in the mangroves of Darwin Harbour (northern Australia) is presented and compared with that of other tropical mangrove areas. Aspects of the feeding guild ecology and the effects of disturbance on mangrove worms are also examined. Data were collected over a period of four years, across four mangrove assemblages. Samples were obtained using three sampling techniques: 1 m × 1 m quadrat searches, epifauna searches and a new type of infaunal sampling technique, the anoxic mat. A total of 75 species (67 polychaetes, 1 oligochaete, 1 echiuran, 3 sipunculans, 2 nemerteans, 1 turbellarian) were recorded from the four main mangrove assemblages. Of these, 30 species are widespread, occurring in mangrove and non-mangrove habitats throughout the Indo-West Pacific. Only seven species (all polychaetes) appear to be restricted to the mangroves of Darwin Harbour and northern Australia. Polychaetes are predominant, comprising 80–96% of all worms sampled, with three families—Nereididae, Capitellidae and Spionidae—accounting for 46% of all species. The highest diversity and abundance was recorded in the soft, unconsolidated substrates of the seaward assemblage, with diversity and abundance decreasing progressively in the landward assemblages. Most of the worm fauna was infaunal (70%), but the intensive sampling regime revealed a hitherto unknown significant percentage of epifaunal species (18%) and species occurring as both infauna and epifauna (12%). Univariate analyses showed annual and seasonal differences in worm species richness and abundance—presumably associated with the intensity of the monsoon and recruitment success. The worm fauna differed between mangrove assemblages but the proportion of species in each feeding guild was relatively consistent across the four assemblages studied. Overall, herbivores were the most species-rich and abundant, followed by carnivores and sub-surface deposit feeders. Multivariate analyses showed that the species composition of urbanised

mangroves differed to that of undisturbed sites, with surface deposit feeders more numerous in disturbed habitats. Overall, the findings demonstrate a dynamic spatial and temporal variation in diversity and abundance, and provide insight on the range of microhabitats in which mangrove worms occur and their response to anthropogenic disturbance.

Keywords: Polychaete, worm, macrofauna, macrobenthos, diversity, abundance, assemblage, feeding guild, disturbance, mangroves, Australia, Indo-west Pacific

1. INTRODUCTION

Invertebrate fauna surveys conducted by the senior author in the mangroves of Darwin Harbour, northern Australia between 2001 and 2005 yielded a considerable amount of data on the distribution, diversity and abundance of macro-invertebrates (Metcalfe, 2004, 2005, in prep.). Crustaceans, molluscs and worms (mainly polychaetes) were the most species-rich groups sampled during these surveys. This study presents the results for the worm fauna, including diversity, abundance and distribution, within the four main mangrove assemblages (hinterland margin, tidal flat, tidal creek and seaward). Although worms comprise an ecologically important element of the macro-invertebrate fauna of mangroves (e.g. Hutchings and Recher, 1982), they have been relatively poorly studied or neglected (e.g. MacIntosh, et al. 2002). Studies in tropical Australia include those of Wells (1983) who found 15 and 12 polychaete species (and one flatworm in each) in *Avicennia* and *Rhizophora* assemblages respectively in North-west Cape, Western Australia; Hanley (1985) who listed nine polychaete species from mangroves at several sites in the Northern Territory; and Dittman (2001) who found 19 species of polychaetes and a couple of oligochaetes at Missionary Bay, north Queensland.

The worm fauna of other tropical Indo-west Pacific mangroves has been documented in several studies including Sasekumar (1974), Frith et al. (1976), Kumar (1995), and Guerreiro et al. (1996). All showed a diverse and abundant polychaete fauna, especially in more seaward parts of the mangroves (also true for Australian mangroves, e.g. Wells, 1983; Hanley, 1985). Kumar (1995) reported higher faunal diversity during pre- and post-monsoon months compared to the monsoon months of June and July. Frith et al. (1976) found 'a distinct and characteristic mangrove fauna' dominated by molluscs, crustaceans and polychaetes in Phuket, Thailand. Several other studies have examined the worm fauna of mudflats immediately adjacent mangrove areas (e.g. Hsieh, 1995; Dittmann, 2002; López et al., 2002). Although these areas may support a similar worm fauna, the habitat is sufficiently different—especially in terms of insolation, exposure to currents, and degree of inundation—that a comparison of species composition and abundance would not be useful. A few studies have attempted to compile the invertebrate mangrove fauna of entire regions (e.g. Saenger et al., 1978; Hutchings and Recher, 1982; Kumar, 2003), but they are also not comparable with this study because of the taxonomic inconsistency between source studies.

Polychaetes in general are good subjects for research on the impacts of anthropogenic disturbance (reviewed by Giangrande, 2005), because of their highly diverse range of feeding and reproductive strategies, which give them different potentials for responding

to disturbance. The use of worm feeding guilds as indicators of ecological change was first proposed by Fauchald and Jumars (1979) and recently examined in the context of environmental assessment by Pagliosa (2005). This study represents an opportunity to further examine the relationship between feeding guild and anthropogenic disturbance, in this case potential differences between disturbed and undisturbed mangrove habitats. It is based on two data sets from Darwin Harbour: a one-year survey in 2001 of three relatively pristine mangrove sites and four sites affected directly or indirectly by anthropogenic disturbance; and a three-year study (2003–2005) of six mangrove sites—including two of the three sites in the 2001 study—which was part of a mangrove monitoring program examining invertebrate biodiversity (Metcalfe, 2004; Metcalfe, 2005; Metcalfe, in prep.). Collectively these data were compared with specimen records in the database of the Museum and Art Gallery of the Northern Territory (NTM)—built from various baseline surveys and environmental assessment projects—and an annotated list of polychaete and other worm species was compiled. Where possible, the feeding guild, ecology and distribution of each species in the wider context of the tropical Indo-Pacific region were recorded.

The specific aims of the study are:

1. To describe the spatial and temporal changes in the diversity and abundance of worm fauna in mangrove habitats of Darwin Harbour;
2. To test for the effects of anthropogenic disturbance on diversity, abundance and trophic composition;
3. To compare the diversity of worm fauna of Darwin Harbour with that of other tropical mangrove regions in northern Australia and the wider Indo-Pacific and assess the level of endemism.

2. STUDY AREA

All data were collected within Darwin Harbour, situated on the north-western coastline of the Northern Territory between latitudes 12°20' and 12°40' S and longitudes 130°45' and 131°05' E. Darwin Harbour is bounded to the west and east by Charles Point and East Point respectively, and contains approximately 20,400 hectares of healthy and relatively intact mangrove and saltflat habitat—representing one of the largest tracts of mangroves in the Northern Territory (Fig. 1).

Darwin's climate is tropical, seasonally humid, with mean annual temperature of 28°C and 54% relative humidity. Annual rainfall is approximately 1,713 mm, with wet summer monsoon and dry winter seasons (Bureau of Meteorology, 2006). The region is macrotidal, with a maximum tidal range of 7.8 m and strong bi-directional tidal velocities. Tides are diurnal (two per day) with a mean spring range of 5.5 m and mean neap range of 1.9 m (Woodroffe, 1995). Despite strong tidal currents, the Darwin Harbour estuary is relatively poorly flushed (Williams et al., 2006) which contributes to characteristically high turbidity levels, particularly during the wet season. Mangrove substrates generally comprise root-structured and bioturbated mud and muddy sands with fine-grained, unconsolidated marine muds in the seaward assemblages (Semeniuk, 1985).

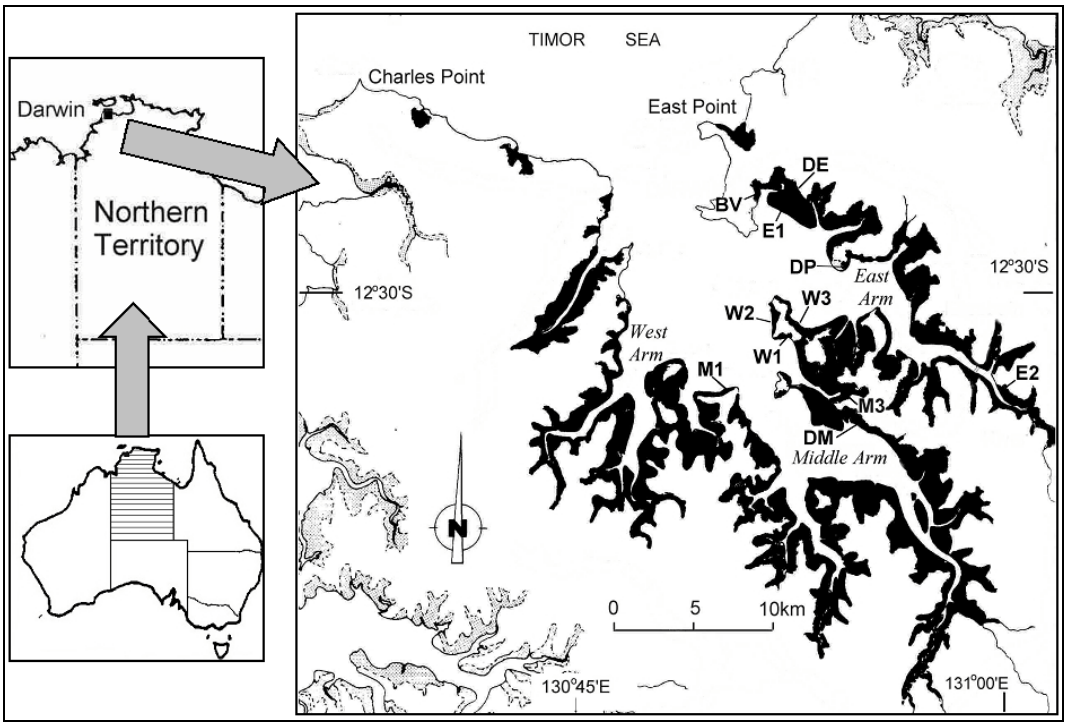


Fig. 1: Map showing location of Darwin in the Northern Territory, Australia (left) and the distribution of mangroves (shaded in black) within Darwin Harbour (right). The seven study sites (E1, E2, M1, M3, W1, W2 and W3) and four disturbed sites (BV, DE, DP and DM) are indicated.

In Darwin Harbour mangroves occur between approximately –1.0 m and 4.0 m Australian Height Datum (AHD) which approximates to mean sea level (MSL). Over 30 species of mangrove are known from the Darwin area, with 21 shrub and tree species commonly occurring in the intertidal zone (Wightman, 1989). Collectively they form dense mangrove forests that comprise a number of distinct habitats, indicated by a predictable pattern of species distribution—each of the major floristic assemblages are confined to discrete elevational ranges (Semeniuk, 1985; Woodroffe and Bardsley, 1987; Metcalfe, 1999). Four of the ten assemblages recognised in Darwin Harbour (Brocklehurst and Edmeades, 1996) occupy 88.2% of the total mangrove area. The tidal flooding regime and the seasonality of the climate are primary factors influencing the distribution and extent of mangroves in Darwin Harbour (Woodroffe and Bardsley, 1987).

At around mean sea level, open woodlands with *Sonneratia alba* occur in soft, unconsolidated substrates. Further to landward, tall *Rhizophora stylosa* forests occur between approximately 0.5 and 2 m AHD. These two assemblages occupy the lower intertidal zone of the mangrove and are largely shaped by marine processes—including wave action, tidal currents and two high tides per day. Only 58% of annual tides exceed 2 m AHD however, and assemblages in the upper intertidal zone are inundated only by spring tides, for one week of every fortnight (Metcalfe, 1999). The landward assemblages are thus more influenced by terrestrial rather than marine processes, including freshwater seepage, seasonal deposition of sediments and desiccation. Dense, low (2 to 4 m high) thickets of *Ceriops australis* occur in this habitat, partly in response to increasing soil salinities.

3. METHODS

3.1 Sampling

Sampling for the 2001 study was conducted at three undisturbed sites (E1, E2 and M3) during wet and dry seasons, and at four disturbed sites (BV, DE, DP and DM) during the dry season of the same year. Disturbed sites included the fringes of the Bayview housing development situated on 103 ha of reclaimed mangroves (site BV) and bulldozed tracks through relatively pristine mangroves (site DE). Disturbed mangroves abutting the Darwin Port precinct, a major industrial port development (site DP) and fringing an outlet channel for a prawn farm in Middle Arm (site DM) were also studied. Sampling for the three year monitoring program (2003–2005) was done at six sites (W1, W2, W3, E1, M3 and M1) during the wet and dry seasons (Fig. 1).

At each site, transects traversing each of the four main assemblages were established from the landward to seaward margin of the mangroves. Listed from landward to seaward these assemblages comprise the hinterland margin, tidal flat, tidal creek and seaward. Transect length varied between approximately 350 and 1500 m and along each transect, one permanent study plot was established in each assemblage (Fig. 2). Study plots for the 2001 study were 50 m x 50 m in size and two transects were established at each site. For the monitoring study, study plots were 20 m x 20 m in size and one transect was established per site. In all other respects, the methodology for both studies was identical.

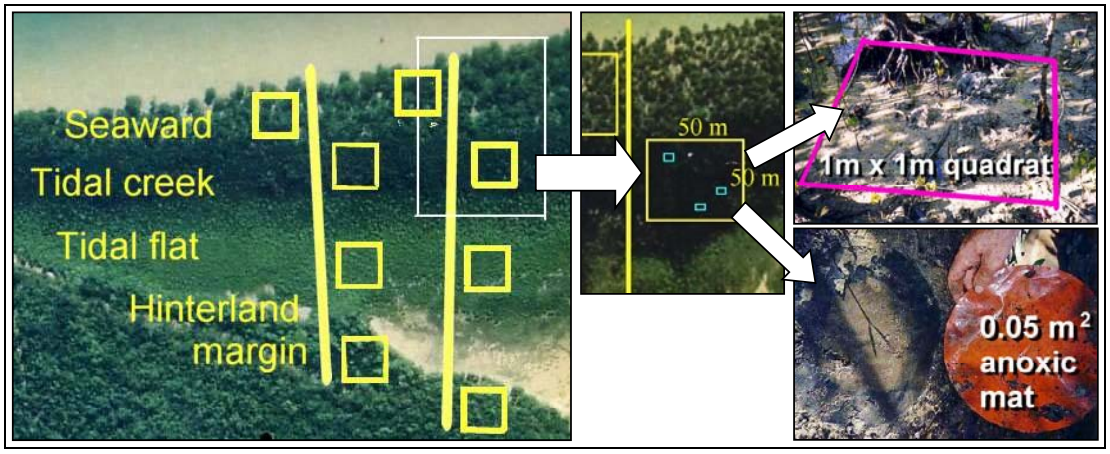


Fig. 2: Permanent study plots were placed within the four assemblages on paired transects from the landward to seaward margin (left). Sampling was conducted at three randomly placed subplots within each study plot (middle) using quadrats and anoxic mats (right).

Worms were sampled from four distinct micro-habitats: (i) on the mud surface (ii) within the substrate (iii) on the surface of tree trunks, roots and rocks and (iv) within rotting logs. Worms in the first two microhabitats were considered infauna and those in the latter two, epifauna. Within each 0.25 ha or 0.04 ha study plot, three randomly selected sampling stations were located at which one pitfall trap, one 0.05 m^2 anoxic mat and one 1m × 1m quadrat were used. The quadrat was placed against the tree nearest to the point designated by random number co-ordinates. Active searches of the quadrat and all surfaces of the tree to a height of 2 m (including roots and foliage) were conducted and quadrats were also dug to a depth of approximately 5–10 cm.

The anoxic mat comprised a plastic disc that temporarily created a localised area of anoxic mud. It was placed flat on the mud surface, covered with a mound of mud to maintain anoxic conditions and left for up to 24 hours. The following day the mat was peeled back and specimens collected, by eye, from the mud surface. The mud beneath the mat was also searched, by digging with a trowel to a depth of approximately 5 cm. The technique was very effective at capturing small polychaetes overlooked by other methods, but possibly under-sampled taxa having a high tolerance of anaerobic conditions (e.g. oligochaetes); the effectiveness of the anoxic mat compared to other benthic sampling devices is described elsewhere (Metcalfe, in prep.). All specimens sampled were preserved in 70% ethanol, and lodged with the NTM for identification (references specimens were registered with the NTM).

3.2 Analyses

Specimens identified to genus or species levels were included in statistical analyses and species tallies. Specimens identified only to family (usually because they were in poor condition) or phylum level (lack of taxonomic expertise) were omitted from the analyses, unless they represented the only member of that family, or phylum. Thus 98 of the total of 1,026 specimen records obtained during all surveys were omitted. Each of the analysed taxa was to assigned one of 22 feeding guilds and five trophic categories—herbivore, carnivore, filter feeder, surface deposit feeder and subsurface deposit feeder [=burrower, after Fauchald and Jumars (1979) and Pagliosa (2005)]—in order to assess trophic characteristics of the worm fauna.

For the 3-year study, species richness and abundance data were compared between years, seasons, sites and assemblages using a 4-factor ANOVA with all factors fixed. Tests for ANOVA assumptions were run prior to the analysis, by examination of normal plots of within-cell residuals and plots of means verses standard deviations, before and after transformation. Abundance data was transformed ($\log10(x + 1)$) but transformation was not necessary for species richness data. Analyses were conducted using either Statistica or the General Linear Model in Minitab. By convention, significance levels were set at $p<0.05$.

All comparisons of disturbed and undisturbed mangroves were based on the dry season survey of 2001. The sampling effort for that survey was double that for surveys in 2003–2005, as paired transects were sampled at each location. ANOVA for species richness, abundance and feeding guild data involved four factor, nested analyses with the factors disturbance, location, transect and assemblage, in which all factors were fixed except transect, which was random and nested in location and disturbance.

The two data sets from undisturbed sites were merged for multivariate analyses, to permit examination of community data spanning four years. Ordination by non-metric multi-dimensional scaling (NMDS) procedures in the Primer (version 5) program (Clarke and Warwick, 1994; Clarke and Gorley, 2001) was used to examine community patterns in worm diversity and abundance, and for comparison of disturbed and undisturbed sites. Ordinations were generated using Bray Curtis dissimilarity on untransformed data after 50 random restarts.

4. RESULTS

A total of 216 records were obtained for worms during three surveys in 2001 (one wet season, two dry season) and 810 records for the three-year survey of six sites (three wet and three dry seasons).

4.1 Diversity, distribution and habitat

The two data sets yielded a total of 76 species of worms from mangrove habitats (Appendix). Polychaetes (Annelida) are predominant, comprising 80–96% of all mangrove worms sampled. In all, 77 species—comprising 69 polychaetes, 1 oligochaete (Annelida), 1 echiuran, 3 sipunculans, 2 nemerteans and 1 turbellarian—were recorded from mangrove habitats of Darwin Harbour (Appendix). Seven species appear to be restricted to mangrove habitats of Darwin Harbour and northern Australia – the polynoid *Lepidonotus* sp. 1, three capitellids (*Heteromastus* sp. 1, sp. 2 and *Mastobranchus* sp.) and three nereidids (*Ceratonereis* sp. NTM6742, *Namalycastis nicolea* and *Paraleonnates bolus*). Thirty-three species occur in mangrove and non-mangrove habitats throughout the Indo-West Pacific; the remainder are too poorly known taxonomically for distributions to be analysed.

In terms of microhabitat, the majority of species are infaunal (70%), but a substantial portion also occurs as epifauna (18%) and about 12% of species occur as both (Appendix). Most infaunal species avoided the surface of the mud, the exception being *Phyllodoce* sp., which mostly were collected in pitfall traps. Epifaunal species mostly occurred under the bark of mangrove trees, but also in fallen timber. Particularly productive microhabitats were beneath the large flakes of bark on the lower trunks of *Sonneratia alba* trees in the seaward assemblage and within rotting, burrow-structured roots and limbs of *Rhizophora stylosa* trees in the tidal creek assemblage. Certain species including *Lepidonotus* sp. 1, *Neanthes* cf. *biseriata* and *Perinereis singaporiensis* were almost exclusively sampled from the trunks of *Sonneratia alba* trees.

4.2 Species richness and abundance

Within the mangroves, the overall species richness and abundance of worms at the six sites sampled during the three year monitoring program was not significantly different. Also, diversity levels for each of the four assemblages were reasonably consistent between sites. However, within each site univariate analysis showed significant annual and seasonal differences in species richness and abundance between assemblages. The seaward assemblage had the highest diversity of worms, with species richness and abundance decreasing progressively to landward, with few worms sampled in the hinterland margin (Table 1; Fig. 3). This distribution pattern reflects the frequency of tidal inundation and the suitability of substrates—muds become increasingly moist and unconsolidated to seaward and the habitat opportunities for infauna increase.

Significant year × assemblage and season × assemblage interactions were also found indicating distinct annual differences amongst assemblages and that the effects of season on diversity are dependent on assemblage. For instance, species richness is higher in the seaward assemblages in the dry season; whereas it decreases in the two landward assemblages in the dry season (Fig. 4). The mean squares indicated that the

most significant factor determining worm species richness and abundance was mangrove assemblage.

Table 1: Mean species richness and abundance of worms per square metre (±SE) in the four mangrove assemblages during wet and dry seasons over three years. Data from 1 m× 1 m quadrats and epifaunal counts were used to calculate means.

Assemblage	**Dry Season**		**Wet season**	
	Mean species richness ± SE	Mean abundance ± SE	Mean species richness ± SE	Mean abundance ± SE
Hinterland margin	0.1 ± 0.03	0.06 ± 0.03	0.1 ± 0.05	0.13 ± 0.05
Tidal flat	0.2 ± 0.05	0.15 ± 0.05	0.5 ± 0.12	0.56 ± 0.13
Tidal creek	1.0 ± 0.16	1.34 ± 0.26	0.7 ± 0.17	0.93 ± 0.22
Seaward	3.1 ± 0.27	6.06 ± 0.64	1.9 ± 0.19	3.19 ± 0.39
TOTAL	1.1 ± 0.12	1.92 ± 0.24	0.83 ± 0.09	1.20 ± 0.14

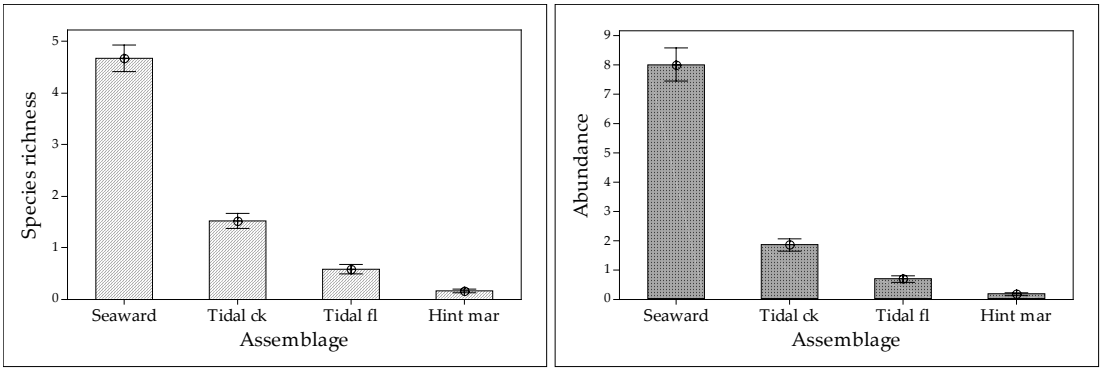


Fig. 3: Variation in worm species richness (left) and abundance (right) in the four main mangrove assemblages. Data are pooled over six sites and three years.

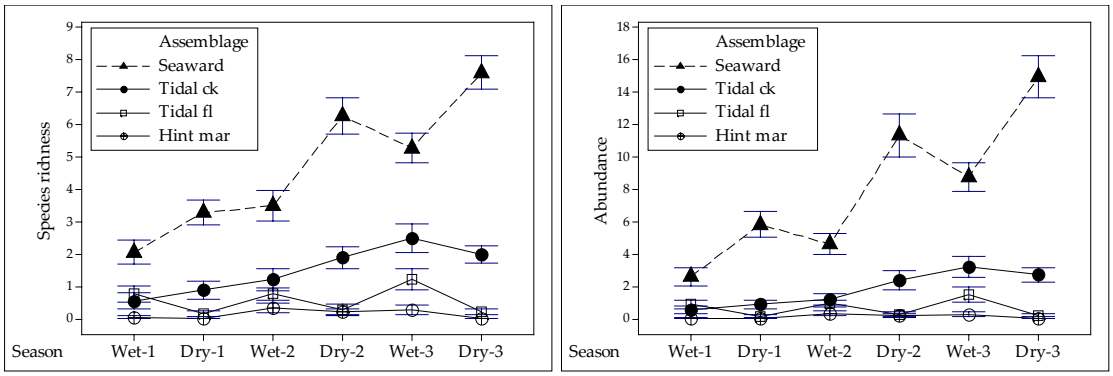


Fig. 4: Annual (and seasonal) variation in worm species richness (left) and abundance (right) in the four main assemblages. Data are pooled over six sites.

Overall mean abundance decreased by almost 50% in the seaward assemblage during the wet (monsoon) season, when rainfall, erosion and wave action peaks. In contrast, abundance increased in both the tidal flat and hinterland margin assemblages during the wet (Fig. 5). Worm abundance varied between years but this was determined by

assemblage, as was the effect of season. Overall worm abundance showed an apparent increase from 2001 to 2005 (Fig. 5), a pattern that was mirrored by other invertebrate groups, e.g. crustaceans and molluscs (Metcalfe, in prep.).

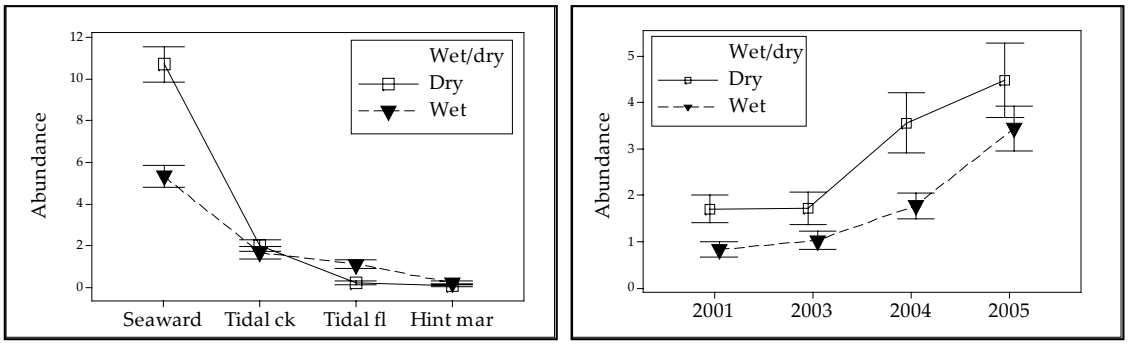


Fig. 5: Mean worm abundance (±SE) indicating seasonal and annual variation. Differences in mean abundance in the four assemblages (left) and during wet and dry season during four years of sampling (right). Points represent mean numbers of worms per sampling station, averaged over three locations (2001 data) or six locations (2003–2005 data) shown from seaward (left) to landward (right)

Multivariate analyses showed that mangrove assemblage is the primary determinant of worm populations. NMDS ordinations indicated the strong similarity between study plots in the seaward mangrove assemblage based on the presence and abundance of worms (Fig. 6). The worm fauna of the tidal creek assemblage shows similar affinity between the different locations sampled, but there is also some overlap with study sites from both other assemblages. The tidal flat and hinterland margin assemblages have a distinct worm fauna, although not as prolific as the seaward assemblages (Fig. 6). Typical species in the hinterland margin and tidal flat are the nereidids *Namanereis malaitae* and *Paraleonnates bolus* and *Phyllodoce* sp. (Phyllodocidae).

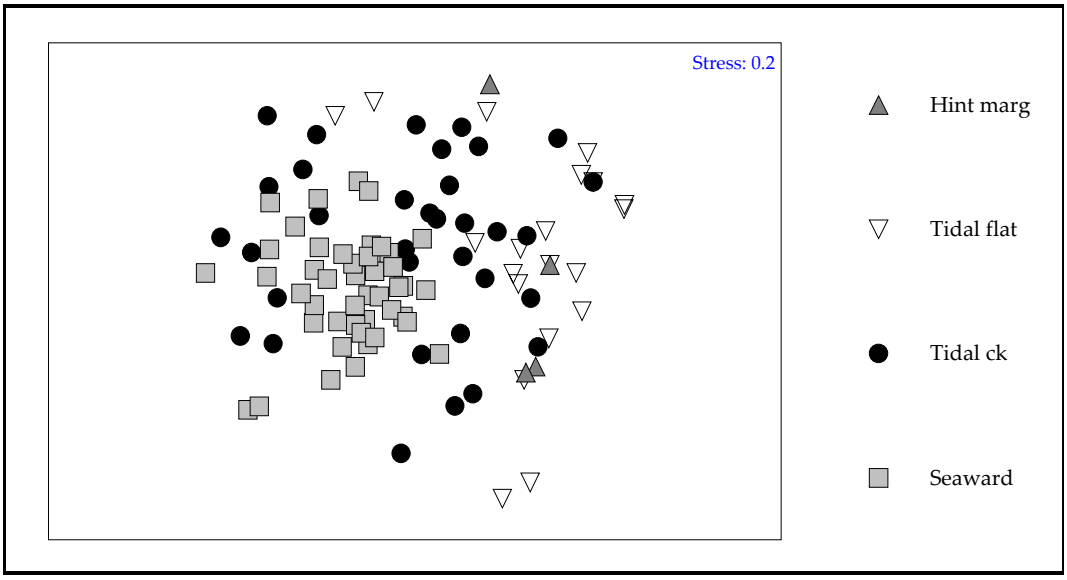


Fig. 6: NMDS ordination of 107 study plots surveyed over four years based on the abundance of 69 polychaete species indicating the similarity of study plots in different assemblages. Points represent data pooled for each sampling technique at three replicate sampling stations per study plot.

Mangrove assemblage also plays a role in the frequency of occurrence of worms in different microhabitats—few species occur as epifauna in the hinterland margin and tidal flat but they are highly numerous and almost as common as infauna in the tidal creek and seaward assemblages. Typical epifaunal species include the eunicid *Nematonereis* sp., the nereidids *Ceratonereis australis*, *Neathes* cf. *biseriata*, *Perinereis singaporiensis*, the scaleworm *Lepidonotus* sp. 1, the serpulid *Pomatoleios kraussii* and a syllid, *Syllis* sp. 1. A few infaunal species are also characteristic of the seaward assemblage including *Isolda pulchella* (Ampharetidae), the lumbrinerids *Arabelloneris broomensis* and *Scoletoma* sp. 1, *Nephtys mesobranchia* (Nephtyidae) and *Nereis* sp. 1 (Nereididae).

4.3 Feeding guild

All five trophic categories and thirteen of the 22 feeding guilds were identified among the worm taxa collected in this study; filter feeders were the only trophic category not well represented (Appendix). The proportion of worms per feeding guild remained relatively consistent in each of the main assemblages, with the exception of the tidal flat (*Ceriops australis*) assemblage where subsurface deposit feeders were more numerous than carnivores and herbivores. Overall, herbivores were the most numerous, with carnivores, subsurface deposit feeders and surface deposit feeders in decreasing order of abundance (Fig. 7). Although herbivores were treated together in one group in this analysis, they can be subdivided further into diatom- and macrophyte-feeders (Fauchald and Jumars, 1979). Probably the majority of herbivores in this study are of the former type (i.e., microphagous), and feed not only on diatoms, but also algae and detritus. Polychaetes are also potentially capable of breaking down whole mangrove leaves (e.g. Camilleri, 1992) so it is likely that some species would also utilise this abundant food source.

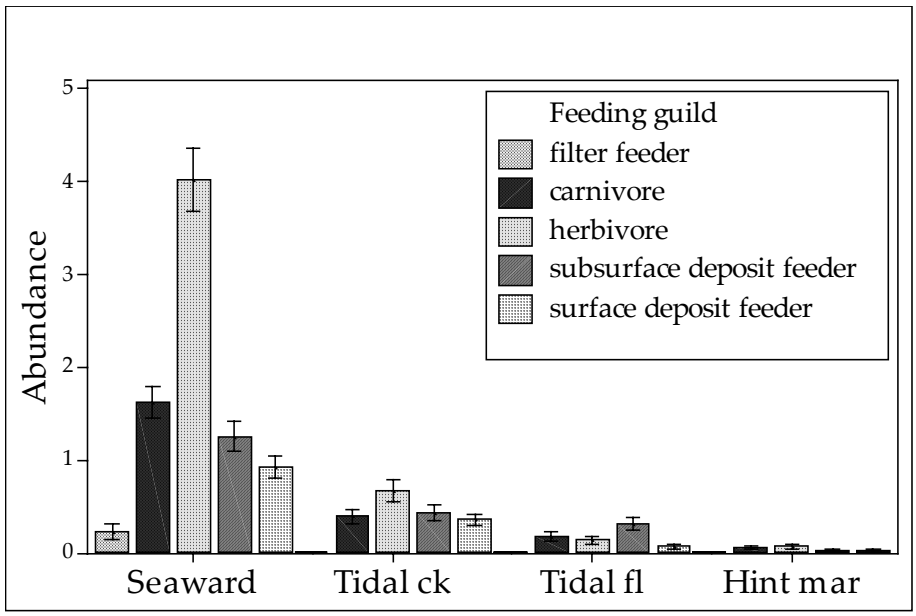


Fig. 7: Mean abundance of worms in the five main feeding guilds at six sites during 2003–2005. Means per sampling station in the four assemblages are shown from seaward (L) to landward (R).

4.4 Fauna of disturbed mangroves

The one-year survey of three undisturbed and four disturbed sites conducted in 2001 allowed comparison of the worm faunal assemblages in mangroves directly or indirectly affected by anthropogenic development, with undisturbed sites. Although mean diversity was lower and abundance slightly higher in disturbed mangroves, univariate analyses found no significant differences in overall mean species richness and abundance between disturbed and undisturbed mangroves. A significant disturbance × assemblage interaction for worm abundance indicated that abundance in disturbed and undisturbed sites differed between assemblages. Mean worm abundance is apparently higher in disturbed sites in the tidal creek and to a lesser extent the seaward assemblage, but is apparently lower than undisturbed sites in the landward assemblages (Fig. 8).

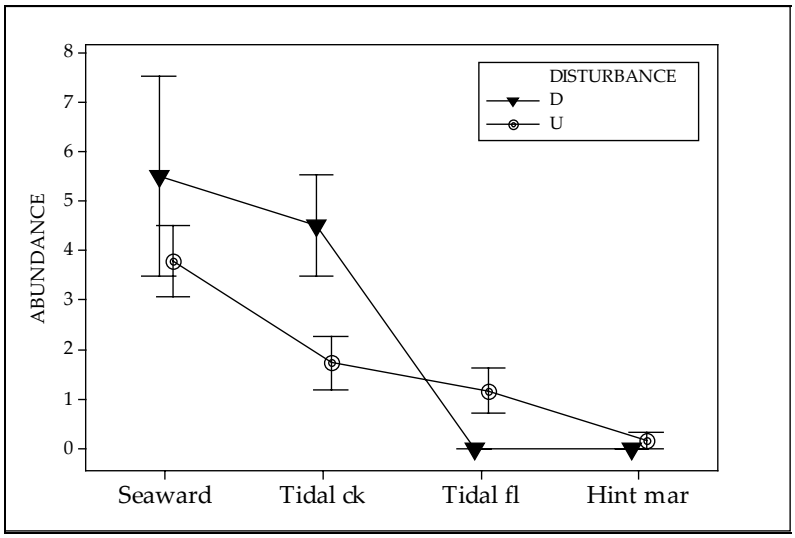


Fig. 8: Mean abundance of worms (±SE) in disturbed (D) and undisturbed (U) sites, in the four assemblages. Means are pooled across three undisturbed and two disturbed sites from one dry season survey in 2001.

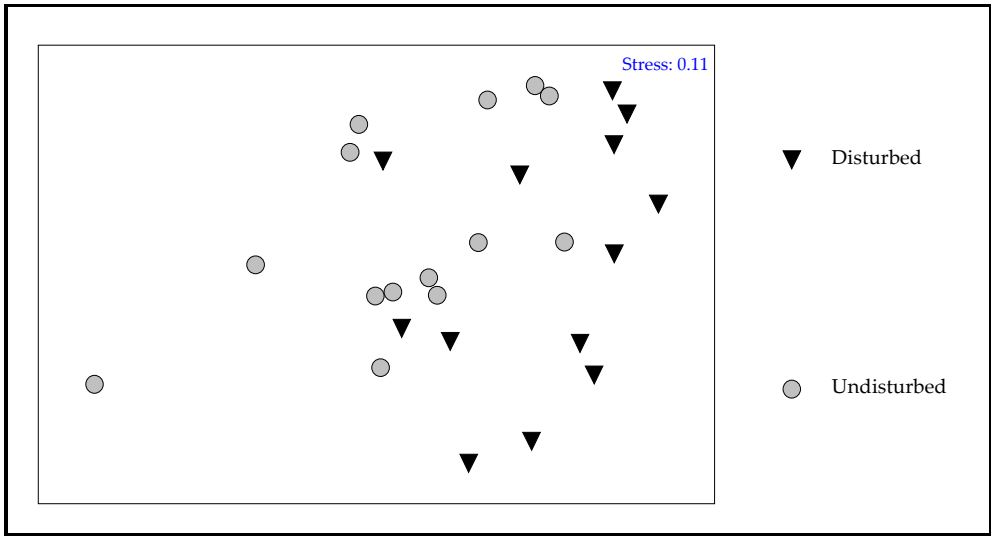


Fig. 9: Ordination of 13 disturbed and 14 undisturbed study plots based on worm taxon presence/absence. Dry season data from three replicate sampling stations were pooled for each study plot.

Multivariate analyses illustrated that the worm fauna of urbanised mangroves differs somewhat to that of undisturbed sites (Fig. 9). Seventeen species, of the total of 49, were recorded only from disturbed sites. Subsequent sampling however, spanning three years and both wet and dry seasons, revealed a wider distribution for many of those species, including undisturbed sites. Although not always exclusive to disturbed habitats, the surface deposit feeders *Aphelochaeta* sp. 1, *Leonnates stephensoni*, *Scolelepis* sp. 1, *Terebellides kowoinka*, and *Terebella tantabiddycreekensis* and the herbivore (detrital) feeder, *Simplisetia* cf *erythraensis* appear characteristic of urbanised mangroves.

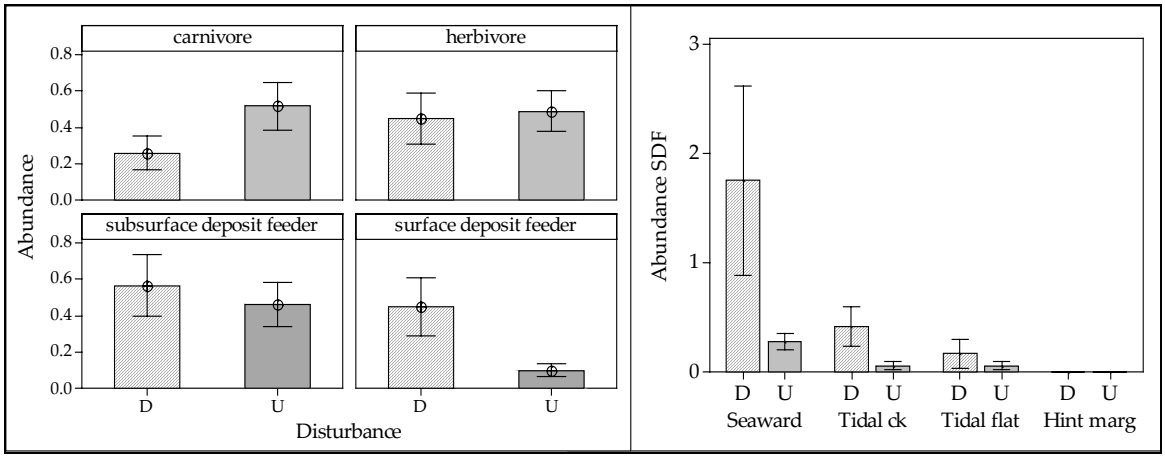


Fig. 10: Mean abundance of worms in the four main feeding guilds in disturbed (D) and undisturbed (U) mangroves (left). Means represent average abundance per sampling station, pooled across 78 disturbed and 72 undisturbed replicates. Mean abundance of surface deposit feeders (±SE) in disturbed (D) and undisturbed sites (U) in the four assemblages (right). Means are pooled for two disturbed (BV, DP) and two undisturbed sites (E2 , M3).

The abundance of worms in three of the four main feeding guilds varied little between disturbed and undisturbed sites (Fig. 10). Univariate analyses found the abundance of surface deposit feeders differed between disturbed and undisturbed sites; this trophic group was more numerous in disturbed sites. A significant disturbance × assemblage interaction also indicated the effects of disturbance on surface deposit feeders varied between assemblages—impacts of disturbance were most pronounced in the seaward assemblage (Fig. 10). These results were, however, based on one dry season survey during 2001 and further sampling is required to substantiate these findings.

5. DISCUSSION

5.1 Diversity and abundance

The diverse and extensive mangrove environments of Darwin Harbour, provide habitat for a surprisingly rich worm fauna in which polychaetes predominate, comprising 80–96% of all worms sampled. Three polychaete families—Nereididae, Capitellidae and Spionidae—accounted for 46% of all species. The dominance of these three polychaete families coincides with the results of other studies of mangrove systems (Frith et al., 1976; Hutchings and Recher, 1982; Kumar, 1995). The total number of taxa reported in the study (76 species; 56 genera) is however, far in excess of any other mangrove study in the Indo-west Pacific, but this is likely to be the result of the more extensive sampling regime over a longer period of time. Studies of 1 year duration or less and those that

consider only the infauna have yielded less than half the number of genera (e.g. Sasekumar, 1974; Guerreiro et al., 1996; Dittmann, 2001). Multi-year studies therefore, are more likely to sample short-lived species (1 year or less), which may be absent altogether in years following poor recruitment. The four year period of this study was sufficient in duration to sample almost all of the polychaete species currently known from Darwin Harbour mangroves, based on literature records and specimen records in the database of NTM (Appendix). The exception is the capitellid, *Mastobranchus* sp., which was also reported by Hanley (1985) as *Heteromastus* sp. A, and may have a specialised habitat (tailings of mud lobster burrows).

Of the other worm taxa recorded in this study, nemerteans were also abundant (8.5% of all records) but the taxonomy of this group is poorly known and apart from the large, rarely encountered *Cerebratulus* species of the seaward zones, other species could not be identified. Sipuncula were also abundant (6.5 % of all records) with most belonging to the widely distributed Indo-west Pacific estuarine species, *Phascolosoma arcuatum;* two other, possibly undescribed, species were also found in the tidal creek zone.

The spatial patterns in diversity and abundance were remarkably consistent between locations in Darwin Harbour such that the species richness and abundance of polychaetes around Darwin Harbour appears reasonably predictable—with highest diversity and abundance in the seaward mangrove assemblage, decreasing progressively to landward, with few worms sampled in the hinterland margin. This distribution pattern presumably reflects the frequency of tidal inundation and the suitability of substrates—muds become increasingly moist and unconsolidated to seaward and the habitat opportunities for epifauna increase. In addition, frequency of tidal inundation directly influences recruitment such that the more frequently inundated seaward zones have a greater potential to receive larvae, and for larvae to survive. For example, species occurring in the tidal creek assemblage (at roughly 1 m AHD) are inundated by 93% of annual tides, whereas those living in the tidal flat assemblage and above (>2 m AHD) are only bathed by 58% of tides. High dry season evaporation rates in the tidal flat create hypersaline conditions which further add to the harshness of the mid- to upper-intertidal zone. Seasonal rainfall and higher tides during the wet season moderate the harsh environmental conditions in the tidal flat and the hinterland margin which may contribute to the higher diversity and abundance observed in landward zones during the wet season. Desiccation and high salinity are likely to be important factors limiting worm populations in these habitats. Species occurring in these landward zones belong to various trophic categories (e.g. BMX, CMX, HMJ, SMX of Appendix), but all are highly mobile.

On the contrary, the levels of diversity in the seaward assemblages decreased during the wet season. Monsoonal conditions during the wet season generate swell and wave action, typically leading to erosion of surface sediment in the seaward assemblages during this period (K. Metcalfe, pers. obs.). Monsoonal conditions may drastically alter sediment characteristics, such as particle size and can exert a strong seasonal impact on the macrobenthos (Alongi and Sasekumar, 1992), especially polychaetous worms (Sarkar et al., 2005). Kumar (1995) also reported lessened faunal diversity during the monsoonal period in the mangroves of Cochin, India. Polychaetes may be seriously affected by erosion and reduced salinity (Kurian, 1984), while other phyla are not (Nandi and Choudhury, 1983 as cited in Alongi and Sasekumar (1992)). Recent research in north Queensland indicates that during intense, short-term freshwater inundations,

the majority of benthic species in mudflats just seaward of mangroves are lost and do not return; a small remnant fauna remains—comprising euryhaline 'resident' species—which slowly recover to pre-disturbance levels (J. Sheaves, pers. com.).

The gradual increase in diversity and abundance observed during 2001 to 2005 may be a response to the impact of one or more extreme wet season events. The wet season of 2003–2004 had an above average rainfall and strong monsoonal activity, which may have contributed to lower worm diversity and abundance during that year, but 2001 values were however, even lower than 2003. Nevertheless, the observed increase may represent gradual recovery of invertebrate populations during years in which the monsoon was more moderate. It is unlikely, given the methodological consistency that the increase is due to an artefact of sampling or improved discrimination in the field or laboratory. Determination of the factors influencing worm populations is, however, beyond the scope of this project. Forthcoming surveys may provide further insight into the long term patterns in diversity and abundance of mangrove worms.

The higher number of subsurface deposit feeders in the tidal flat may be associated with the number of mud lobster mounds, which provide excellent habitat (soft, reworked mud) for worms. The capitellids – *Heteromastus* sp. 1, *Mediomastus* sp. 1 and *Notomastus* sp. – appear to be the main taxa responsible for this pattern. The higher number of surface deposit feeders in disturbed sites is the only significant difference detected between disturbed and undisturbed mangroves, but it was only based on one year's sampling and therefore requires corroboration. If supported, it suggests that a shift in polychaete trophic assemblages, such as the sudden dominance of surface deposit feeders, could be a good indicator of disturbance, such as increased sedimentation.

5.2 Effects of anthropogenic disturbance

Probably the most significant type of anthropogenic disturbance to the mangroves of Darwin Harbour is associated with urbanisation. Urbanisation can affect sediment properties when runoff, currents, tidal flow and the ability of mangrove trees to capture sediments is altered (Kaly et al., 1997). By contrast, organic enrichment associated with pollution is anticipated to be relatively minor, if present, at the disturbed study sites in Darwin Harbour. Sediment properties are a primary factor determining polychaete populations especially grain size (Alongi, 1987; Pagliosa, 2005; Sarkar et al., 2005) and silt and clay content (Hsieh, 1995). Increased populations of polychaetes at several sites and increases in the abundance of surface deposit feeders may have been related to changes in the sediment.

The findings of this study need to be interpreted with caution however, as the work did not document the direct response of the worm fauna to disturbance. The faunal differences observed in disturbed sites may, to some extent, also be due to intrinsic environmental differences between sites. Substrates at the port site for example, may naturally have been more sandy, gravely or rocky than at the undisturbed sites studied—with a specialised worm fauna that reflected this. Pre-disturbance surveys are required to eliminate such possibilities. Nevertheless, these studies have provided valuable baseline information and further research on the response of mangrove polychaetes to anthropogenic disturbance is seen as a priority for environmental assessment and management of mangrove communities in Darwin Harbour. The preliminary results obtained here suggest that of all the invertebrate groups studied in

mangrove environments, polychaetes may be the most useful as key indicators of anthropogenic disturbances.

5.3 Mangrove worms: characteristic or specialised fauna?

Hutchings and Recher (1982: 102) point out that 'Relatively few animals are restricted to mangroves or show specific adaptations to the mangrove environment.' This appears to be the case for the majority of species encountered in this study. Of the 77 worm species reported from Darwin Harbour mangroves, only seven may be restricted to this environment. The remainder that are well enough known (at least 33 species) are also present on adjacent mudflats and channels, and other intertidal non-mangrove shallow coastal habitats in northern Australia. Several species including the polychaetes *Marphysa mossambica*, *Dendronereides heteropoda*, *Namalycastis abiuma*, *Perinereis aibuhitensis*, *Simplisetia cf erythraensis*, and the sipunculan, *Phascolosoma arcuatum* have been reported from other mangrove areas in northern Australia and the Indo-West Pacific and are characteristic members of the Indo-west Pacific mangrove fauna.

No previous study has identified an endemic or specialised mangrove worm fauna, perhaps because the knowledge of polychaetes and other worms (especially of the tropics) is not mature enough to know with any degree of confidence the taxonomic limits and distributions of each species. This is also true of the seven species (10% of total) identified here as possible endemics (Appendix). Of these seven species, the three most likely to be endemics are: *Mastobranchus* sp., which appears to be confined to the mounds of the mud-lobster *Thalassina squamifera*. This species was not collected in the present study, possibly because *Thalassina* mounds were rarely sampled in the sampling strategy which placed 1 m × 1 m quadrats against randomly selected trees. It was one of only two species found by Hanley (1985) to be exclusively associated with *Thalassina* mounds; the other one *Neanthes* sp. B (=*Perinereis aibuhitensis*) was found here to occur more widely across all mangrove assemblages both as epifauna and infauna. Another nereidid, the epifaunal *Namalycastis nicoleae* is mainly found under the bark of *Sonneratia alba* trees and within fallen mangrove timber and so far, is only known from Darwin Harbour mangroves and a drainage channel of reclaimed mangroves near Brisbane (Glasby, 1999). The epifaunal scaleworm *Lepidonotus* sp. 1 also appears to be restricted to Darwin Harbour mangroves. The occurrence of endemic polychaetes in Darwin Harbour mangroves may be the result of isolation, spatial extent, floristic diversity and the habitat complexity they provide. Other mangrove specialists/endemics are known from other animal groups occurring in tropical mangroves (Hutchings and Recher, 1982: 102).

At the generic level, a similar suite of 'characteristic' worm taxa exists. Polychaete genera common to both Darwin Harbour mangroves and the mangroves of other Indo-West Pacific mangroves include, the ampharetid *Amphicteis*, the nereidids *Composetia*, *Dendronereides*, *Dendronereis, Neanthes*, *Nereis, Perinereis and Simplisetia,* the onuphid *Diopatra,* the maldanid *Euclymene,* the glycerid, *Glycera,* the capitellids *Heteromastus and Mediomastus,* the polynoid *Lepidonotus,* the eunicid *Marphysa,* the phyllodocid *Phyllodoce,* the lumbrinerid *Scoletoma,* the spionids *Polydora, Prionospio* and the orbiniid, *Scoloplos.* The only non-polychaete so far reported from more than one Indo-Pacific mangrove area is the sipunculan, *Phascolosoma*, which is a genus typical of Indo-West Pacific hard substrates (Cutler and Cutler 1990). Most of these genera are species-rich and whose

members occupy a wide variety of habitats globally. Thus, while these genera can be considered characteristic of mangroves, they are not mangrove specialists. The high number of genera (56) in Darwin Harbour mangroves that have not been previously reported from other Indo-west Pacific mangroves probably reflects the poor state of taxonomic knowledge of polychaetes, particularly in the tropics.

6. CONCLUSIONS

1. The diverse mangrove worm fauna of Darwin Harbour is dominated by polychaetes, especially Nereididae, Capitellidae and Spionidae.
2. The majority of species, and many genera, are characteristic of mangrove areas across the Indo-Pacific; only 10% of species may be endemic to the mangroves of northern Australia, but further studies are required to test this hypothesis.
3. The distribution and abundance of species in Darwin Harbour mangroves was found to vary in time (between years and seasons) and space (between mangrove assemblages). High consistency was observed from site to site however, with a reasonably predictable suite of species occurring at particular tidal elevations.
4. The microhabitats from which worms were sampled and the species composition of landward assemblages differed markedly from the seaward assemblages.
5. The seasonal pattern of increased dry season diversity and abundance to seaward is reversed to landward, where it declined in response to desiccation.
6. A different species and trophic composition between disturbed and undisturbed mangroves is also suggested by the data.
7. Herbivores are the most abundant trophic group overall, but in disturbed habitats surface deposit feeders are relatively more common.

Acknowledgements

We thank Julie Crawford and Joe Darcy for field assistance, Keith McGuinness and Tim Glasby for comments on the manuscript and Joe Lee for the invitation to present the paper at the Second International Mangrove Macrobenthos Meeting, Coolangata, 25-30 June 2006. In particular, we acknowledge the proponents of the mangrove monitoring program for permission to publish this valuable baseline data. This work was undertaken with support from an Australian Postgraduate Award and the Parks and Wildlife Commission of the Northern Territory.

REFERENCES

Alongi DM (1987) Intertidal zonation and seasonality of meiobenthos in tropical mangrove estuaries. Marine Biology 95 447-458

Alongi, D.M., Sasekumar, A., 1992. Benthic communities. In: Robertson, A.I., Alongi, D.M. (Eds) Tropical Mangrove Ecosystems. American Geophysical Union: Washington, DC, pp. 137–172.

Blake, J.A., Kudenov, J.D., 1978. The Spionidae (Polychaeta) from southeastern Australia and adjacent areas with a revision of the genera. Memoirs of the National Museum of Victoria 39, 171–280.

Böggemann, M. 2005. Revision of the Goniadidae (Annelida, Polychaeta). Abhandlungun des Naturwissenschaftlichen Vereins in Hamburg (NF) 39, 1–354.

Brocklehurst, P.S., Edmeades, B.F., 1996. Mangrove Survey of Darwin Harbour, Northern Territory, Australia. Land Conservation Unit, Conservation Commission of the Northern Territory, Darwin, NT.

Bureau of Meteorology, 2006. Climate averages for Station 014015 Darwin Airport, NT during the period 1941–2006, Commonwealth Bureau of Meteorology Website www.bom.gov.au. 2006.

Camilleri, J.C., 1992. Leaf-litter processing by invertebrates in a mangrove forest in Queenland. Marine Biology 114, 139–145.

Clarke, K.R., Gorley, R.N., 2001. Primer v5: User manual, Plymouth Marine Laboratory.

Clarke, K.R., Warwick, R.M., 1994. Change in marine communities: An approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Primer-E Ltd.

Cutler, N.J., Cutler, E.B., 1990. Revision of the genus *Phascolosoma* (Sipuncula: Phascolosomatidae). Proceedings of the Biological Society of Washington. 103, 691–730.

Day, J.H., 1977. A review of the Australian and New Zealand Orbiniidae (Annelida: Polychaeta). In: Reish, D.J., Fauchald, K. (Eds). Essays on polychaetous annelids in memory of Dr. Olga Hartman. Los Angeles, Allan Hancock Foundation, pp. 217–246.

Dittman, S., 2001. Abundance and distribution of small infauna in mangroves of Missionary Bay, North Queensland Australia. Revista de Biología Tropical 49, 535–544.

Dittmann, S., 2002. Benthic fauna in tropical tidal flats of Hinchinbrook Channel, NE Australia: diversity, abundance and their spatial and temporal variation. Wetlands Ecology and Management 10, 323–333.

Edmonds, S.J., 1987. Echiurans from Australia (Echiura). Records of the South Australian Museum 21, 119–138.

Fauchald, K., Jumars, P.A., 1979. The diet of worms: A study of polychaete feeding guilds. Oceanography and Marine Biology Annual Review 17, 193–284.

Frith, D.W., Tantanasiriwong R., Bhatia, O., 1976. Zonation of macrofauna on a mangrove shore, Phuket Island. Research Bulletin of the Phuket Marine Biological Center 10, 1–37.

Giangrande, A., Licciano, M., Musco, L. 2005. Polychaetes as environmental indicators revisited. Marine Pollution Bulletin 50, 1153–1162.

Glasby, C.J., 1999. The Namanereidinae (Polychaeta: Nereididae). Part 1. Taxonomy and Phylogeny. Records of the Australian Museum Supplement 25, 1–129.

Guerreiro, J., Freitas, S., Pereira, P., Paula, J., Macia, A., Jr., 1996. Sediment macrobenthos of mangrove flats at Inhaca Island, Mozambique. Cahiers de Biologie Marine 37, 309–327.

Hanley, J.R., 1985. Why are there so few Polychaetes (Annelida) in northern Australian mangroves? In: Bardsley, K.N., Davie, J.D.S., Woodroffe, C.D. (Eds) Coasts and Tidal Wetlands of the Australian Monsoon Region. North Australia Research Unit, Australian National University, Darwin, NT, pp. 239–250.

Hartmann-Schröder, G., 1979. Teil 2. Die Polychaeten der tropischen Nordwestküste Australiens (zwischen Derby im Norden und Port Hedland im Süden). In: Hartmann-Schröder, G., Hartmann, G. (Eds) Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 76, 75–218.

Hartmann-Schröder, G., 1985. Revision der Gattung Ceratonereis Kinberg (Nereididae, Polychaeta) (mit besonderer Berucksichtigung der Arten mit eingeschnittenem Prostomium). Mitteilungen aus dem Zoologischen Institut und Zoologische Museum der Universität Hamburg 82, 37–59.

Hsieh, H.-L., 1995. Spatial and temporal patterns of polychaete communities in a subtropical mangrove swamp: influences of sediment and microhabitat. Marine Ecology Progress Series 127, 157–167.

Hutchings, P., 1997. The Terebellidae (Polychaeta) of northern Australia with a key to all the described species of the region. In: Hanley, J.R., Caswell, G., Megirian, D., Larson, H.K. (Eds). Proceedings of the sixth international marine biological workshop: The marine flora and fauna of Darwin Harbour, northern Australia. Museums and Art Galleries of the Northern Territory: Darwin, NT, pp. 133–161.

Hutchings, P., Peart, R., 2000. A revision of the Australian Trichobranchidae (Polychaeta). Invertebrate Taxonomy 14, 225–272.

Hutchings, P., Recher, H.F., 1982. The fauna of Australian mangroves. Proceedings of the Linnaean Society of New South Wales 106, 83–121.

Hutchings, P.A., Reid, A., 1990. The Nereididae (Polychaeta) from Australia - Gymnonereidinae sensu Fitzhugh, 1987: *Australonereis, Ceratocephale, Dendronereides, Gymnonereis, Nicon, Olganereis* and *Websterinereis*. Records of the Australian Museum 42, 69–100.

Hutchings, P.A., Reid, A., 1991. The Nereididae (Polychaeta) from Australia – *Leonnates*, *Platynereis* and *Solomonereis*. Records of the Australian Museum 43, 47–62.

Hutchings, P.A., Reid, A., Wilson, R.S., 1991. *Perinereis* (Polychaeta, Nereididae) from Australia, with redescriptions of six additional species. Records of the Australian Museum 43, 241–274.

Imajima, M., 1989. Spionidae (Annelida, Polychaeta) from Japan. I. The genera *Aonides* and *Apoprionospio*. Bulletin of the National Science Museum, series A (Zoology) 15, 213–222.

Kaly, U.L., Eugelink, G., Roberston, A.I., 1997. Soil conditions in damaged north Queensland mangroves. Estuaries 20, 291–300.

Kumar, R.S., 1995. Macrobenthos in the mangrove ecosystem of Cochin backwaters, Kerala (southwest coast of India). Indian Journal of Marine Sciences 24, 56–61.

Kumar, R.S., 2003. A checklist of polychaete species some mangroves of Asia. Zoos' Print Journal 18(2): 1017–1020.

Kurian, C.V., 1984. Fauna of the mangrove swamps in Cochin estuary. In: Soepadmo, E., Rao, A.N., Macintosh, D.J. (Eds) Proceedings of the Asian Symposium on Mangrove Environments: Research and Management, University of Malaya and UNESCO, Kuala Lumpur, pp 226–230.

López, E., Cladera, P., San Martín, G., Laborda, A., Aguado, M.T., 2002. Polychaete assemblages inhabiting intertidal soft bottoms associated with mangrove systems in Coiba National Park (East Pacific, Panama). Wetlands Ecology and Management 10, 233–242.

Macintosh D.J., Ashton E.C., Havanond, S., 2002. Mangrove rehabilitation and intertidal biodiversity: a study in the Ranong mangrove ecosystem, Thailand. Estuarine, Coastal and Shelf Science 55: 331–345.

Mackie, A.S.Y., 1987. A review of species currently assigned to the genus *Leitoscoloplos* Day, 1977 (Polychaeta: Orbiniidae), with descriptions of species newly referred to *Scoloplos* Blainville, 1828. Sarsia 72, 1–28.

Metcalfe, K., 1999. Mangrove litter production, Darwin Harbour. A study of litter fall as a measure of primary productivity in the mangrove communities of Darwin Harbour. Master of Tropical Environmental Management Thesis, Faculty of Biological and Environmental Science, Northern Territory University, 84 pp.

Metcalfe, K., 2004. Mangrove Invertebrate Fauna. Darwin LNG Project Environmental Monitoring Program. Darwin, NT, Prepared for URS Australia Pty Ltd, 55 pp.

Metcalfe, K., 2005. Mangrove Invertebrate Fauna. Darwin LNG Project Mangrove Monitoring Program, Annual Report 2004–2005. Prepared for URS Australia, 94 pp.

Metcalfe, K., 2007. The biological diversity, recovery from disturbance and rehabilitation of mangroves, Darwin Harbour, NT. PhD thesis, Charles Darwin University, Darwin, Northern Territory, Australia.

Pagliosa P.R., 2005. Another diet of worms: the applicability of polychaete feeding guilds as a useful conceptual framework and biological variable. Marine Ecology 26, 246–254.

Qiu, J.-W., Qian, P.-Y., 2000. Revision of the genus *Leonnates* Kinberg, 1866 (Polychaeta: Nereididae), with descriptions and comments on other species described in *Leonnates*. Proceedings of the Biological Society of Washington 113, 1111–1146.

Rainer, S.F., Hutchings, P.A., 1977. Nephtyidae (Polychaeta: Errantia) from Australia. Records of the Australian Museum 31, 307–347.

Sarkar, S.K., Bhattacharya, S.G., Bhattacharya, B., Sarkar, D., Nayak, D.C., Chattopadhaya, A.K. (2005) Spatiotemporal variation in benthic polychaetes (Annelida) and relationships with environmental variables in a tropical estuary. Wetands ecology and management 13: 55-67

Saenger, P., Specht, M.M., Specht, R.L., Chapman, V.J., 1978. Mangal and Coastal Salt-Marsh Communities in Australasia. In: Chapman, V.J. (Ed.) Ecosystems of the World Volume I, Wet Coastal Ecosystems. Elsevier, Amsterdam, pp. 293–345.

Sasekumar, A., 1974. Distribution of macrofauna on a Malayan mangrove shore. Journal of Animal Ecology 43, 51–69.

Semeniuk, V., 1985. Mangrove environments of Port Darwin, Northern Territory: the physical framework and habitats. Journal of the Royal Society of Western Australia 67, 81–97.

Wells, F.E., 1983 An analysis of marine invertebrate distributions in a mangrove swamp in northwestern Australia. Bulletin of Marine Science 33, 736–744.

Wightman, G.M., 1989. Mangroves of the Northern Territory. Palmerston, Conservation Commission of the Northern Territory.

Williams, D, Wolanski, E., Spagnol, S., 2006. The hydrodynamics of Darwin Harbour. In: Wolanski, E. (Ed.). The environments in Asia Pacific Harbours. Springer Dordrecht, the Netherlands, pp 461–476.

Woodroffe, C.D., 1995. Response of tide-dominated mangrove shorelines in northern Australia to anticipated sea-level rise. Earth surface processes and landforms 20, 65–85.

Woodroffe, C.D., Bardsley, K.N., 1987. The distribution and productivity of mangroves in Creek H, Darwin Harbour. In: Larson, H.K., Michie, M.G., Hanley, J.R. (Eds). Proceedings of a workshop on research and management held in Darwin, 2–3 September 1987. Darwin, North Australia Research Unit, the Australian National University. Mangrove Monograph No. 4, 82–122.

Appendix

Annotated list of polychaete and other worm species from Darwin Harbour mangrove habitats. Macrohabitat categories *=known only from mangroves; **=occurring in both mangroves and non-mangrove intertidal flats. One species, *Mastobranchus* sp., was not collected in this study – it is only know from *Thalassina* mounds. Codes for feeding guilds as follows:

Higher Taxon	Family	Species	Assemblage - tally of abundance				Micro-habitat	Macro-habitat	Feeding guild	Trophic category	Distribution	Additional data source
			Hint marg	Tidal flat	Tidal ck	Seawd						
Echiura	Thalassematidae	*Listriolobus bulbocaudatus*			1	2	Infauna	**	SDX	surface deposit feeder	Indo-west Pacific	Edmonds (1987)
Nemertea		*Cerebratulus* sp.			1	1	Infauna		CMX	carnivore		
Nemertea		Nemertea spp.	5	20	25	49	Epi/Infauna		CMX	carnivore		
Oligochaeta		Oligochaeta sp.				1	Infauna		BMX	subsurface deposit feeder		
Polychaeta	Ampharetidae	*Amphicteis* sp.1				1	Infauna		SST	surface deposit feeder		
Polychaeta	Ampharetidae	*Isolda pulchella*			10	34	Infauna	**	SST	surface deposit feeder	NT	NTM database
Polychaeta	Ampharetidae	*Pavelius* sp.			1		Infauna		SST	surface deposit feeder		
Polychaeta	Capitellidae	*Capitella* sp.1			1		Infauna		SMX	surface deposit feeder		
Polychaeta	Capitellidae	*Heteromastus* sp. 2				2	Infauna	*	BMX	subsurface deposit feeder	Darwin Harbour	NTM database
Polychaeta	Capitellidae	*Heteromastus* sp.1		13	9	22	Infauna	*	BMX	subsurface deposit feeder	Darwin Harbour	NTM database; Hanley (1985) as Heteromastides sp.
Polychaeta	Capitellidae	*Mastobranchus* sp.					Infauna	*			Darwin Harbour	NTM database; Hanley (1985) as Heteromastus sp. A
Polychaeta	Capitellidae	*Mediomastus* sp. 1		4	6	11	Infauna	**	BMX	subsurface deposit feeder	NT	NTM database
Polychaeta	Capitellidae	*Notomastus* sp.		2		1	Infauna	**	BMX	subsurface deposit feeder	NT	NTM database; Hanley (1985)
Polychaeta	Cirratulidae	*Aphelochaeta* sp. 1			1	12	Infauna		SMT	surface deposit feeder		

Polychaeta	Cirratulidae	*Cirriformia* sp. 1			1	7	Infauna		SMT	surface deposit feeder		
Polychaeta	Cirratulidae	*Protocirrineris* sp.			7	1	Infauna		SMT	surface deposit feeder		
Polychaeta	Dorvilleidae	*Schistomeringos* sp.				1	Infauna		HMJ	herbivore		
Polychaeta	Eunicidae	*Marphysa mossambica*			4	4	Epi/Infauna	**	CMJ	carnivore	Indo-west Pacific	NTM database; Hanley (1985)
Polychaeta	Eunicidae	*Nematonereis* sp.				4	Epifauna	**	CMJ	carnivore	northern Australia	NTM database; Hanley (1985) as N. unicornis
Polychaeta	Glyceridae	*Glycera nicobarica*		3	17	67	Infauna	**	CDJ	carnivore	Indo-west Pacific	NTM database; Hanley (1985) reports Glycera Sp. A,B,C but cannot reconcile his ids with this study
Polychaeta	Glyceridae	*Glycera* sp.2			4	3	Infauna		CDJ	carnivore		Hanley (1985) reports Glycera Sp. A,B,C but cannot reconcile his ids with this study
Polychaeta	Goniadidae	*Glycinde bonhourei*				3	Infauna	**	CDJ	carnivore	northern Australia	Boggemann (2005)
Polychaeta	Lumbrineridae	*Arabelloneris broomensis*				10	Infauna	**	BMJ	subsurface deposit feeder	Darwin Harbour and Broome	Hartmann-Schroder (1979)
Polychaeta	Lumbrineridae	*Scoletoma* sp. 1			10	87	Infauna		BMJ	subsurface deposit feeder		
Polychaeta	Magelonidae	*Magelona* sp. 1			3	25	Infauna		SDT	surface deposit feeder		
Polychaeta	Nephtyidae	*Nephtys mesobranchia*				21	Infauna	**	CMJ	carnivore	northern Australia, eastern Australia	Rainer and Hutchings (1977)
Polychaeta	Nereididae	*Ceratonereis australis*				6	Epifauna	**	HMJ	herbivore	north and north-west Australia	NTM database; Hartmann-Schroder (1985)
Polychaeta	Nereididae	*Ceratonereis* NTMW6742			2	2	Epi/Infauna	*	HMJ	herbivore	northern Australia	NTM database; Hanley (1985) as Ceratonereis mirabilis

Polychaeta	Nereididae	*Composetia* sp.			1		Infauna		HMJ	herbivore		
Polychaeta	Nereididae	*Dendronereides heteropoda*				1	Infauna	**	SDJ	surface deposit feeder	Indo-west Pacific	NTM database; Hutchings and Reid (1990), Hanley (1985)
Polychaeta	Nereididae	*Dendronereides* sp.		2			Infauna		SDJ	surface deposit feeder		
Polychaeta	Nereididae	*Leonnates crinitus*			1		Epifauna	**	SDJ	surface deposit feeder	northern Australia	NTM database; Hutchings and Reid (1991); Qiu and Qian (2000)
Polychaeta	Nereididae	*Leonnates stephensoni*			2	3	Infauna	**	SDJ	surface deposit feeder	Indo-west Pacific	NTM database; Hutchings and Reid (1991); Qiu and Qian (2000)
Polychaeta	Nereididae	*Namalycastis abiuma*	3		4		Epi/Infauna	**	HMJ	herbivore	Pan-tropical	NTM database; Glasby (1999)
Polychaeta	Nereididae	*Namalycastis nicoleae*	1		6	6	Epifauna	*	HMJ	herbivore	northern and eastern Australia	NTM database; Glasby (1999)
Polychaeta	Nereididae	*Namanereis malaitae*	5	1			Infauna	**	HMJ	herbivore	Indo-west Pacific	NTM database; Glasby (1999)
Polychaeta	Nereididae	*Namereis amboinensis*			4		Epifauna	**	HMJ	herbivore	Pan-tropical	NTM database
Polychaeta	Nereididae	*Neanthes cf. biseriata*	1			28	Epifauna	**	HMJ	herbivore	north and north-west Australia	NTM database; Glasby (1999)
Polychaeta	Nereididae	*Neanthes* sp.2				1	Infauna		HMJ	herbivore		
Polychaeta	Nereididae	*Nereis* sp. 1		2	16	235	Infauna		HMJ	herbivore		
Polychaeta	Nereididae	*Paraleonnates bolus*	2	8		1	Epi/Infauna	*	SDJ	surface deposit feeder	northern Australia	NTM database; Hutchings and Reid (1991) [as Leonnates bolus]; Qiu and Qian (2000)

Polychaeta	Nereididae	*Perinereis aibuhitensis*	2	15	14	18	Epi/Infauna	**	HMJ	herbivore	Indo-west Pacific	NTM database; Hutchings, Reid and Wilson (1991); Hanley (1985) as Neanthes sp. B
Polychaeta	Nereididae	*Perinereis nigropunctata*			4	1	Epi/Infauna	**	HMJ	herbivore	Indo-west Pacific	NTM database; Hutchings, Reid and Wilson (1991)
Polychaeta	Nereididae	*Perinereis singaporiensis*		1	26	186	Epifauna	**	HMJ	herbivore	Indo-west Pacific	NTM database; Hanley (1985) as P. vancaurica
Polychaeta	Nereididae	*Simplisetia* cf. *erythraensis*			10		Infauna	**	HMJ	herbivore	northern Australia	NTM database
Polychaeta	Oenonidae	*Drilonereis* sp.				1	Infauna		CMJ	carnivore		
Polychaeta	Onuphiidae	Onuphid unident.			1		Infauna		HDJ	herbivore		
Polychaeta	Orbiniidae	*Leitoscoloplos latibranchus*			5	19	Infauna	**	BMX	subsurface deposit feeder	Australia	NTM database; Day (1977); Mackie (1987)
Polychaeta	Orbiniidae	*Scoloplos normalis*			1		Infauna	**	BMX	subsurface deposit feeder	Australia	NTM database; Day (1977); Mackie (1987)
Polychaeta	Paranoidae	Paraonidae unident.				1	Infauna		SMX	surface deposit feeder		
Polychaeta	Phyllodocidae	*Eteone* sp. 1			1		Infauna		CMX	carnivore		
Polychaeta	Phyllodocidae	*Phyllodoce* sp. 1		12		3	Infauna	**	CMX	carnivore	?Indo-Pacific	NTM database
Polychaeta	Phyllodocidae	*Sige* sp.				1	Epifauna		CMX	carnivore		
Polychaeta	Pilagidae	*Parandalia* sp.				1	Infauna		CMJ	carnivore		
Polychaeta	Polynoidae	*Lepidonotus kumari*			7		Epi/Infauna	**	CMJ	carnivore	northern Australia	NTM database
Polychaeta	Polynoidae	*Lepidonotus* sp. 1			2	52	Epifauna	*	CMJ	carnivore	Darwin Harbour	NTM database; Hanley (1985) as Lepidonotus sp. D
Polychaeta	Sabellidae	*Branchiomma* sp.1				8	Epifauna		FST	filter feeder		
Polychaeta	Sabellidae	*Demonax* sp. 1				1	Epifauna		FST	filter feeder		

Polychaeta	Serpulidae	*Pomatoleios kraussii*				16	Epifauna	**	FST	filter feeder	Indo-west Pacific	NTM database
Polychaeta	Spionidae	*Aonides oxycephala*				1	Infauna	**	SDT	surface deposit feeder	cosmopolitan	NTM database; Blake and Kudenov (1978); Imajima (1989)
Polychaeta	Spionidae	*Polydora* sp. 1			1	4	Infauna		SDT	surface deposit feeder		
Polychaeta	Spionidae	*Polydora* sp. 2			1		Infauna		SDT	surface deposit feeder		
Polychaeta	Spionidae	*Polydora* sp. 3				3	Infauna		SDT	surface deposit feeder		
Polychaeta	Spionidae	*Prionospio* cirrifera complex			2		Infauna	**	SDT	surface deposit feeder	cosmopolitan	NTM database; Blake and Kudenov (1978)
Polychaeta	Spionidae	*Prionospio* sp. 1			1	15	Infauna		SDT	surface deposit feeder		
Polychaeta	Spionidae	*Prionospio* steenstrupi complex			1	1	Infauna	**	SDT	surface deposit feeder	cosmopolitan	NTM database; Blake and Kudenov (1978)
Polychaeta	Spionidae	*Scolelepis* sp. 1			1		Infauna		SDT	surface deposit feeder		
Polychaeta	Sternaspidae	*Sternaspis* sp.			2		Infauna		SDT	surface deposit feeder		
Polychaeta	Syllidae	*Branchiosyllis* sp.1				1	Epifauna		CMJ	carnivore		
Polychaeta	Syllidae	*Syllis* sp. 1				9	Epifauna		CMJ	carnivore		
Polychaeta	Terebellidae	*Terebella tantabiddycreekensis*			5		Epi/Infauna	**	SST	surface deposit feeder	northern Australia	NTM database; Hutchings (1997)
Polychaeta	Trichobranchidae	*Terebellides kowinka*			5		Infauna	**	SST	surface deposit feeder	Australia	NTM database; Hutchings (2000)
Polychaeta	Trochochaetidae	*Trochochaeta* sp.				1	Infauna		SDT	surface deposit feeder		
Sipunculida		*Phascolosoma arcuatum*	2	24	54	14	Infauna	**	SDT	surface deposit feeder	Indo-west Pacific	Cutler and Cutler (1990)
Sipunculida		Sipuncula sp. 2			5		Infauna		SDT	surface deposit feeder		
Sipunculida		Sipuncula sp. 3			1		Infauna		SDT	surface deposit feeder		
Turbellaria		Turbellaria spp.	1	4	3	16	Epifauna		SMX	surface deposit feeder		
Total abundance per assemblage			**22**	**111**	**290**	**1025**						

Table available online : http://www.nt.gov.au/nreta/museums/magnt/collectionsresearch/naturalsciences/annelids.html.

APPENDIX D

Manuscript published in *Zoological Science,* Volume 24, pages 563-570 (2007).

An Amphibious Bryozoan from Living Mangrove Leaves—*Amphibiobeania* new genus (Beaniidae)

Kristin Metcalfe[1], Dennis P. Gordon[2], and Ellie Hayward[1]

[1]School of Science and Primary Industries, Faculty of Education, Health and Science, Charles Darwin University, Darwin, NT 0909, Australia

[2]National Institute of Water & Atmospheric Research (NIWA), Private Bag,14-901 Kilbirnie, Wellington, New Zealand

ABSTRACT—*Amphibiobeania epiphylla* is a new, monotypic taxon of Beaniidae (Cheilostomata) from Darwin, Northern Territory. It is unique among the 6000 living species of Bryozoa in that it encrusts mainly living tree leaves (chiefly the mangrove *Rhizophora stylosa*). The consequence of living in such a specialized habitat is that colonies are emergent (subaerial) for a significant part of the tidal cycle—around 12 of every 24 hours during spring tides and for several days during neap tides. Desiccation is prevented or minimized by the high humidity of the habitat and a cohesive coating of silt covering the colony. Zooids are weakly calcified and lie alternately on their left and right sides in a lineal series, with opercula displaced to the outer corner of the distal zooidal rim. Organisms associated with *A. epiphylla* include a colony-damaging ceratopogonid (Diptera) larva and a tarsonemid mite that may use dead zooidal interiors, beneath the silt crust, for shelter.

Keywords: Bryozoa, Beaniidae, new genus, *Amphibiobeania*, mangroves, Darwin, Northern Territory

INTRODUCTION

Mangrove forest habitats host a rich diversity of invertebrates (Alfaro, 2006; Ashton *et al.*, 2003; Hutchings and Recher, 1983)—the dense canopy typically offers protection from desiccation and the roots, tree trunks, and unconsolidated sediments provide microhabitats for abundant epifauna, infauna, and benthic species. In the mangroves of Darwin Harbour (Fig. 1), the main macro-invertebrate groups are molluscs (95 species) and crustaceans (89 species), with polychaete and other worm taxa also well represented by over 75 species (Metcalfe, 2005, 2007). Similar to the flora, mangrove faunal assemblages are also patterned in response to tidal rhythms, and geomorphological, ecological, and microtopographic factors, with the seaward assemblage supporting the greatest diversity and abundance of fauna.

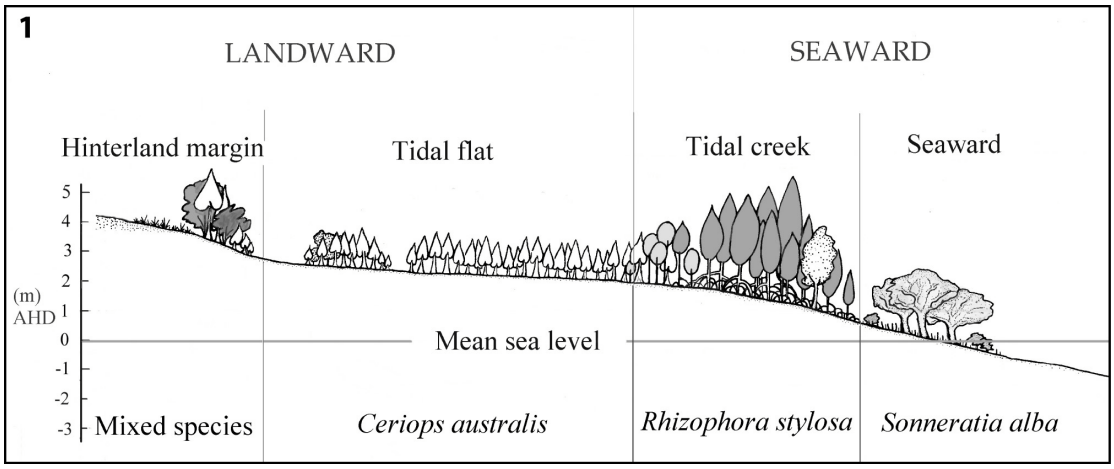
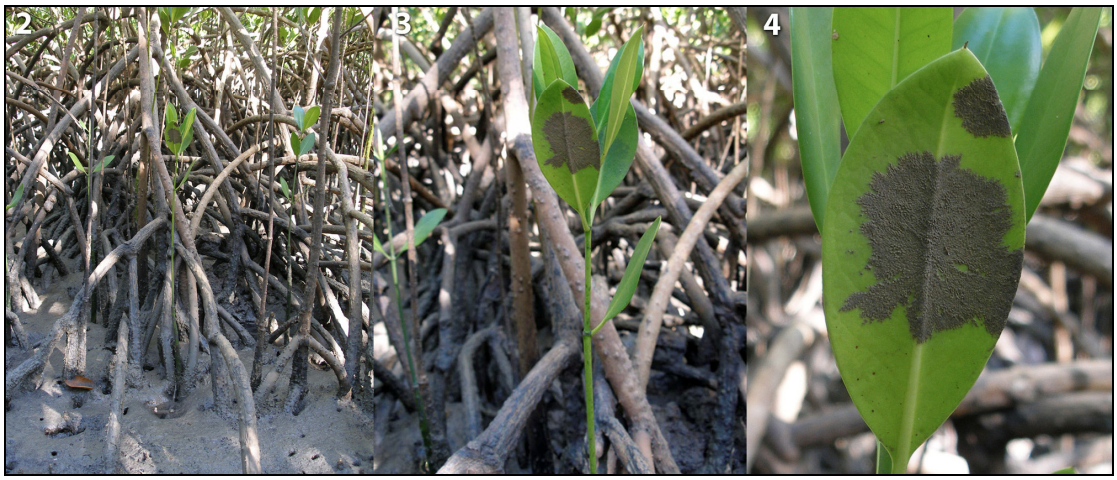


Fig. 1. Generalised profile of the pattern of mangrove assemblages in the upper intertidal zone of Darwin Harbour, indicating the tidal elevation (m AHD) and the dominant tree species in the four main assemblages.

In the course of ecological studies of the mangal environment, a species of bryozoan was found that primarily encrusts living mangrove leaves in seaward assemblages (Figs 2 - 4). The obvious consequence of living in such a specialized habitat is that the bryozoan is emergent (subaerial) for a significant part of the tidal cycle. Indeed, in its primary habitat, the bryozoan is exposed for longer than it is submerged—for at least 12 of every 24 hours during spring tides and for periods of several days during neap tides. So far as is known, both the substratum (living tree leaves) and the duration of the amphibious mode of existence are unique among the approximately 6000 extant species of Bryozoa, whereas seagrass leaves are well-known substrata for bryozoans. A study was begun to ascertain the taxonomic affinities of the bryozoan, the diversity of host mangrove species, any other substrata occupied, and its ecology relative to individual mangrove hosts and the tidal cycle. Our results include the recognition of a new genus of cheilostome bryozoan with a unique zooidal orientation and budding pattern.



Figs. 2 - 4. Tidal-creek mangrove habitat in Darwin Harbour with Amphibiobeania epiphylla colonies encrusting the underside of a leaf of a Rhizophora stylosa seedling (magnified in 2 through 4).

STUDY AREA AND METHODS

Mangrove environments of northern Australia are floristically diverse and extensive, spanning over 4,120 km^2 of the Northern Territory coast (Wightman, 1989). Darwin Harbour, an embayment of some 450 km^2, comprises over 20,400 hectares of relatively pristine mangrove habitat, representing one of the most extensive stands in the region (Woodroffe, 1995). Over 30 species of mangrove are known from the Darwin area, with 21 shrub and tree species commonly occurring in the intertidal zone (Wightman, 1989). Collectively, they form dense mangrove forests that comprise a number of distinct habitats or assemblages, indicated by a predictable pattern of species distribution (Fig. 1). Indeed, each of the major floristic assemblages is confined to quite discrete elevational ranges (Metcalfe, 1999; Semeniuk, 1985; Woodroffe and Bardsley, 1987). Of the ten assemblages recognised in a recent classification of Darwin Harbour, just four occupy 88.2% of the total area

(Brocklehurst and Edmeades, 1996). Darwin's climate is tropical humid, with mean annual temperature of 28°C and 63% relative humidity, with wet summer monsoon and dry winter seasons. There are some 111 rainy days per year and the mean annual rainfall of 1,713 mm is exceeded by mean evaporation of 2,591 mm yr^{-1} (Bureau of Meteorology, 2006). Salinities in the seaward mangrove habitat remain close to that of oceanic seawater, at 33 - 36 psu throughout the year.The region is macro-tidal, with a maximum tidal range of 7.8 m. Tides are semidiurnal (two lows and highs per day) with a mean spring range of 5.5 m and mean neap range of 1.9 m (Woodroffe, 1995). In Darwin Harbour, mangroves occur between –1.0 and 4.0 m Australian Height Datum (AHD)—which approximates to mean sea level (MSL). Mangrove forests occurring at 0 m AHD are inundated by all tides and during neap tides regularly undergo periods of inundation spanning over 18 hours and exposure lasting approximately nine hours. To landward, the frequency and duration of tidal inundation progressively decreases, such that 93% of annual tides exceed 1 m AHD and only 58% exceed 2 m AHD (Metcalfe 1999). Mangroves occurring to landward of approximately 2 m AHD, including the extensive tidal-flat assemblage, are inundated only every fortnight by spring tides. Dense, low (2 – 4 m high) thickets of *Ceriops australis* (Perr.) C.B. Robinson (Rhizophoraceae) occur in this habitat, partly in response to increasing soil salinities. Below 2 m AHD, however, the two seaward assemblages receive more frequent tidal flushing and comprise taller (9 - 16 m high), more luxuriant forests, dominated by *Rhizophora stylosa* Griff. (Rhizophoraceae) and *Sonneratia alba* J. Smith (Lythraceae)

Colonies of the new, leaf-encrusting bryozoan were collected from the *Rhizophora* assemblages during several different months over a period of five years, from April 2001 to April 2006. Some were studied live, while others were narcotised in a magnesium chloride solution, prior to preservation in either 70% ethanol or in buffered 3% glutaraldehyde and seawater, with post-fixation in osmium tetroxide. Scanning electron microscopy was carried out on uncoated specimens viewed at low vacuum and on whole and dissected parts of colonies coated with gold-palladium and viewed under high vacuum. Elemental composition of the zooidal body wall and silt matrix of the colony was carried out using a LEO 440 SEM and energy-dispersive X-ray analysis. For light microscopy, specimens were embedded in Spurrs resin, stained using toluidine blue, and sectioned at a thickness 1 μm.

SYSTEMATICS

Phylum **Bryozoa** Ehrenberg, 1831

Class **Gymnolaemata** Allman, 1856

Order **Cheilostomata** Busk, 1852

Suborder **Neocheilostomina** d'Hondt, 1985

Infraorder **Flustrina** Smitt, 1868

Superfamily **Buguloidea** Gray, 1848

Family **Beaniidae** Canu & Bassler, 1927

Genus **Amphibiobeania** nov.

Diagnosis: Colony encrusting, concealed by firm opaque layer of silt particles. Individual zooids dinghy-shaped, very weakly calcified and lying on their left or right sides; highly disjunct, joined by tubular connections to daughter zooids and neighbouring lateral zooids. Orifice displaced to outer distolateral rim of zooid, closed by an opercular flap with sclerotized rim. No spines or avicularia. Ovicells not seen. Ancestrula not seen.

Etymology: The genus name reflects the uniquely amphibious life habit of the bryozoan as well as its likely affinities to *Beania*.

Type species: *Amphibiobeania epiphylla* n. sp., by monotypy.

Amphibiobeania epiphylla sp. nov.

Material examined: Holotype: NTM G268 (colony on a leaf of *Rhizophora stylosa*; preserved in alcohol), Museum and Art Gallery of the Northern Territory, Darwin, collected at a tidal elevation of c. 1.5 m Australian Height Datum from 12° 27.389′ S 130° 52.135′ E, Darwin Harbour, December 2004. Paratypes: NHM 2006.8.7.1 - 2, London, same locality as holotype; NIWA 23892, National Institute of Water & Atmospheric Research, Wellington, on *R. stylosa* leaf fragments, same locality as holotype (NIWA Stn Z15114). All colonies collected by K. Metcalfe.

Description: Colony encrusting, unilaminar, mostly multiserial, frequently more or less circular but sometimes with pluriserial lobes and/or uniserial extensions of zooids at the colony margin (Figs 4, 5, 19) that give the colony a stellate outline; maximum colony diameter 48 mm. Zooids and interzooidal spaces completely concealed by adherent opaque coating of silt but their general disposition in the colony evidenced by regularly spaced zooidal orifices and sometimes a longitudinal slit in the coating above each zooid (Fig. 5); the slit sometimes evident in live zooids, especially when lophophores (Fig. 10) are retracted. Removal of silt coating reveals that zooids are dinghy-shaped, very weakly calcified, and lie on their sides (Figs 6, 8, 19). Individual zooids 380 - 530 μm long, 90 - 110 μm wide highly disjunct, lying on their left or their right, and joined by tubular connections to daughter zooids and neighbouring lateral zooids. Daughter zooids originating from the distal body wall or from a tubular connection budded mid-

basally; alternatively, the basally budded tube crosses the substratum to connect to the mid-lateral rim of an adjacent zooid produced by a different parent. Zooids in a lineal series lying alternately on their left and right sides along the series (Fig. 19). Opercular area displaced to the outer distolateral rim of each zooid (Figs 6, 8 12), thickened where lophophore everts (Fig. 13); number of tentacles 8, no intertentacular organ. No gizzard in the alimentary tract. No spines, avicularia, or basal attachment rhizoids. Ovicells not seen, nor evidence of internal brooding. Ancestrula and early astogeny not seen.

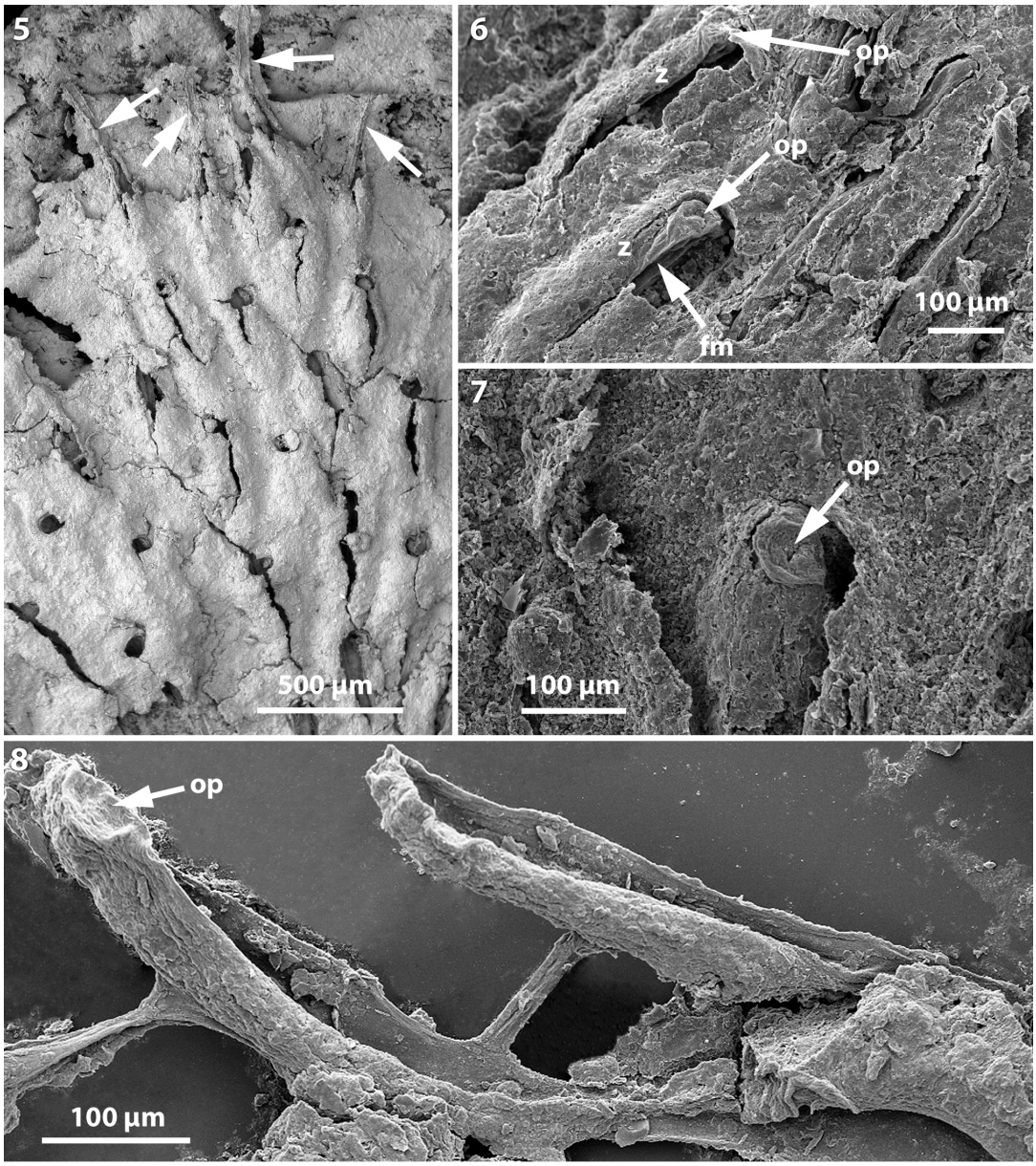
Remarks: Initial microscopic examination of colonies to ascertain their identity was handicapped by an opaque muddy coating that conceals all diagnostic characters. Immersion of colonies in seawater, however, elicited emergence of lophophores for feeding, unequivocally demonstrating the bryozoan nature of the organism. Careful removal of the silt layer is possible using a fine paintbrush.

Tubular zooidal buds at the colony periphery resemble those seen in some ctenostomes and the very thin zooidal walls give the initial impression of a ctenostome bryozoan. The dinghy shape is more typically cheilostomate, however, and the presence of calcium carbonate in the walls is confirmed by strong birefringence under polarized light with crossed nicols. An SEM elemental analysis also shows a calcium spike (Figs 16, 17).

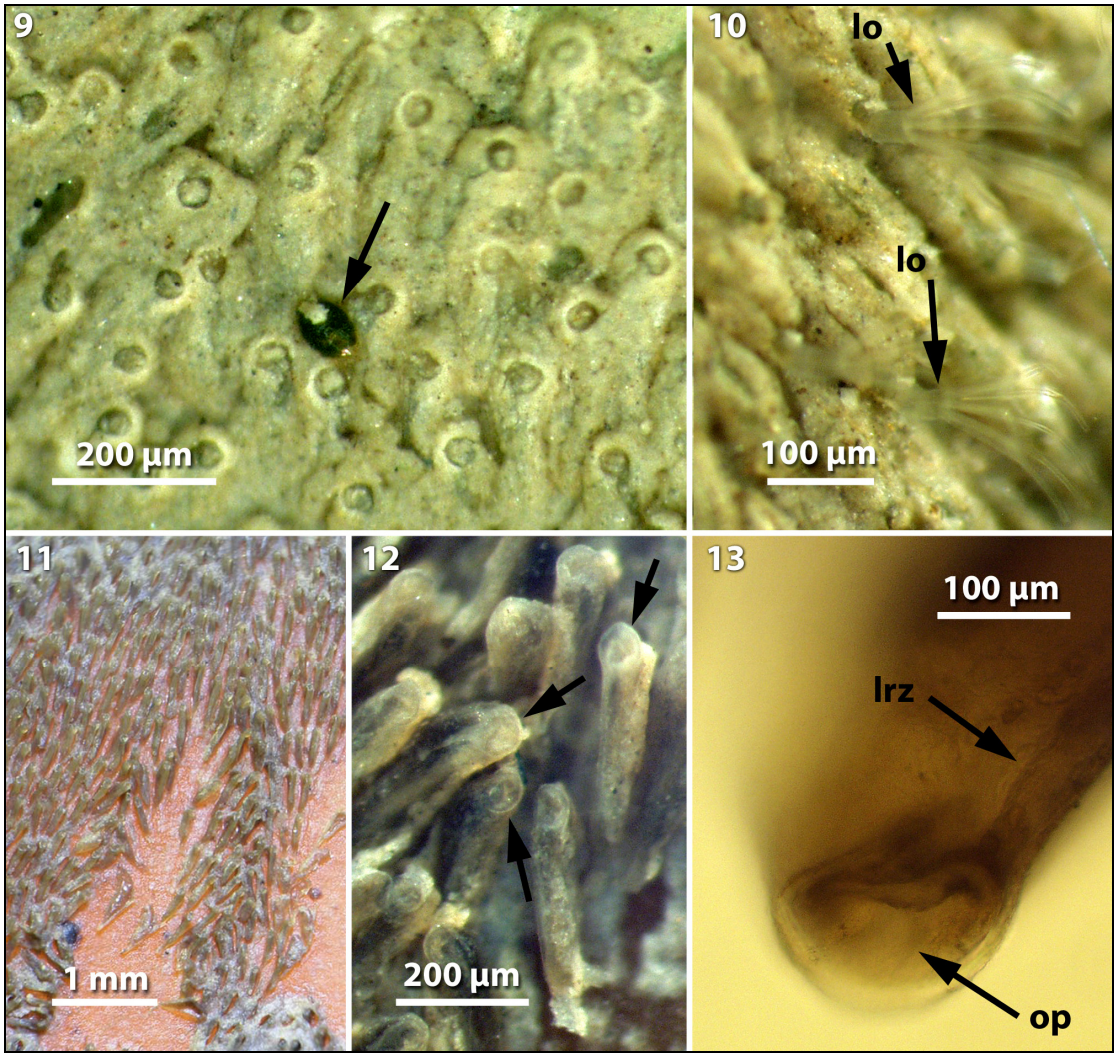
Amphibiobeania epiphylla is unique among bryozoans. Not only is it the only bryozoan known to encrust tree leaves, no other has been reported to have zooids orientated so as to lie on their sides. This in turn has particular consequences, viz the emergence of lophophores past one corner of the distal zooidal rim, and the disposition of lateral zooid connections in a manner not seen in other cheilostomes. The discovery that zooids lie on their sides explains an unusual feature that was seen in histological sections taken through the colony above the plane of the mangrove leaf. These show a clear area on one side of each zooid (Fig. 14). Although the sectioned zooids have retracted lophophores, we interpret the clear area as reflecting the space in which the membranous frontal wall of the zooid flexes outwards and inwards upon invagination and evagination of the lophophore; in this case, frontalwards is sideways in the colony, beneath the silt layer. One can only guess how the sideways orientation may have evolved but it is possible that partial desiccation of the inflexible silt layer during tidal emergence, making it harder, may have been a driving factor in selection for sideways orientation; with a hardened overlying surface layer, the zooidal frontal membrane cannot flex upwards, in contrast to a sideways flexure.

The disjunct arrangement of zooids in *A. epiphylla*, with tubular connections, allows us to classify our new genus in the Beaniidae, which comprises only two other recognized genera—*Beania* Johnston, 1840 and *Stolonella* Hincks, 1883. Unless they are uniserial, species of *Beania* for the most part have obviously disjunct zooids, connected by tubular extensions of neighbouring zooids. Further, zooids of many species are boat-shaped and the anterior half or more of the zooid can be elevated near vertically such that budding of distal zooids is essentially from the basal wall, similar to that in *A. epiphylla*. Beaniids are all lightly calcified, typical of the majority of species in the superfamily Buguloidea, although few are as weakly mineralized as *A. epiphylla*. *Amphibiobeania* differs from all species of *Beania* in having zooids orientated on their sides, basal tubes that either bud a new distal zooid or connect with the lateral walls of an adjacent zooid, a displaced orifice, and the lack of rhizoids with attachment disks. The accretion of a silt layer is also distinctive, as is the complete lack of both avicularia and spines. Of the many disparate species of *Beania*, *A. epiphylla* is closer to uniserial forms like *Beania mirabilis* Johnston,

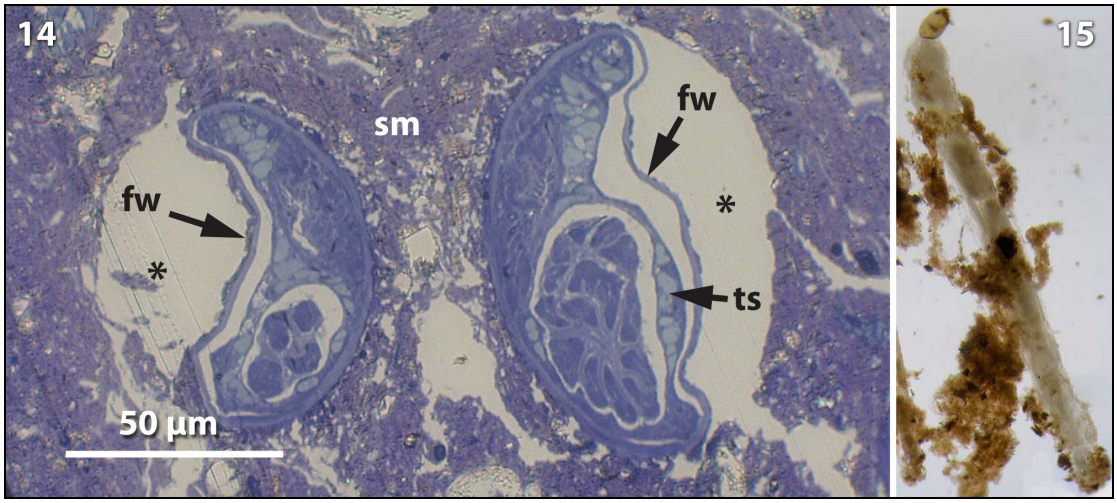
1840 than to species with four or six tubular connections with adjacent zooids. *Stolonella* differs in having all autozooids arise from stolons, not from other autozooids.



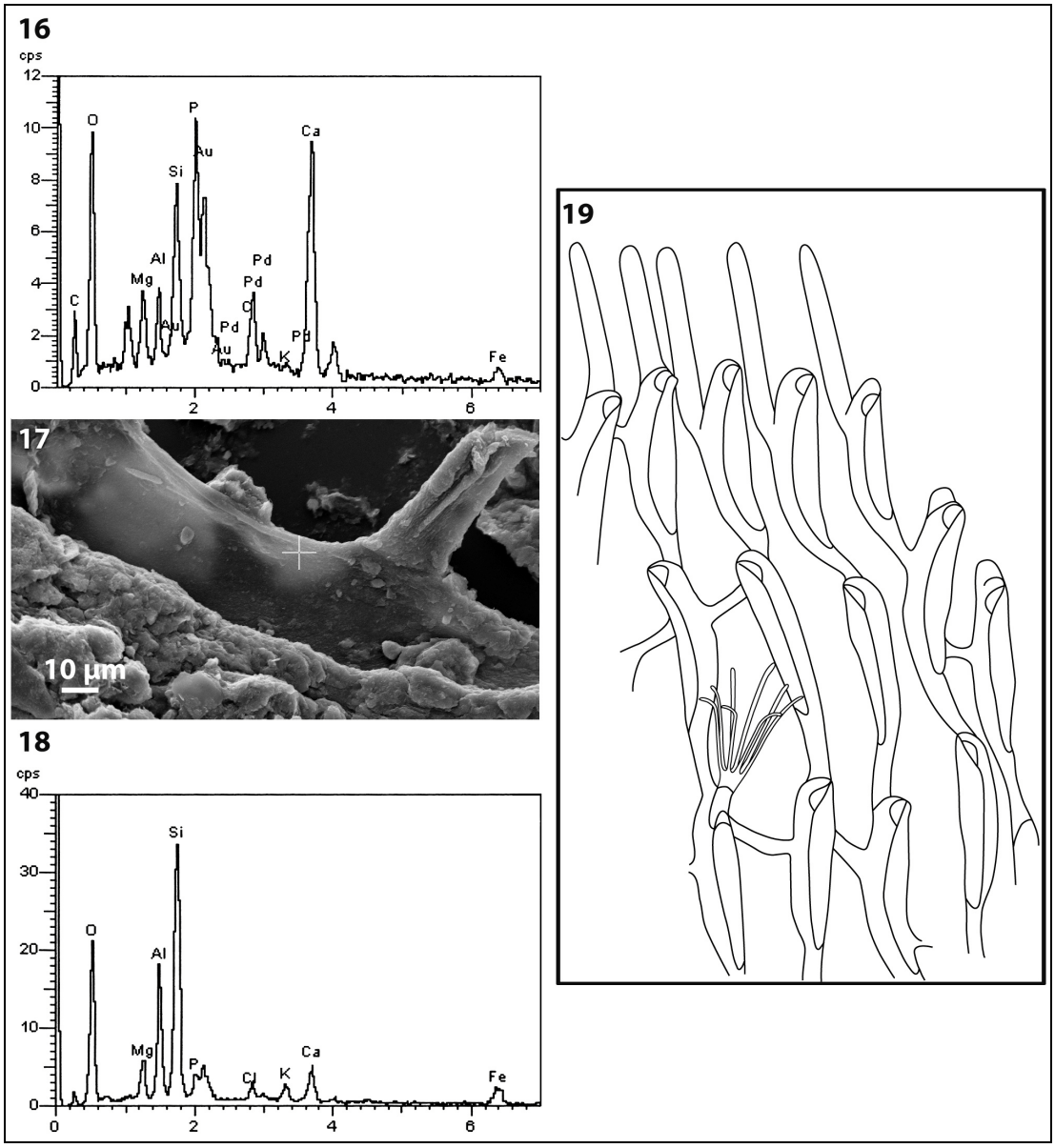
Figs. 5 - 8. *Amphibiobeania epiphylla* gen. et sp. nov. 5. Surface of part of a colony with a thick silt crust. Zooidal orifices are visible as subcircular to irregular openings and there are cracks in the crust. Arrows indicate tubular zooidal buds (collapsed through drying) at the colony margin. 6. part of colony surface with the silt crust mostly covering zooids. Two zooids (z) are indicated where the crust is partially missing, showing them lying on their sides (fm, membranous frontal wall; op, operculum). 7. Close-up of an individual operculum surrounded by the silt crust of adjacent zooids. 8. SEM view of two zooids from which the crust has been removed and which have been partially treated in hypochlorite solution; they are orientated in life position, i.e. on their sides. The opercular area (op) is visible in the zooid at left, and two tubular connections are evident.



Figs. 9 - 13. *Amphibiobeania epiphylla* gen. et sp. nov. 9. Surface of a live colony showing orifices and a tarsonemid mite (arrow). 10. Living zooids with two emergent lophophores (lo). 11. Part of fresh colony with silt crust removed, showing relative disposition of zooids. 12. Close-up of zooids from which the silt crust has been removed, showing opercula (arrows). 13. Distal view of an operculum (op); lrz, lateral zooidal rim.



Figs. 14, 15. (opposite page). *Amphibiobeania epiphylla* gen. et sp. nov. 14. Section through a colony, more or less in the same plane as the leaf surface but just above it, showing two zooids with their curved basal walls facing each other. The zooids are lying on their sides, with a space (*) for each membranous frontal wall to flex into. The zooid at left shows profiles of four tentacle tips, whereas that at right shows profiles of bent retracted tentacles; ts, tentacle sheath; sm, silt matrix. 15. A dipteran larva, probably of *Dasyhelea* (Ceratopogonidae), associated with *A. epiphylla*.



Figs. 16 – 19. *Amphibiobeania epiphylla* gen. et sp. nov. 16. Elemental composition of the zooidal body wall shown in Fig. 17 (based on energy-dispersive X-ray analysis using a LEO 440 SEM). Elements are represented by their symbols. Magnesium-calcite in the body wall is indicated by the high calcium (Ca) spike and the presence of carbon (C), oxygen (O), and magnesium (Mg). [The gold-palladium (Au-Pd) metal coating of the specimen is also indicated.] 17. View of the hypochlorite-cleaned inner wall of a zooid showing the location (+) of the elemental analysis. 18. Elemental analysis of the silt matrix surrounding the zooids, showing spikes indicating soil aluminosilicate. 19. Pattern of budding in adjacent zooids. Notice the alternating left and right disposition of zooids in a lineal series.

DISCUSSION

Bryozoans have been noted previously on mangroves. For example, Fransen (1986) reported bryozoans on permanently submerged roots of *Rhizophora mangle* Linnaeus in Curaçao, but not on the leaves of this species, which were aerial. Colonies of *Amphibiobeania epiphylla* were found to occur primarily on the undersides of the lowermost leaves of one species—*Rhizophora stylosa*. Occasionally, colonies were also found on the leaves of *Aegiceras corniculatum* (L.) (Myrsinaceae), which occurs as a sparse, low shrub or small tree at similar tidal elevations. Colonies were typically found on the leaves of either seedlings or saplings of *Rhizophora stylosa* and the height of encrusted leaves above the estuarine mud at low tide ranged from 0.35 - 1.7 m. On two occasions, colonies in the field were observed attached to PVC (polyvinyl chloride) pipes used to demarcate quadrats, but not to pneumatophores. Specimens were first collected from within the tidal-creek habitat in Charles Darwin Park (12° 27.389′ S 130° 52.135′ E), where the linear distance from the encrusted plants to the high tide mark was approximately 1.3 km. The distance to this habitat varies however, with the width of the intertidal zone at different locations within Darwin Harbour.

Given the nature of the tidal cycle, individual colonies are emergent at ebb tide for a minimum of 5 hours to a maximum of 21 hours during the wet season. During the dry season, tidal amplitude is diminished slightly, which increases the duration of exposure from a minimum of 8 hours to a maximum period of 2 - 3 days. Other intertidal bryozoan species may be nominally amphibious insofar as they are emergent (though usually under rocks, on shaded pilings, or in seaweed holdfasts) during ebb tide. At northern temperate latitudes, several cheilostome species survive abundantly quite high in the intertidal zone in regions where the tidal range is c. 4 m (Dick & Ross 1988) but actual durations of emergence have not been measured and are therefore difficult to compare with the situation for *A. epiphylla*.

Two factors make survival of *A. epiphylla* possible under conditions of long-duration emergence. One is the high humidity of the mangal habitat where the bryozoan occurs. The dense evergreen canopy above and the saturated substratum beneath the host plants contributes to the persistently humid conditions within the forest. Considerable protection from desiccation is also sustained by the humid tropical climate—mean relative humidity at 1500 h is 70% in January and 38% in July, with a seasonal average of 81% for the wet season and 67% for the dry. Presumably, the formation of colonies on the undersurface of leaves also offers additional protection from the sun. The second factor is the silt layer that coats the colony. Scanning electron microscopy reveals that, although this layer is intimately associated with the bryozoan (it does not occur beyond the colony on the substratum surface), it is not biological in composition. Not only are there no traces of embedded diatoms or coccoliths (sponge spicules are rare), for example, but elemental analysis yielded high levels of silicon, aluminium, and oxygen, with the occurrence of iron (Fig. 18), indicating soil particles. We did not ascertain if the bryozoan secretes a mucus that binds the soil particles.

We speculate that one selective advantage to living in a semi-terrestrial situation with significant periods of emergence in air may be to lower predation intensity, but there are no indicative data. We did not study submerged colonies in the field, but those observed under a stereomicroscope in the laboratory yielded, on more than one occasion, several organisms associated with *A. epiphylla* collected at low tide, including a

tiny, possibly juvenile, gastropod, a burrowing dipteran larva (Fig. 15), and a mite (Fig. 9). The mite, which has a black body with a white spot distally, was often found inside dead zooids in old or moribund parts of the colony. It was identified as a prostigmatan mite (family Tarsonemidae). Most tarsonemids feed on plant fluids or fungus (H. Proctor pers. com.) and one mite was found to contain a green substance, suggesting that it had been feeding on plant material—not the bryozoan zooids. These terrestrial mites probably feed on plant material during low tide and retreat into empty zooids during high tide for protection. The insect larvae associated with the bryozoan belong to the ceratopogonid (biting midge) genus *Dasyhelea* Kieffer (A. Borkent, pers comm.). The adults of a number of *Dasyhelea* species are found only in the intertidal zone; only two, however (*D. bajensis* Wirth, *D. griseola* Wirth), have been reared or emerged directly from the intertidal (in Mexico) but their immatures are unknown, and a third (*D. calvescens* Macfie) has immatures present in the upper splash zone in Hawaii (Linley 1976; Wirth 1978; Borkent, pers. obs.). Larvae of this genus have not previously been found associated with a bryozoan. The species discovered here may be a predator of *A. epiphylla* but we have no direct evidence Nevertheless, it removes the bryozoan from the leaf surface by burrowing into or through colonies, contributing to the highly convoluted colony margins seen in many instance. Larvae of some other *Dasyhelea* species are detritivores (eating microorganisms, algae, and fungi) or eat insect carrion (A. Borkent, pers. comm.).

ACKNOWLEDGMENTS

The authors wish to thank Stephen Eagar (Victoria University of Wellington) for petrographic analysis and Kay Card (Industrial Research Ltd, Lower Hutt) for elemental analysis. Dr Ilse Bartsch (Forschungsinstitut Senckenberg, Hamburg) provided tentative identification of mites to family level and (Dr Heather Proctor (University of Alberta, Canada) confirmed the taxonomy and provided additional ecological information on the mites. Dr Art Borkent (Research Associate, Royal British Columbia Museum, Victoria, Canada) identified a ceratopogonid dipteran. Two anonymous referees provided helpful comments.

REFERENCES

Alfaro AC (2006) Benthic macro-invertebrate community composition within a mangrove/seagrass estuary in northern New Zealand. *Estuar Coast Shelf Sci* 66: 97–110

Allman G (1856) A Monograph of the Freshwater Polyzoa, including all the known species, both British and foreign The Ray Society, London. viii + 119 p, 11 pls

Ashton EC, Macintosh DJ, Hogarth PJ (2003) A baseline study of the diversity and community ecology of crab and molluscan macrofauna in the Semantan margrove forest, Sarawak, Malaysia. *J Trop Ecol* 19: 127–142

Brocklehurst PS, Edmeades BF (1996) Mangrove Survey of Darwin Harbour, Northern Territory, Australia. Land Conservation Unit, Conservation Commission of the Northern Territory, Darwin, NT

Bureau of Meteorology (2006) Climate averages for Station 014015 Darwin Airport, NT during the period 1941–2006. Available from: http://www.bom.gov.au

Busk G (1852) An account of the Polyzoa, and sertularian zoophytes, collected in the voyage of the Rattlesnake, on the coasts of Australia and the Louisiade Archipelago, &c. In "Narrative of the Voyage of HMSRattlesnake, commanded by the late Captain Owen Stanley … 1846–1850; including discoveries and surveys in New Guinea, the Louisiade Archipelago, etc., to which is added the account of Mr E. B. Kennedy's expedition of the Cape York Peninsula [including Mr W. Carron's narrative]". Vol. 1. Ed by J. MacGillivray. T.W. Boone, London. pp 343–402, pl. 1 (Appendix No. IV)

Canu F, Bassler RS (1927) Classification of the cheilostomatous Bryozoa. *Proc US Natl Mus* 69(14): 1–42, pl. 1

Dick MH, Ross JRP (1988) Intertidal Bryozoa (Cheilostomata) of the Kodiak vicinity, Alaska. Center Pacif NW Stud W Wash Univ Occ Pap 23: 1–133

Ehrenberg CG (1831) Symbolae Physicae, seu icones et descriptiones corporum naturalium novorum aut minus cognitorum, quae ex itineribus per Libyam, Aegyptum, Nubiam, Dongalam, Syriam, Arabiam et Habessiniam … studio annis 1820–25 redierunt … Pars Zoologica. Vol. 4, Animalia Evertebrata exclusis Insectis. Berlin. 10 pls

Fransen CHJM (1986) Caribbean Bryozoa: Anasca and Ascophora Imperfecta of the inner bays of Curaçao and Bonaire. *Stud Fauna Curaçao other Caribbean Is* 68 [No. 210]: 1–119

Gray JE (1848) List of the Specimens of British Animals in the Collection of the British Museum. Part 1. Centroniae or Radiated Animals. Trustees of the British Museum (Natural History), London. xiii + 173 p. [Polyzoa, pp 91–151.]

Hincks T (1883) Contributions towards a general history of the marine Polyzoa. XI. Foreign Cheilostomata (Australia and New Zealand). *Ann Mag Nat Hist ser* 5, 11: 193–202, pls 6, 7

Hondt J-L d' (1985) Contribution à la systématique des Bryozoaire eurystomes. Apports récents et nouvelles propositions. *Annales Sci Natur, Zool sér 13*, 7:1–12

Hutchings P, Recher HF (1983) The faunal communities of Australian mangroves. In "*Biology and Ecology of mangroves*" Ed by HJ Teas, W. Junk, The Hague, pp 103–110

Johnston G (1840) Miscellanea Zoologica. Description of a new genus of British zoophyte. *Ann Mag Nat Hist* 5: 272–274

Linley JR (1976) Biting midges of mangrove swamps and salt marshes. In "Marine Insects" Ed by L. Cheng, Elsevier, Amsterdam, pp 335–376

Metcalfe K (1999) *Mangrove litter production, Darwin Harbour*. A study of litter fall as a measure of primary productivity in the mangrove communities of Darwin Harbour. Master of Tropical Environmental Management thesis, Northern Territory University, Darwin

Metcalfe K (2005) Mangrove invertebrate fauna. Darwin LNG Project — Mangrove Monitoring Program. Annual Report 2004–2005. Prepared by URS Australia for Conoco-Phillips. 94 p

Metcalfe K (2007) The biological diversity, recovery from disturbance and rehabilitation of mangroves in Darwin Harbour, Northern Territory. PhD thesis, Charles Darwin University, Darwin

Semeniuk V (1985) Mangrove environments of Port Darwin, Northern Territory: the physical framework and habitats. *J R Soc West Austr* 67: 81–97

Smitt FA (1868) Kritisk förteckning öfver Skandinaviens Hafs-Bryozoer. III. *Öfver Kongl Vetensk-Akad Förh* 24: 279–429, pls 16–20

Wightman GM (1989) *Mangroves of the Northern Territory*. N T Bot Bull 7: 1–130

Wirth WW (1978) New species and records of intertidal biting midges of the genus *Dasyhelea* Kieffer from the Gulf of California (Diptera: Ceratopogonidae). *Pacific Insects* 18: 191–198

Woodroffe CD (1995) Response of tide-dominated mangrove shorelines in northern Australia to anticipated sea-level rise. *Earth Surface Processes Landforms* 20: 65–85

Woodroffe CD, Bardsley KN (1987) The distribution and productivity of mangroves in Creek H, Darwin Harbour. In "*Proceedings of a Workshop on Research and Management held in Darwin, 2–3 September 1987*" Eds HK Larson, MG Michie and JR Hanley, North Australia Research Unit, Australian National University, Darwin

APPENDIX E

APPENDIX E – ANALYSES FOR CHAPTER 6

SPECIES RICHNESS OF INVERTEBRATES IN DISTURBED SITES:

Table E-1: Three factor nested ANOVA comparing **species richness** of **invertebrate fauna** between sites (random), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites (Sites BV and DP)**. Data from the four sampling techniques pooled and means calculated per sampling station from three replicate samples

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Site	1	82.69	2	19.77	4.18	0.178
Transect	2	19.77	32	10.67	1.85	0.173
Assemblage	3	602.699	3	78.35	7.69	0.064
Site*Assemblage	3	78.35	6	6.77	11.57	0.007*
Transect*Assemblage	6	6.77	32	10.67	0.63	0.701

Table E-2: Three factor nested ANOVA comparing **species richness** of **invertebrate fauna** between sites (random), transects (random, nested in site) and assemblage (fixed) **at three disturbed sites (Sites BV, DM and DP)**. Data from the four sampling techniques pooled and means calculated per sampling station from three replicate samples

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Site	2	2.056	3	6.389	0.322	0.747
Transect	3	6.389	36	9.093	0.703	0.557
Assemblage	2	294.1	4	57.611	5.104	0.079
Site*Assemblage	4	57.61	6	2.944	19.566	0.001*
Transect*Assemblage	6	2.94	36	9.093	0.324	0.920

Table E-3: Three factor nested ANOVA comparing **species richness** of **invertebrate fauna** between sites (random), transects (random, nested in site) and assemblage (fixed) **at four disturbed sites (Sites BV, DM, DE and DP)**. Data from the four sampling techniques pooled and means calculated per sampling station from three replicate samples

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Site	3	6.56	4	10.92	0.60	0.650
Transect	4	10.92	32	11.17	0.98	0.433
Assemblage	1	352.081	3	105.42	3.34	0.165
Site*Assemblage	3	105.42	4	3.42	30.85	0.003*
Transect*Assemblage	4	3.42	32	11.17	0.31	0.872

SPECIES RICHNESS OF INVERTEBRATES IN DISTURBED & UNDISTURBED SITES:

Table E-4: Four factor nested ANOVA comparing **species richness** of **invertebrate fauna** between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites (Sites BV and DP) and three undisturbed sites (E1, E2 and M3) in all four assemblages**. Data from the four sampling techniques pooled and means calculated per sampling station from three replicate samples

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Disturbance	1	37.81	3	73.65	0.51	0.525
Site	3	73.65	8.52	59.59	1.24	0.355
Assemblage	3	982.93	9	37.24	26.40	0.000*
Transect*	5	35.45	15	13.09	2.71	0.062
Disturbance*Assemblage	3	114.08	9	37.24	3.06	0.084
Assemblage*Site	9	37.24	15	13.09	2.84	0.036*
Assemblage*Transect	15	13.09	80	8.91	1.47	0.137

Table E-5: Four factor nested ANOVA comparing **species richness** of **invertebrate fauna** between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites (Sites BV, DM and DP) and three undisturbed sites (E1, E2 and M3) in three landward assemblages**. Data from the four sampling techniques pooled and means calculated per sampling station from three replicate samples

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Disturbance	1	96.33	4	28.472	3.38	0.140
Site	4	28.47	7.55	42.917	0.66	0.636
Assemblage	2	401.36	8	41.083	9.77	0.007*
Transect	6	12.04	12	10.204	1.18	0.379
Disturbance*Assemblage	2	105.86	8	41.083	2.58	0.137
Assemblage*Site	8	41.08	12	10.204	4.03	0.015*
Assemblage*Transect	12	10.20	72	7.926	1.28	0.245

ABUNDANCE OF INVERTEBRATES IN DISTURBED SITES:

Table E-6: Three factor nested ANOVA comparing **abundance** ($\log_{10}(x + 1)$ transformed total abundance) of **invertebrate fauna** between sites (random), transects (random, nested in site) and assemblage (fixed) **at two disturbed sites (Sites BV and DP**) **in four assemblages**. Data from the four sampling techniques pooled and means calculated per sampling station from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Site	1	0.342	2	0.245	1.40	0.359
Transect	2	0.245	32	0.047	5.23	0.011*
Assemblage	3	4.694	3	1.075	4.36	0.129
Site*Assemblage	3	1.075	6	0.223	4.82	0.049*
Transect*Assemblage	6	0.223	32	0.047	4.77	0.001*

Table E-7: Three factor nested ANOVA comparing **abundance** ($\log_{10}(x + 1)$ transformed total abundance) of **invertebrate fauna** between sites (random), transects (random, nested in site) and assemblage (fixed) **at three disturbed sites (Sites BV, DM and DP**) **in three assemblages**. Data from the four sampling techniques pooled and means calculated per sampling station from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Site	2	0.431	3	0.309	1.40	0.373
Transect	3	0.309	36	0.071	4.33	0.010*
Assemblage	2	4.040	4	0.822	4.91	0.084
Site*Assemblage	4	0.822	6	0.164	5.01	0.041*
Transect*Assemblage	6	0.164	36	0.071	2.30	0.055

Table E-8: Three factor nested ANOVA comparing **abundance** ($\log_{10}(x + 1)$ transformed total abundance) of **invertebrate fauna** between sites (random), transects (random, nested in site) and assemblage (fixed) **at four disturbed sites (Sites BV, DE, DM and DP**) **in two assemblages**. Data from the four sampling techniques pooled and means calculated per sampling station from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Site	3	0.571	4	0.204	2.79	0.173
Transect	4	0.204	32	0.025	8.03	0.000*
Assemblage	1	3.659	3	1.001	3.65	0.152
Site*Assemblage	3	1.001	4	0.228	4.39	0.094
Transect*Assemblage	4	0.228	32	0.025	8.96	0.000*

ABUNDANCE OF INVERTEBRATE FAUNA IN DISTUBED & UNDISTURBED SITES:

Table E-9: Four factor nested ANOVA comparing **abundance** ($\log_{10}(x + 1)$ transformed total abundance) of **invertebrate fauna** between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites (Sites BV and DP) and three undisturbed sites (E1, E2 and M3)**. Data from the four sampling techniques pooled and means calculated per sampling station from three replicate samples

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Disturbance	1	0.770	3	0.326	2.37	0.222
Site	3	0.326	7	0.468	0.69	0.581
Assemblage	3	7.873	9	0.432	18.23	0.000*
Transect	5	0.169	15	0.133	1.28	0.325
Disturbance*Assemblage	3	1.091	9	0.432	2.53	0.123
Assemblage*Site	9	0.432	15	0.133	3.25	0.021*
Assemblage*Transect	15	0.133	80	0.053	2.54	0.004*

Table E-10: Four factor nested ANOVA comparing **abundance** ($\log_{10}(x + 1)$ transformed total abundance) of **invertebrate fauna** between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites (Sites BV, DM and DP) and three undisturbed sites (E1, E2 and M3) in three landward assemblages**. Data from the four sampling techniques pooled and means calculated per sampling station from three replicate samples

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Disturbance	1	1.231	4	0.335	3.67	0.128
Site	4	0.335	7.89	0.544	0.62	0.664
Assemblage	2	6.831	8	0.490	13.94	0.002*
Transect	6	0.190	12	0.136	1.40	0.291
Disturbance*Assemblage	2	1.060	8	0.490	2.16	0.178
Assemblage*Site	8	0.490	12	0.136	3.61	0.023*
Assemblage*Transect	12	0.136	72	0.067	2.03	0.034*

WORMS IN DISTURBED SITES:

Table E-11: Three factor nested ANOVA comparing **species richness** of **worms** between sites (random), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites (Sites BV and DP)**. Data from the four sampling techniques pooled and means calculated per sampling station from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Site	1	2.083	2	2.417	0.86	0.451
Transect	2	2.417	32	2.229	1.08	0.350
Assemblage	3	26.917	3	4.250	6.33	0.082
Site*Assemblage	3	4.250	6	1.694	2.51	0.156
Transect*Assemblage	6	1.694	32	2.229	0.76	0.606

Table E-12: Three factor nested ANOVA comparing **species richness** of **worms** between sites (random), transects (random, nested in site) and assemblage (fixed) **at three disturbed sites (Sites BV, DM and DP)**. Data from the four sampling techniques pooled and means calculated per sampling station from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Site	2	0.167	3	0.111	1.50	0.354
Transect	3	0.111	36	0.926	0.12	0.948
Assemblage	2	20.667	4	2.667	7.75	0.042*
Site*Assemblage	4	2.667	6	0.222	12.00	0.005*
Transect*Assemblage	6	0.222	36	0.926	0.24	0.960

Table E-13: Three factor nested ANOVA comparing **abundance** ($\log_{10}(x + 1)$ transformed total abundance) of **worms** between sites (random), transects (random, nested in site) and assemblage (fixed) at two disturbed sites (Sites BV and DP). Data from the four sampling techniques pooled and means calculated per sampling station from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Site	1	0.017	2	0.070	0.25	0.669
Transect	2	0.070	32	0.086	0.82	0.451
Assemblage	3	1.456	6	0.097	15.01	0.003*
Site*Assemblage	3	0.166	6	0.097	1.72	0.261
Transect*Assemblage	6	0.097	32	0.086	1.12	0.373

Table E-14 Three factor nested ANOVA comparing **abundance** ($(\log_{10}(x + 1)$ transformed total abundance) of **worms** between sites (random), transects (random, nested in site) and assemblage (fixed) **at three disturbed sites (Sites BV, DM and DP**). Data from the four sampling techniques pooled and means calculated per sampling station from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Site	2	0.023	3	0.004	5.97	0.090
Transect	3	0.004	36	0.056	0.07	0.976
Assemblage	2	1.348	4	0.221	6.10	0.061
Site*Assemblage	4	0.221	6	0.009	24.04	0.001*
Transect*Assemblage	6	0.009	36	0.056	0.17	0.984

WORMS IN DISTURBED AND UNDISTURBED SITES:

Table E-15: Four factor nested ANOVA comparing **species richness** of **worms** between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites (Sites BV and DP) and three undisturbed sites (E1, E2 and M3)**. Data from the four sampling techniques pooled and means calculated per sampling station from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	0.200	3	4.28	0.05	0.843
Site	3	4.278	6.85	4.72	0.91	0.486
Assemblage	3	46.878	9	4.74	9.89	0.003*
Transect	5	1.675	15	1.70	0.99	0.458
Disturbance*Assemblage	3	4.011	9	4.74	0.85	0.503
Assemblage*Site	9	4.741	15	1.70	2.79	0.038*
Assemblage*Transect	15	1.697	80	1.68	1.01	0.451

Table E-16: Four factor nested ANOVA comparing **species richness** of **worms** between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites (Sites BV, DM and DP) and three undisturbed sites (E1, E2 and M3) in three landward assemblages**.

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	1.494	4.46	1.646	0.91	0.390
Site	4	1.755	5.53	2.477	0.71	0.617
Assemblage	2	21.086	8.57	2.560	8.24	0.010*
Transect	6	0.640	12.00	0.944	0.68	0.672
Disturbance*Assemblage	2	8.346	8.57	2.560	3.26	0.089
Assemblage*Site	8	2.782	12.00	0.944	2.95	0.045*
Assemblage*Transect	12	0.944	126.00	0.780	1.21	0.283

Table E-17: Four factor nested ANOVA comparing **abundance** ($\log_{10}(x + 1)$ transformed total abundance) of **worms** between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites (Sites BV and DP) and three undisturbed sites (E1, E2 and M3)**. Data from the four sampling techniques pooled and means calculated per sampling station from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	0.001	3	0.146	0.01	0.930
Site	3	0.146	5.98	0.120	0.73	0.572
Assemblage	3	2.198	9	0.233	9.43	0.004*
Transect	5	0.039	15	0.072	0.54	0.743
Disturbance*Assemblage	3	0.346	9	0.233	1.49	0.283
Assemblage*Site	9	0.233	15	0.072	3.23	0.022*
Assemblage*Transect	15	0.072	80	0.062	1.17	0.310

Table E-18: Four factor nested ANOVA comparing **abundance** ($\log_{10}(x + 1)$ transformed total abundance) of **worms** between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites (Sites BV, DM and DP) and three undisturbed sites (E1, E2 and M3), in three landward assemblages**. Data from the four sampling techniques pooled and means calculated per sampling station from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	0.053	4.56	0.08	0.63	0.467
Site	4	0.089	5.7	0.18	0.50	0.739
Assemblage	2	1.247	8.47	0.19	6.58	0.019*
Transect	6	0.019	12	0.05	0.40	0.863
Disturbance*Assemblage	2	0.648	8.47	0.19	3.42	0.081
Assemblage*Site	8	0.207	12	0.047	4.36	0.011*
Assemblage*Transect	12	0.047	126	0.048	0.98	0.469

WORM FEEDING GUILD IN DISTURBED AND UNDISTURBED SITES:

Table E-19: Four factor nested ANOVA comparing **abundance** ($\log_{10}(x + 1)$ transformed total abundance) of **surface deposit feeding worms** between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites (Sites BV and DP) and three undisturbed sites (E1, E2 and M3)**. Data from the four sampling techniques pooled and means calculated per sampling station from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	0.610	4.45	0.035	17.33	0.011*
Site	3	0.039	5.52	0.053	0.72	0.577
Assemblage	3	0.472	11.65	0.052	9.09	0.002*
Transect	5	0.017	15.00	0.024	0.70	0.632
Disturbance*Assemblage	3	0.325	11.65	0.052	6.25	0.009*
Assemblage*Site	9	0.061	13.77	0.024	2.53	0.059
Assemblage*Transect	15	0.024	152.00	0.025	0.95	0.507

ANTS IN DISTURBED SITES:

Table E-20: Three factor nested ANOVA comparing **ant species richness** (untransformed data) between sites (random), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites (Sites BV and DP) in four assemblages**. Means calculated for each sampling station from three replicates.

	df effect	MS effect	df error	MS error	F	P
Site	1	0.188	2	0.771	0.24	0.671
Transect	2	0.771	32	0.750	1.03	0.369
Assemblage	3	4.354	3	0.410	10.63	0.042*
Site*Assemblage	3	0.410	6	0.215	1.90	0.230
Transect*Assemblage	6	0.215	32	0.750	0.29	0.939

Table E-21: Three factor nested ANOVA comparing **ant species richness** (untransformed data) between sites (random), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites (Sites BV, DM and DP) in three assemblages**. Means calculated for each sampling station from three replicates.

	df effect	MS effect	df error	MS error	F	P
Site	2	0.389	3	0.185	2.10	0.269
Transect	3	0.185	36	0.796	0.23	0.873
Assemblage	2	10.889	4	0.194	56.00	0.001*
Site*Assemblage	4	0.194	6	0.130	1.50	0.313
Transect*Assemblage	6	0.130	36	0.796	0.16	0.985

Table E-22: Three factor nested ANOVA comparing **ant species richness** (untransformed data) between sites (random), transects (random, nested in site) and assemblage (fixed) at **four disturbed sites (Sites BV, DM, DE and DP) in two assemblages**. Means calculated for each sampling station from three replicates.

	df effect	MS effect	df error	MS error	F	P
Site	3	1.056	32	0.563	1.88	0.154
Transect	4	0.125	32	0.563	0.22	0.924
Assemblage	1	0.083	3	0.250	0.33	0.604
Site*Assemblage	3	0.250	4	0.042	6.00	0.058
Transect*Assemblage	4	0.042	32	0.563	0.07	0.990

ANTS IN DISTURBED AND UNDISTURBED SITES:

Table E-23: Four factor nested ANOVA comparing **ant species richness** between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites (Sites BV and DP) and three undisturbed sites (E1, E2 and M3) in all four assemblages**. Means calculated per sampling station from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	0.402	3	3.572	0.11	0.760
Site	3	3.572	8.26	1.589	2.25	0.158
Assemblage	3	9.216	9	1.300	7.09	0.010*
Transect*	5	0.725	15	0.436	1.66	0.204
Disturbance*Assemblage	3	1.061	9	1.300	0.82	0.517
Assemblage*Site	9	1.300	80	0.750	1.33	0.234
Assemblage*Transect	15	0.436	80	0.750	0.58	0.881

Table E-24: Four factor nested ANOVA comparing **ant species richness** between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites (Sites BV, DM and DP) and three undisturbed sites (E1, E2 and M3) in three landward assemblages**.

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	0.009	4	1.315	0.01	0.937
Site	4	1.315	8.26	1.204	1.09	0.421
Assemblage	2	19.620	8	0.870	22.54	0.001*
Transect	6	0.657	12	0.324	2.03	0.140
Disturbance*Assemblage	2	0.287	8	0.870	.033	0.728
Assemblage*Site	8	0.870	12	0.324	2.69	0.060
Assemblage*Transect	12	0.324	72	0.713	0.45	0.934

CRUSTACEANS IN DISTURBED SITES:

Table E-25: Three factor nested ANOVA comparing **crustacean species richness** (untransformed data) between sites (random), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites (Sites BV and DP) in four assemblages**. Means calculated for each sampling station from three replicates.

	df effect	MS effect	df error	MS error	F	P
Site	1	4.083	3.77	16.472	0.25	0.646
Transect	3	123.611	3	13.361	9.25	0.050*
Assemblage	2	4.875	6	1.764	2.76	0.141
Site*Assemblage	3	13.361	6	1.764	7.57	0.018*
Transect*Assemblage	6	1.764	32	3.292	0.54	0.777

Table E-26: Three factor nested ANOVA comparing **crustacean species richness** (untransformed data) between sites (random), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites (Sites BV, DM and DP) in three assemblages**.

	df effect	MS effect	df error	MS error	F	P
Site	2	1.685	5.25	8.102	0.21	0.819
Transect	2	69.796	4	6.546	10.66	0.025*
Assemblage	3	2.259	6	0.704	3.21	0.104
Site*Assemblage	4	6.546	6	0.704	9.30	0.010*
Transect*Assemblage	6	0.704	36	1.481	0.47	0.822

Table E-27: Three factor nested ANOVA comparing **crustacean species richness** (untransformed data) between sites (random), transects (random, nested in site) and assemblage (fixed) at **four disturbed sites (Sites BV, DM, DE and DP) in two assemblages**.

	df effect	MS effect	df error	MS error	F	P
Site	3	2.465	3.49	14.993	0.16	0.914
Transect	1	72.521	3	13.743	5.28	0.105
Assemblage	4	2.187	4	0.937	2.33	0.216
Site*Assemblage	3	13.743	4	0.937	14.66	0.013*
Transect*Assemblage	4	0.937	32	1.771	0.53	0.715

Table E-28: Three factor nested ANOVA comparing **crustacean abundance** ($\log_{10}(x + 1)$ transformed) between sites (random), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites (Sites BV and DP) in four assemblages**. Means calculated for each sampling station from three replicates.

	df effect	MS effect	df error	MS error	F	P
Site	1	0.566	1.71	0.628	0.90	0.457
Transect	3	3.037	3	0.743	4.09	0.139
Assemblage	2	0.232	6	0.346	0.67	0.546
Site*Assemblage	3	0.743	6	0.346	2.14	0.196
Transect*Assemblage	6	0.346	32	0.049	7.09	0.00*

Table E-29: Three factor nested ANOVA comparing **crustacean abundance abundance** ($\log_{10}(x + 1)$ transformed) between sites (random), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites (Sites BV, DM and DP) in three assemblages**.

	df effect	MS effect	df error	MS error	F	P
Site	2	0.398	3.31	0.688	0.58	0.609
Transect	2	2.488	4	0.599	4.15	0.106
Assemblage	3	0.354	6	0.265	1.33	0.348
Site*Assemblage	4	0.599	6	0.265	2.26	0.178
Transect*Assemblage	6	0.265	36	0.064	4.12	0.003*

Table E-30: Three factor nested ANOVA comparing **crustacean abundance** ($\log_{10}(x + 1)$ transformed) between sites (random), transects (random, nested in site) and assemblage (fixed) at **four disturbed sites (Sites BV, DM, DE and DP) in two assemblages**.

	df effect	MS effect	df error	MS error	F	P
Site	3	0.653	1.38	0.466	1.40	0.492
Transect	1	2.363	3	0.568	4.16	0.134
Assemblage	4	0.260	4	0.362	0.72	0.621
Site*Assemblage	3	0.568	4	0.362	1.57	0.329
Transect*Assemblage	4	0.362	32	0.026	13.80	0.000*

CRUSTACEANS IN DISTURBED AND UNDISTURBED SITES:

Table E-31: Four factor nested ANOVA comparing **crustacean species richness** between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites (Sites BV and DP) and three undisturbed sites (E1, E2 and M3) in all four assemblages**. Means calculated per sampling station from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	1.324	2.98	4.416	0.30	0.622
Site	3	4.408	7.75	10.809	0.41	0.752
Assemblage	3	224.186	8.96	5.066	44.26	0.000*
Transect	5	7.749	15.05	1.985	3.90	0.018*
Disturbance*Assemblage	3	9.678	8.96	5.066	1.91	0.199
Assemblage*Site	9	5.056	15.08	1.985	2.55	0.053
Assemblage*Transect	15	1.984	79.00	2.825	0.70	0.775

Table E-32: Four factor nested ANOVA comparing **crustacean species richness** between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites (Sites BV, DM and DP) and three undisturbed sites (E1, E2 and M3) in three landward assemblages**.

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	4.083	4	2.657	1.54	0.283
Site	4	2.657	6.11	6.352	0.42	0.791
Assemblage	2	119.565	8	3.880	30.82	0.000*
Transect	6	5.009	12	2.537	1.97	0.149
Disturbance*Assemblage	2	5.361	8	3.880	1.38	0.305
Assemblage*Site	8	3.880	12	2.537	1.53	0.245
Assemblage*Transect	12	2.537	72	1.528	1.66	0.094

Table E-33: Four factor nested ANOVA comparing **crustacean abundance** ($\log_{10}(x + 1)$ transformed) between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) **at two disturbed sites (Sites BV and DP) and three undisturbed sites (E1, E2 and M3) in all four assemblages**.

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	0.310	2.99	0.317	0.98	0.396
Site	3	0.316	4.69	0.294	1.07	0.443
Assemblage	3	5.938	8.98	0.277	21.45	0.000*
Transect	5	0.198	15.01	0.180	1.10	0.401
Disturbance*Assemblage	3	0.378	8.98	0.277	1.36	0.315
Assemblage*Site	9	0.276	15.02	0.180	1.53	0.222
Assemblage*Transect	15	0.178	79.00	0.062	2.90	0.001*

Table E-34: Four factor nested ANOVA comparing **crustacean abundance** ($\log_{10}(x + 1)$ transformed) between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites (Sites BV, DM and DP) and three undisturbed sites (E1, E2 and M3) in three landward assemblages**.

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	0.417	4	0.253	1.65	0.269
Site	4	0.253	5.87	0.384	0.66	0.643
Assemblage	2	4.620	8	0.329	14.05	0.002*
Transect	6	0.232	12	0.177	1.31	0.323
Disturbance*Assemblage	2	0.336	8	0.329	1.02	0.403
Assemblage*Site	8	0.329	12	0.177	1.86	0.161
Assemblage*Transect	12	0.177	72	0.063	2.82	0.003*

GRAPSID CRABS IN DISTURBED SITES:

Table E-35: Three factor nested ANOVA comparing **grapsid crab species richness** (untransformed data) between sites (random), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites (Sites BV and DP) in four assemblages**. Means calculated for each sampling station from three replicates.

	df effect	MS effect	df error	MS error	F	P
Site	1	0.083	2	0.542	0.15	0.733
Transect	2	0.542	32	0.625	0.87	0.430
Assemblage	3	11.611	3	0.250	46.44	0.005*
Site*Assemblage	3	0.250	6	0.319	0.78	0.546
Transect*Assemblage	6	0.319	32	0.625	0.51	0.795

Table E-36: Three factor nested ANOVA comparing **grapsid crab species richness** (untransformed data) between sites (random), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites (Sites BV, DM and DP) in three assemblages**.

	df effect	MS effect	df error	MS error	F	P
Site	2	2.074	3	0.352	5.89	0.091
Transect	3	0.352	36	0.796	0.44	0.724
Assemblage	2	3.130	4	0.935	3.35	0.140
Site*Assemblage	4	0.935	6	0.519	1.80	0.247
Transect*Assemblage	6	0.519	36	0.796	0.65	0.689

Table E-37: Three factor nested ANOVA comparing **grapsid crab species richness** (untransformed data) between sites (random), transects (random, nested in site) and assemblage (fixed) at **four disturbed sites (Sites BV, DM, DE and DP) in two assemblages**..

	df effect	MS effect	df error	MS error	F	P
Site	3	2.076	4	0.438	4.75	0.083
Transect	4	0.438	32	0.833	0.52	0.718
Assemblage	1	1.688	3	2.132	0.79	0.439
Site*Assemblage	3	2.132	4	0.938	2.27	0.222
Transect*Assemblage	4	0.938	32	0.833	1.13	0.362

Table E-38: Three factor nested ANOVA comparing **grapsid crab abundance** ($\log_{10}(x + 1)$ transformed) between sites (random), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites (Sites BV and DP) in four assemblages**. Means calculated for each sampling station from three replicates.

	df effect	MS effect	df error	MS error	F	P
Site	1	0.041	2	0.074	0.55	0.535
Transect	2	0.074	32	0.049	1.53	0.232
Assemblage	3	2.359	3	0.025	94.92	0.002*
Site*Assemblage	3	0.025	6	0.036	0.69	0.591
Transect*Assemblage	6	0.036	32	0.049	0.74	0.620

Table E-39: Three factor nested ANOVA comparing **grapsid crab abundance** ($\log_{10}(x + 1)$ transformed) between sites (random), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites (Sites BV, DM and DP) in three assemblages**.

	df effect	MS effect	df error	MS error	F	P
Site	2	0.507	3	0.021	24.51	0.014*
Transect	3	0.021	36	0.078	0.27	0.850
Assemblage	2	0.405	4	0.236	1.71	0.290
Site*Assemblage	4	0.236	6	0.079	2.98	0.112
Transect*Assemblage	6	0.079	36	0.078	1.02	0.430

Table E-40: Three factor nested ANOVA comparing **grapsid crab abundance** ($\log_{10}(x + 1)$ transformed) between sites (random), transects (random, nested in site) and assemblage (fixed) at **four disturbed sites (Sites BV, DM, DE and DP) in two assemblages**.

	df effect	MS effect	df error	MS error	F	P
Site	3	0.680	4	0.111	6.13	0.056
Transect	4	0.111	32	0.068	1.64	0.189
Assemblage	1	0.295	3	0.125	2.35	0.222
Site*Assemblage	3	0.125	4	0.060	2.08	0.245
Transect*Assemblage	4	0.060	32	0.068	0.89	0.482

GRAPSID CRABS IN DISTURBED AND UNDISTURBED SITES:

Table E-41: Four factor nested ANOVA comparing **grapsid crab species richness** between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites** (Sites BV and DP) **and three undisturbed sites** (E1, E2 and M3**) in all four assemblages**. Means calculated per sampling station from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	4.835	3	1.294	3.74	0.149
Site	3	1.29410.	7.93	1.068	1.21	0.367
Assemblage	3	10.101	9	0.868	11.64	0.002*
Transect	5	0.517	15	0.317	1.63	0.212
Disturbance*Assemblage	3	1.2680.8	9	0.868	1.46	0.289
Assemblage*Site	9	0.868	15	0.317	2.74	0.041*
Assemblage*Transect	15	0.317	80	0.742	0.43	0.967

Table E-42: Four factor nested ANOVA comparing **grapsid crab species richness** between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites** (Sites BV, DM and DP) **and three undisturbed sites** (E1, E2 and M3) **in three landward assemblages**.

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	2.370	4	2.157	1.10	0.534
Site	4	2.157	5.34	0.782	2.76	0.141
Assemblage	2	6.333	8	0.866	7.32	0.016*
Transect	6	0.259	12	0.343	0.76	0.617
Disturbance*Assemblage	2	1.037	8	0.866	1.20	0.351
Assemblage*Site	8	0.866	12	0.343	2.53	0.072
Assemblage*Transect	12	0.343	72	0.759	0.45	0.936

Table E-43: Four factor nested ANOVA comparing **grapsid crab abundance** ($\log_{10}(x + 1)$ transformed) between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites (**Sites BV and DP) **and three undisturbed sites** (E1, E2 and M3) **in all four assemblages**.

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	1.785	5.08	0.146	12.23	0.017*
Site	3	0.256	5.08	0.146	1.75	0.270
Assemblage	3	2.287	9	0.183	12.49	0.001*
Transect*	5	0.030	15	0.067	0.45	0.808
Disturbance*Assemblage	3	0.487	9	0.183	2.66	0.112
Assemblage*Site	9	0.183	15	0.067	2.73	0.041*
Assemblage*Transect	15	0.067	80	0.066	1.02	0.447

Table E-44: Four factor nested ANOVA comparing **grapsid crab abundance** ($\log_{10}(x + 1)$ transformed) between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites** (Sites BV, DM and DP) **and three undisturbed sites** (E1, E2 and M3) **in three landward assemblages**.

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	1.467	4.87	0.179	8.20	0.046*
Site	4	0.297	4.87	0.179	1.65	0.298
Assemblage	2	1.455	8	0.225	6.47	0.021*
Transect*	6	0.012	12	0.057	0.21	0.968
Disturbance*Assemblage	2	0.359	8	0.225	1.59	0.261
Assemblage*Site	8	0.225	12	0.057	3.93	0.017*
Assemblage*Transect	12	0.057	72	0.069	0.83	0.619

OCYPODID CRABS IN DISTURBED SITES:

Table E-45: Three factor nested ANOVA comparing **ocypodid crab species richness** (untransformed data) between sites (random), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites** (Sites BV and DP) **in four assemblages**. Means calculated for each sampling station from three replicates.

	df effect	MS effect	df error	MS error	F	P
Site	1	1.333	2	2.708	0.49	0.556
Transect	2	2.708	32	1.021	2.65	0.086
Assemblage	3	15.250	3	2.944	5.18	0.105
Site*Assemblage	3	2.944	6	1.319	2.23	0.185
Transect*Assemblage	6	1.319	32	1.021	1.29	0.289

Table E-46: Three factor nested ANOVA comparing **ocypodid crab species richness** (untransformed data) between sites (random), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites** (Sites BV, DM and DP) **in three assemblages**.

	df effect	MS effect	df error	MS error	F	P
Site	2	0.056	3	1.870	0.03	0.971
Transect	3	1.870	36	0.426	4.39	0.010*
Assemblage	2	9.056	4	1.278	7.09	0.048*
Site*Assemblage	4	1.278	6	1.426	0.90	0.521
Transect*Assemblage	6	1.426	36	0.426	3.35	0.010*

Table E-47: Three factor nested ANOVA comparing **ocypodid crab species richness** (untransformed data) between sites (random), transects (random, nested in site) and assemblage (fixed) at **four disturbed sites** (Sites BV, DM, DE and DP) **in two assemblages**.

	df effect	MS effect	df error	MS error	F	P
Site	3	0.028	4	1.625	0.02	0.996
Transect	4	1.625	32	0.500	3.25	0.024*
Assemblage	1	12.000	3	1.722	6.97	0.078
Site*Assemblage	3	1.722	4	2.042	0.84	0.537
Transect*Assemblage	4	2.042	32	0.500	4.08	0.009*

Table E-48: Three factor nested ANOVA comparing **ocypodid crab abundance** ($\log_{10}(x + 1)$ transformed) between sites (random), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites (**Sites BV and DP) **in four assemblages**.

	df effect	MS effect	df error	MS error	F	P
Site	1	0.944	2	0.250	3.77	0.192
Transect	2	0.250	32	0.070	3.55	0.040*
Assemblage	3	2.007	3	0.407	4.93	0.112
Site*Assemblage	3	0.407	6	0.618	0.66	0.607
Transect*Assemblage	6	0.618	32	0.070	8.77	0.000*

Table E-49: Three factor nested ANOVA comparing **ocypodid crab abundance** ($\log_{10}(x + 1)$ transformed) between sites (random), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites** (Sites BV, DM and DP) **in three assemblages**..

	df effect	MS effect	df error	MS error	F	P
Site	2	0.585	3	0.521	1.12	0.432
Transect	3	0.521	36	0.092	5.66	0.003*
Assemblage	2	1.432	4	0.272	5.27	0.076
Site*Assemblage	4	0.272	6	0.470	0.58	0.690
Transect*Assemblage	6	0.470	36	0.092	5.11	0.001*

Table E-50: Three factor nested ANOVA comparing **ocypodid crab abundance** ($\log_{10}(x + 1)$ transformed) between sites (random), transects (random, nested in site) and assemblage (fixed) at **four disturbed sites** (Sites BV, DM, DE and DP) **in two assemblages**.

	df effect	MS effect	df error	MS error	F	P
Site	3	0.401	4	0.457	0.88	0.524
Transect	4	0.457	32	0.093	4.89	0.003*
Assemblage	1	1.478	3	0.429	3.45	0.160
Site*Assemblage	3	0.429	4	0.717	0.60	0.649
Transect*Assemblage	4	0.717	32	0.093	7.67	0.000*

OCYPODID CRABS IN DISTURBED AND UNDISTURBED SITES:

Table E-51: Four factor nested ANOVA comparing **ocypodid crab species richness** between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites** (Sites BV and DP) **and three undisturbed sites** (E1, E2 and M3) **in all four assemblages**. Means calculated per sampling station from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	10.755	3	0.509	21.12	0.019*
Site	3	0.509	6.78	2.291	0.22	0.878
Assemblage	3	21.367	9	1.380	15.49	0.001*
Transect	5	1.625	15	0.714	2.28	0.100
Disturbance*Assemblage	3	2.278	9	1.380	1.65	0.246
Assemblage*Site	9	1.380	15	0.714	1.93	0.125
Assemblage*Transect	15	0.714	80	0.633	1.13	0.347

Table E-52: Four factor nested ANOVA comparing **ocypodid crab species richness** between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites (Sites BV, DM and DP) and three undisturbed sites (E1, E2 and M3) in three landward assemblages**.

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	4.482	3.86	1.287	3.48	0.159
Site	4	0.093	3.86	1.287	0.07	0.987
Assemblage	2	8.787	8	0.982	8.95	0.009*
Transect	6	1.204	12	0.898	1.34	0.313
Disturbance*Assemblage	2	1.676	8	0.982	1.71	0.241
Assemblage*Site	8	0.982	12	0.898	1.09	0.429
Assemblage*Transect	12	0.898	72	0.324	2.77	0.004*

Table E-53: Four factor nested ANOVA comparing **ocypodid crab abundance** ($\log_{10}(x + 1)$ transformed) between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites** (Sites BV and DP) **and three undisturbed sites** (E1, E2 and M3) **in all four assemblages**.

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	2.024	3	0.354	5.71	0.097
Site	3	0.354	0.04	0.022	16.22	0.881
Assemblage	3	3.334	9	0.166	20.12	0.000*
Transect	5	0.140	15	0.284	0.49	0.777
Disturbance*Assemblage	3	0.215	9	0.166	1.30	0.334
Assemblage*Site	9	0.166	15	0.284	0.58	0.791
Assemblage*Transect	15	0.284	80	0.062	4.58	0.000*

Table E-54: Four factor nested ANOVA comparing **ocypcodid crab abundance** ($\log_{10}(x + 1)$ transformed) between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites** (Sites BV, DM and DP) **and three undisturbed sites** (E1, E2 and M3) **in three landward assemblages**. Means calculated per sampling station from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	1.081	4	0.305	3.54	0.133
Site	4	0.305	1.1	0.157	1.95	0.469
Assemblage	2	1.576	8	0.157	10.07	0.007*
Transect	6	0.277	12	0.277	1	0.468
Disturbance*Assemblage	2	0.305	8	0.157	1.95	0.205
Assemblage*Site	8	0.157	12	0.277	0.57	0.787
Assemblage*Transect	12	0.277	72	0.067	4.11	0.000*

MOLLUSCS IN DISTURBED SITES:

Table E-55: Three factor nested ANOVA comparing **gastropod species richness** (untransformed data) between sites (random), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites** (Sites BV and DP) **in four assemblages**. Means calculated for each sampling station from three replicates.

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Site	1	2.083	2	3.542	0.59	0.523
Transect	2	3.542	32	1.813	1.95	0.158
Assemblage	3	14.889	6	2.208	6.47	0.024*
Site*Assemblage	3	2.528	6	2.208	1.14	0.404
Transect*Assemblage	6	2.208	32	1.813	1.22	0.323

Table E-56: Three factor nested ANOVA comparing **gastropod species richness** (untransformed data) between sites (random), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites** (Sites BV, DM and DP) **in three assemblages**.

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Site	2	0.296	3	1.537	0.19	0.834
Transect	3	1.537	36	1.759	0.87	0.464
Assemblage	2	7.630	4	2.130	3.58	0.128*
Site*Assemblage	4	2.130	6	2.259	0.94	0.500
Transect*Assemblage	6	2.259	36	1.759	1.28	0.289

Table E-57: Three factor nested ANOVA comparing **gastropod species richness** between sites (random), transects (random, nested in site) and assemblage (fixed) at **four disturbed sites** (Sites BV, DM, DE and DP) **in two assemblages**.

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Site	3	0.556	4	3.000	0.19	0.901
Transect	4	3.000	32	2.063	1.45	0.239
Assemblage	1	5.333	3	4.000	1.33	0.332
Site*Assemblage	3	4.000	4	2.167	1.85	0.279
Transect*Assemblage	4	2.167	32	2.063	1.05	0.397

Table E-58: Three factor nested ANOVA comparing **bivalve species richness** (untransformed data) between sites (random), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites** (Sites BV and DP) **in four assemblages**.

	df effect	MS effect	df error	MS error	F	P
Site	1	0.750	2	0.042	18.00	0.051
Transect	2	0.042	32	1.250	0.03	0.967
Assemblage	3	9.222	6	1.264	7.30	0.020*
Site*Assemblage	3	1.639	6	1.264	1.30	0.359
Transect*Assemblage	6	1.264	32	1.250	1.01	0.436

Table E-59: Three factor nested ANOVA comparing **bivalve species richness** (untransformed data) between sites (random), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites** (Sites BV, DM and DP) **in three assemblages**.

	df effect	MS effect	df error	MS error	F	P
Site	2	1.796	3	0.389	4.62	0.121
Transect	3	0.389	36	0.630	0.62	0.608
Assemblage	2	5.352	4	1.796	2.98	0.161
Site*Assemblage	4	1.796	6	0.389	4.62	0.048*
Transect*Assemblage	6	0.389	36	0.630	0.62	0.715

Table E-60: Three factor nested ANOVA comparing **bivalve abundance** ($\log_{10}(x + 1)$ transformed) between sites (random), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites** (Sites BV and DP) **in four assemblages**.

	df effect	MS effect	df error	MS error	F	P
Site	1	0.009	2	0.003	2.92	0.229
Transect	2	0.003	32	0.038	0.08	0.926
Assemblage	3	0.422	6	0.033	12.79	0.005*
Site*Assemblage	3	0.059	6	0.033	1.75	0.256
Transect*Assemblage	6	0.033	32	0.038	0.88	0.518

Table E-61: Three factor nested ANOVA comparing **bivalve abundance** ($\log_{10}(x + 1)$ transformed) between sites (random), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites** (Sites BV, DM and DP) **in three assemblages**.

	df effect	MS effect	df error	MS error	F	P
Site	2	0.063	3	0.010	6.03	0.089
Transect	3	0.010	36	0.016	0.64	0.595
Assemblage	2	0.265	4	0.063	4.23	0.103
Site*Assemblage	4	0.063	6	0.010	6.03	0.027*
Transect*Assemblage	6	0.010	36	0.016	0.64	0.699

MOLLUSCS IN DISTURBED & UNDISTURBED SITES:

Table E-62: Four factor nested ANOVA comparing **gastropod species richness** between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites** (Sites BV and DP) **and three undisturbed sites** (E1, E2 and M3**) in all four assemblages**. Means calculated per sampling station from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	22.050	3	11.889	1.85	0.266
Site	3	11.889	6.63	7.459	1.59	0.279
Assemblage	3	25.161	9	6.259	4.02	0.045*
Transect*	5	4.158	15	2.958	1.41	0.278
Disturbance*Assemblage	3	25.339	9	6.259	4.05	0.045*
Assemblage*Site	9	6.259	15	2.958	2.12	0.096
Assemblage*Transect	15	2.958	80	1.367	2.16	0.014*

Table E-63: Four factor nested ANOVA comparing **gastropod species richness** between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites** (Sites BV, DM, and DP) **and three undisturbed sites** (E1, E2 and M3**) in three assemblages**.

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	39.120	6.8	6.505	6.01	0.050*
Site	4	9.935	6.8	6.505	1.53	0.295
Assemblage	2	32.444	8	6.282	5.16	0.036*
Transect*	6	2.343	12	2.120	1.10	0.414
Disturbance*Assemblage	2	35.704	8	6.282	5.68	0.029*
Assemblage*Site	8	6.282	12	2.120	2.96	0.044*
Assemblage*Transect	12	2.120	72	1.444	1.47	0.157

Table E-64: Four factor nested ANOVA comparing **gastropod species richness** between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites** (Sites BV, DM and DE) **and three undisturbed sites** (E1, E2 and M3) **in two landward assemblages**.

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	64.222	4	10.181	6.31	0.066
Site	4	10.181	6.2	11.264	0.90	0.516
Assemblage	1	26.889	4	8.653	3.11	0.153
Transect*	6	3.194	6	0.583	5.48	0.029*
Disturbance*Assemblage	1	32.000	4	8.653	3.70	0.127
Assemblage*Site	4	8.653	6	0.583	14.83	0.003*
Assemblage*Transect	6	0.583	48	1.319	0.44	0.847

Table E-65: Four factor nested ANOVA comparing **gastropod abundance** ($\log_{10}(x + 1)$ transformed) between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites** (Sites BV and DP) **and three undisturbed sites** (E1, E2 and M3**) in all four assemblages**.

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	1.582	3	0.636	2.49	0.213
Site	3	0.636	5.9	0.253	2.52	0.156
Assemblage	3	1.685	9	0.260	6.48	0.013*
Transect*	5	0.110	15	0.117	0.94	0.484
Disturbance*Assemblage	3	0.866	9	0.260	3.33	0.070
Assemblage*Site	9	0.260	15	0.117	2.22	0.083
Assemblage*Transect	15	0.117	80	0.071	1.64	0.081

Table E-66: Four factor nested ANOVA comparing **gastropod abundance** ($\log_{10}(x + 1)$ transformed) between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites** (Sites BV, DM and DP) **and three undisturbed sites** (E1, E2 and M3**) in three assemblages** (Hint mar, Tidal fl and Tidal ck).

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	2.219	4	0.512	4.33	0.106
Site	4	0.512	5.21	0.199	2.58	0.159
Assemblage	2	1.498	8	0.217	6.89	0.018*
Transect	6	0.075	12	0.093	0.80	0.589
Disturbance*Assemblage	2	1.260	8	0.217	5.80	0.028*
Assemblage*Site	8	0.217	72	0.078	2.78	0.010*
Assemblage*Transect	12	0.093	72	0.078	1.20	0.301

Table E-67: Four factor nested ANOVA comparing **gastropod abundance** ($\log_{10}(x + 1)$ transformed) between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites** (Sites BV, DM and DE) **and three undisturbed sites** (E1, E2 and M3) **in two landward assemblages**.

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	3.011	4	0.377	7.99	0.047*
Site	4	0.377	6.74	0.435	0.87	0.530
Assemblage	1	0.498	4	0.308	1.62	0.272
Transect	6	0.159	6	0.032	4.97	0.036*
Disturbance*Assemblage	1	0.977	4	0.308	3.18	0.149
Assemblage*Site	4	0.308	6	0.032	9.6	0.009*
Assemblage*Transect	6	0.032	48	0.081	0.40	0.878

Table E-68: Four factor nested ANOVA comparing **bivalve species richness** between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites** (Sites BV and DP) **and three undisturbed sites** (E1, E2 and M3**) in all four assemblages**.

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	0.450	3	2.500	0.18	0.700
Site	3	2.500	2.45	1.206	2.07	0.311
Assemblage	3	22.154	9	1.228	18.03	0.000*
Transect	5	1.258	15	1.281	0.98	0.460
Disturbance*Assemblage	3	0.776	9	1.228	0.63	0.613
Assemblage*Site	9	1.228	15	1.281	0.96	0.507
Assemblage*Transect	15	1.281	80	0.958	1.34	0.201

Table E-69: Four factor nested ANOVA comparing **bivalve abundance** ($\log_{10}(x + 1)$ transformed) between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites** (Sites BVand DP) **and three undisturbed sites** (E1, E2 and M3) **in four assemblages**.

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	0.276	3	0.115	2.39	0.220
Site	3	0.115	4.58	0.107	1.08	0.443
Assemblage	3	1.359	9	0.062	22.21	0.000*
Transect*	5	0.097	15	0.052	1.88	0.158
Disturbance*Assemblage	3	0.069	9	0.062	1.13	0.389
Assemblage*Site	9	0.061	15	0.052	1.18	0.372
Assemblage*Transect	15	0.052	80	0.051	1.02	0.442

Table E-70: Four factor nested ANOVA comparing **bivalve species richness** between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites** (Sites BV, DM and DP) **and three undisturbed sites** (E1, E2 and M3**) in three assemblages** (Hint mar, Tidal fl and Tidal ck).

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	0.593	4	1.241	0.48	0.528
Site	4	1.241	5.5	1.129	1.10	0.442
Assemblage	2	9.194	8	1.074	8.56	0.010
Transect	6	0.611	12	0.556	1.10	0.416
Disturbance*Assemblage	2	0.065	8	1.074	0.06	0.942
Assemblage*Site	8	1.074	12	0.556	1.93	0.146
Assemblage*Transect	12	0.556	72	0.565	0.98	0.473

Table E-71: Four factor nested ANOVA comparing **bivalve abundance** ($\log_{10}(x + 1)$ transformed) between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites** (Sites BV, DM and DP) **and three undisturbed sites** (E1, E2 and M3) **in three assemblages** (Hint mar, Tidal fl and Tidal ck).

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	0.159	4	0.048	3.29	0.144
Site	4	0.048	3.65	0.044	1.11	0.468
Assemblage	2	0.637	8	0.040	15.76	0.002*
Transect*	6	0.037	12	0.033	1.09	0.419
Disturbance*Assemblage	2	0.006	8	0.040	0.16	0.856
Assemblage*Site	8	0.040	12	0.033	1.21	0.370
Assemblage*Transect	12	0.033	72	0.032	1.06	0.408

FISH IN DISTURBED SITES:

Table E-72: Three factor nested ANOVA comparing **fish species richness** (untransformed data) between sites (random), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites** (Sites BV and DP) **in four assemblages**. Means calculated for each sampling station from three replicates.

	df effect	MS effect	df error	MS error	F	P
Site	1	4.084	3.29	3.028	1.35	0.323
Transect	3	0.542	6	0.319	1.70	0.261
Assemblage	2	11.056	3	2.806	3.94	0.145
Site*Assemblage	3	2.806	6	0.319	8.78	0.013*
Transect*Assemblage	6	0.319	32	0.375	0.85	0.540

Table E-73: Three factor nested ANOVA comparing **fish species richness** (untransformed data) between sites (random), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites** (Sites BV, DM and DP) **in three assemblages**. Means calculated for each sampling station from three replicates.

	df effect	MS effect	df error	MS error	F	P
Site	2	0.130	2.7	0.907	0.014	0.873
Transect	3	0.259	6	0.370	0.70	0.586
Assemblage	2	3.185	4	1.019	3.13	0.152
Site*Assemblage	4	1.019	6	0.370	2.75	0.129
Transect*Assemblage	6	0.370	36	0.259	1.43	0.231

Table E-74: Three factor nested ANOVA comparing **fish abundance** ($\log_{10}(x + 1)$ transformed) between sites (random), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites** (Sites BV and DP) **in four assemblages**. Means calculated for each sampling station from three replicates.

	df effect	MS effect	df error	MS error	F	P
Site	1	0.606	3.44	0.447	1.36	0.319
Transect	2	0.143	6	0.071	4.20	0.216
Assemblage	3	1.579	3	0.376	2.00	0.134
Site*Assemblage	3	0.376	6	0.071	5.26	0.041*
Transect*Assemblage	6	0.071	32	0.029	2.44	0.047*

Table E-75: Three factor nested ANOVA comparing **fish abundance** ($\log_{10}(x + 1)$ transformed) between sites (random), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites** (Sites BV, DM and DP) **in three assemblages**.

	df effect	MS effect	df error	MS error	F	P
Site	2	0.023	3.79	0.182	0.13	0.884
Transect	3	0.073	6	0.052	1.39	0.333
Assemblage	2	0.524	4	0.161	3.24	0.145
Site*Assemblage	4	0.161	6	0.052	3.08	0.106
Transect*Assemblage	6	0.052	36	0.034	1.54	0.195

FISH IN DISTURBED & UNDISTURBED SITES:

Table E-76: Four factor nested ANOVA comparing **fish species richness** between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites** (Sites BV and DP) **and three undisturbed sites** (E1, E2 and M3**) in all four assemblages**. Means calculated per sampling station from three replicate samples

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	1.250	3	3.056	0.41	0.568
Site	3	3.056	6.34	2.432	1.26	0.366
Assemblage	3	17.632	9	1.543	11.43	0.002*
Transect	5	1.758	15	0.869	2.02	0.134
Disturbance*Assemblage	3	2.965	9	1.543	1.92	0.197
Assemblage*Site	9	1.543	15	0.869	1.77	0.157
Assemblage*Transect	15	0.869	80	0.650	1.34	0.200

Table E-77: Four factor nested ANOVA comparing **fish species richness** between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites** (Sites BV, DM, and DP) **and three undisturbed sites** (E1, E2 and M3**) in three assemblages**.

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	5.787	4	1.102	5.25	0.084
Site	4	1.102	3.89	0.991	1.11	0.462
Assemblage	2	11.194	8	0.880	12.73	0.003*
Transect	6	0.824	12	0.713	1.16	0.390
Disturbance*Assemblage	2	2.565	8	0.880	2.92	0.112
Assemblage*Site	8	0.880	12	0.713	1.23	0.358
Assemblage*Transect	12	0.713	72	0.482	1.48	0.152

Table E-78: Four factor nested ANOVA comparing **fish abundance** ($\log_{10}(x + 1)$ transformed) between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **two disturbed sites** (Sites BV and DP) **and three undisturbed sites** (E1, E2 and M3**) in all four assemblages**.

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	0.240	3	0.312	0.76	0.446
Site	3	0.312	7.65	0.203	1.54	0.281
Assemblage	3	1.710	9	0.149	11.49	0.002*
Transect	5	0.116	15	0.061	1.89	0.157
Disturbance*Assemblage	3	0.528	9	0.149	3.55	0.061
Assemblage*Site	9	0.149	15	0.061	2.42	0.063
Assemblage*Transect	15	0.061	80	0.041	1.50	0.126

Table E-79: Four factor nested ANOVA comparing **fish abundance** ($\log_{10}(x + 1)$ transformed) between disturbance (fixed), sites (random, nested in disturbance), transects (random, nested in site) and assemblage (fixed) at **three disturbed sites** (Sites BV, DM and DP) **and three undisturbed sites** (E1, E2 and M3**) in three assemblages** (Hint mar, Tidal fl and Tidal ck).

	df effect	MS effect	df error	MS error	F	P
Disturbance	1	0.009	4	0.062	0.14	0.725
Site	4	0.062	6.04	0.114	0.54	0.711
Assemblage	2	0.812	8	0.098	8.26	0.011*
Transect	6	0.067	12	0.051	1.32	0.322
Disturbance*Assemblage	2	0.170	8	0.098	1.73	0.238
Assemblage*Site	8	0.098	12	0.051	1.94	0.145
Assemblage*Transect	12	0.051	72	0.039	1.29	0.241

APPENDIX F

ANALYSES for RHIZOPHORA STYLOSA

Table F-1: Four factor nested ANOVA comparing **mean height** (square root transformed) of planted *Rhizophora stylosa* seedlings on **bulldozed tracks**, at **66 weeks** (T7), between sites (random), treatment (fixed), collection method (fixed) and plot (random, nested in treatment and site).

	df effect	MS effect	df error	MS error	F	P
Site	1	19.837	4	17.648	1.12	0.349
Treatment	4	24.019	20	20.483	1.17	0.353
Collection method	1	11.882	4	4.254	2.79	0.170
Plot	20	20.483	0	0.000		
Site* Treatment	4	17.648	20	20.483	0.86	0.504
Site* Collection method	1	1.504	4	3.727	0.40	0.560
Treatment* Collection method	4	4.254	20	3.196	1.33	0.293
Collection method* Plot	20	3.196	0	0.000		
Site* Treatment*Collection method	4	3.727	20	3.196	1.17	0.355

Table F-2: Four factor nested ANOVA comparing **mean height** (square root transformed) of planted *Rhizophora stylosa* seedlings on **bulldozed tracks**, at **106 weeks** (T8), between sites (random), treatment (fixed), collection method (fixed) and plot (random, nested in treatment and site).

	df effect	MS effect	df error	MS error	F	P
Site	1	2.993	20	35.423	0.08	0.774
Treatment	4	109.76	20	35.423	3.10	0.039*
Collection method	1	13.824	1	2.904	4.76	0.274
Plot	20	35.423	0	0.000		
Site* Treatment	4	19.199	20	35.423	0.54	0.707
Site* Collection method	1	2.904	20	4.220	0.69	0.417
Treatment* Collection method	4	4.926	4	2.581	1.91	0.273
Collection method* Plot	20	4.220	0	0		
Site* Treatment*Collection method	4	2.581	20	4.220	0.61	0.659

Table F-3 : Four factor nested ANOVA comparing **leaf scars** (data not transformed) for *Rhizophora stylosa* seedlings on **bulldozed tracks**, 66 weeks (T7) after planting between sites (random), treatment (fixed), collection method (fixed) and plot (random, nested in treatment and site).

	df effect	MS effect	df error	MS error	F	P
Site	1	286.308	20	65.022	4.40	0.049*
Treatment	4	317.698	20	65.022	4.89	0.007*
Collection method	1	53.834	1	1.656	32.52	0.111
Plot	20	65.022	0	0.000	-	-
Site* Treatment	4	81.357	20	65.022	1.25	0.322
Site* Collection method	1	1.656	20	4.503	0.37	0.551
Treatment* Collection method	4	14.539	4	5.841	2.49	0.199
Collection method* Plot	20	4.503	0	0.000	-	-
Site* Treatment*Collection method	4	5.841	20	4.503	1.30	0.305

Table F-4: Four factor nested ANOVA comparing **total leaf scars (log 10 (x + 1) transformed)** on *Rhizophora stylosa* seedlings on **bulldozed tracks**, **106** weeks (T8) after planting between sites (random), treatment (fixed), collection method (fixed) and plot (random, nested in treatment and site).

	df effect	MS effect	df error	MS error	F	P
Site	1	1.102	20	0.041	26.95	0.000*
Treatment	4	0.714	4	0.089	8.04	0.034*
Collection method	1	0.018	1	0.008	2.32	0.370
Plot	20	0.041	0	0.000		
Site* Treatment	4	0.089	20	0.041	2.17	0.109
Site* Collection method	1	0.008	20	0.008	1.03	0.323
Treatment* Collection method	4	0.011	4	0.008	1.25	0.417
Collection method* Plot	20	0.008	0	0.000		
Site* Treatment*Collection method	4	0.008	20	0.008	1.10	0.383

Table F-5: Five factor nested ANOVA comparing **survival** of *Rhizophora stylosa* seedlings (data not transformed) in **cyclone-damaged and bulldozed** areas **66 weeks** after planting (T7), between site type (fixed), sites (random, nested in type), treatment (fixed), collection method (fixed) and plot (random, nested in treatment, site and type).

	df effect	MS effect	df error	MS error	F	P
Site type	1	9.861	2	0.048	205.44	0.005*
Site	2	0.048	40	0.032	1.48	0.239
Treatment	4	1.393	8	0.039	35.87	0.000*
Collection method	1	0.133	2	0.005	25.00	0.038*
Plot	40	0.032	0	0.000		
Site type* Treatment*	4	0.721	8	0.039	18.58	0.000*
Site No.* Treatment	8	0.039	40	0.032	1.20	0.323
Site type* Collection method	1	0.005	2	0.005	1.00	0.423
Site No.* Collection method	2	0.005	40	0.024	0.23	0.799
Treatment* Collection method	4	0.012	8	0.018	0.65	0.640
Collection method* Plot	40	0.024	0	0.000		
Site type* Treatment*Collection method	4	0.029	8	0.018	1.61	0.263
Site No.* Treatment* Collection method	8	0.018	40	0.024	0.75	0.645

Table F-6: Five factor nested ANOVA comparing **survival** of *Rhizophora stylosa* seedlings (data not transformed in **cyclone damaged and bulldozed** areas **106 weeks** after planting (T8), between site type (fixed), sites (random, nested in type), treatment (fixed), collection method (fixed) and plot (random, nested in treatment, site and type).

	df effect	MS effect	df error	MS error	F	P
Site type	1	11.781	2	0.059	198.56	0.005*
Site	2	0.059	40	0.034	1.73	0.191
Treatment	4	1.156	8	0.019	62.50	0.000*
Collection method	1	0.033	2	0.011	2.94	0.228
Plot	40	0.034	0	0.000		
Site type* Treatment*	4	0.662	8	0.019	35.79	0.000*
Site No.* Treatment	8	0.019	40	0.034	0.54	0.820
Site type* Collection method	1	0.048	2	0.011	4.24	0.176
Site No.* Collection method	2	0.011	40	0.020	0.58	0.567
Treatment* Collection method	4	0.007	8	0.032	0.23	0.912
Collection method* Plot	40	0.020	0	0.000		
Site type* Treatment*Collection	4	0.015	8	0.032	0.48	0.749
Site No.* Treatment* Collection	8	0.032	40	0.020	1.64	0.145

ANALYSES for CERIOPS AUSTRALIS

Table F-7 : Four factor nested ANOVA comparing **mean height** of planted *Ceriops australis* seedlings on **bulldozed tracks**, at **70 weeks** (T8) between sites (random), treatment (fixed), collection method (fixed) and plot (random, nested in treatment and site).

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Site	1	5603.875	8	587.927	9.53	0.015*
Treatment	3	1444.048	3	712.258	2.03	0.288
Collection method	1	766.035	1	281.833	2.72	0.347
Plot	8	587.927	0	0.000	-	-
Site* Treatment	3	712.258	8	587.927	1.21	0.366
Site* Collection method	1	281.833	8	424.349	0.66	0.439
Treatment* Collection method	3	79.918	3	675.908	0.12	0.944
Collection method* Plot	8	424.349	0	0.000	-	-
Site* Treatment*Collection method	3	675.908	8	424.349	1.59	0.266

Table F-8 : Four factor nested ANOVA comparing **mean height** of planted *Ceriops australis* seedlings on **bulldozed tracks**, at **101 weeks** (T9) between sites (random), treatment (fixed), collection method (fixed) and plot (random, nested in treatment and site).

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Site	1	6856.693	8	1665.480	4.12	0.077
Treatment	3	9438.731	3	3596.953	2.62	0.225
Collection method	1	904.365	8	1589.70.	0.57	0.470
Plot	8	1665.480	0	0.000	-	-
Site* Treatment	3	3596.953	8	1665.480	2.16	0.171
Site* Collection method	1	0.547	8	1589.697	0.00	0.986
Treatment* Collection method	3	792.223	3	968.728	0.82	0.564
Collection method* Plot	8	1589.697	0	0.000	-	-
Site* Treatment*Collection method	3	968.728	8	1589.697	0.61	0.628

Table F-9: Four factor nested ANOVA comparing total numbers of **leaf scars** (log 10 (x + 1) transformed) for *Ceriops australis* seedlings on **bulldozed tracks 70 weeks** (T8) after planting between sites (random), treatment (fixed), collection method (fixed) and plot (random, nested in treatment and site).

	df effect	MS effect	df error	MS error	F	P
Site	1	0.127	8	0.012	10.26	0.013*
Treatment	3	0.024	3	0.007	3.64	0.158
Collection method	1	0.005	1	0.001	5.73	0.252
Plot	8	0.012	0	0.000		
Site* Treatment	3	0.007	8	0.012	0.52	0.678
Site* Collection method	1	0.001	8	0.009	0.09	0.770
Treatment* Collection method	3	0.002	3	0.003	0.56	0.676
Collection method* Plot	8	0.009	0	0.000		
Site* Treatment*Collection method	3	0.003	8	0.009	0.37	0.778

Table F-10 : Four factor nested ANOVA comparing total numbers of **leaf scars** (log 10 (x + 1) transformed) for *Ceriops australis* seedlings on **bulldozed tracks 101 weeks** (T9) after planting between sites (random), treatment (fixed), collection method (fixed) and plot (random, nested in treatment and site).

	df effect	MS effect	df error	MS error	F	P
Site	1	0.052	8	0.028	1.90	0.206
Treatment	3	0.046	3	0.022	2.03	0.288
Collection method	1	0.001	1	0.004	0.14	0.775
Plot	8	0.028	0	0.000		
Site* Treatment	3	0.022	8	0.028	0.81	0.521
Site* Collection method	1	0.004	8	0.014	0.27	0.617
Treatment* Collection method	3	0.000	3	0.003	0.06	0.975
Collection method* Plot	8	0.014	0	0.000		
Site* Treatment*Collection method	3	0.003	8	0.014	0.23	0.870

Table F-11: Five factor nested ANOVA comparing **survival** (proportion arcsine square root transformed) of *Ceriops australis* seedlings in **cyclone damaged** and **bulldozed areas** at **70 weeks** (T8) between site type (fixed), sites (random, nested in type), treatment (fixed), collection method (fixed) and plot (random, nested in treatment, site and type).

	df effect	MS effect	df error	MS error	F	P
Site type	1	4.342	2	0.168	25.82	0.037*
Site	2	0.168	16	0.389	0.43	0.656
Treatment	3	0.300	16	0.389	0.77	0.530
Collection method	1	0.335	2	0.054	6.24	0.130
Plot	16	0.389	0	0.000	-	-
Site type* Treatment*	3	0.164	6	0.044	3.72	0.080
Site No.* Treatment	6	0.044	16	0.389	0.11	0.993
Site type* Collection method	1	0.329	2	0.054	6.13	0.132
Site No.* Collection method	2	0.054	16	0.078	0.69	0.517
Treatment* Collection method	3	0.197	6	0.047	4.22	0.063
Collection method* Plot	16	0.078	0	0.000	-	-
Site type* Treatment*Collection	3	0.106	6	0.047	2.27	0.181
Site No.* Treatment* Collection	6	0.047	16	0.078	0.60	0.727

Table F-12: Five factor nested ANOVA comparing **survival** (proportion arcsine square root transformed) of *Ceriops australis* seedlings in **cyclone damaged** and **bulldozed areas** at **101 weeks** (T9) between site type (fixed), sites (random, nested in type), treatment (fixed), collection method (fixed) and plot (random, nested in treatment, site and type).

	df effect	MS effect	df error	MS error	F	P
Site type	1	4.792	2	0.093	51.56	0.019*
Site	2	0.093	16	0.362	0.26	0.776
Treatment	3	0.252	6	0.067	3.78	0.078
Collection method	1	0.268	2	0.022	12.31	0.073
Plot	16	0.362	0	0.000	-	-
Site type* Treatment*	3	0.177	6	0.067	2.67	0.142
Site No.* Treatment	6	0.067	16	0.362	0.18	0.977
Site type* Collection method	1	0.555	2	0.022	25.45	0.037*
Site No.* Collection method	2	0.022	16	0.049	0.45	0.646
Treatment* Collection method	3	0.246	6	0.055	4.46	0.057
Collection method* Plot	16	0.049	0	0.000	-	-
Site type* Treatment*Collection method	3	0.096	6	0.055	1.74	0.258
Site No.* Treatment* Collection method	6	0.055	16	0.049	1.14	0.385

Table F-13 : Four factor nested ANOVA comparing **mean height** (log10 (x + 1) transformed) of planted *Ceriops australis* seedlings in **cyclone damaged** areas, at **70 weeks** (T8) between sites (random), treatment (fixed), collection method (fixed) and plot (random, nested in treatment and site).

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Site	1	0.198	1.11	0.013	15.28	0.140
Treatment	3	0.020	3.00	0.010	2.07	0.282
Collection method	1	0.043	1.00	0.010	4.17	0.290
Plot	6	0.033	3.00	0.033	0.99	0.548
Site* Treatment	3	0.010	0.07	0.007	1.45	0.879
Site* Collection method	1	0.010	3.31	0.007	1.41	0.313
Treatment* Collection method	3	0.022	3.00	0.007	3.22	0.181
Collection method* Plot	3	0.033	0	0.000	-	-
Site* Treatment*Collection method	3	0.007	3.00	0.033	0.21	0.883

Table F-14 : Four factor nested ANOVA comparing **mean height** (log 10 (x + 1) transformed) of planted *Ceriops australis* seedlings in **cyclone damaged** areas, at **101 weeks** (T9) between sites (random), treatment (fixed), collection method (fixed) and plot (random, nested in treatment and site).

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Site	1	0.421	2.01	0.092	4.59	0.165
Treatment	3	0.031	3.00	0.038	0.81	0.566
Collection method	1	0.058	1.00	0.061	0.96	0.507
Plot	6	0.176	3.00	0.023	7.71	0.061
Site* Treatment	3	0.038	4.68	0.166	0.23	0.872
Site* Collection method	1	0.061	3.29	0.005	11.11	0.039*
Treatment* Collection method	3	0.016	3.00	0.005	3.02	0.194
Collection method* Plot	3	0.023				
Site* Treatment*Collection method	3	0.005	3.00	0.023	0.23	0.870

Table F-15 : Four factor nested ANOVA comparing total numbers of **leaf scars** (log 10 (x + 1) transformed) for *Ceriops australis* seedlings in **cyclone damaged** areas **70 weeks** (T8) after planting between sites (random), treatment (fixed), collection method (fixed) and plot (random, nested in treatment and site).

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Site	1	0.025	0.64	0.010	2.45	0.448
Treatment	3	0.009	3.00	0.003	2.67	0.221
Collection method	1	0.005	1.00	0.012	0.45	0.624
Plot	6	0.011	3.00	0.002	5.31	0.099
Site* Treatment	3	0.003	6.50	0.015	0.23	0.869
Site* Collection method	1	0.012	3.03	0.005	2.24	0.231
Treatment* Collection method	3	0.005	3.00	0.005	0.90	0.532
Collection method* Plot	3	0.005	0.00			
Site* Treatment*Collection method	3	0.033	3.00	0.002	2.58	0.229

Table F-16 : Four factor nested ANOVA comparing total numbers of **leaf scars** (log 10 (x + 1) transformed) for *Ceriops australis* seedlings in **cyclone damaged** areas **101 weeks** (T9) after planting between sites (random), treatment (fixed), collection method (fixed) and plot (random, nested in treatment and site).

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Site	1	0.136	1.04	0.029	4.69	0.268
Treatment	3	0.020	3.00	0.013	1.53	0.368
Collection method	1	0.000	1.00	0.027	0.00	0.989
Plot	6	0.129	3.00	0.023	5.54	0.094
Site* Treatment	3	0.013	4.46	0.120	0.11	0.949
Site* Collection method	1	0.027	3.15	0.010	2.61	0.200
Treatment* Collection method	3	0.009	3.00	0.010	0.94	0.520
Collection method* Plot	3	0.023	0.00	0.00	0.00	
Site* Treatment*Collection method	3	0.010	3.00	0.023	0.44	0.743

HERBIVORE EXCLOSURE EXPERIMENT – RHIZOPHORA STYLOSA

Table F-17 : Three factor nested ANOVA comparing total numbers of **leaf scars** (square-root transformed) for *R. stylosa* seedlings in **cyclone damaged** areas **44 weeks** (T5) after planting between sites (random), treatment (fixed), and plots (random, nested in treatment and site).

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Site	1	0.22	8	0.124	1.82	0.215
Treatment	1	3.31	1	0.269	12.30	0.177
Plot	8	0.12	0	0.000	-	-
Site* Treatment	1	0.27	8	0.124	2.17	0.179

Table F-18 : Three factor nested ANOVA comparing survival (untransformed) of *R. stylosa* seedlings in **cyclone damaged** areas **44 weeks** (T5) after planting between sites (random), treatment (fixed), and plots (random, nested in treatment and site).

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Site	1	0.00	8	0.044	0.02	0.894
Treatment	1	0.19	8	0.044	4.25	0.070
Plot	8	0.04	0	0.000		
Site* Treatment	1	0.04	8	0.044	0.92	0.364

Table F-19 : Three factor nested ANOVA comparing total numbers of **leaf scars** (square-root transformed) for *R. stylosa* seedlings in **cyclone damaged** areas **73 weeks** (T6) after planting between sites (random), treatment (fixed), and plots (random, nested in treatment and site).

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Site	1	2.305	8.00	0.539	4.28	0.072
Treatment	1	8.628	8.00	0.540	16.016	0.004*
Plot	8	0.539	0.00	0.000	-	-
Site* Treatment	1	0.399	8.00	0.539	0.74	0.415

Table F-20 : Three factor nested ANOVA comparing **survival** (arcsine square-root transformed) for *R. stylosa* in **cyclone damaged** areas at **73 weeks** (T6) between sites (random), treatment (fixed), and plots (random, nested in treatment and site).

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Site	1	0.130	8.00	0.133	0.98	0.352
Treatment	1	1.821	1.00	1.000	1.82	0.406
Plot	8	0.133	0.00	0.000		
Site* Treatment	1	1.000	8.00	0.133	7.52	0.025*

ANALYSES FOR CHAPTER 8

REHABILITATION— CERIOPS AUSTRALIS

Table F-21: Three factor nested ANOVA comparing **number of leaves** ($\log_{10}(x + 1)$ transformed) of container grown and transplanted *Ceriops australis* seedlings in **bulldozed** areas **58 weeks** (T8) after planting between sites (random), treatment (fixed), and plots (random, nested in site).

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Site	1	1.202	16.00	0.028	42.19	0.000*
Treatment	1	0.397	16.00	0.030	13.00	0.002*
Plot	16	0.028	0.00	0.000	-	-
Site*Treatment	1	0.007	16.00	0.030	0.23	0.641
Treatment*Plot	16	0.030	0.00	0.000	-	-

Table F-22: Three factor nested ANOVA comparing **number of leaves** (not transformed) of container grown and transplanted *Ceriops australis* seedlings in **bulldozed** areas **84 weeks** (T10) after planting between sites (random), treatment (fixed), and plots (random, nested in site).

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Site	1	6872.410	16	107.463	63.95	0.000*
Treatment	1	2131.361	16	146.662	14.53	0.002*
Plot	16	107.463	0	0.000	-	-
Site* Treatment	1	402.671	16	146.662	2.75	0.117
Treatment*Plot	16	146.662	0	0.000	-	-

Table F-23: Three factor nested ANOVA comparing leaf **survival** (arcsine square-root transformed) of container grown and transplanted *Ceriops australis* seedlings in **bulldozed** areas **58 weeks** (T8) after planting between sites (random), treatment (fixed), and plots (random, nested in site).

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Site	1	4.296	16.00	0.068	63.56	0.000*
Treatment	1	0.000	1.00	0.000	0.78	0.540
Plot	16	0.068	0.00	0.000	-	-
Site* Treatment	1	0.000	16.00	0.041	0.01	0.921
Treatment*Plot	16	0.041	0.00	0.000	-	-

Table F-24: Three factor nested ANOVA comparing **survival** (arcsine square-root transformed) of container grown and transplanted *Ceriops australis* seedlings in **bulldozed** areas **84 weeks** (T10) after planting between sites (random), treatment (fixed), and plots (random, nested in site).

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Site	1	3.996	16	0.034	118.43	0.000*
Treatment	1	0.003	1	0.018	0.14	0.769
Plot	16	0.034	0	0.000	-	-
Site* Treatment	1	0.018	16	0.078	0.23	0.641
Treatment*Plot	16	0.078	0	0.000	-	-

REHABILITATION—RHIZOPHORA STYLOSA, CERIOPS AUSTRALIS, AVICENNIA MARINA and AEGIALITIS ANNULATA

Table F-25: Three factor nested ANOVA comparing **total number of leaves** (not transformed) of implanted *Ceriops australis* and *Rhizophora stylosa* propagules and transplanted *Avicennia marina* and *Aegialitis annuala* in **disturbed** mangroves **58 weeks** (T9) after planting between sites (random), species (fixed)and plots (random, nested in site and species).

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Site	2	145.360	72	39.273	3.70	0.030*
Species	3	180.705	6	84.955	2.13	0.198
Plot	72	39.273	0	0.000	-	-
Site* Species	6	84.955	72	39.273	2.16	0.056

Table F-26: Three factor nested ANOVA comparing **survival** (not transformed) of implanted *Ceriops australis* and *Rhizophora stylosa* propagules and transplanted *Avicennia marina* and *Aegialitis annuala* in **disturbed** mangroves **56 weeks** (T9) after planting between sites (random), species (fixed) and plots (random, nested in site and species).

	df effect	**MS effect**	**df error**	**MS error**	**F**	**P**
Site	2	0.218	108	0.055	3.97	0.022*
Species	3	0.082	6	0.494	0.17	0.915
Plot	108	0.055	0	0.000	-	-
Site* Species	6	0.494	108	0.055	8.98	0.000*

Table F-27: Three factor nested ANOVA comparing **total number of leaves** ($\log_{10}(x + 1)$ transformed) of implanted *C. australis* and *R. stylosa* propagules and transplanted *A. marina* and *A. annuala* in **disturbed** mangroves **89 weeks** (T11) after planting between sites (random), species (fixed) and plots (random, nested in site and species).

	df effect	MS effect	df error	MS error	F	P
Site	2	0.34	72	0.052	6.48	0.003*
Species	3	0.23	6	0.091	2.50	0.157
Plot	72	0.05	0	0.000	-	-
Site* Species	6	0.09	72	0.052	1.75	0.121

Table F-28: Three factor nested ANOVA comparing **survival** (not transformed) of implanted *C. australis* and *R. stylosa* propagules and transplanted *A. marina* and *A. annuala* in **disturbed** mangroves **89 weeks** (T11) after planting between sites (random), species (fixed) and plots (random, nested in site and species).

	df effect	MS effect	df error	MS error	F	P
Site	2	0.373	108	0.065	5.74	0.004*
Species	3	0.089	6	0.464	0.19	0.899
Plot	108	0.065	0	0.000	-	-
Site* Species	6	0.464	108	0.065	7.15	0.000*

Table F-29: Three factor nested ANOVA comparing **height** ($\log_{10}(x + 1)$ transformed) of implanted *C. australis* and *R. stylosa* propagules and transplanted *A. marina* and *A. annuala* in **disturbed** mangroves, **89 weeks** (T11) after planting between sites (random), species (fixed) and plots (random, nested in site and species).

	df effect	MS effect	df error	MS error	F	P
Site	2	0.66	72	0.034	19.36	0.000*
Species	3	2.08	6	0.052	40.10	0.000*
Plot	72	0.03	0	0.000	-	-
Site* Species	6	0.05	72	0.034	1.52	0.184

NATURAL RECRUITMENT EXPERIMENT (Fences *vs* Control)

Table F-30: Five factor nested ANOVA comparing **number of seedling** ($\log_{10}(x+1)$ transformed) at three **disturbed sites** after **9 months** (T5) between treatments (fixed), sites (random), assemblages (fixed), plots (random, nested in assemblage and site) and replicates (random, nested in plot, assemblage and site).

	df effect	MS effect	df error	MS error	F	P
Treatment	1	1.466	9	0.040	37.00	0.000*
Site	2	0.514	9	0.120	4.27	0.050*
Assemblage	2	0.478	9	0.120	3.97	0.058
Plot	9	0.120	18	0.125	0.96	0.501
Replicate	18	0.125	0	0.000	-	-
Treatment*Site	2	0.046	9	0.040	1.15	0.359
Treatment*Assemblage	2	0.662	9	0.040	16.71	0.001*
Site*Assemblage	4	0.043	9	0.120	0.36	0.833
Treatment*Plot	9	0.040	18	0.086	0.46	0.883
Treatment*Replicate	18	0.086	0	0.000	-	-
Treatment*Site*Assemblage	4	0.066	9	0.040	1.66	0.242

Table F-31: Four factor nested ANOVA comparing **species richness of seedlings** ($\log_{10}(x+1)$ transformed) at three **disturbed sites** after **9 months** (T5) between treatments (fixed), sites (random), assemblages (fixed), plots (random, nested in assemblage and site) and replicates (random, nested in plot, assemblage and site).

	df effect	MS effect	df error	MS error	F	P
Treatment	1	0.869	9	0.037	23.68	0.001*
Site	2	0.290	9	0.073	3.99	0.057
Assemblage	2	0.200	9	0.073	2.76	0.116
Plot	9	0.073	18	0.087	0.84	0.593
Replicate	18	0.087	0	0.000	-	-
Treatment*Site	2	0.040	9	0.037	1.10	0.373
Treatment*Assemblage	2	0.279	9	0.037	7.59	0.012*
Site*Assemblage	4	0.036	9	0.073	0.50	0.739
Treatment*Plot	9	0.037	18	0.069	0.53	0.834
Treatment*Replicate	18	0.069	0	0.000	-	-
Treatment*Site*Assemblage	4	0.048	9	0.037	1.32	0.334

Table F-32: Four factor nested ANOVA comparing **number of seedlings** ($\log_{10}(x+1)$ transformed) at three **disturbed sites** after **13 months** (T8) between treatments (fixed), sites (random), assemblages (fixed), plots (random, nested in assemblage and site) and replicates (random, nested in plot, assemblage and site).

	df effect	MS effect	df error	MS error	F	P
Treatment	1	2.420	9	0.087	27.94	0.001*
Site	2	4.743	9	0.120	39.47	0.000*
Assemblage	2	0.109	9	0.120	0.91	0.438
Plot	9	0.120	18	0.075	1.61	0.185
Replicate	18	0.075	0	0.000	-	-
Treatment*Site	2	0.528	9	0.087	6.10	0.021*
Treatment*Assemblage	2	0.240	9	0.087	2.77	0.115
Site*Assemblage	4	0.508	9	0.120	4.23	0.034*
Treatment*Plot	9	0.087	18	0.077	1.12	0.399
Treatment*Replicate	18	0.077	0	0.000	-	-
Treatment*Site*Assemblage	4	0.132	9	0.087	1.52	0.275

Table F-33: Four factor nested ANOVA comparing **species richness of seedlings** ($\log_{10}(x+1)$ transformed) at three **disturbed sites** after **13 months** (T8) between treatments (fixed), sites (random), assemblages (fixed), plots (random, nested in assemblage and site) and replicates (random, nested in plot, assemblage and site).

	df effect	MS effect	df error	MS error	F	P
Treatment	1	0.240	9	0.014	16.97	0.003*
Site	2	1.015	9	0.036	28.15	0.000*
Assemblage	2	0.037	9	0.036	1.01	0.401
Plot	9	0.036	18	0.029	1.26	0.323
Replicate	18	0.029	0	0.000	-	-
Treatment*Site	2	0.064	9	0.014	4.50	0.044*
Treatment*Assemblage	2	0.043	9	0.014	3.05	0.098
Site*Assemblage	4	0.013	9	0.036	0.36	0.829
Treatment*Plot	9	0.014	18	0.040	0.35	0.943
Treatment*Replicate	18	0.040	0	0.000	-	-
Treatment*Site*Assemblage	4	0.010	9	0.014	0.72	0.602

Table F-34: Four factor nested ANOVA comparing **number of seedlings** ($\log_{10}(x+1)$ transformed) at three **disturbed sites** after **17 months** (T9) between treatments (fixed), sites (random), assemblages (fixed), plots (random, nested in assemblage and site) and replicates (random, nested in plot, assemblage and site). and site).

	df effect	MS effect	df error	MS error	F	P
Treatment	1	3.234	9	0.131	24.70	0.001*
Site	2	3.658	9	0.207	17.65	0.001*
Assemblage	2	0.507	9	0.207	2.44	0.142
Plot	9	0.207	18	0.059	3.49	0.011*
Replicate	18	0.059	0	0.000	-	-
Treatment*Site	2	0.490	9	0.131	3.75	0.066
Treatment*Assemblage	2	0.107	9	0.131	0.82	0.471
Site*Assemblage	4	0.307	9	0.207	1.48	0.286
Treatment*Plot	9	0.131	18	0.062	2.10	0.086
Treatment*Replicate	18	0.062	0	0.000	-	-
Treatment*Site*Assemblage	4	0.087	9	0.131	0.67	0.630

Table F-35: Four factor nested ANOVA comparing **species richness of seedlings** ($\log_{10}(x+1)$ transformed) at three **disturbed sites** after **17 months** (T9) between treatments (fixed), sites (random), assemblages (fixed), plots (random, nested in assemblage and site) and replicates (random, nested in plot, assemblage and site).

	df effect	MS effect	df error	MS error	F	P
Treatment	1	0.532	9	0.024	21.87	0.001*
Site	2	0.636	9	0.047	13.66	0.002*
Assemblage	2	0.115	9	0.047	2.46	0.141
Plot	9	0.047	18	0.022	2.12	0.084
Replicate	18	0.022	0	0.000	-	-
Treatment*Site	2	0.085	9	0.024	3.47	0.076
Treatment*Assemblage	2	0.037	9	0.024	1.54	0.267
Site*Assemblage	4	0.003	9	0.047	0.07	0.988
Treatment*Plot	9	0.024	18	0.037	0.66	0.732
Treatment*Replicate	18	0.037	0	0.000	-	-
Treatment*Site*Assemblage	4	0.010	9	0.024	0.39	0.811