

**THE EFFECT OF URBAN STORM-WATER RUNOFF ON
SESARMID CRABS**

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Dedicated to:

My father Garry Ball,
Who taught me the most important lessons.
Left this world 7th July 1982

ABSTRACT

Urban development is becoming increasingly common along landward margins of mangroves and results in increased impervious surfaces which collect and facilitate discharge of storm-water at point locations into the mangrove swamp. In contrast, natural storm-water inputs into mangroves are largely diffuse flows.

Along the central Queensland coast *Neosarmatium trispinosum* and *Parasesarma erythrodactyla* are the most abundant species of sesarmid crabs occurring within these mangroves. Following a trial that found burrow counts were the most reliable estimate of relative crab abundance, comparisons were made between mangroves receiving storm-water input and control sites that were not affected.

Paired site comparisons were conducted at two spatio-temporal scales; a three year comparison using three paired sites and a one year comparison using 10 paired sites. The relative abundance of crabs was found to be less at storm-water input sites, which is a new finding for sesarmid crabs and particularly relevant as they are considered to be keystone species within mangrove communities. Soil core water salinity, pH and characteristics of the mangrove vegetation were examined to determine if they varied between storm-water input sites and controls. Soil core water salinity was significantly lower at storm-water input sites, but its relationship with burrow numbers was complex. There was no correlation between salinity and burrow numbers but nevertheless, there was a threshold at approximately 35‰ (that of undiluted seawater), above which *Neosarmatium* spp. burrows were more numerous. For *P. erythrodactyla* there was also evidence of a threshold effect, and at control sites (and therefore with

higher salinity) there was a positive correlation between burrow numbers and salinity.

The mangrove vegetation at all sites was described. Bray Curtis dissimilarity measures were used within an Analysis of Similarity (ANOSIM) to compare vegetation between storm-water input sites and control sites. There was a significant difference between the two groups, but multidimensional scaling plots using vegetation similarity and burrow numbers of both *Neosarmatium* spp. and *P. erythrodactyla* found that vegetation characteristics and burrow numbers were not related. Most control sites were dominated by *Ceriops tagal* and in storm-water input sites dominated by this mangrove there may have been more burrows of both taxa than at other sites. Consequently, it was hypothesised that crabs may have a feeding preference for *C. tagal* over *B. exaristata*. It was also hypothesised that crabs may prefer to eat leaves from mangroves not affected by storm-water, as other studies suggested that mangroves receiving storm-water input may have had more tannins and phenols in their leaves.

Within the study area *Neosarmatium* spp. was found to be the only leaf litter remover and in most areas the only species present was *N. trispinosum*. In addition, it was found that individuals of this species foraged no more than 30cm from their burrows. These findings enabled the design of *in situ* experiments for assessing whether this species showed a preference for feeding on leaves of *C. tagal* over *B. exaristata* or for leaves sourced from control sites over those from storm-water input sites. It was found that *N. trispinosum* had no preference for either species, nor for leaves from control sites over those from storm-water input

sites. These findings are notable because most previous feeding preference experiments have been conducted within the laboratory where captivity may affect behaviour.

Leaf litter removal and subsequent processing is a key role of sesarmids. If a decline in abundance of crabs results in decreased leaf litter processing, the mangrove ecosystem may be affected. During the dry season crabs removed 4.10 to 5.76 t/ha/year (37-63% of total leaf litter fall) and in the wet season 1.96 to 6.35 t/ha/year (8-42% of total leaf litter fall). From these data it appeared that leaf litter was not a limiting resource to *N. trispinosum*. Burrows of this species were contagiously dispersed within the mangrove habitat with more found in gaps between tree stems, in close association with above ground root structures. Within this micro-habitat, the spatial organisation of burrows was such that foraging radii overlapped, but an area close to the burrow entrance was used exclusively by the occupant crab. Foraging radii were found to increase as the distance to the nearest burrow increased, however, this was limited to when the distance between burrows was 30cm or less. This was consistent with an expansion of spatial foraging effort, with a reduction in overlap with the foraging space of neighbouring crabs, which would be expected if competition influenced burrow distribution. Based on these findings, the predictions were that leaf litter removal might be similar when the abundance of *N. trispinosum* remained relatively high, but foraging radii would not continue to increase when burrows became far apart and this would result in decreased leaf litter removal. Sesarmids perform other important roles within mangroves through their burrowing: they aerate the soil, thereby decreasing phytotoxins such as sulphide

and ammonium and they influence nutrient cycling by processing leaf litter.

Further work is required to estimate the effects of a reduction in the abundance of these crabs. In addition, further investigations are required to better understand how storm-water input causes a reduction in sesarmid abundance, in order to provide more guidance in designing urban storm-water drainage.

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DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is provided.

10th December 2013

Derek Stafford Ball

Date

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1 General introduction

1.1 Scope of Thesis

This thesis is an investigation into the influence of urban storm-water runoff on mangrove crabs of the family . Different species are unlikely to respond to changes in their environment in the same way. Thus, this investigation was informed by a review of the known biology of sesarmid species (section 1.2 below). As sesarmid crabs are recognised as keystone species in mangroves (section 1.3), the thesis also considered the potential impacts of a decline in sesarmids on the mangrove ecosystem. To understand any observed patterns in sesarmid populations, it was first necessary to understand the determinants of their distribution and abundance such as; soil characteristics, the mangrove habitat, tidal regime, and the interactions between sesarmids and their habitat (section 1.4). Subsequently, an understanding of the mechanisms by which sesarmids may be affected required knowledge of how storm-water runoff may influence these determinants (section 1.5).

1.2 The family Sesarmidae

Crabs of the family Sesarmidae (infraorder Brachyura, superfamily Grapsoidea) are conspicuous residents of mangrove and saltmarsh habitats within temperate and tropical regions worldwide (Davie 2002). The Sesarmids were formally recognised as a subfamily within the family Grapsidae, along with the subfamilies Cyclograpsinae, Grapsinae and Varuninae. Thus sesarmids were most often referred to in the literature

as 'Grapsids'. Davie (2002) provides general descriptions of these groups. Within Australia the family Sesarmidae contains 35 species from 15 genera consisting mostly of semi-terrestrial, burrowing species that occur in mid to upper tidal limits within mangrove and estuarine environments. Sesarmids have a number of morphological adaptations that allow them to maximise uptake of dissolved oxygen from surrounding water and thus appear to be better adapted to the typically anoxic mangrove environment than members of the family Grapsidae (Davie, pers comm). The family Sesarmidae remains under active taxonomic review with an additional Australian species (*Parasesarma hartogi*) having been described recently (Davie & Pabriks, 2010).

Studies of the larval development and ecology of sesarmids are fewer than for strictly marine species (Anger & Moreira, 2002). *Neosarmatium trispinosum*, that is common in the study area, develops through five zoeal and a megalopa stage over a period of 23 days based on laboratory studies (Islam *et al.*, 2004). *N. indicum* (Islam *et al.*, 2002), and *Perisesarma guttatum* (Lago, 1993) also have this number of larval stages. A Brazilian species *Armases angustipes* (Sesarmidae) develops through four planktonic zoeal stages and a megalopa before metamorphosis into a post-larvae (juvenile) benthic stage (Anger and Moreira, 2002). Similar development occurs in *Sesarma cinerum* (Costlow & Bookhout, 1960) and *Perisesarma fasciatum* (Guerao *et al.*, 2004). However, a Caribbean species *Armases miersii* has abbreviated development of only three zoeal stages (Cuesta *et al.*, 1999). This shows some

variability in development is present within the family and that larval and juvenile ecology varies among species.

The life cycle of many estuarine crabs includes a planktonic stage; embryonic development takes place whilst attached to the female abdominal pleopods, followed by zoeal transport downstream. Further development takes place in higher salinities, followed by return of megalopae upstream into the lower salinity adult habitat where they then metamorphose and settle as juveniles (Taylor and Seneviratna, 2005; Torres *et al.*, 2006). Ryan & Choy (1990) reported a mass upstream migration by megalopa by *Varuna litterata* (Varunidae) in Fiji, and Yates (1978) found that *Parasesarma erythrodactyla* in a temperate habitat undertook migrations associated with spawning. Gebauer *et al.* (1998) found that for *Chasmagnathus granulata* (Varunidae) the presence of both the adults and the adult habitat substratum decreased time to metamorphosis of the megalopa stage. Further, Gebauer *et al.* (2002) demonstrated that megalopa stages of *Sesarma curacoense* settled in response to the odour from conspecific and inter-specific crabs. Luppi *et al.* (2001) showed that adults of *Chasmagnathus granulata* and *Cyrtograpsus angulatus* (Varunidae) prey on settling juveniles.

Sesarmid larvae vary in their ability to survive and metamorphose in low salinities. Anger *et al.* (1990) found that *Sesarma angustipes* zoea survived for two to three days in low salinity water (0-3‰), and were only able to develop through instars at higher salinities. Taylor and Seneviratna (2005) investigated survivorship of two mid

to high shore sesarmids, *Hemigrapsus edwardsii* and *H. crenulatus*, and found a capacity for hyper-osmoregulation at the post gastrulation stage. Both species survived well (approx 80-100% survivorship) in a salinity range of 1-100‰ seawater for 96 hours. Luppi *et al.* (2003) examined survival and the duration of the intermolt period of the zoeal stage of the sesarmid *Armases rubripes*. Survival was higher, and development rate faster, at higher salinity. Nevertheless, such experiments do not account for the natural variations in salinity that would be expected during transport of larvae along estuarine gradients and consequently the potential for larvae to acclimate. For example, Torres *et al.* (2006), compared survivorship of post-moult megalopae in fixed salinities and in treatments where salinity was progressively reduced to simulate upstream migration. In the fixed salinity treatments, megalopae survived in salinities between 5 and 25‰ with 46-96% survivorship respectively. Larvae exposed to 3‰ died within 24 hours. In contrast, when salinity was gradually decreased, larvae survived and metamorphosed in salinities as low as 0.2‰. These studies indicate that sesarmid larvae can survive in low salinities but only if they have undergone a period of acclimation.

1.3 Sesarmids as keystone species

Sesarmid crabs are considered to be keystone species within mangrove communities since their activities have a major influence on ecosystem-level processes (Smith *et al.*, 1991; Lee, 1998; Kristensen, 2008; Alongi, 2009). They have been shown to process large quantities of mangrove leaves and propagules and therefore form an important link between primary and secondary producers (Lee, 1998), although the

amount of litter processed varies by species, mangrove community and height in the intertidal zone. Also, leaf litter processing occurs at a higher rate in tropical systems than in temperate areas (Imgraben & Dittman, 2008). Sesarmids are important consumers of mangrove propagules and thus may influence the recruitment and consequently the structure and floristics of mangrove communities (Smith, 1987; McGuinness, 1997a; Clarke and Kerrigan, 2002; Clarke, 2004). A large proportion of the organic matter within sesarmid faecal material is derived from leaf litter, but is more nutritious than the leaves in terms of its carbon to nitrogen ratio and decreased tannin content (Lee, 1997). Consequently, sesarmids may support an important coprophagous food chain. Bio-turbation by sesarmids can effectively provide aeration of the soil (Kristensen, 2008), thereby decreasing sulphide and ammonium concentrations (Smith *et al.*, 1991). Reduction of such phytotoxins could contribute to increased primary production within mangrove communities (Lee, 1998). Crab burrows can have a great influence on nutrient cycling (Kristensen *et al.*, 1995) and further, Lee (1997) suggests that burrowing activities might make organic matter from deeper soil layers available to other mangrove fauna.

1.4 Determinants of the distribution and abundance of sesarmids

1.4.0 Soil characteristics

Few studies to date have considered the full influence of soil characteristics on the distribution and abundance of sesarmids, apart from Frusher *et al.* (1994) who conducted a series of field surveys in mangrove communities in north Queensland.

Soil pore water salinity did not explain variability in the pattern of distribution for any of the sesarmid species studied, and laboratory trials demonstrated that these species could survive in salinities well outside the range within which they were found. For example, *Perisesarma messa* was found to survive at all salinities tested from 2.5 ‰ to 60 ‰ but was sometimes absent from sites with pore water salinities within this range. The results of this study should be interpreted with caution, however, as crab abundance was estimated by pitfall trapping, a method affected by crab activity and one which can be biased by species and crab size (Lee, 1998). Seiple (1979) did, however, find a difference in the distribution of *Sesarma cinerum* compared to *S. reticulatum* which was attributed to both sediment particle size and salinity. The osmoregulatory ability of two congeners, *Neosarmatium meinerti*, and *N. smithi* was investigated in laboratory trials by Gillikin *et al.* (2004). These species reacted differently to salinity; *N. smithi* had poor survivorship at all salinities trialled except 32‰, whilst *N. meinerti* survived well at all salinities between 16 to 65‰. However, the energy budget of the latter species was reduced at higher salinities indicating that extreme salinities may negatively affect populations through longer-term exposure.

In east Africa, the abundance of *N. meinerti* showed no relationship to soil particle size or organic matter (Hartnoll *et al.*, 2002). Frusher *et al.* (1994), however, found that of the four species within their study, *Perisesarma brevipes* appeared to be more abundant in areas of relatively acidic sediment but no difference was observed for the other species. The percentage of sand and organic matter within the soil explained a

significant amount of the variability in the abundance of *P. brevipes* and *P. messa*. Spivak *et al.* (1994) in a South American study also found a relationship between distribution and sediment types for *Cyrtograpsus angulatus* and *Chasmagnathus granulata* and this varied depending on size and sex. However, for *C. granulata* at least, these result need to be interpreted with caution as another study found that this species can also significantly influence sediment characteristics (Botto & Iribarne, 2000).

1.4.1 The mangrove habitat

A number of studies have attempted to relate sesarmid distribution and abundance to the different mangrove species present in various habitats. In Kenya, Dahdouh-Guebas *et al.* (2002) concluded that different sesarmid assemblages were present within different mangrove zones. However, each zone showed considerable variation in canopy dominance, which raises some uncertainty regarding interpretation of these results. Lee and Kwok (2002) examined population characteristics of *Perisesarma bidens* and *Parasesarma affinis* within two contiguous but different mangrove communities. The abundance of both species was higher in *Kandelia candel* forest than in *Avicennia marina* forest, as were their gonosomatic and hepatosomatic indices (measures of reproductive capability which are independent of body size). It was proposed by Lee and Kwok (2002) that the habitat value of each forest was different, with *Kandelia candel* buttress roots affording better refugia.

Several studies have investigated feeding preferences of sesarmids for leaves and propagules of different mangrove species. Such preferences may at least partially explain patterns of distribution and abundance of sesarmids within different mangrove forest types. Camilleri (1989) in south-east Queensland showed that *Sesarma* (= *Parasesarma*) *erythodactyla* displayed a preference for leaves of *Avicennia marina* over *Rhizophora stylosa* and *Bruguiera gymnorhiza*. This was explained by the lower tannin and higher nitrogen content of *A. marina* leaves. Micheli (1993) established that at five north Queensland field sites and in laboratory tests, *Sesarma* (= *Perisesarma*) *messa* did not display preferences for feeding among mangrove leaves of the species *Rhizophora stylosa*, *Avicennia marina*, *Bruguiera exaristata*, or *Ceriops tagal*. *Sesarma smithii* (= *Neosarmatium trispinosum*) preferred *Rhizophora stylosa* over the other species in laboratory experiments but this was not displayed in the field. In peninsular Malaysia, Ashton (2002) investigated sesarmid feeding preferences for different mangrove leaves in different mangrove zones, using both fresh and senescent leaves. The results were complicated, but no consistent preferences could be demonstrated at all sites. Nevertheless, at sites dominated by the genus *Bruguiera*, greater numbers of *Bruguiera gymnorhiza* leaves were removed and deposited in burrows. In a Kenyan study, Dahdouh-Guebas *et al.* (1997) concluded that *Neosarmatium meinerti* had no distinct preference for the leaves of any mangrove species present within their habitat.

A number of studies have demonstrated some degree of preference for feeding on propagules of different mangrove species (for example Clarke & Kerrigan, 2002;

Dahdouh-Guebas, 1998; Smith 1987), but these deal with preferences of the entire sesarmid assemblage rather than of particular species. It would appear that some sesarmids may have dietary preferences which could influence their distribution and abundance, but these studies have been geographically restricted and often conducted over short time frames. Additional work is required to determine if food type limits the distribution and/or abundance of sesarmids.

1.4.2 Tidal regime

The height of the substratum above tidal datum can be used as a measure of inundation frequency and period, of mangroves occurring within the intertidal zone. Zonation of crab species across the intertidal gradient has been demonstrated on all continents where mangroves occur (Frusher *et al.*, 1994). Broadly, sesarmids occur in higher intertidal areas and the family Ocypodidae (particularly the genus *Uca*) occurs in lower ones. Hartnoll *et al.* (2002) found greater sesarmid biomass in higher shore areas but cautioned that this explained only a small proportion of the observed variability. Dahdouh-Guebas *et al.* (2002) report that the population density of *Perisesarma guttatum* and *Metopograpsus thukuhar* did not correlate with height above tidal datum although the population density of *Neosarmatium meinerti* did. The latter finding was confirmed by Hartnoll *et al.* (2002) who found a highly significant negative correlation between the abundance of this species and immersion period. In a south-east Queensland study, Prosser (2004) found *Parasesarma erythodactyla* from the high water mark (HWM) to approximately 0.8m below HWM, while *Perisesarma messa* was restricted to the area between HWM and 0.4m

below HWM. However, no comprehensive mapping of sesarmid distributions versus height above tidal datum has been undertaken in Queensland.

1.4.3 Interactions between sesarmids and their habitat

In considering the importance of habitat parameters on the distribution and abundance of sesarmids, actual causal relationships need to be established. Such ‘cause and effect’ considerations are important when comparing patterns of variation in benthos and sediment properties (Chapman and Tolhurst, 2004). Evidence is available which demonstrates that while some benthos react to properties of the sediment, the benthos itself may significantly alter the sediment (Ford *et al.*, 1999). For example, bio-turbation by sesarmids could influence particle size and organic matter within the soil. Furthermore, burrowing activity could also influence soil salinity and pH. Consequently, attributing these environmental parameters as *determinants* of sesarmid distribution or abundance needs to be done with considerable caution. Sesarmid crabs are important consumers of mangrove propagules and can themselves influence mangrove population structure (Lee, 1998) since some species of mangrove propagules are more readily removed by crabs (Clarke and Kerrigan 2002). Given that sesarmids are important consumers of leaf fall it should also be considered whether, in the absence of sesarmids, accumulation of leaf litter could eventually affect the height and soil chemistry of the substratum.

1.5 The impacts of storm-water runoff on sesarmid crabs and their habitat.

1.5.0 Introduction

The economic and ecological values of mangrove communities have become increasingly well known and accepted (see for example; Abuodha & Kairo, 2001; Bridgewater & Cresswell, 1999). Consequently, mangroves within northern Australia are now largely protected from obvious or known impacts, including clearing. Unfortunately, indirect impacts resulting from land use activities in catchments have only rarely been investigated. No studies of the impact of urban storm-water run-off into mangrove communities have been identified by this review; the most relevant appears to be by Walsh (2004) who provides results of studies in sixteen catchments of urban storm-water runoff into near coastal freshwater communities near Melbourne, Australia. Catchments were described in terms of the degree of storm-water impervious area they contained and the degree of drainage connection from these areas to the receiving communities. Drainage connection was defined by Walsh (2004) as “the proportion of impervious area directly connected to streams by storm-water pipes”. Communities receiving water from relatively impervious catchments supported only depauperate assemblages of disturbance tolerant species. In addition, few species were present at sites with greater than 20% connection. Indeed, the author claims “this study has identified piped storm-water drainage connection as a likely causal factor explaining the widely observed loss of taxa from streams draining urbanized catchments”.

1.5.1 Soil characteristics

Abuodha & Kairo (2001) suggested that in Kenya, groundwater (freshwater) seepage facilitates colonization and growth of mangroves in areas not subject to freshwater outflows by rivers and that alteration of this seepage could then impact on mangroves. Due to its high clay content, mangrove soil is typically highly impermeable (Stieglitz *et al.*, 2000). Frusher *et al.* (1994) observed that during a very high rainfall event in their study area, estuarine water salinities dropped to 0‰, but soil pore water salinities were lowered only by 1.4‰. However, sesarmid crab burrows may alter this situation. Stieglitz *et al.* (2000) concluded that the burrows of *P. messa* facilitate tidal flushing within mangrove sediments and thus remove excess salt accumulated in the soil. An extension of this conclusion is that large quantities of freshwater from storm-water drains could result in even more effective flushing of accumulated salt than relatively saline tidal waters, and thus a greater reduction in pore water salinity.

Periodic water exchange within mangrove soils can lead to fluctuations in soil pH (Chowdhury, 2001). It is reasonable to assume that both sesarmid burrowing activity and storm-water inputs (in addition to normal tidal flushing) would contribute to these fluctuations.

1.5.2 The mangrove habitat

Moritz-Zimmerman *et al.* (2002) examined the impacts of storm-water channels draining into mangrove forests associated with Darwin Harbour. The channels were constructed in the 1980's to reduce habitat for mosquito breeding. In this study,

survivorship of experimentally planted *Ceriops australis* was lower directly adjacent to the channels than in forest further away. The basal area of mangrove trees was also greater further away from channels. Adjacent to some channels, the forest had a greater proportion of *Lumnitzera racemosa* and *Avicennia marina*. These results suggest that creation of channels could have an effect on the floristics of the mangrove forest. Given that in some cases sesarmids display preferences for some mangrove community types, such vegetation changes may also affect sesarmid abundance and/or distribution. There is some evidence that alterations of drainage patterns can affect sesarmid crab populations. Breitfuss (2003b) examined the impact of drainage channels (again constructed for purposes of mosquito control) on saltmarsh crabs. Complex patterns of change were reported including a decrease in overall burrow densities and changes in crab size classes present adjacent to channels.

A key feature of the biology of sesarmids is their ability to eat mangrove leaf litter, despite it being high in tannins and polyphenols which reduce palatability. Basak *et al.* (1998) examined polyphenol, tannin and protein concentrations in the leaves of nine mangrove species throughout a full year. Polyphenol and tannin concentrations increased during the wet season and protein concentration was negatively correlated with these compounds. Considerable variation in the concentration of all three constituents was found among mangrove species and the study highlights the possibility that leaf chemistry of mangrove trees subjected to higher freshwater inputs (i.e. by point discharge of urban storm-water) may differ from unaffected areas, which in turn, may affect palatability of leaf litter to the sesarmid assemblage.

Whether or not similar changes in propagule composition also occurs, remains unknown.

1.6 Thesis objectives

This thesis aimed to determine if changes in mangrove hydrology resulted in impacts at ecosystem level. This was undertaken by testing whether point discharge of urban storm-water into the landward margin of mangrove communities caused a decline in sesarmid crabs and what related changes in the sesarmid habitat may have caused the decline. The implications of a decline are examined with respect to the keystone species role of leaf litter removal from the mangrove substratum.

1.7 Thesis outline

1) To compare the abundance of sesarmids between sites that receive point discharge of urban storm-water and sites not so affected.

A study was completed to determine the most effective way to estimate relative abundance of sesarmids within the study area. This study showed that burrow counts were the most reliable. Comparisons were made of sesarmid burrow abundance at sites that received point discharge of storm-water (henceforth referred to as storm-water input sites) and at sites not so affected by storm-water discharge (henceforth referred to as control sites). These were made over three years at three localities and over one year at 10 localities.

2) *To compare soil core water and vegetation characteristics between storm-water input and control sites and relate these to sesarmid burrow abundance.*

Comparisons were made of soil core water salinity and pH between storm-water input sites and control sites to determine if there were differences between these groups, and if these could be related to the abundance of sesarmid burrows. Structural and floristic characteristics of the mangrove communities were compared between storm-water input sites and control and any differences related to sesarmid burrow abundance.

3) *To determine if sesarmids in the study area showed preferences for feeding on leaves of different mangroves and between leaves from storm-water input sites and control sites.*

Neosarmatium trispinosum was identified as the principle leaf removing sesarmid within the study area. Experiments were conducted *in situ* to determine if this species preferred to feed on leaves of *Ceriops tagal* over those of *Bruguiera exaristata*, and if leaves were preferentially removed, if they were sourced from control sites rather than storm-water input sites.

4) *To determine if a decline in abundance of sesarmids could be predicted to result in reduced leaf litter removal.*

This was done by directly measuring leaf litter fall and removal at three sites during two seasons. Natural leaf litter rates were measured and compared to the amount removed from the substratum with the difference between these two measurements

allowing calculation of the net amount of leaf litter left remaining. Removal rates were compared to the estimated biomass of *N. trispinosum* at each area where measurements were taken.

5) To examine the micro-distribution of N. trispinosum burrows to determine if there is evidence of habitat partitioning, and/or if it is related to vegetation structures within the mangrove community.

The dispersion of mangrove trees and of *N. trispinosum* burrows within the mangrove habitat was examined. The spatial distribution of burrows was studied in relation to the proximity of mangrove tree stems and above ground root structures. The distance between *N. trispinosum* burrows was measured and related to the distance that crabs forage away from burrow entrances, to determine if burrows are located in a way that might reduce competition amongst crabs.

1.8 The study area

This study was conducted in central Coastal Queensland (Australia) in the vicinity of the urban centres of Sarina, Mackay City and Airlie Beach. Study sites consisted of mangrove communities close to the urban residential areas of Armstrong's Beach, Slade Point, Eimeo, Bucasia, Cannonvale and Mandalay. This area lies within the Mackay to Lucinda coastal (meso-scale) bioregion (Anon, 1998) that is characterised by less diverse mangrove communities and associated lower littoral fauna and lower structural complexity than in the more northern tropics. Tidal amplitudes are large, from 7.14m at Hay Point in the south, to 6.41m at Mackay Harbour and 4.30m at

Shute Harbour (Anon, 2011a). Net movement of near coastal water and sediment is dominated by a northerly longshore drift driven by a predominant south-easterly wind direction (Anon, 2004). Within the region there are extensive areas of mangrove dominated estuarine ecosystems associated with both large and small waterways. The estimated pre-European extent of mangrove communities was approximately 33701ha, of which 794ha was cleared prior to 2005 (Anon, 2011b).

2 Estimating sesarmid abundance and population structure

2.1 Introduction - methods for estimating crab abundance

In a review of the ecological role of sesarmid crabs, Lee (1998) noted that no satisfactory method existed for accurate field estimation of population density, although more recent studies have improved that situation. Several methods have been used including burrow counts (Breitfuss, 2003a; Emmerson, 2001; Piou *et al.*, 2009; Schories *et al.*, 2003; Warren, 1990), direct visual census (Hartnoll *et al.*, 2002; Warren, 1990) excavation (Lee & Kwok, 2002; Schories *et al.*, 2003) and pitfall traps (Frusher *et al.*, 1994; Salgado-Kent & McGuinness, 2006). There have been limited attempts to combine two or more methods (Salgado-Kent & McGuinness, 2006; Skov & Hartnoll, 2002).

Direct visual census underestimates numbers (Skov & Hartnoll, 2002) and is of little use for cryptic or nocturnal species. Excavation can provide accurate estimates of abundance but presents problems with repeatability, as this technique is destructive and very difficult to conduct in areas of high root densities (Skov & Hartnoll, 2002).

Burrow counts may be useful in estimating relative abundance but may not provide accurate estimates of actual abundance as many species construct more than one opening (Lee, 1998) and more than one individual may occupy a burrow (McKillup & Butler 1979). Salgado-Kent & McGuinness (2006) noted that some crabs

(*Neosarmatium meinerti*) construct visually distinctive burrows which can be used to obtain species-specific abundance estimates. Further, multiple burrow entrances constructed by this species were readily recognisable and thus ‘over-counting’ of burrows could be avoided. *Neosarmatium trispinosum* also builds characteristic mounds at the entrance to the burrow (Islam *et al.*, 2004) and as this species lies outside the range of *N. meinerti* (ABRS, 2009) these too can be used in species-specific abundance estimates. Breitfuss (2003b) found that for *Helograpsus haswellianus*, a large increase in accuracy of abundance estimates (from 33% to 97%), obtained by burrow counts could be achieved by only counting those that were obviously recently used by crabs. Burrow counts can also be useful in examining size frequencies of populations, as there is a relationship between burrow opening width (aperture) and crab size (Breitfuss, 2003a; Emmerson, 2001; Piou *et al.*, 2009; Prosser, 2004).

Pitfall traps are biased for species, sex and size (Skov *et al.*, 2002) and more accurately measure activity levels (Lee, 1998). Further compounding these difficulties is that activity varies temporally and is highest after spring high tides (Frusher *et al.*, 1994; Hartnoll *et al.*, 2002). Lee and Kwok (2002) note that some species hibernate during the year, and both juveniles and ovigerous stages of some species are also known to stay buried or hidden. Thus this component of the population would not be sampled by pitfalls during some periods of the year.

Despite the limitations of pitfall trapping, it can be used to obtain specimens and therefore allow accurate recording of size, sex and possibly reproductive status of females enabling calculation of important population parameters. Estimates using burrow counts are less likely to be biased by activity patterns, but yield less information on crab populations.

In summary, the method chosen to estimate crab abundance must take into consideration the species of crabs present and the type of estimate required (i.e. relative or actual abundance). Thus the advice of Salgado-Kent & McGuinness (2006) that “the selection of a method should be made after careful evaluation of the questions and relevant information required for any particular study” is most appropriate.

For the purposes of this study, comparison of sesarmid abundance between storm-water input sites and control sites was required. Because sesarmids have differing tolerances to the salinity of their habitat (see review in Chapter 1), it was also necessary to compare abundance of different taxa, as they may have different responses to exposure to storm-water input. Further, knowledge of the size frequency distribution within populations would be useful as an indicator of recruitment of crabs back into storm-water input sites during the dry season. In consideration of these needs, extensive qualitative observations and a series of pilot studies were undertaken to assess the efficacy of various methods for estimating sesarmid abundance within the study area.

2.2 Methods

2.2.0 Qualitative observations

Qualitative observations were undertaken to initially establish which sesarmid species were present within the study area and note any relevant behaviour. The observations included extensive diurnal and nocturnal searches on the substratum, under and around mangrove roots and fallen debris, and on tree trunks. Any moulted shell or crab parts left remaining on the substratum after predation were collected and examined. Where possible, taxonomy of these remains was resolved to the lowest level practical. Crabs were observed (either at close quarters or through binoculars) and/or captured at the entrance of burrows to establish if particular burrow morphology could be reliably attributed to a single species. Crabs captured by pitfall traps were also identified.

2.2.1 Pitfalls and direct visual census

A number of pilot studies were undertaken to investigate whether pitfall trapping and/or direct visual census were suitable techniques for estimating abundance of sesarmid species present within the study area.

Initially, a single area of mangrove forest was selected at Bucasia. It contained *Cerriops tagal* with occasional *Bruguiera exaristata* and was representative of the mangrove community under investigation. Part of the area was divided into nine 10m

× 10m grids within which three replicates of each sampling technique were randomly allocated. Sampling techniques consisted of:

- Five pitfall traps placed in the fashion described by Frusher *et al.* (1994) at each corner of a 2m × 2m square with another trap in the centre. This grid was placed at the centre of the larger 10m × 10m grid. Each pitfall consisted of a 13cm diameter and 15cm deep straight-sided plastic flower pot.
- Five pitfall traps, positioned as described above, but with a 15cm high drift fence placed in a crossed pattern over the pitfall traps (in the fashion often used by terrestrial ecologists) to increase trapping success. The drift fence was held in place by steel pegs and was constructed of aluminium fly screen.
- Timed (15 minute) observations within a 5m × 5m area in the centre of the 10m × 10m grid. This was undertaken at night using a low power (Petzel) headlamp (using both white and red lights) to observe the nocturnal *Neosarmatium* spp., and by day to assess the presence of other species.

Sampling was conducted during two five day periods; 27th September 2004 to the 1st November 2004 (after spring tides, starting with a nightly high tide of 5.86m declining over the sampling period to 4.90m), and 12th – 16th October 2004 (after neap tides, starting with a nightly high tide of 5.42m and declining over the sampling period to 4.97m).

Further studies were conducted at three locations; Bucasia, Eimeo and Slade Point, to further examine the usefulness of pitfall traps for sampling sesarmids. Fenced pitfalls were used as the previous study showed that they collected larger and possibly more representative samples of at least one species (*P. erythrodactyla*), than unfenced pitfalls. At each location paired sites were selected; a storm-water input site and a control site. At each site, three fenced pitfalls (as described above) were installed at random positions. Sampling was undertaken during two periods; 11th – 13th November 2004 (after spring tides, starting with a nightly high tide of 5.22m declining to 4.95m) and 27th – 29th November 2004 (after neap tides, starting with a nightly high tide of 4.37m declining to 3.91m).

2.3 Results

2.3.0 Qualitative observations

Within the study area, five species of sesarmid were observed; *Neosarmatium trispinosum*, *N. fourmanoiri*, *Parasesarma erythrodactyla*, *Perisesarma messa*, and *Metopograpsus frontalis*. Davie (pers comm., 2004) provided assistance in identifying collected specimens. *N. trispinosum* and *P. erythrodactyla* were observed to be the markedly most abundant species. Both *N. trispinosum* and *N. fourmanoiri* were consistently associated with distinctive hooded burrows. *N. trispinosum* was only ever observed at night time or from dead material, but *N. fourmanoiri* was observed on multiple occasions during the day, particularly in overcast conditions. This latter species was only ever observed at two locations, close to a storm-water

drain at Bucasia and at Cannonvale. These two species are easily distinguished when closely examined as *N. trispinosum* males have three prominent spines at the base of the dactyl (compared to shallow pits in females) whereas *N. fourmanoiri* has no such features. *P. erythrodactyla* was the most commonly observed species and smaller specimens could be readily captured from the entrance of simple burrows in the substratum. These burrows were consistently found in flat areas of substratum usually away from roots and debris and had no other distinctive features. *Perisesarma messa* was rarely observed or captured and then only along the moister lower margins of the study area which were frequently inundated by tides. This species was observed close to unhooded burrows with slightly laterally compressed apertures in close association with roots or more often with debris lying on the substratum. *Metopograpsus frontalis* was rarely observed (although often captured in pitfalls) and was more commonly associated with tree trunks or on roots and debris lying on the substratum, but never seen at the entrance to burrows. Davie (2002) does not record this latter species as a burrower and notes that it is cosmopolitan in its habitat utilisation, being found in a variety of shore types.

2.3.1 Direct visual census

Visual observation of *N. trispinosum* was virtually impossible due to its nocturnal and cryptic behaviour. Individuals were readily disturbed upon approach and immediately retreated into their burrows, not reappearing unless the observer's headlight was switched off for at least 10 minutes. Both white and red lights were found to have a similar affect. Upon turning the light back on, the crabs immediately retreated again.

Efforts at visual census of this species were abandoned after the first few nights as this behaviour precluded any meaningful census. Although less sensitive to disturbance, observation of *P. erythrodactyla* was also abandoned for similar reasons as the recovery time between disturbance and re-emergence from burrows made visual census of the large number of burrows in the sampling area logistically unviable.

2.3.2 Efficacy of fenced pitfall vs. unfenced pitfall traps

During 27th September 2004 to the 1st November 2004 (after spring tides, starting with a nightly high tide of 5.86m and declining over the sampling period to 4.90m), a total of 89 crabs were captured, 54 from fenced pitfalls and 35 from unfenced pitfalls (Table 2.1). Captures were numerically dominated by *P. erythrodactyla* ($n = 73$) with fewer *M. frontalis*, ($n = 14$) and *N. trispinosum* ($n = 2$). In contrast, during the second sampling period (after neap tides) only eleven crabs were captured; ten within fenced pitfalls and one within unfenced pitfalls (Table 2.2). These captures were again largely dominated by *P. erythrodactyla* ($n = 10$) with only a single *M. frontalis*.

Table 2.1 Fenced and unfenced pitfall trap captures made after spring tides (5.86 – 4.90m).

Date	UF1	UF2	UF3	F1	F2	F3
27/09/04	3	4	7	13	4	6
28/09/04	3	3	1	7	6	2# ¹
29/09/04	3# ²	2# ¹	2# ¹	3*	2# ¹	2# ²
30/09/04	1# ¹	2 #	4# ¹ *	0	1# ¹	1
1/10/04	1	0	0	2	3# ¹	2
Replicate total	11	11	14	25	16	13
Treatment total		35			54	

UF = unfenced pitfall; F = fenced pitfall. Captures are of *Parasesarma erythodactyla* unless otherwise noted: #¹ = number of *M. frontalis* captures; * includes 1 individual of *N. trispinosum*

Table 2.2 Fenced and unfenced pitfall trap captures made after neap tides (5.42-4.97m).

Date	UF1	UF2	UF3	F1	F2	F3
12/10/04	0	0	0	1	1# ¹	0
13/10/04	0	0	0	1	0	0
14/10/04	1	0	0	0	1	2
15/10/04	0	0	0	0	2	1
16/10/04	0	0	0	1	0	0
Replicate total	1	0	0	3	4	3
Treatment total		1			10	

UF = unfenced pitfall; F = fenced pitfall. Captures are of *Parasesarma erythodactyla* unless otherwise noted: #¹ = number of *M. frontalis* captures.

The differences in captures between treatments (fenced vs. unfenced pitfall), between each sampling time (after spring tide vs. after neap tide) and amongst tides (= sampling nights) were tested by a repeated measures ANOVA. Data were transformed $[\log (x+1)]$ to reduce heteroscedasticity and Mauchly's Test subsequently found no significant deviation from sphericity ($df = 9$, $W = 0.262$, $P = 0.49$). Tests of within-subject effects are shown in Table 2.3. There was no significant difference in captures among tides (Sphericity Assumed; $F_{4, 32} = 0.756$, $P = 0.562$). However, there were significant interactions in captures between sampling time and tide (Sphericity Assumed; $F_{4, 32} = 7.109$, $P < 0.001$), between treatment and tide (Sphericity Assumed; $F_{4, 32} = 3.322$, $P = 0.022$) and between time, treatment and tide (Sphericity Assumed; $F_{4, 32} = 3.086$, $P = 0.029$). These interactions are further explored with use of the estimated marginal means given in Tables 2.4 to 2.6. After spring tides there was a significant difference between captures on the last tide and the first two. In the fenced treatment there was a significant difference in captures between the 4th and 5th tide. After spring tides the unfenced treatment captured significantly more on the last tide than the 2nd, 3rd or 4th. After neap tides the fenced treatment captured significantly more on the 5th tide than the 2nd.

Table 2.3 Tests of within-subjects effects of sesarmid crab captures at different tides, sampling times and for different treatments (fenced and unfenced pitfall traps).

Measure: Captures						
Source		Type III Sum of Squares	df	Mean Square	F	Sig.
Tide	Sphericity Assumed	.092	4	.023	.756	.562
	Lower-bound	.092	1.000	.092	.756	.410
Tide * Time	Sphericity Assumed	.870	4	.217	7.109	<.001
	Lower-bound	.870	1.000	.870	7.109	.029
Tide * Treatment	Sphericity Assumed	.406	4	.102	3.322	.022
	Lower-bound	.406	1.000	.406	3.322	.106
Tide * Time * Treatment	Sphericity Assumed	.378	4	.094	3.086	.029
	Lower-bound	.378	1.000	.378	3.086	.117
Error (Tide)	Sphericity Assumed	.979	32	.031		
	Lower-bound	.979	8.000	.122		

Table 2.4 **Estimated marginal means for the Time * Tide interaction for pitfall trap captures.**

Measure: Captures

Time	Tide	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
Spring tide	1	.667	.097	.443	.890
	2	.622	.069	.464	.780
	3	.520	.064	.372	.668
	4	.347	.058	.213	.481
	5	.310	.053	.187	.433
Neap tide	1	.100	.097	-.124	.324
	2	.050	.069	-.108	.208
	3	.180	.064	.032	.328
	4	.180	.058	.046	.314
	5	.367	.053	.244	.490

Table 2.5 **Estimated marginal means for the Treatment * Tide interaction for pitfall trap captures.**

Measure: Captures

Treatment	Tide	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
Fenced	1	.550	.097	.326	.774
	2	.422	.069	.264	.580
	3	.390	.064	.242	.538
	4	.280	.058	.146	.414
	5	.577	.053	.454	.700
Unfenced	1	.217	.097	-.007	.440
	2	.250	.069	.092	.408
	3	.310	.064	.162	.458
	4	.247	.058	.113	.381
	5	.100	.053	-.023	.223

Table 2.6 Estimated marginal means for the Time * Treatment * Tide interaction for pitfall trap captures.

Measure: Captures

Time	Treatment	Tide	Mean	Std. Error	95% Confidence Interval	
					Lower Bound	Upper Bound
Spring tide	Fenced	1	.900	.137	.584	1.216
		2	.743	.097	.520	.967
		3	.520	.091	.311	.729
		4	.200	.082	.011	.389
		5	.520	.075	.346	.694
	Unfenced	1	.433	.137	.117	.750
		2	.500	.097	.277	.723
		3	.520	.091	.311	.729
		4	.493	.082	.304	.683
		5	.100	.075	-.074	.274
Neap tide	Fenced	1	.200	.137	-.116	.516
		2	.100	.097	-.123	.323
		3	.260	.091	.051	.469
		4	.360	.082	.171	.549
		5	.633	.075	.460	.807
	Unfenced	1	5.551E-17	.137	-.316	.316
		2	1.527E-16	.097	-.223	.223
		3	.100	.091	-.109	.309
		4	-1.110E-16	.082	-.189	.189
		5	.100	.075	-.074	.274

Tests of between-subject effects (Table 2.7) found a significant difference in captures between sampling times ($F_{1,8} = 62.756, P < 0.001$) and treatments ($F_{1,8} = 29.826, P = 0.001$). There was no significant interaction between sampling time and treatment.

Table 2.7 Tests of between-subjects effects of sesarmid captures at different times and for different treatments (fenced and unfenced pitfall traps).

Measure: Captures					
Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Intercept	6.700	1	6.700	277.780	< .001
Time	1.514	1	1.514	62.756	< .001
Treatment	.719	1	.719	29.826	.001
Time * Treatment	.040	1	.040	1.660	.234
Error	.193	8	.024		

The mean captures of crabs made by fenced and unfenced pitfall traps during the two sampling times is shown in Figure 2.1. Fewer captures were made in the time after neap tides with the effect being most noticeable in unfenced pitfall traps.

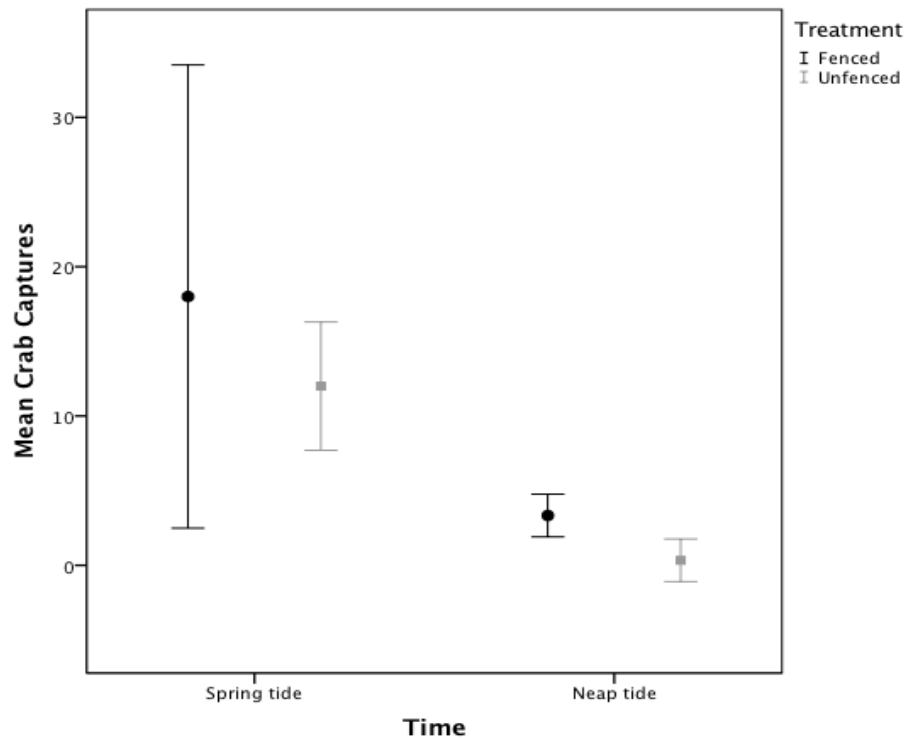


Figure 2.1 Mean captures of crabs made by fenced and unfenced pitfall traps during the spring tide and neap tide sampling times (bars are 95% confidence intervals of the means).

There appeared to be some tendency for captures by fenced pitfalls to increase during higher tidal heights although wider confidence intervals of the means at these times precludes more definitive interpretation. Figures 2.2 and 2.3 show mean captures at each tidal height (data from both sampling times combined) for fenced and unfenced pitfalls respectively. A similar comparison for unfenced pitfalls illustrates a possible peak in captures at a mid-range tidal amplitude with higher tidal levels resulting in a similar tendency for increased captures as seen in fenced pitfalls.

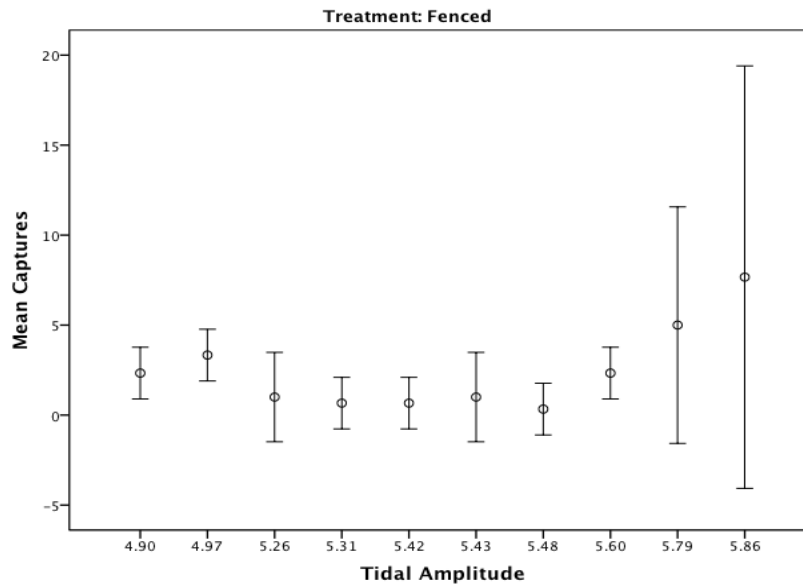


Figure 2.2 Mean captures of crabs vs. tidal amplitude for fenced pitfall traps (bars are 95% confidence intervals of the mean).

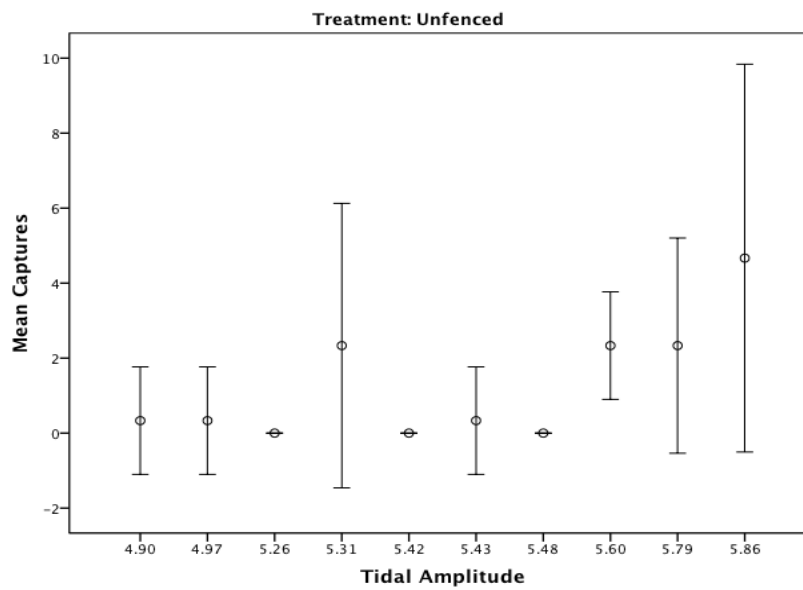


Figure 2.3 Mean captures of crabs vs. tidal amplitude for unfenced pitfall traps (bars are 95% confidence intervals of the mean).

During 11th to the 13th November 2004 (after spring tides; starting with a nightly high tide of 5.22m and declining over the sampling period to 4.95m), only five crabs were captured, four from control sites and one from the Bucasia storm-water input site (Table 2.8). Captures were made of all species known to be present; *P. erythodactyla*, *M. frontalis*, *N. trispinosum*, *N. fourmanoiri* and *P. messa*. In contrast, during the second sampling period (after neap tides: starting with a nightly high tide of 4.37 declining to 3.91m) 39 crabs were captured (Table 2.9), but of these 32 were caught at the Eimeo control site and consisted of *P. erythodactyla* ($n = 17$), *M. frontalis* ($n = 12$) and *P. messa* ($n = 3$). Only one individual of *N. trispinosum* was captured at the Bucasia storm-water input site.

Table 2.8 Comparison of fenced pitfall trap captures among sites 11-13th November (night-time tides of 5.22m to 4.95m).

Date	SPC	SPSW	EC	ESW	BC	BSW
11/11/04	0	0	0	0	0	1**
12/11/04	1^	0	1# ¹	0	0	0
13/11/04	0	0	1	0	1*	0
Total	1	0	2	0	1	1

Captures are of *Parasesarma erythodactyla* unless otherwise noted: #¹ = number of *M. frontalis* captures; ^ = 1 *Perisesarma messa* capture; * = 1 *N. trispinosum* capture; ** = 1 *N. fourmanoiri* capture. SPC = Slade Point Control, SPSW = Slade Point storm-water input, EC = Eimeo Control, ESW = Eimeo storm-water input, BC = Bucasia control, BSW = Bucasia storm-water input.

Table 2.9 Comparison of fenced pitfall trap captures among sites 27-29th
November (night-time tides of 4.37m to 3.91m).

Date	SPC	SPSW	EC	ESW	BC	BSW
27/11/04	2# ¹	0	7# ⁴ ^	0	0	1 ^
28/11/04	0	0	15# ⁶ ^	0	1	1*
29/11/04	0	0	10# ² ^	1# ¹	1# ¹	0
Replicate total	2	0	32	1	2	2

Captures are of *Parasesarma erythodactyla* unless otherwise noted: #¹ = number of *M. frontalis* captures; ^ = 1 *Perisesarma messa* capture; * = 1 *N. trispinosum* capture. SPC = Slade Point Control, SPSW = Slade Point storm-water input, EC = Eimeo Control, ESW = Eimeo storm-water input, BC = Bucasia control, BSW = Bucasia storm-water input.

2.4 Discussion

The landward mangrove community under investigation in this study is best defined as a forest of *Cerriops tagal* with other species such as *Brugueira* spp. being less common. Intensive searching detected four grapsids of the sub-family Seserminae: *P. erythodactyla*, *N. trispinosum*, *N. fourmanoiri* and *P. messa*. Hooded burrow entrances of *N. trispinosum* were found to be a characteristic feature and their abundance (sometimes up to 8 per m²) suggested that this species was present in large numbers. *P. erythodactyla* was readily captured at burrow entrances and was also observed to be numerous. *N. fourmanoiri* was rare. *M. frontalis*, a member of the sub-family Grapsinae was often captured in pitfall traps but otherwise rarely observed. This species is far more cosmopolitan than the mangrove specific Sesarminae (Davie,

2002) and is not known to construct burrows. *P. messa* was rarely observed or captured.

Attempts to estimate abundance of sesarmids by direct visual observation proved unviable.

The initial pilot study at Bucasia showed that fenced pitfall traps were more effective at capturing sesarmids, particularly *P. erythodactyla* and that more were captured in the sampling period after spring tides. This latter finding is consistent with other studies (Frusher *et al.*, 1994; Hartnoll *et al.*, 2002) and supports Lee's (1998) assertion that pitfall-trapping success may be more a measurement of activity level than sesarmid abundance. Although there appeared to be a general trend for increased nightly capture rates during higher amplitude tides, the numbers differ between types of traps (fenced vs. unfenced) and within different sampling periods (after spring vs. after neap tides). Further, there was a large difference in the mean number of captures amongst traps of the same type during the same tidal height. Thus actual tidal height was not considered as a definitive guide to timing of further pitfall trapping pilot studies.

Further pilot studies used fenced pitfall traps as these appeared to capture larger and probably more representative samples of the sesarmid population, especially of *P. erythodactyla*. Comparisons were made of paired sites (storm-water input vs. control sites) at three locations during two periods of different tidal height. The results of

these studies cast considerable doubt on the efficacy of pitfall traps in estimating sesarmid abundance. The number of sesarmid captures was very low during the period after spring tides compared to that found during the first study. Even casual visual observation revealed that several of the sites sampled supported large populations of sesarmids, however, this was clearly not reflected in the number of captures. During the lower tidal period, results were similar except that at Eimeo a large number of captures were made compared to other sites and also compared to the same site during the period after spring tides. This is in contrast to the findings of the first pilot study.

Throughout the studies all species detected by intensive searching were also captured by fenced pitfalls, and all but *N. fourmanoiri* by unfenced pitfalls. As such, fenced pitfall trapping may be a useful technique for undertaking a census of species present. However, it was clear that pitfall trapping using either technique failed to capture *Neosarmatium* spp. in the numbers expected given the presence of large numbers of burrows at the study sites. This may be due to limited foraging range and thus a reduced probability of this species encountering a pitfall trap, compared to more mobile species. Alternatively, *Neosarmatium* spp, being typically much larger than other species, may have an ability to avoid pitfall traps. In addition, the results of these studies showed that pitfall trapping was not a suitable method for comparing the abundance of other sesarmid species among sites and time, as it was highly sensitive to crab activity levels, which may not be consistent over time. If accurate comparisons of abundance are to be made between treatments (storm-water input vs.

control) and amongst locations by pitfall trapping, as is required; a key assumption would be that activity levels are the same at each place of sampling and at each sampling time. Whilst tidal period (i.e. spring vs. neap tides) may be one determinant of activity level as noted by Frusher *et al.* (1994) and Hartnoll *et al.* (2002), there appear to be other unknown stimuli. Actual tidal height may be one of these, but inconsistencies in the relationship between capture rates and tidal heights suggest there were others. Without knowledge of these, or an ability to accurately predict activity levels amongst sampling places and times, pitfall trapping would not provide any meaningful estimates of abundance by which comparisons could be made.

The two most common sesarmids in the study area were *Neosarmatium* spp. and *P. erythodactyla*. The former was almost always represented by *N. trispinosum*. The burrows of both species within the study area could be confidently identified and thus counted. Based on previous studies (Breitfuss, 2003; Emmerson, 2001; Piou *et al.*, 2009; Prosser, 2004; Salgado-Kent & McGuinness 2006) the potential bias in estimating sesarmid abundance by burrow counts can be reduced and estimates of crab size made, by measuring burrow apertures. Further, the comparisons between storm-water input sites and controls can be effectively and appropriately undertaken using the measures of relative abundance that burrow counts provide. Therefore, this method was used as it was considered more reliable within the study area than direct visual census or pitfall trapping and because the need for repeatability of measurements precluded excavation of the substratum.

3 Long-term comparisons among mangroves receiving storm-water input and control sites

3.1 Introduction

This chapter provides quantitative comparisons of sesarmid burrow abundance within mangrove communities that received storm-water input and those that did not (controls), at three localities, over a three-year period. Chapter 2 outlined the difficulties in estimating absolute sesarmid abundance and discussed the efficacy of using burrow counts to compare relative abundance. Differences in burrow morphology (also discussed in Chapter 2) allowed the abundance of *Neosarmatium* spp. and *Parasesarma erythrodactyla* burrows to be quantified and comparisons were initially made between paired sites at three localities. The times of sampling and increased spatial coverage of sampling represented an iterative approach to development of the sampling design. The initial sampling allowed examination of the spatial and temporal variability amongst three paired sites within the study area (Figure 3.1). This gave a total of three controls and three impact sites within the study area amongst which comparisons were made. Preliminary analysis showed that even amongst storm-water input sites, there appeared to be markedly different numbers of crab burrows. Additional storm-water input and control sites were added over the study period to assist in a better understanding of the possible magnitude of impact on sesarmids as a result of differences among storm-water sites. Key soil chemical characteristics were measured and were examined in relation to burrow abundance and presence/absence of storm-water input.

The primary prediction tested was that sesarmid burrow abundance would be lower at storm-water input sites than at control sites. The relationships between storm-water input, soil characteristics and burrow abundance were also examined.

3.2 Methods

3.2.0 Site Selection

The study initially used a matched pairs design at three locations; Slade Point, Bucasia and Eimeo (Figure 3.1). At each location two sites were sampled from December 2004 to December 2007; a storm-water input site and a control site (Table 3.1). At each location, an additional storm-water input site was identified and sampled from May 2006 to December 2007. All sites were sampled at approximately quarterly intervals and at monthly intervals during the late dry season in 2005 and 2006. The monthly samples were taken to investigate whether burrow abundance changed as storm-water input decreased during the dry season. In May and December 2007, an additional control site was also sampled at each location as part of a wider regional comparison (see Chapter 4). All control sites were selected on the basis that they occupied a similar position along the tidal gradient, and had as similar floristics and vegetation structure as possible to storm-water input sites. Selection of control sites was assisted by use of existing mangrove vegetation mapping (Winter and Wild, 1995) and aerial photographs. Once chosen, the positions of control sites were marked on aerial photographs and then located in the field by use of recognisable landmarks. This procedure was used to avoid bias in selection of control sites (e.g. through unintentionally selecting those that appeared to have large numbers of burrows). Storm-water sites extended approximately 25m away from the storm-water input at the littoral

margin and control sites were the same size, with the centre point being the location of the site as identified on aerial photographs.

For Bucasia, examination of historical aerial photographs revealed that storm-water input sites had been receiving agricultural derived storm-water discharge for at least 30 years with likely increased volumes from residential areas beginning in 1998. BSW(a) received considerably more storm-water input as estimated by the number and size of discharge points (Figure 3.2) than BSW(b). BSW(b) did not receive storm-water input directly, but via a retention basin in which water accumulated before being released by several much smaller pipes along the littoral edge (Figure 3.3).

At Eimeo, storm-water input sites were free of point storm-water discharge until 1999 when adjacent residential development began. ESW(a) received input from a relatively much smaller discharge point (Figure 3.4) than ESW(b) (Figure 3.5).

At Slade Point, storm-water input sites were known to have received point storm-water discharge from well established earthen drainage lines for at least 40 years (Figures 3.6 and 3.7).

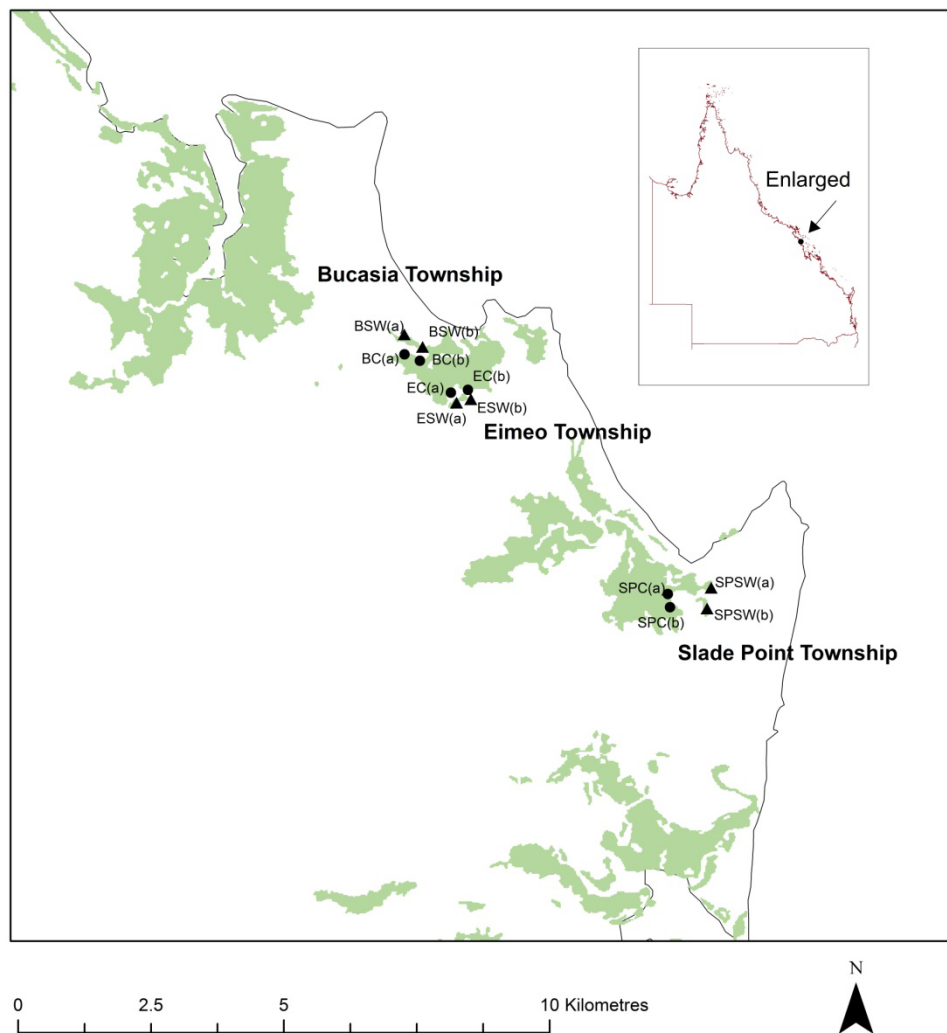


Figure 3.1 Study site locations. ▲ = Storm-water input sites, ● = Control sites. Green shading shows the extent of mangrove communities.



Figure 3.2 Storm-water input into BSW(a) via multiple, large discharge pipes.



Figure 3.3 Storm-water input into BSW(b) from a retention basin via a small pipe.



Figure 3.4 Storm-water input into ESW(a) from a small (400mm diameter) pipe.



Figure 3.5 Storm-water input into ESW(b) via a large (600mm diameter) pipe and then a short earthen drain.



Figure 3.6 Storm-water input into SPSW(a) via a well established earthen drain.



Figure 3.7 Storm-water input into SPSW(b) via a well established earthen drain.

3.2.1 Sesarmid Burrow Abundance

At each site, ten 1m² quadrats were randomly placed on the substratum by haphazardly casting the quadrat backwards to an area out of sight, thus avoiding bias through unintentionally selecting areas with the expected numbers of burrows. Within each quadrat, the number of burrows was recorded, and each burrow aperture was measured across its widest diameter and assigned to one of the two mutually exclusive morphological types; lateral (*Neosarmatium* spp., Figure 3.8) or simple (*Parasesarma erythroductyla*, Figure 3.9). Burrows were only recorded if they were mostly contained within the quadrat.



Figure 3.8 Lateral burrow (*Neosarmatium* spp.) morphology.



Figure 3.9 Simple burrow (*Parasesarma erythrodactyla*) morphology.

3.2.2 Substratum

At each of the three pairs of sites initially sampled, the height of the substratum relative to lowest astronomical tide (LAT) was identified at one point, by placing a 1.5m long chalk-covered stake, which protruded 1m vertically from the substratum, during a spring high tide of known height. The maximum height of the tide was clearly distinguishable as a wash line in the chalk. This reference point was then used to measure the height of 20 other randomly selected points within each site, using a builder's 'dumpy' level, thus enabling calculation of the mean height above LAT for each site.

Salinity, pH and redox potential of the soil core water were measured in five randomly located replicate pits dug into the ground at each site until the water table was reached. Salinity and pH measurements were taken in May 2005 (i.e. at the end of the wet season), and then during all months that soil core water was

accessible, commencing in May 2006. Where possible, monthly measurements were taken during periods of both neap and spring tides. Measurements of redox potential were made in May 2005 but were not continued as values typically varied as much within sites as among sites, and differed markedly even at scales of a few centimetres.

Table 3.1 Sampling times outlining the increasing number of comparisons made among sites within the three locations (X = sampled, * = although sampling was planned, burrow abundance could not be estimated during this period due to very heavy rainfall resulting from Cyclone Justin).

Sampling Time	Bucasia Control(a)	Bucasia Control(b)	Bucasia Storm-water(a)	Bucasia Storm-water(b)	Eimeo Control(a)	Eimeo Control(b)	Eimeo Storm-water(a)	Eimeo Storm-water (b)	Slade Point Control(a)	Slade Point Control(b)	Slade Point Storm-water(a)	Slade Point Storm-water(b)
Dec 04	X	-	X	-	X	-	X	-	X	-	X	-
Feb 05	X	-	X	-	X	-	X	-	X	-	X	-
May 05	X	-	X	-	X	-	X	-	X	-	X	-
Sept 05	X	-	X	-	X	-	X	-	X	-	X	-
Oct 05	X	-	X	-	X	-	X	-	X	-	X	-

The effect of urban storm-water runoff on Sesarmid crabs

Sampling Time	Bucasia Control(a)	Bucasia Control(b)	Bucasia Storm-water(a)	Bucasia Storm-water(b)	Eimeo Control(a)	Eimeo Control(b)	Eimeo Storm-water(a)	Eimeo Storm-water (b)	Slade Point Control(a)	Slade Point Control(b)	Slade Point Storm-water(a)	Slade Point Storm-water(b)
Nov 05	X	-	X	-	X	-	X	-	X	-	X	-
Feb 06	*	-	*	-	*	-	*	-	*	-	*	-
May 06	X	-	X	X	X	-	X	X	X	-	X	X
Aug 06	X	-	X	X	X	-	X	X	X	-	X	X
Sept 06	X	-	X	X	X	-	X	X	X	-	X	X
Oct 06	X	-	X	X	X	-	X	X	X	-	X	X
Nov 06	X	-	X	X	X	-	X	X	X	-	X	X
Feb 07	X	-	X	X	X	-	X	X	X	-	X	X
May 07	X	X	X	X	X	X	X	X	X	X	X	X
Sept 07	X	-	X	X	X	-	X	X	X	-	X	X
Dec 07	X	X	X	X	X	X	X	X	X	X	X	X

3.3 Results

3.3.0 *Neosarmatium* spp. burrow abundance

Although the magnitude of the difference varied, burrow numbers were lower at storm-water input sites than at control sites at all three locations at all 15 sampling times with the single exception of December 2004 at Eimeo. Figures 3.10, 3.11 and 3.12 show the mean number of *Neosarmatium* spp. burrows at Bucasia, Eimeo and Slade Point respectively during the period from December 2004 to December 2007. There were also marked differences among locations. At Slade Point storm-water input sites, *Neosarmatium* spp. burrows were very rare and often absent, whilst control sites usually had between four and 10 burrows/m². At Bucasia the storm-water sites had up to three burrows/m² and control sites had similar numbers to the Slade Point controls. BSW(b) had more than two burrows/m² on seven of nine occasions and more burrows than at BSW(a) on eight out of nine occasions. At Eimeo there was less difference between storm-water input and control sites but burrow abundances at storm-water input sites, with the single noted exception, were always less than at control sites. ESW(a) always had more burrows than ESW(b).

During 2006, *Neosarmatium* spp. burrow numbers at control sites did not show any strong seasonal pattern with numbers remaining similar from the late wet season through to the late dry season.

There were large differences in sample variances both among sites and among times, nor were the data normally distributed. Transformation did not remedy this

to enable parametric statistical comparisons between burrow abundance at storm-water input and control sites, or among times of sampling. Therefore, for each of the three locations, the data were expressed as the number of occasions on which each treatment (the mutually exclusive categories of storm-water and control) had the higher number of burrows. Under the null hypothesis of no difference between treatments, there would be equal numbers in each of the two categories (Table 3.2). Chi Square tests were applied to the data for each location (noting that $df = 1$ and thus Yates' correction was used). In each location there was a highly significant difference between storm-water input sites and controls (Table 3.2).

Table 3.2 The number of cases when a particular site (storm-water or control) had the higher number of *Neosarmatium* spp. burrows for the three locations

		Location			Total
		Bucasia	Eimeo	Slade Point	
Highest number of burrows	Control	15	14	15	44
	Storm-water	0	1	0	1
Total		15	15	15	45
$\chi^2 (df = 1)$		13.067	11.267	13.067	
P		<0.001	<0.001	<0.001	

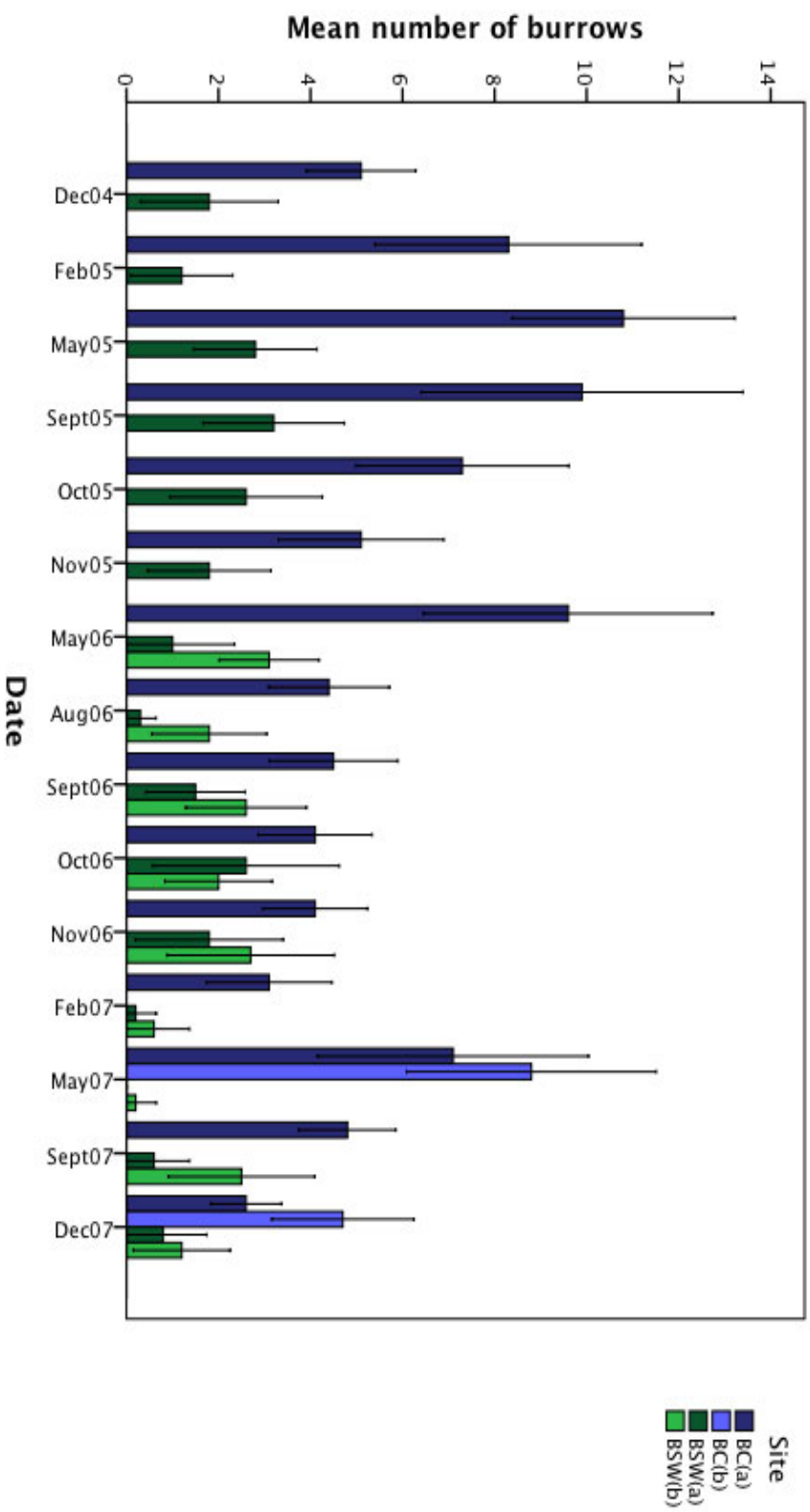


Figure 3.10 Mean number of *Neosartium* spp. burrows/m² at Bucasia from December 2004 to December 2007 (bars show the 95% confidence intervals).

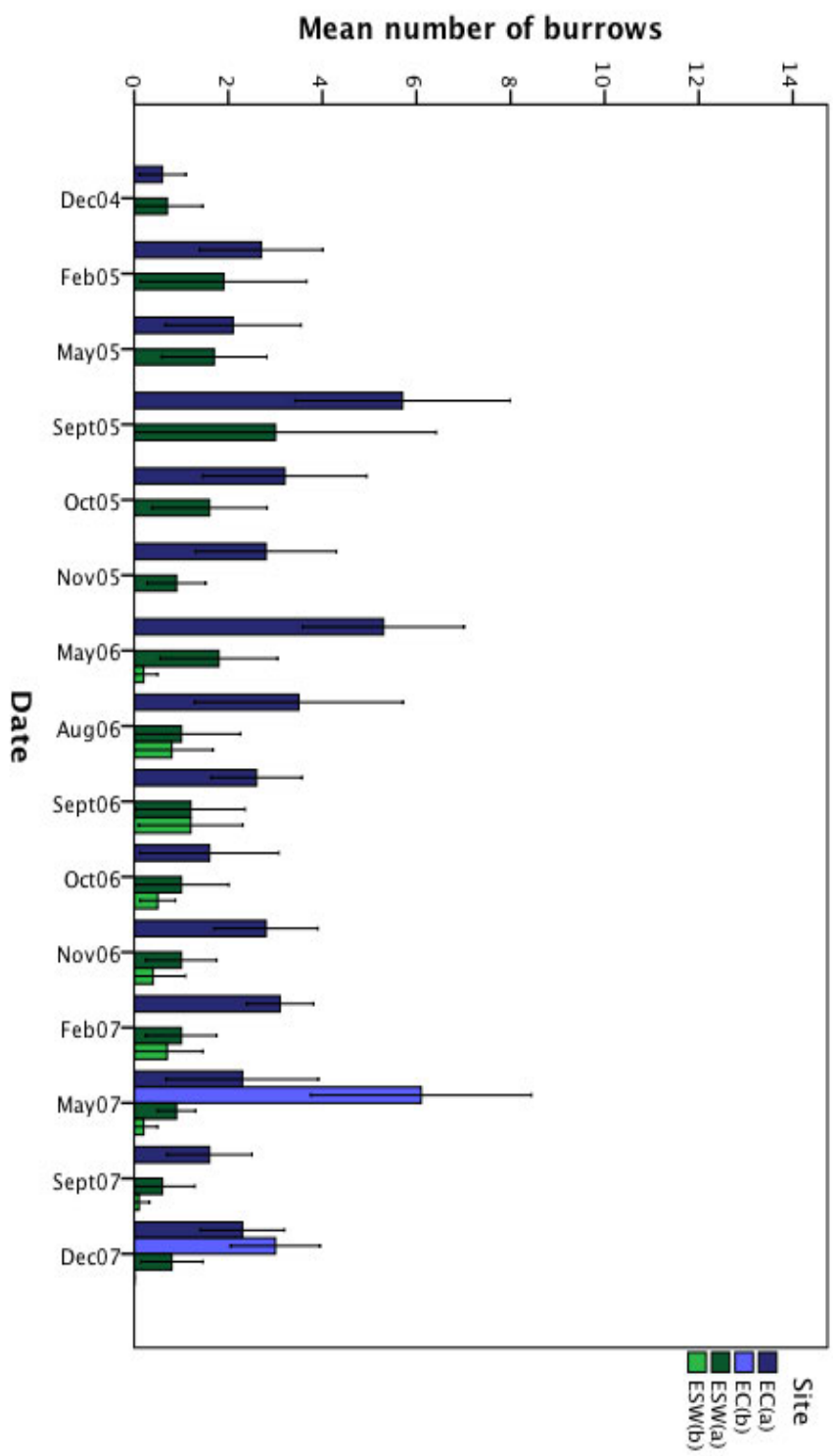


Figure 3.11 Mean number of *Neosarum* spp. burrows/m² at Eimeo from December 2004 to December 2007 (bars show the 95% confidence intervals).

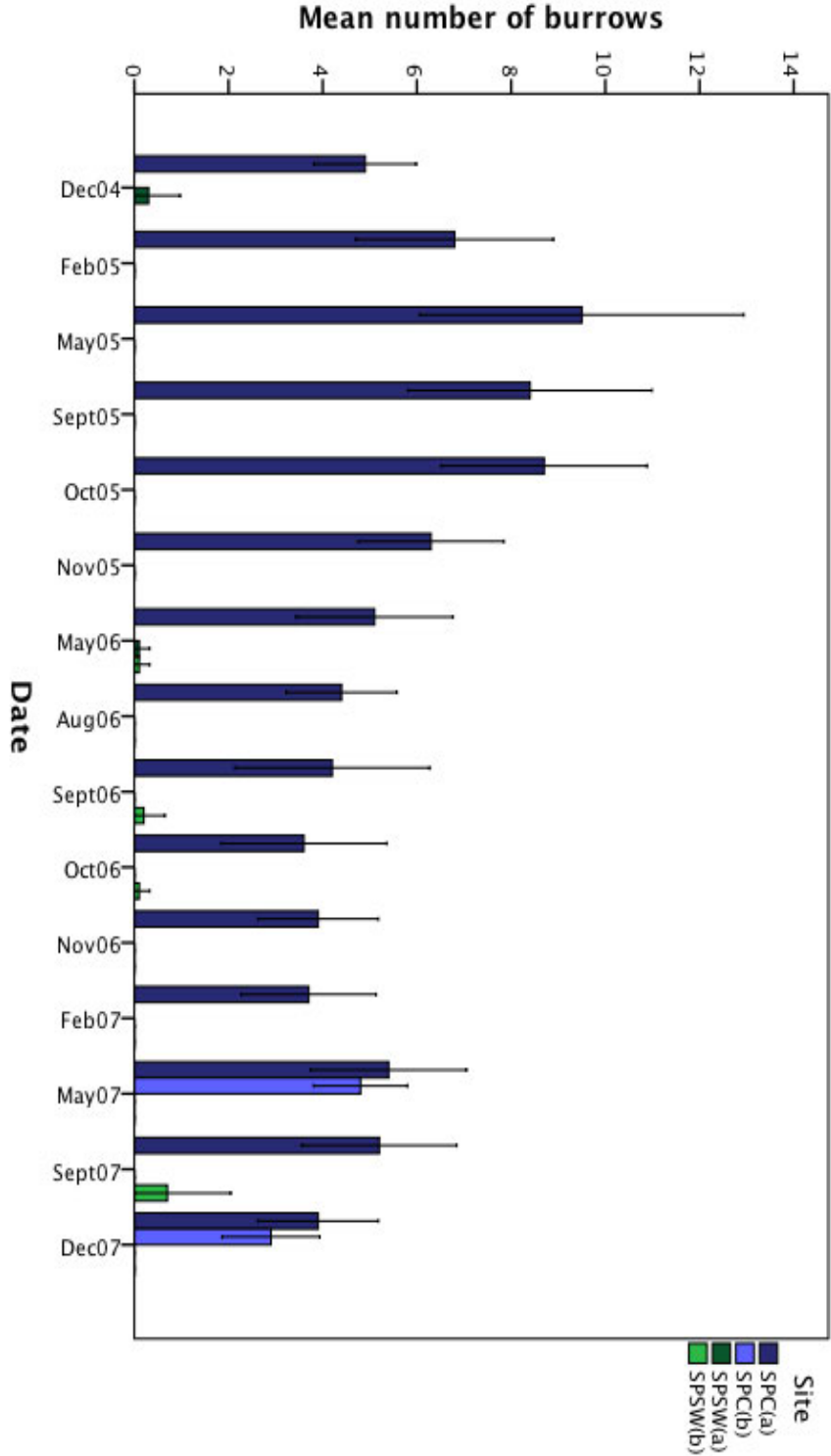


Figure 3.12 Mean number of *Neosarum* spp. burrows/m² at Slade Point from December 2004 to December 2007 (bars show the 95% confidence intervals).

3.3.1 *Parasesarma erythrodictyla* burrow abundance

Burrow numbers were lower at storm-water input sites than at control sites at all three locations at all 15 times. Figures 3.13, 3.14 and 3.15 show the mean number of *Parasesarma erythrodictyla* (simple) burrows at Bucasia, Eimeo and Slade Point respectively over the period December 2004 to December 2007. There were very few burrows at Slade Point storm-water input sites and considerable variation among the controls. Whilst there were few burrows at storm-water input sites at Eimeo, they were usually found in relatively high numbers at control sites. On seven of nine occasions there were more burrows at ESW(a) than at ESW(b). Fewer burrows were found at Bucasia compared to the other locations, but numbers at control sites were still higher than at storm-water input sites. On seven of nine occasions there were more burrows at BSW(b) than at BSW(a).

Seasonal trends in burrow abundance were inconsistent and varied among sites. Here too, there were large differences in sample variances both among sites and among times, nor were the data normally distributed, and again transformation did not adequately remedy this. Therefore, as for *Neosarmatium* spp. burrows, for each of the three locations, the data were expressed as the number of occasions on which each treatment (the mutually exclusive categories of storm-water input and control) had the higher number of burrows. Under the null hypothesis of no difference between treatments, there would be equal numbers in each of the two categories (Table 3.3) and Chi Square tests applied. In each case there was a significant difference between storm-water input sites and controls (Table 3.3).

Table 3.3 **The number of cases when a particular site (storm-water or control) had the higher number of *Parasesearma erythrodactyla* burrows for the three locations**

		Location			Total
		Bucasia	Eimeo	Slade Point	
Highest number of burrows	Control	15	15	15	45
	Storm-water	0	0	0	0
Total		15	15	15	45
χ^2 ($df = 1$)		13.067	13.067	13.067	
P		<0.001	<0.001	<0.001	

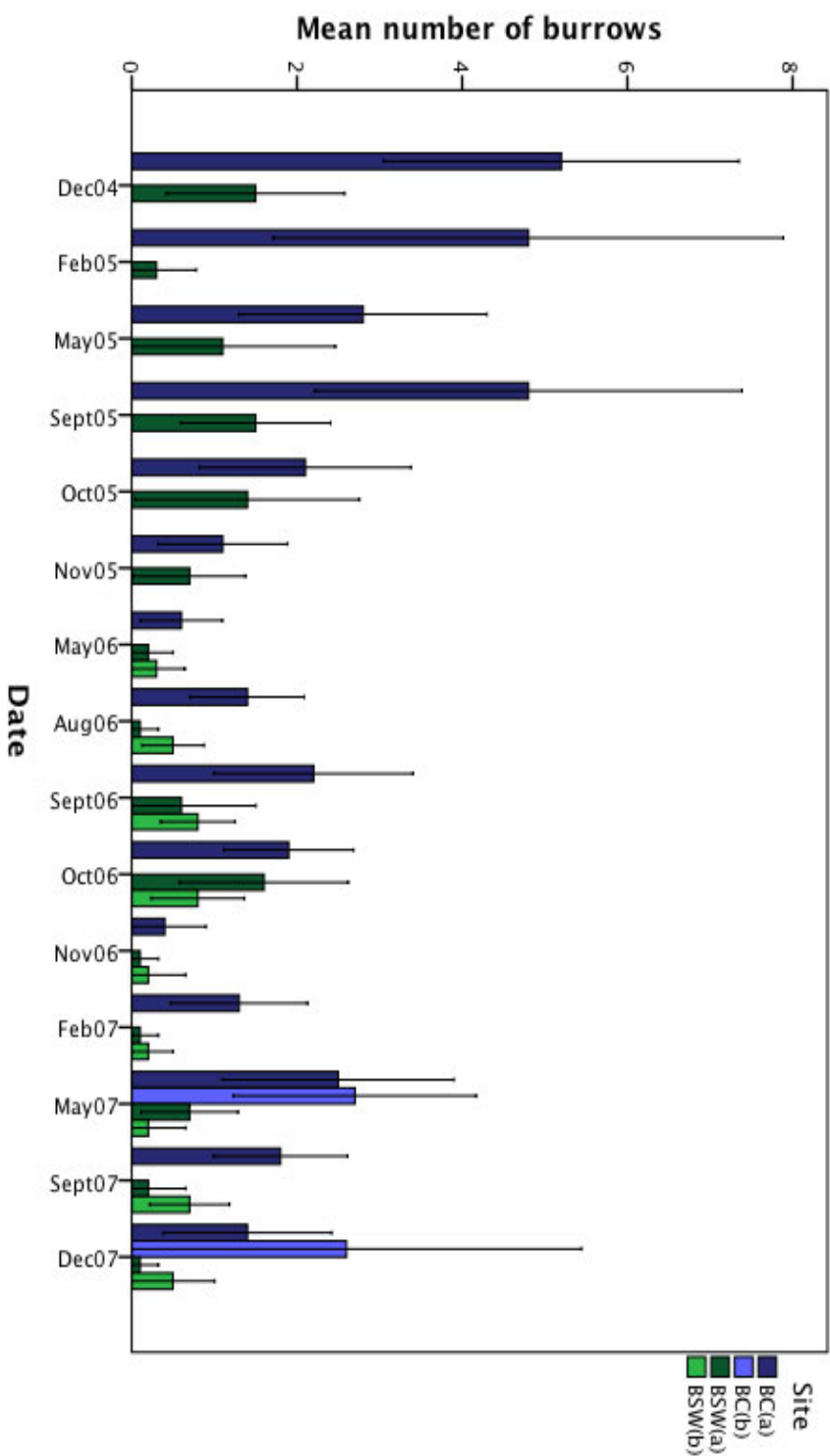


Figure 3.13 Mean number of *Parusesarma erythrodayla* (simple) burrows/m² at Bucasia from December 2004 to December 2007 (bars show the 95% confidence intervals).

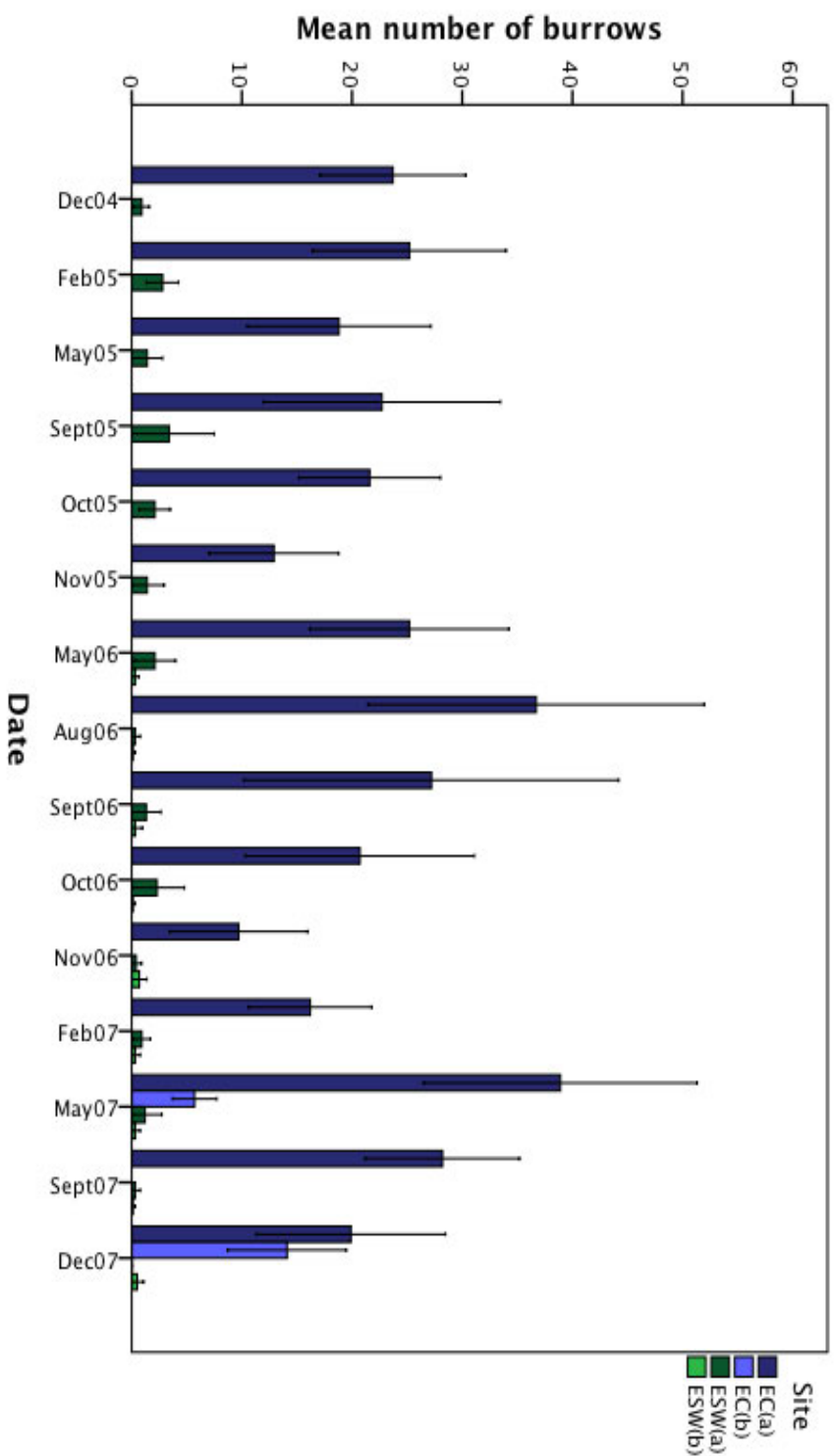


Figure 3.14 Mean number of *Parasesarma erythrodayla* (simple) burrows/m² at Eimeo from December 2004 to December 2007 (bars show the 95% confidence intervals).

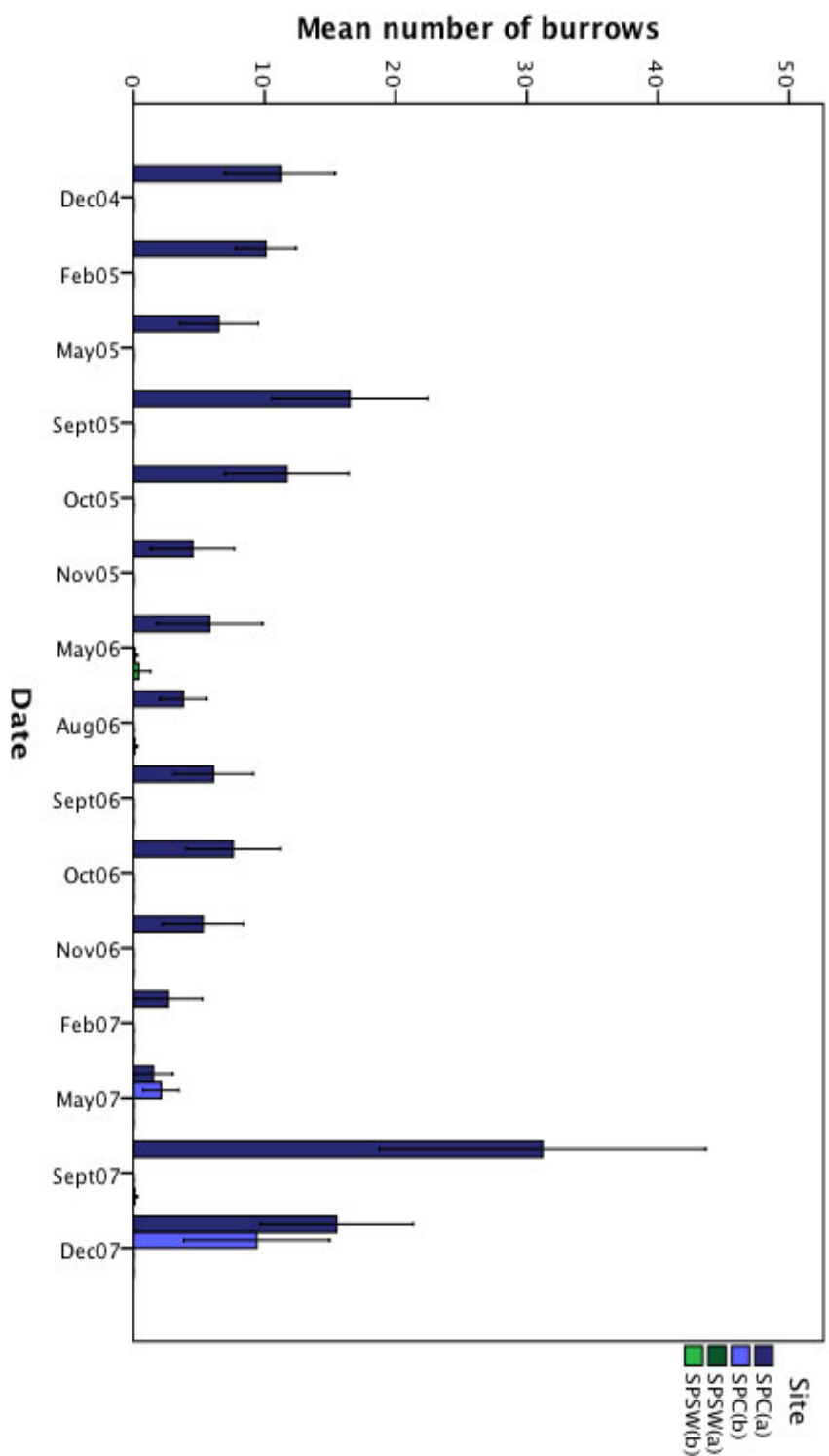


Figure 3.15 Mean number of *Parusesarma erythrodayla* (simple) burrows/m² at Slade Point from December 2004 to December 2007 (bars show the 95% confidence intervals).

3.3.2 Substratum

The mean height of the substratum above tidal datum was very similar amongst sites (Figure 3.16) only differing by a maximum of 0.15m (compared to the full intertidal range within the locations of 6.41m). The lowest site was EC(a) (mean = 5.843m $\pm$ 0.017m; 95% CI) and the highest was ESW(a) (mean = 5.99m $\pm$ 0.016m; 95% CI). Sites added to the experimental design at later dates were located in exactly the same intertidal area and examination of ortho-photos of the study sites confirmed there were no substantial differences in their heights.

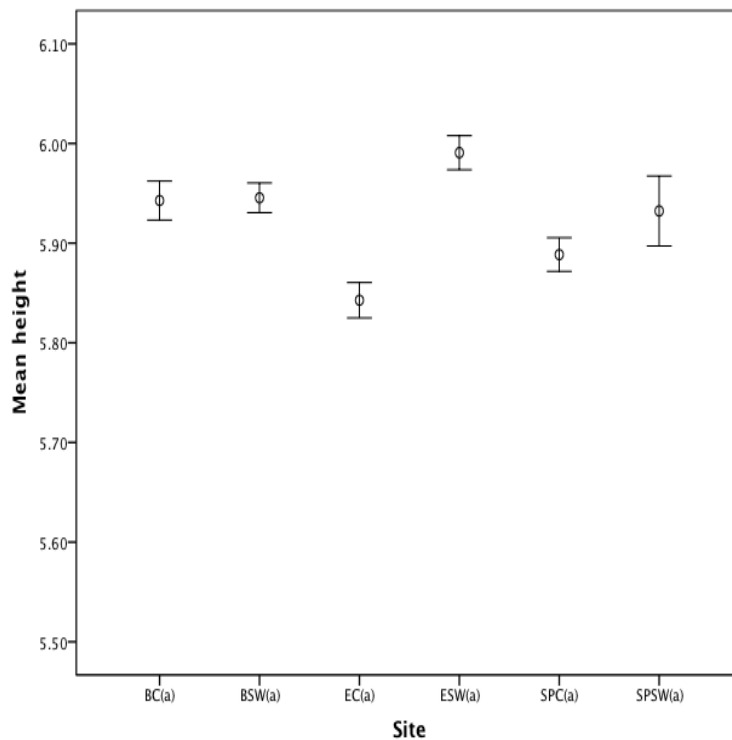


Figure 3.16 Comparisons of the mean height in metres above datum of the matched pair sites at three locations (Bucasia, Eimeo and Slade Point). Bars are the 95% confidence intervals.

3.3.3 Soil Core Water Salinity

With a single exception (Bucasia, January 2007), soil core water salinity was always lower at storm-water input sites compared to respective control sites. During drier conditions the ground water table was sometimes not accessible so measurements were not taken in some months. Figures 3.17 to 3.19 show core water salinity over time at Bucasia, Eimeo and Slade Point sites respectively. Declines in salinity during the wet season were obvious at storm-water input sites and substantially greater in magnitude than at control sites. The lowest salinity was recorded at SPSW(a) followed in turn by ESW(b) and BSW(a), SPSW(b), BSW(b), ESW(a). Mean salinity at storm-water input sites, across the study period was lowest at ESW(b) followed by BSW(a), SPSW(a), BSW(b), SPSW(b) and ESW(a). Mean salinity at BSW(b) was higher than at BSW(a) on 11 of 12 occasions, and higher at ESW(a) than ESW(b) on nine of 11 occasions.

Control sites also had relatively lower soil core water salinity during periods of higher rainfall (the wet season), in some cases dropping to approximately the salinity of undiluted seawater for the broader study area (app 35‰). Salinity increased during the dry season. Core water salinity maxima at Eimeo and Slade Point were approximately the same and slightly higher than at Bucasia. Mean salinity at control sites, across the study period was lowest at BC(a) followed by EC(b), SPC(b), SPC(a), BC(b) and EC(a).

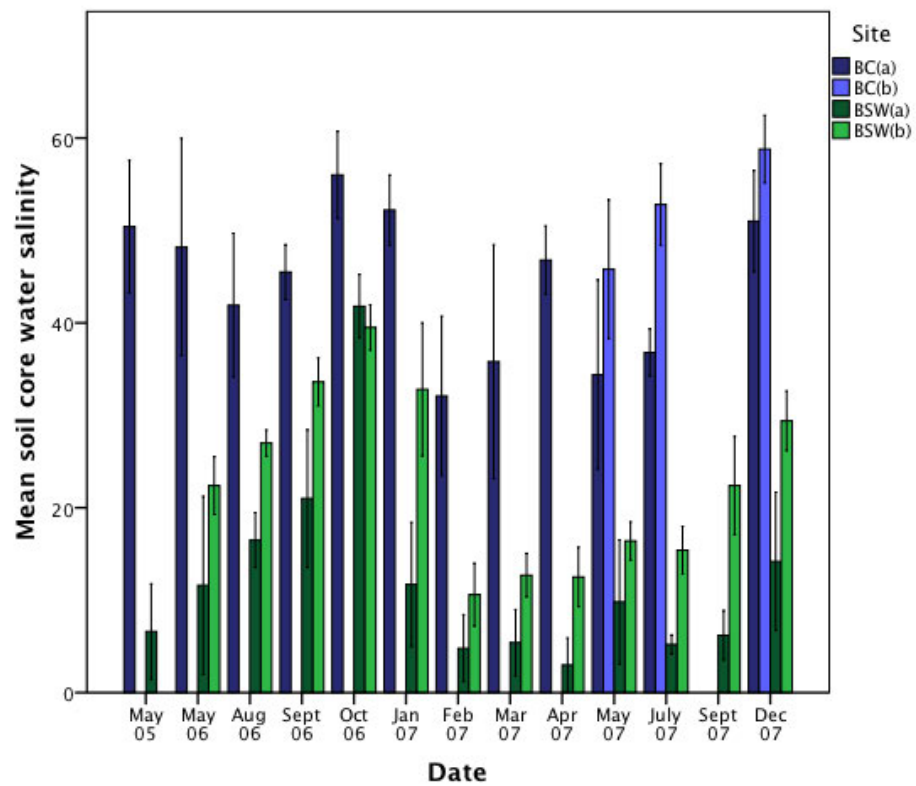


Figure 3.17 Bucasia. Mean soil core water salinity over time (bars are the 95% confidence intervals).

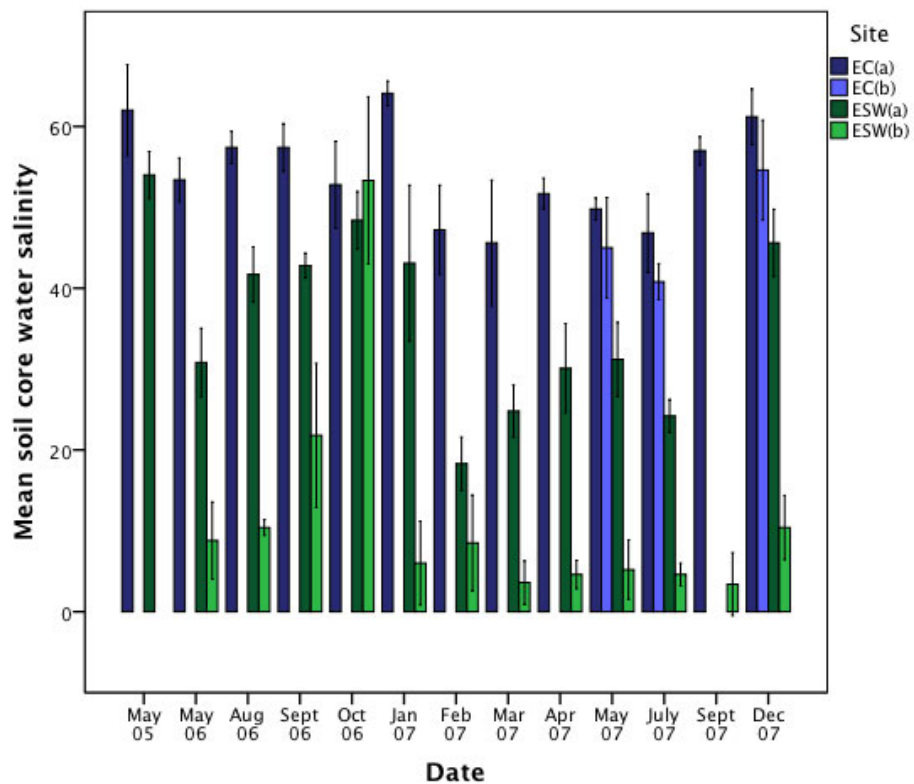


Figure 3.18 Eimeo. Mean soil core water salinity over time (bars are the 95% confidence intervals).

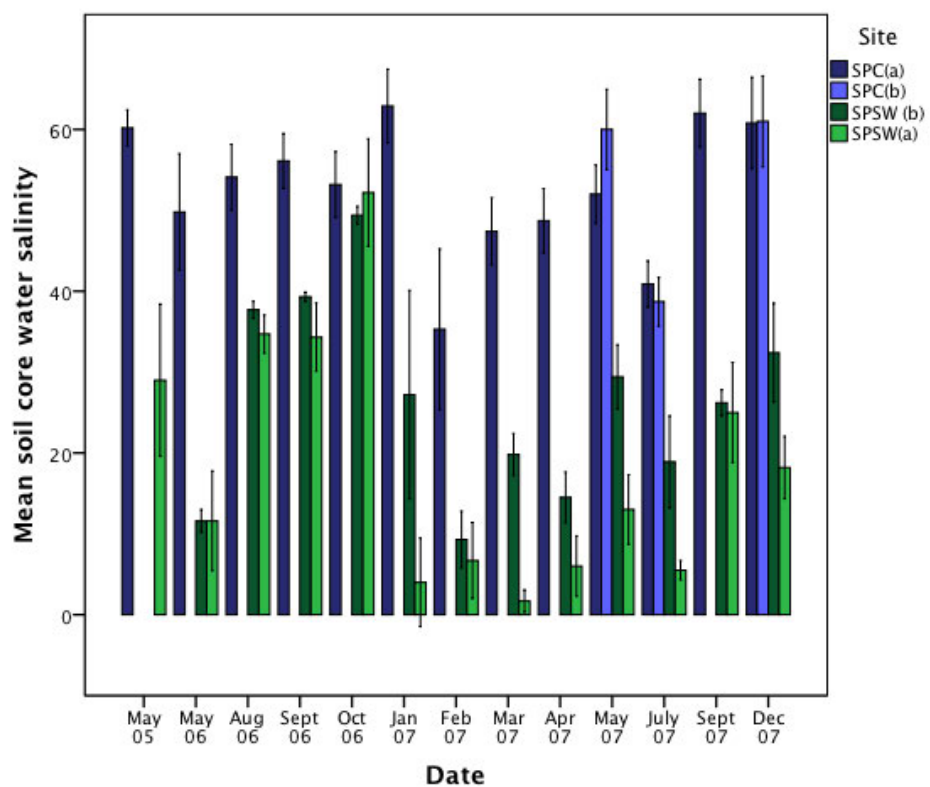


Figure 3.19 Slade Point. Mean soil core water salinity over time (bars are the 95% confidence intervals).

3.3.4 The relationship between soil core water salinity and sesarmid burrow abundance

3.3.4.1 Statistical Analysis

Neosarmatium trispinosum was the only species of this genus found at all sites except at BSW(a) where only *N. fourmanoiri* was present. Thus, data for these species are treated separately. For *N. trispinosum* the samples consisted of burrow counts from five storm-water input sites and three control sites taken on nine different occasions. On one occasion (September 2007) salinity measurements were unable to be taken at ESW(a) or BC(a), thus the total number of comparisons between salinity and burrow numbers was 32 for controls and 41 for storm-water input sites. For *N. fourmanoiri* the total number of comparisons was nine, all of which were from a storm-water input site. For *Parasesarma erythrodactyla* there were 32 comparisons from control sites and 50 from storm-water input sites.

Comparisons were made between mean salinity and burrow numbers and minimum salinity and burrow numbers, for each species. Tests for correlation were not performed using data from both storm-water input and control sites, because they are two distinct groups and there are problems with independence because repeated measurements were taken at each site over time. Instead, and still bearing in mind the likely lack of independence, two-tailed Spearman's rank correlations (as the data did not fit bivariate normal distribution) were performed on storm-water input and control sites separately for illustrative purposes.

To examine the possibility of a salinity threshold effect, a Chi Square test was used to determine if there were significant differences in the number of cases in which there were no burrows, and some burrows, in the two categories of core soil water salinity of (a) less than 35‰ and (b) equal or greater to 35‰. The value of 35‰ was used because that is the salinity of undiluted seawater within the study area, and at this level there appeared to be an increase in burrow numbers for each taxa.

3.3.4.2 The relationship between *N. trispinosum* burrow numbers and mean salinity

The relationship between the mean number of *N. trispinosum* burrows, and the mean soil core water salinity at all times when both were measured, is shown in Figure 3.20. There are two distinct groupings present; storm-water input sites with relatively few burrows and low to high soil core water salinities, and control sites with larger numbers of burrows and intermediate to high soil core water salinity. When the data are viewed as a whole, there appears to be an exponential increase in burrow numbers commencing at a threshold mean salinity of about 35‰ but, it is important to note that some burrows were present at sites with very low mean core water salinity. There was no significant correlation between mean salinity and burrow numbers for control sites (Spearman's $r = -0.220$, $P = 0.226$, $n = 32$) or for storm-water input sites (Spearman's $r = 0.210$, $P = 0.187$, $n = 41$).

A Chi Square test used to examine the possibility of a salinity threshold effect at 35‰ found a significant difference between the observed and expected frequencies of cases in which there were no, and some burrows, in the categories of (a) less than 35‰ and (b) equal or greater to 35‰ ($\chi^2 = 9.217$, $df = 1$, $P = 0.006$) (Table 3.4).

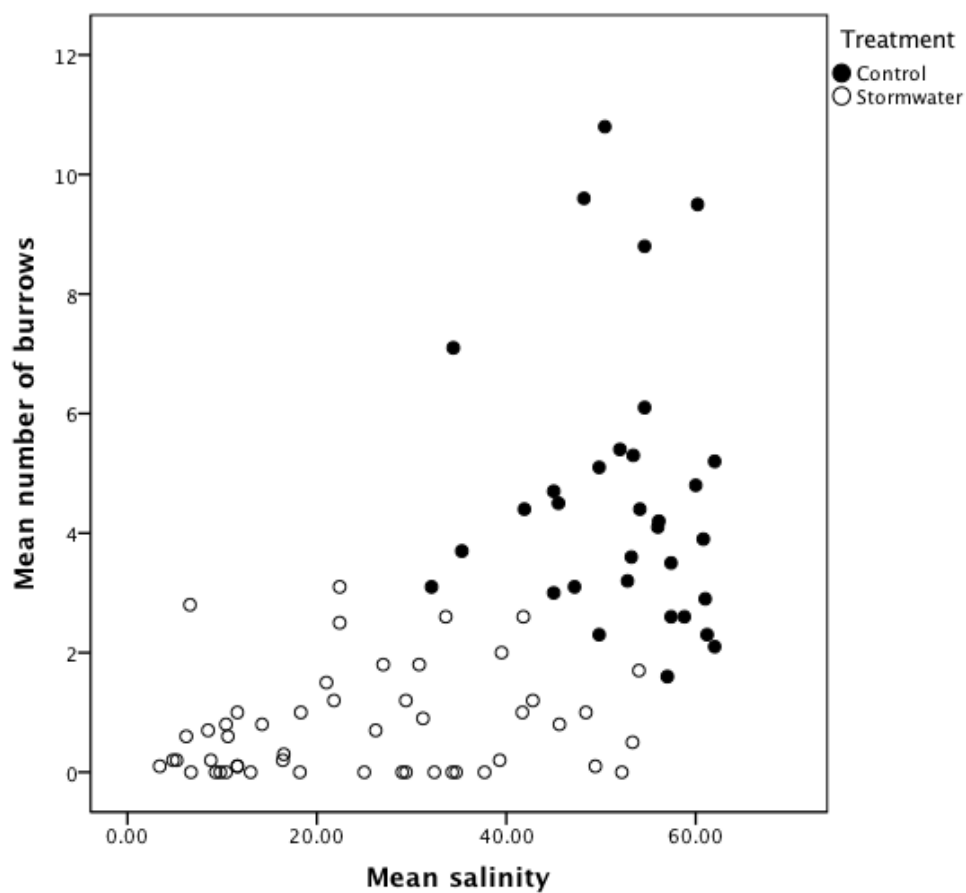


Figure 3.20 Mean *Neosarmatium trispinosum* burrows/m² vs. mean soil core water salinity.

Table 3.4 **The number of cases of zero *N. trispinosum* burrow numbers and greater than zero mean burrow numbers when mean soil core water salinity was < 35‰ and ≥ 35‰.**

		Burrows		Total
		0	>0	
Salinity	< 35‰	12	28	40
	≥ 35‰	2	40	42
Total		14	68	82

3.3.4.3 *The relationship between N. fourmanoiri burrow numbers and mean salinity*

The relationship between the mean number of *N. fourmanoiri* burrows, and the mean soil core water salinity at all times when both were measured, is shown in Figure 3.21. A two-tailed Spearman's rank correlation was not significant (Spearman's $r = 0.417$, $P = 0.265$, $n = 9$).

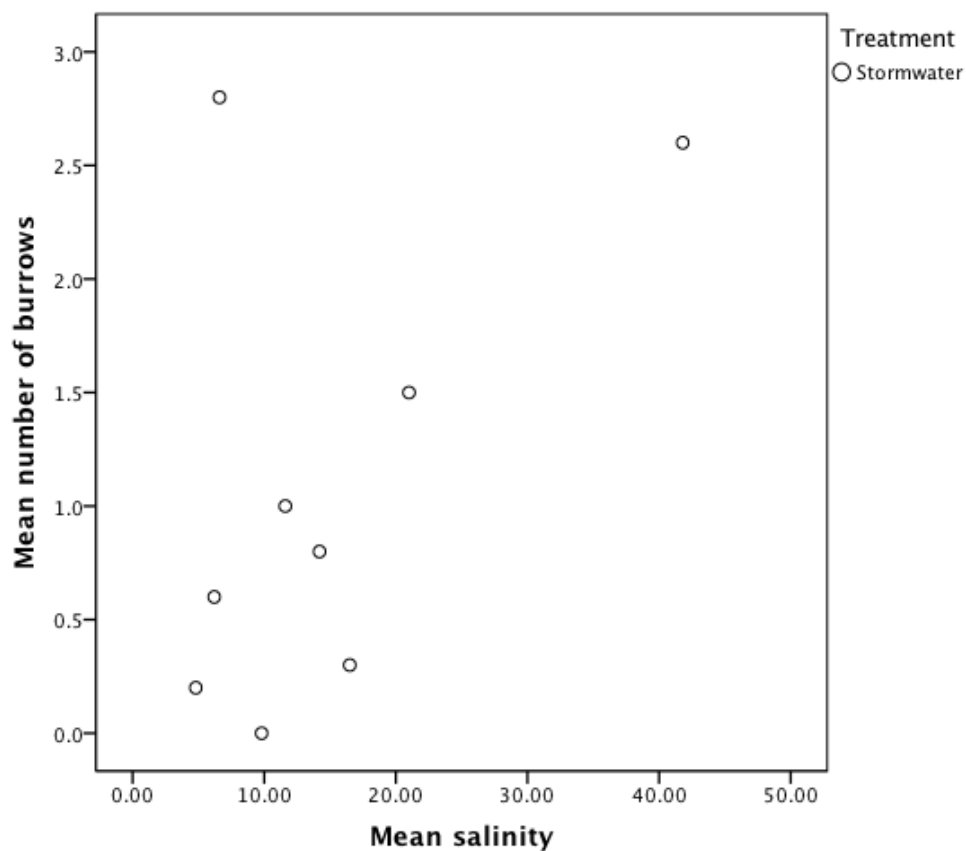


Figure 3.21 Mean *Neosarmatium fourmanoiri* burrows/m² vs. mean soil core water salinity.

3.3.4.4 The relationship between *P. erythrodactyla* burrow numbers and mean salinity

The relationship between the mean number of *P. erythrodactyla* burrows and the mean soil core water salinity at all times when both were measured, is shown in Figure 3.22. Here also, two distinct groupings are present. Storm-water input sites had relatively few burrows and low to high soil core water salinities, and control sites

had low to high numbers of burrows, and intermediate to high soil core water salinity.

As for *N. trispinosum*, when the data are viewed as a whole, there appears to be an exponential increase in burrow numbers commencing at a threshold mean salinity of about 35‰. However, there were some burrows present at sites with very low mean core water salinity. There was a significant positive correlation between burrow numbers and salinity for control sites (Spearman's $r = 0.470$, $P = 0.007$, $n = 32$) but not for storm-water input sites (Spearman's $r = 0.046$, $P = 0.749$, $n = 50$).

A Chi Square test found a significant difference between the observed and expected frequencies of cases in which there were no, and some burrows, in the categories of (a) less than 35‰ and (b) equal or greater to 35‰ ($\chi^2 = 9.024$, $df = 1$, $P = 0.007$) (Table 3.5).

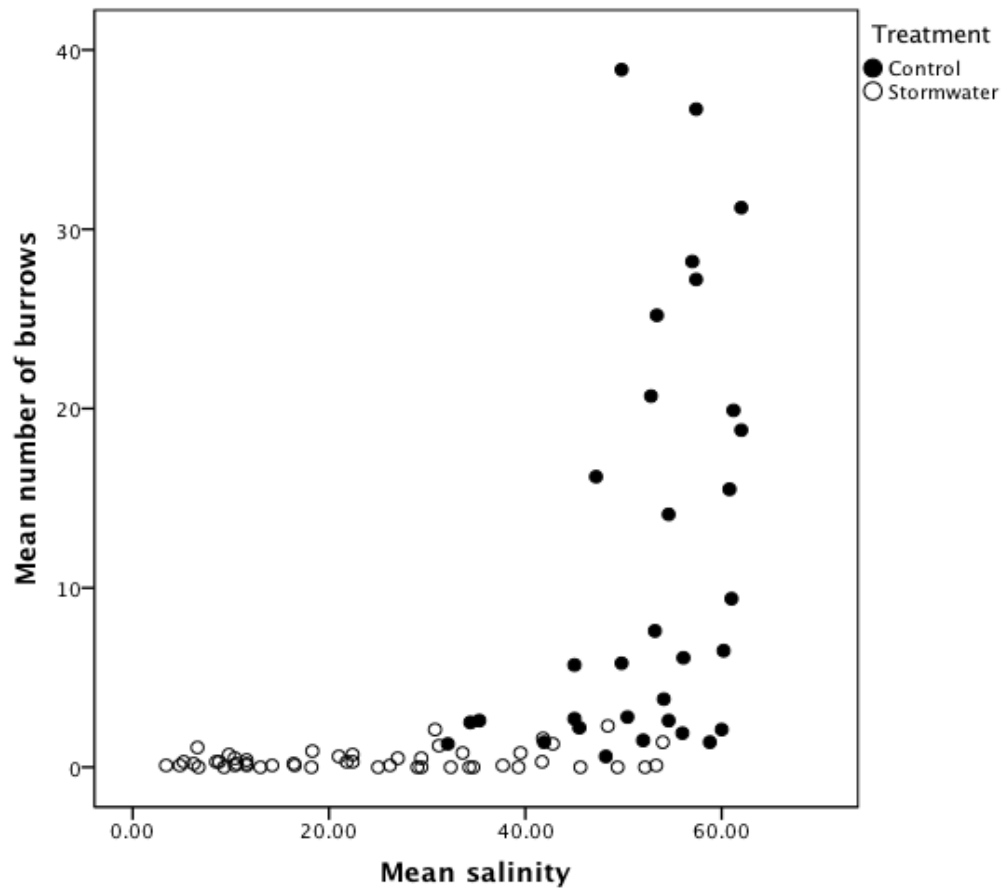


Figure 3.22 Mean *Parasesarma erythrodactyla* burrows /m² vs. mean soil core water salinity.

Table 3.5 The number of cases of zero *P. erythrodactyla* burrow numbers and greater than zero mean burrow numbers when mean soil core water salinity was < 35‰ and ≥ 35‰.

		Burrows		Total
		0	>0	
Salinity	< 35‰	10	30	40
	≥ 35‰	1	41	42
Total		11	71	82

3.3.4.5 *The relationship between N. trispinosum burrow numbers and minimum salinity*

The relationship between the mean number of *N. trispinosum* burrows and the minimum soil core water salinity at all times when both were measured, is shown in Figure 3.23. Once again, two distinct groupings are present; storm-water input sites with relatively few burrows and low to high soil core water salinities, and control sites with larger numbers of burrows, and intermediate to high soil core water salinity. There was a trend of higher burrow numbers as minimum salinity increased, but again it is important to note that some crabs were present at sites with very low minimum salinity. There was no significant correlation for control sites (Spearman's

$r = -0.145$, $P = 0.430$, $n = 32$) or for storm-water input sites (Spearman's $r = 0.192$, $P = 0.230$, $n = 41$).

A Chi Square test found a significant difference between the observed and expected frequencies of cases in which there were no, and some burrows, in the categories of (a) less than 35‰ and (b) equal or greater to 35‰ ($\chi^2 = 7.495$, $df = 1$, $P = 0.015$) (Table 3.6).

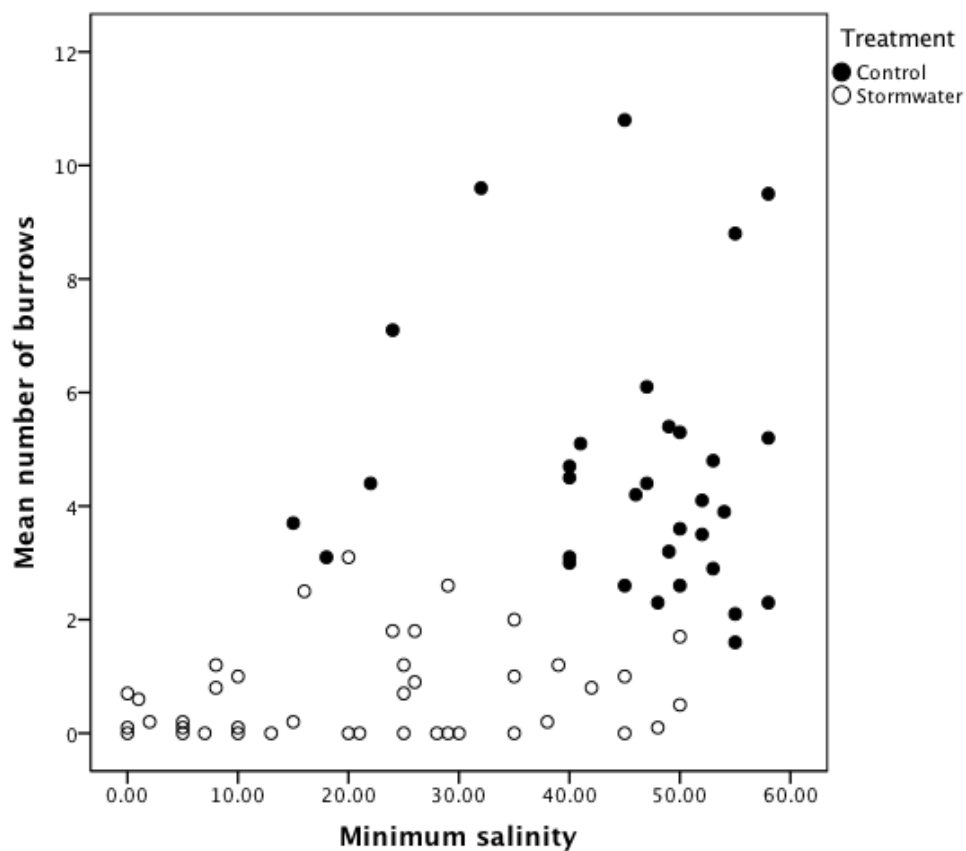


Figure 3.23 Mean *Neosarmatium trispinosum* burrows /m² vs. minimum soil core water salinity.

Table 3.6 **The number of cases of zero *N. trispinosum* burrow number and greater than zero mean burrow numbers when minimum soil core water salinity was < 35‰ and ≥ 35‰.**

		Burrows		Total
		0	>0	
Salinity	< 35‰	12	31	43
	≥ 35‰	2	37	39
Total		14	68	82

3.3.4.6 *The relationship between N. fourmanoiri burrow numbers and minimum salinity*

The relationship between the mean number of *N. fourmanoiri* burrows, and the minimum soil core water salinity at all times when both were measured, is shown in Figure 3.24. A two-tailed Spearman's rank correlation was not significant (Spearman's $r = 0.226$, $P = 0.559$, $n = 9$).

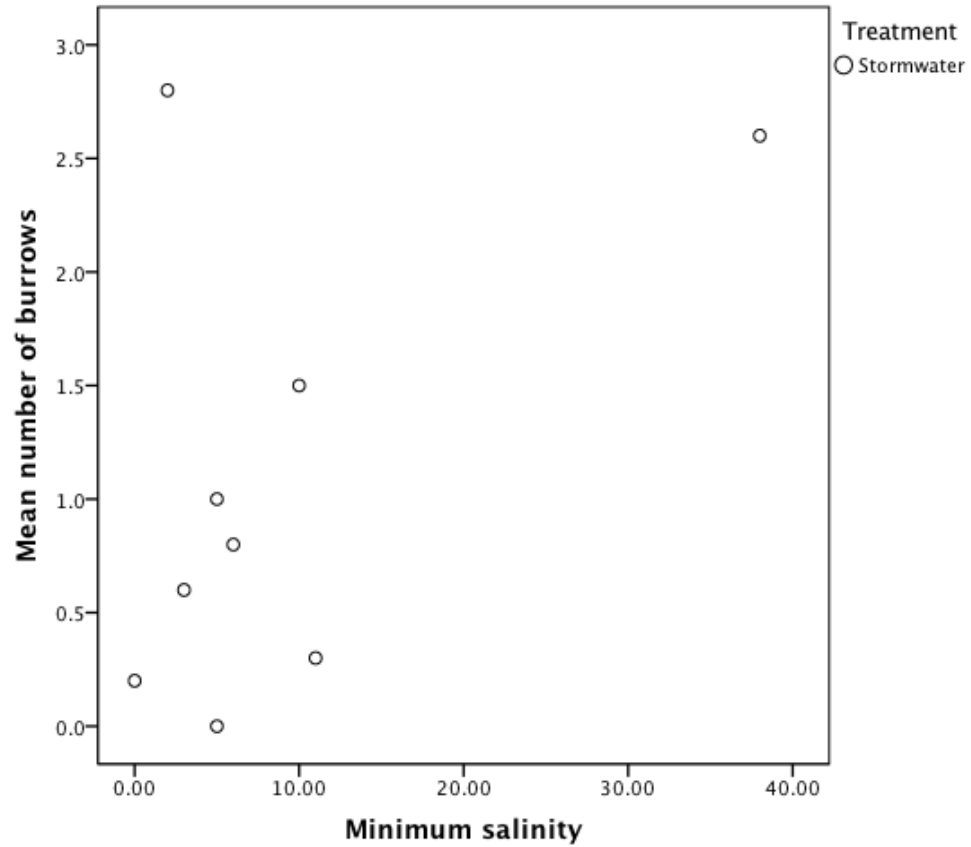


Figure 3.24 Mean *Neosarmatium fourmanoiri* burrows /m² vs. minimum soil core water salinity.

3.3.4.7 The relationship between *P. erythrodactyla* and minimum salinity

The relationship between the mean number of *P. erythrodactyla* burrows and the minimum soil core water salinity at all times when both were measured is shown in Figure 3.25. There are less distinct groupings, but when the data are viewed as a whole, there again appears to be an exponential increase in burrow numbers commencing at a threshold salinity of about 35‰. Storm-water input sites had relatively few burrows and low to high soil core water salinities. Control sites had few to large numbers of burrows, and intermediate to high soil core water salinity with a large increase in numbers corresponding to a minimum salinity of approximately 35‰. However, within the upper range of minimum salinity, there is still considerable variation in the number of burrows even when salinity is very similar. There was a significant positive correlation for control sites (Spearman's $r = 0.555$, $P = 0.001$, $n = 32$) but not for storm-water input sites (Spearman's $r = 0.037$, $P = 0.797$, $n = 50$).

A Chi Square test found a significant difference between the observed and expected frequencies of cases in which there were no, and some burrows, in the categories of (a) less than 35‰ and (b) equal or greater to 35‰ ($\chi^2 = 7.539$, $df = 1$, $P = 0.015$) (Table 3.7).

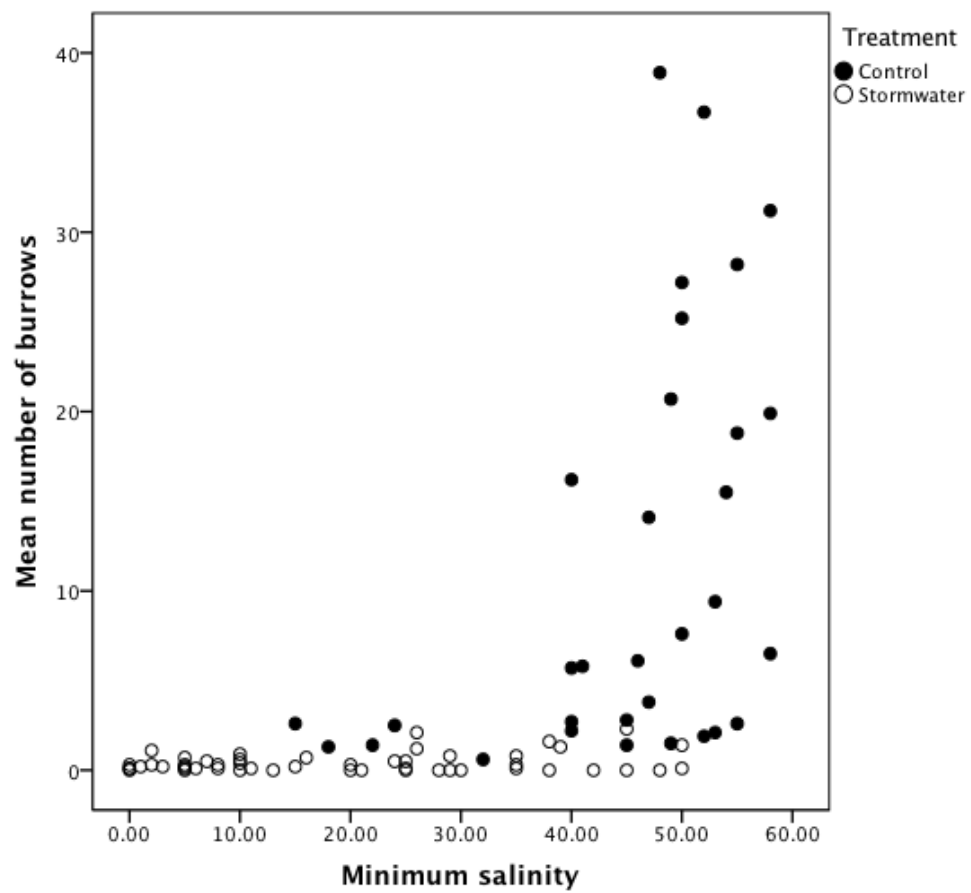


Figure 3.25 Mean *Parasesarma erythroductyla* burrows /m² vs. minimum soil core water salinity.

Table 3.7 The number of cases of zero *P. erythrodactyla* burrow numbers and greater than zero mean burrow numbers when minimum soil core water salinity was < 35‰ and ≥ 35‰.

		Burrows		Total
		0	>0	
Salinity	< 35‰	10	33	43
	≥ 35‰	1	38	39
Total		11	71	82

3.3.5 Soil core water pH

For December 2007 pH values were consistently higher at all sites compared to other sampling periods and are outside of the range generally expected for mangrove soils (Boto & Wellington, 1984). Although care was taken to appropriately calibrate and maintain the instrument used to measure pH, the December 2007 data are considered erroneous and are not considered in further discussion. For the remaining data, there does not appear to be any consistent trend for pH between storm-water input and control sites. Figures 3.26 to 3.28 show soil core water pH over time at Bucasia, Eimeo and Slade Point respectively. As expected most sites were acidic with pH generally from 5.5 to 6.5. These values are within the range found by Clarke (1985) for littoral mangrove communities. SPSW(a) was at times strongly acidic but this was not the case for other storm-water input sites: for example ESW(b) had broadly similar core water salinity to SPSW(a) but tended to have close to neutral pH.

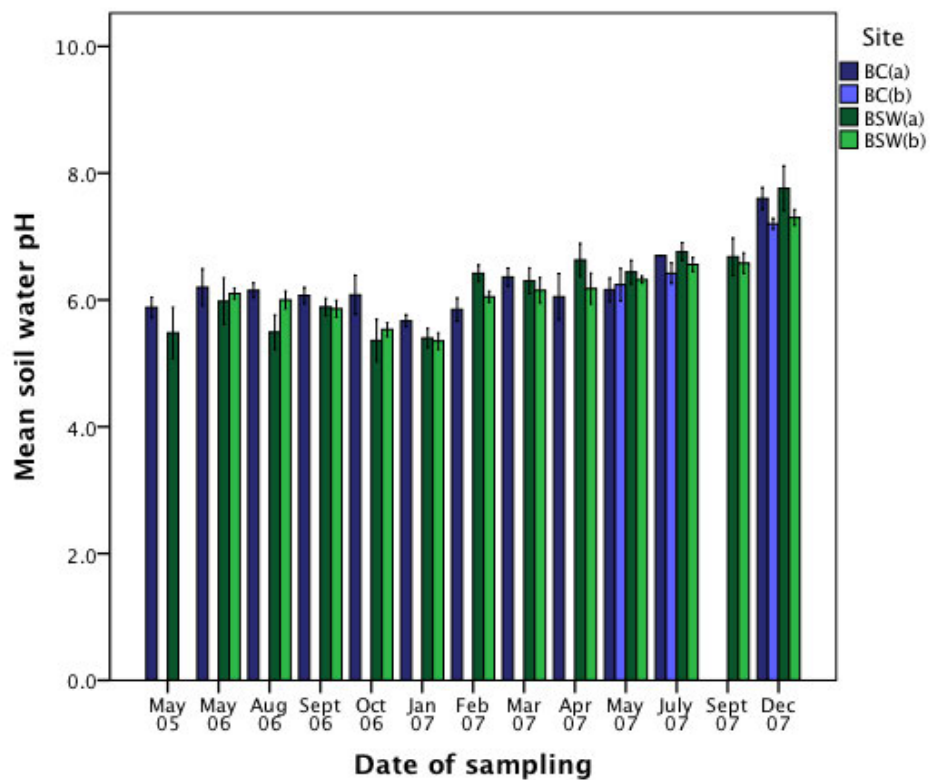


Figure 3.26 Soil core water pH over time at Bucasia (bars are the 95% confidence interval of the mean).

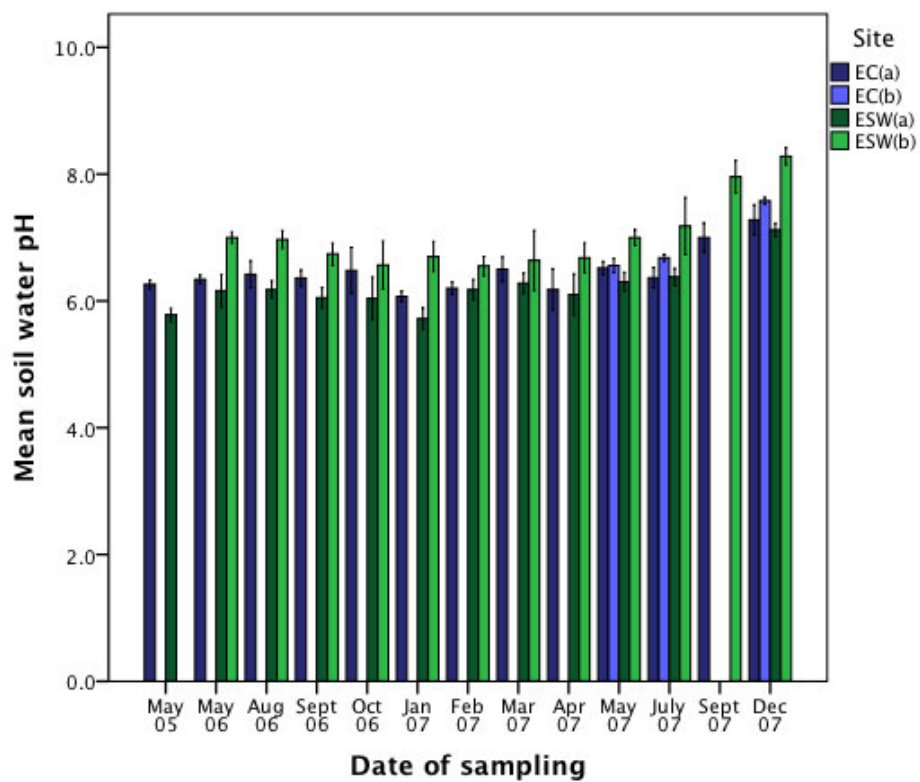


Figure 3.27 Soil core water pH over time at Eimeo (bars are the 95% confidence interval of the mean).

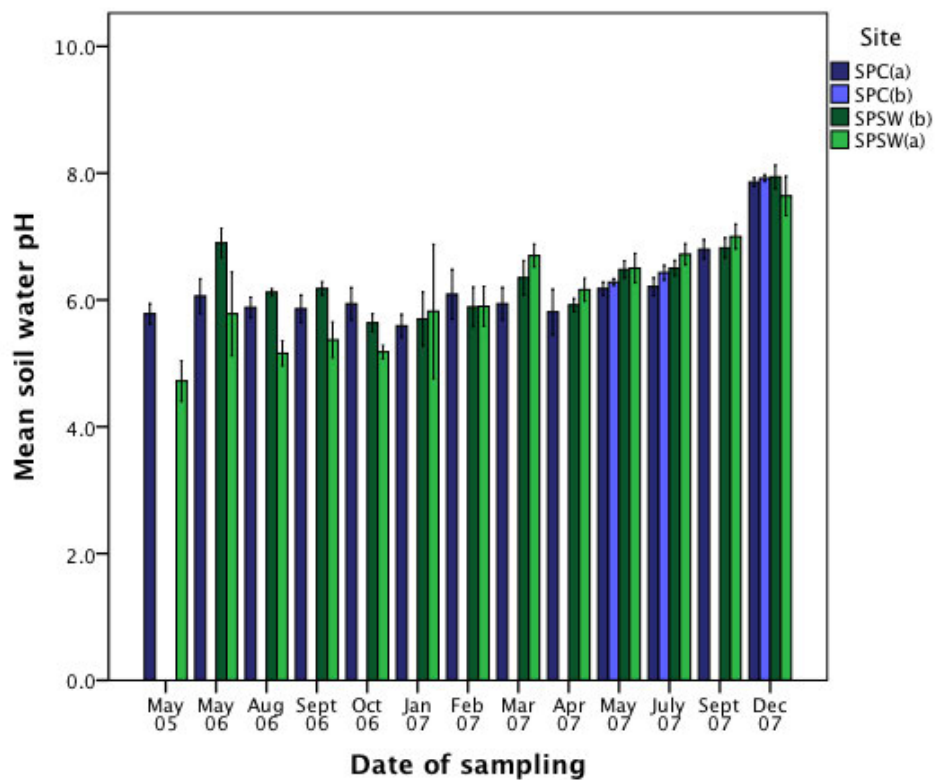


Figure 3.28 Soil core water pH over time at Slade Point (bars are the 95% confidence interval of the mean)

3.3.6 Recruitment

Figure 3.29 shows the number of *Neosarmatium* spp. burrows in the two size classes 0-9.9mm and 10-19.9mm at the control site BC(a) and the paired storm-water input site BSW(a) at all dates surveyed. Figure 3.30 illustrates this at the Eimeo paired sites [EC(a) and ESW(a)], and Figure 3.31 at the Slade Point paired sites [SPC(a) and SPSW(a)].

The most pronounced feature of these data was the complete lack of burrows with an aperture width of < 20mm at SPSW(a) despite the presence of recruits within the locality as demonstrated by the number of burrows in this size class at the respective control site. At Bucasia, there were no clear patterns in the abundance of burrows with an aperture of 10-19.9mm between the control and storm-water input site; at times they were only present at one site or the other, or in higher numbers at one site or the other. At Eimeo, burrows in the 0-9.9mm and 10-19.9mm size classes were generally more numerous at control sites than storm-water sites. There were no obvious patterns in the presence or abundance of burrows in the 0-19.9mm size range amongst seasons.

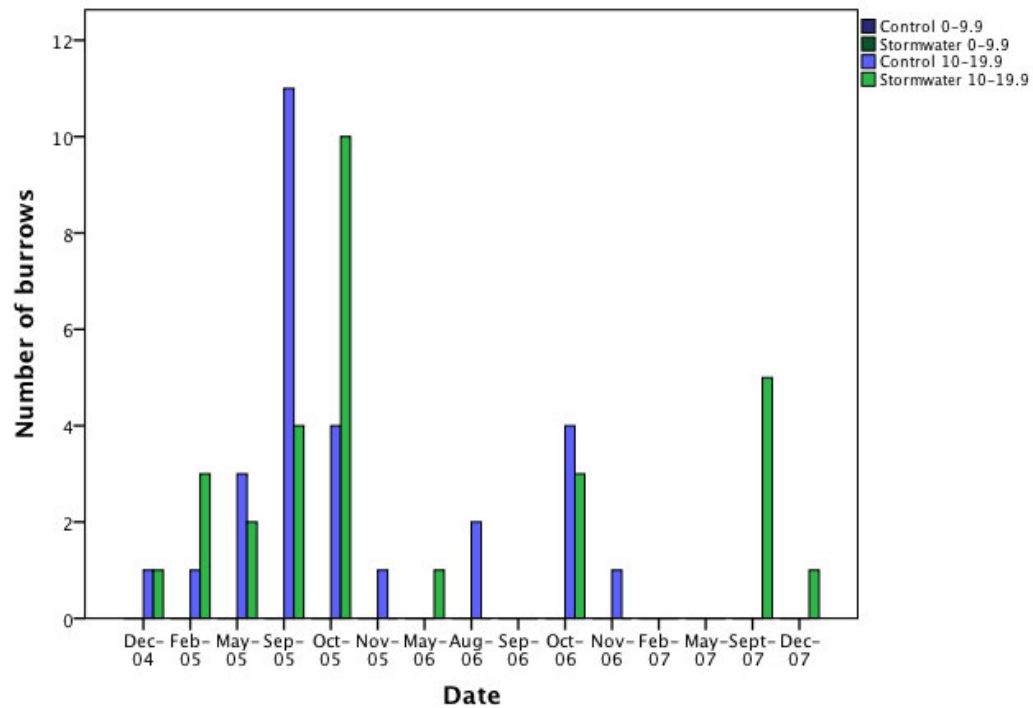


Figure 3.29 Number of *Neosarmatium* spp. burrows in the 0-9.9mm and 10-19.9mm at the paired control and storm-water input sites (a) at Bucasia.

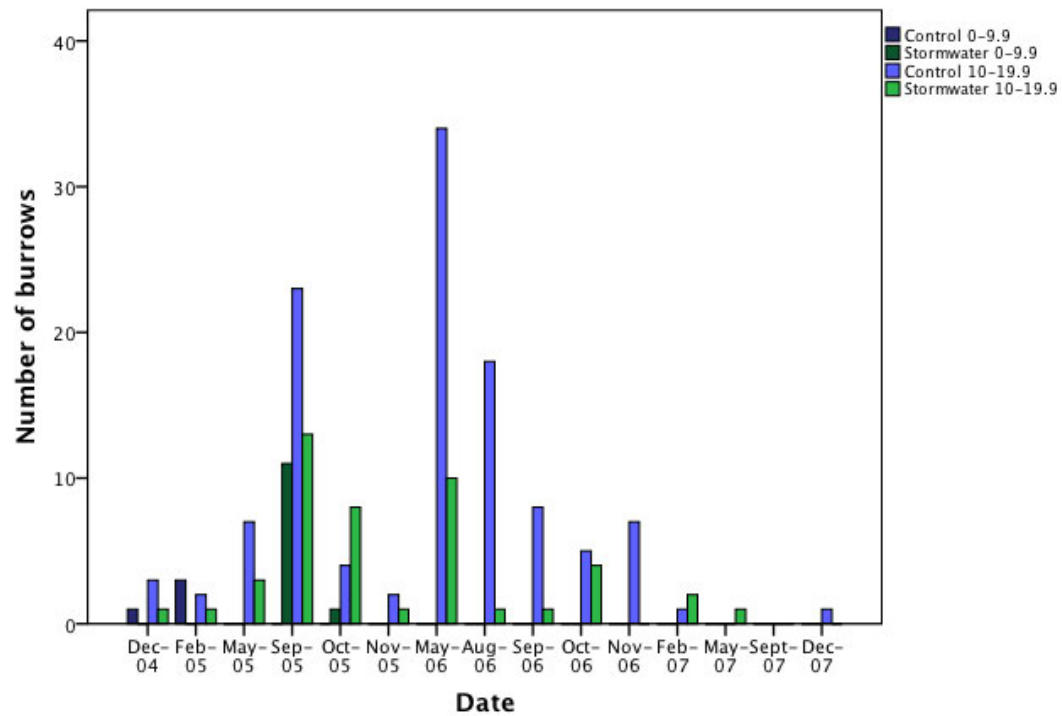


Figure 3.30 Number of *Neosarmatium* spp. burrows in the 0-9.9mm and 10-19.9mm at the paired control and storm-water input sites (a) at Eimeo.

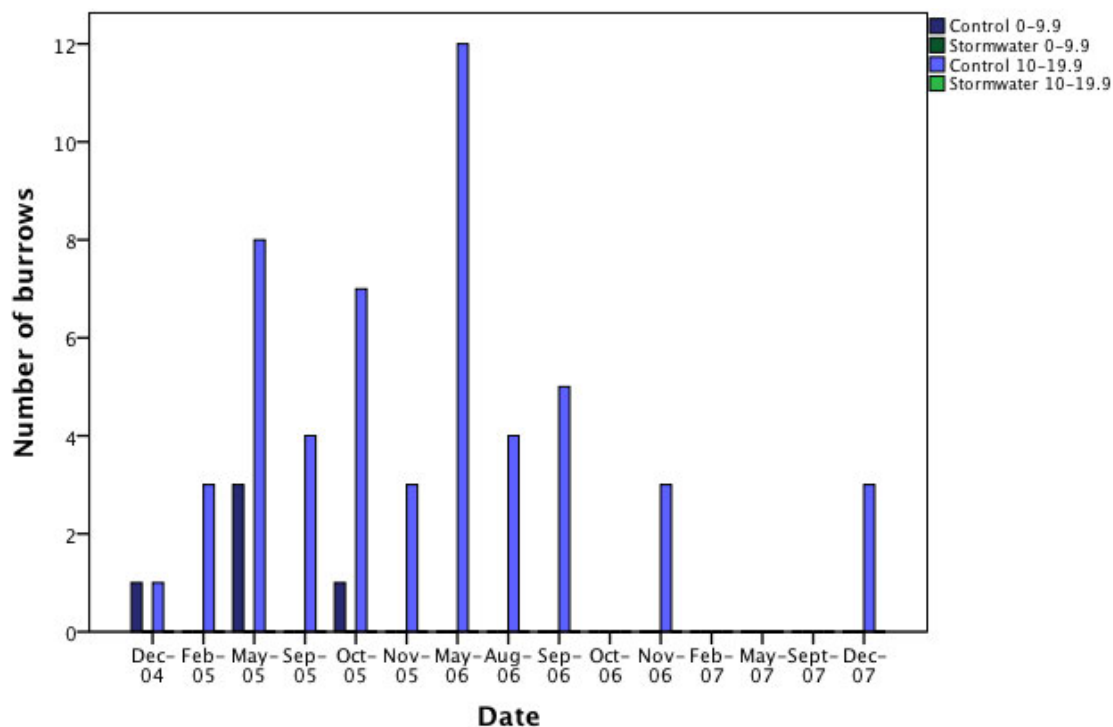


Figure 3.31 Number of *Neosarmatium* spp. burrows in the 0-9.9mm and 10-19.9mm at the paired control and storm-water input sites (a) at Slade Point.

Figure 3.32 shows the relationship between the number of *N. trispinosum* burrows with an aperture width ≤ 19.9 mm and > 19.9 mm for control sites (noting that *N. fourmanoiri* only occurs at BSW(a) as noted above). These data need to be analysed with caution because the data are not strictly independent because multiple observations are present for each site. This relationship appeared poor, and this was confirmed by a two-tailed Spearman's rank correlation (Spearman's $r = -0.176$, $P = 0.216$, $n = 48$).

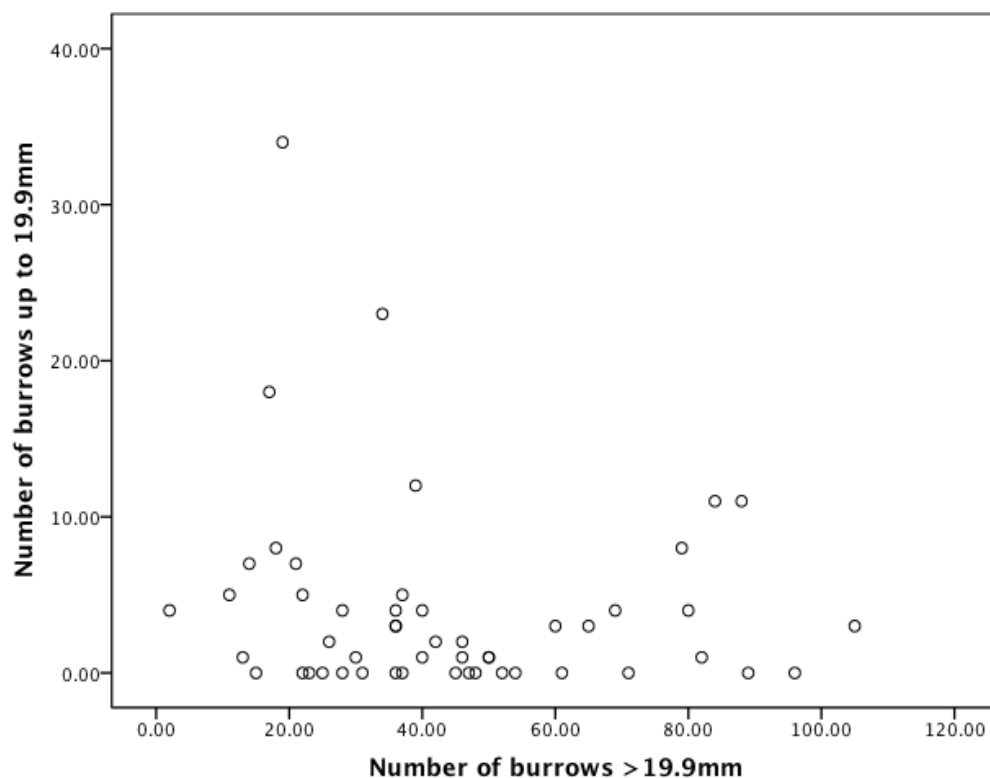


Figure 3.32 The relationship between the number of *N. trispinosum* burrows with an aperture width $\leq 19.9\text{mm}$ and $> 19.9\text{mm}$.

Figure 3.33 shows the number of *Parasesarma erythrodictyla* burrows in size classes 0-4.9mm and 5-9.9mm at the BC(a) and the paired site BSW(b) at all dates surveyed. Figure 3.34 illustrates this at the Eimeo paired sites [EC(a) and ESW(a)] and Figure 3.35 at the Slade Point paired sites [SPC(a) and SPWS(a)].

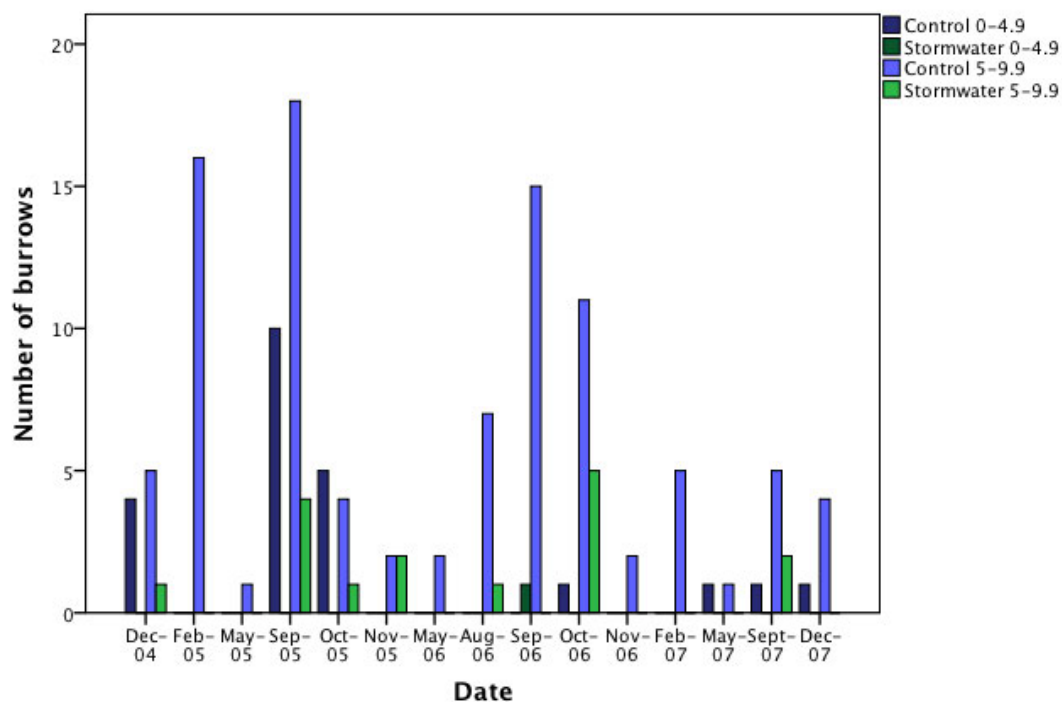


Figure 3.33 Number of *Parasesarma erythrodictyla* burrows in the 0-4.9mm and 5-9.9mm at the paired control and storm-water input sites (a) at Bucasia.

As for *Neosarmatium* spp. burrows, there was a complete lack of *Parasesarma erythrodictyla* burrows with an aperture width of < 10mm at the Slade Point storm-water input site (a), despite the presence of recruits within the locality as demonstrated by the number of burrows in this size class within the respective control site. At both Bucasia and Eimeo, there were markedly fewer burrows with an aperture width of < 10mm at storm-water influenced sites that as the paired control site. There were no obvious patterns in the presence or abundance of burrows in the 0-9.9mm size range amongst seasons.

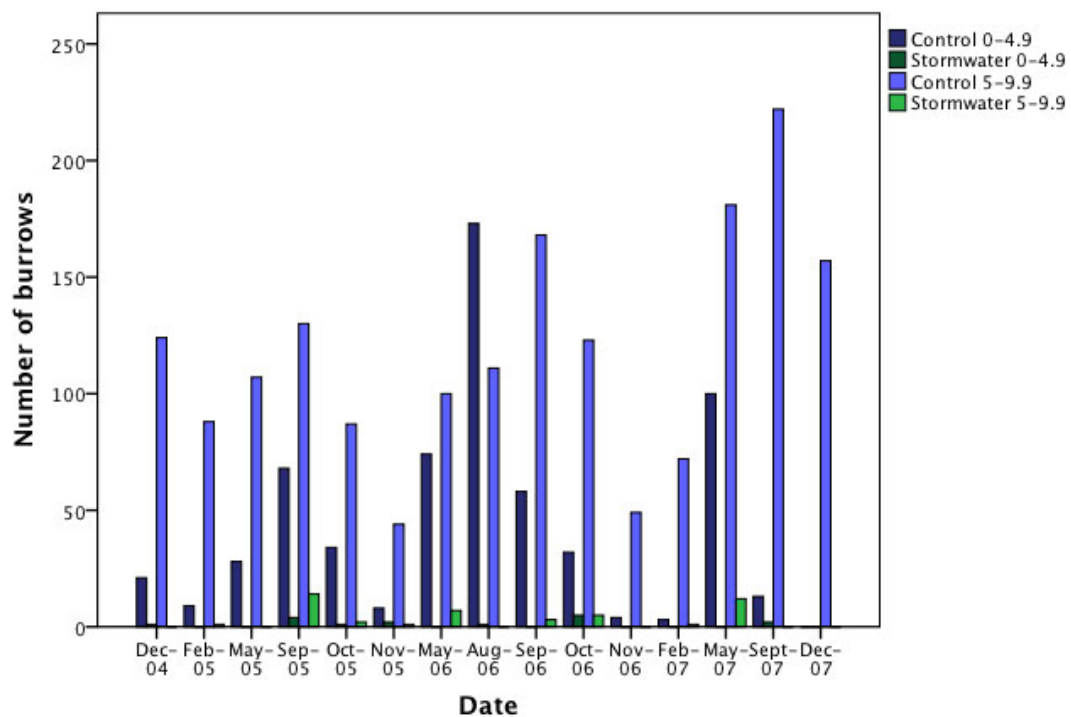


Figure 3.34 Number of *Parasesarma erythrodictyla* burrows in the 0-4.9mm and 5-9.9mm at the paired control and storm-water input sites (a) at Eimeo.

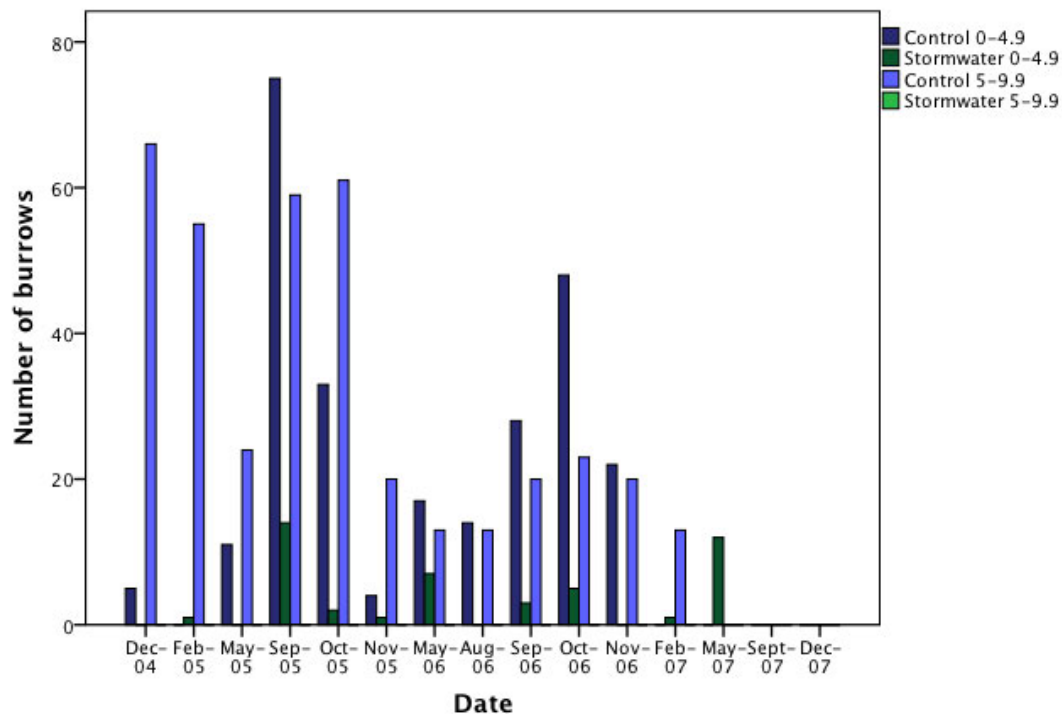
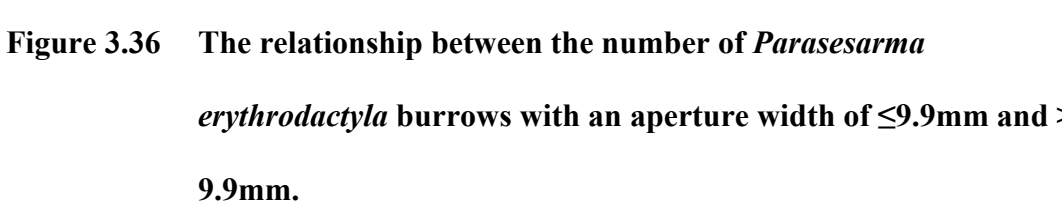


Figure 3.35 Number of *Parasesarma erythrodictyla* burrows in the 0-4.9mm and 5-9.9mm at the paired control and storm-water input sites (a) at Slade Point.

Figure 3.36 illustrates the relationship between the number of *Parasesarma erythrodictyla* burrows with an aperture width ≤ 9.9 mm and > 9.9 mm for control sites. These data also need to be analysed with caution because they are not strictly independent because multiple observations are present for each site. There is however, a highly significant correlation between the two variables (Spearman's $r = 0.735$, $P < 0.001$, $n = 46$).



3.3.7 Rainfall patterns within the study area

Total wet season rainfall (December of previous year to May the following year inclusive) was very similar in 2005 and 2006, but was greater in 2007 (2005, 909.6mm; 2006, 935.6mm; 2007; 1385.0mm). Figures 3.37 to 3.40 show the monthly rainfall from 2004 to 2007 respectively. Mean soil core water salinity measured in May (after the end of the wet season) in 2005, 2006, and 2007 was not closely related to total wet season rainfall. For example, at all three locations salinity was different between 2005 and 2006 despite these years having similar rainfall. This may be because distribution of rainfall amongst months in the wet season varied noticeably amongst years. However, it is also obvious that the decline in soil core water salinity during the wet season varied greatly amongst storm-water input sites, even within the same location. The most likely reason is the different amounts of storm-water input occurring at each site because of the different geographical extent of the catchment linked to each site by storm-water discharge infrastructure.

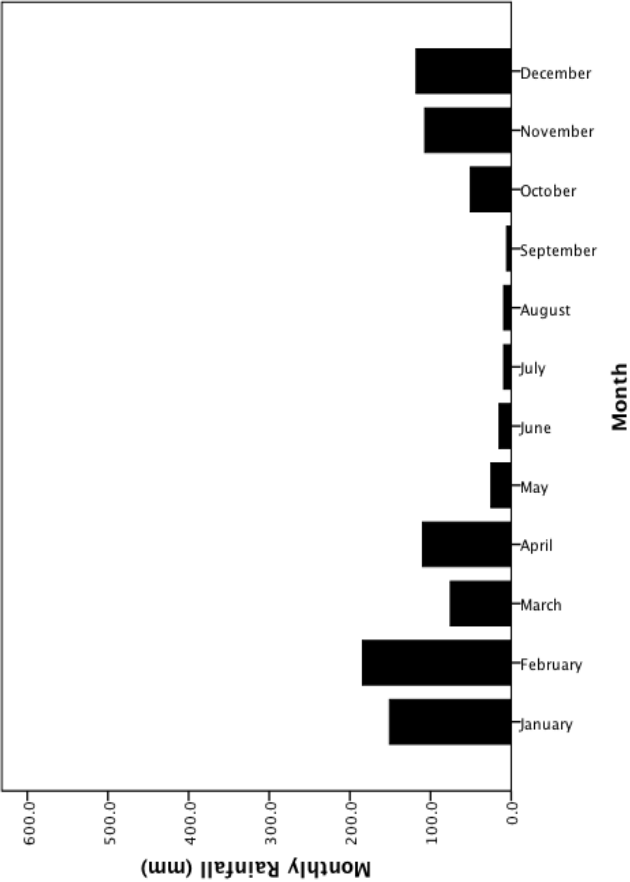


Figure 3.37 Monthly rainfall received in 2004.

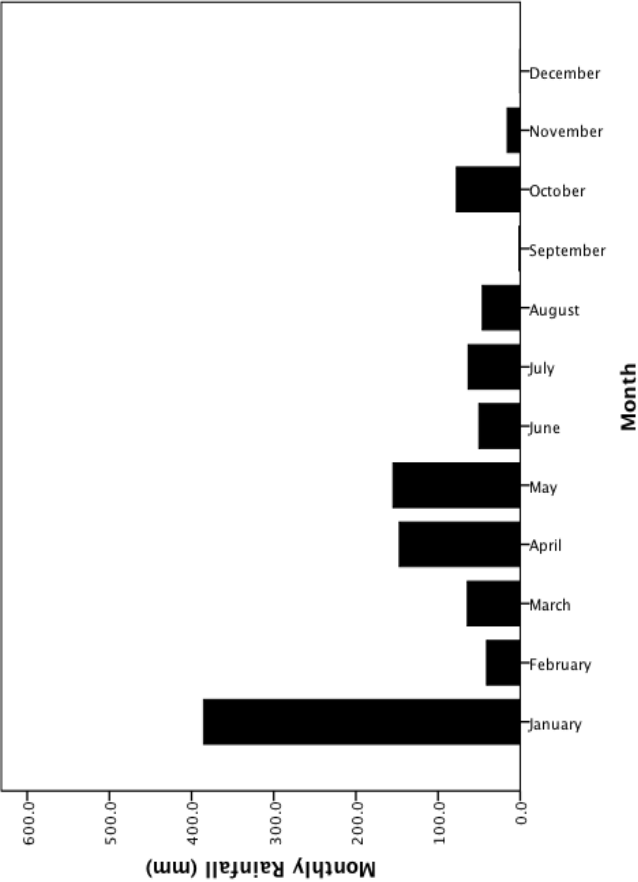


Figure 3.38 Monthly rainfall received in 2005.

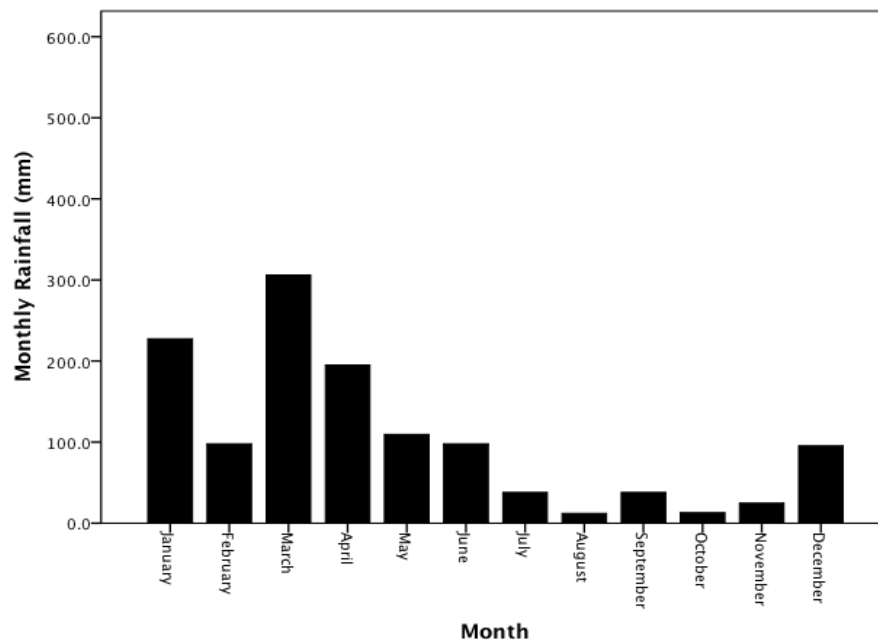


Figure 3.39 Monthly rainfall received in 2006.

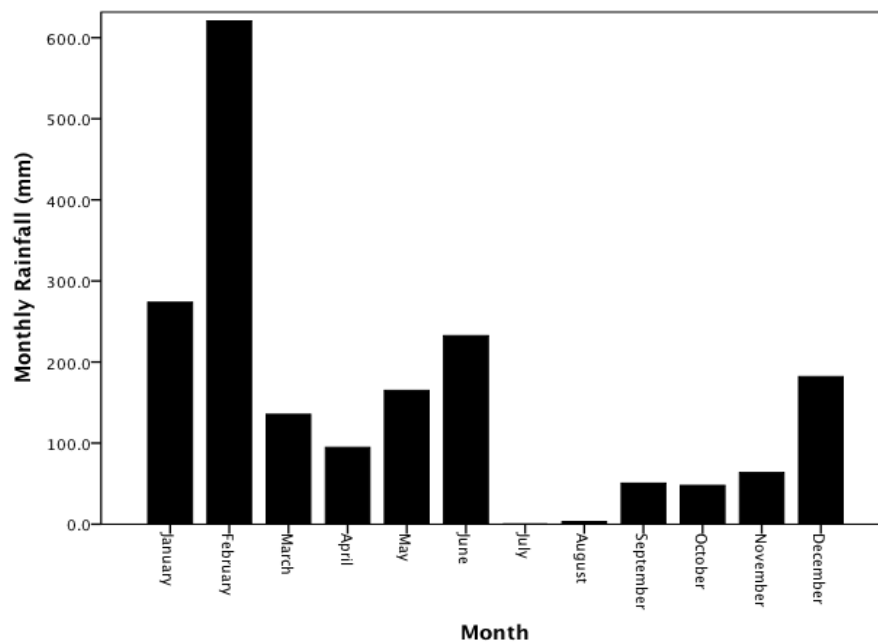


Figure 3.40 Monthly rainfall received in 2007.

3.4 Discussion

3.4.0 Differences in sesarmid burrow abundance

This study found fewer burrows at storm-water input sites compared to control sites. The results are consistent with discharge of urban storm-water into mangrove communities resulting in a decline in abundance of both *Neosarmatium* spp. and *Parasesarma erythrodactyla*. Parametric statistical analysis was not advisable because there were large differences in sample variances both among sites and among times and the data could not be adequately transformed. Nevertheless, there were a large number of comparisons (15 in each of three locations) over a three-year period and for only one of these 45 was burrow abundance of either taxon, higher at storm-water input sites than at controls. As expected, non-parametric testing of these data showed that there were significantly more cases where burrow abundance was higher at control sites, than at storm-water input sites, at all three localities. In addition, the magnitude of the difference in burrow abundance of both taxa between storm-water input and control sites was typically large. Other studies have investigated the potential impacts on mangrove biota from hydrological changes resulting from urbanisation including runnelling of saltmarsh: on adjacent mangrove vegetation in Darwin Harbour (NT, Aust) (Moritz-Zimmerman *et al.*, 2002); and on sesarmid crabs in south-east Queensland (Breitfuss, 2003). The principal finding of Moritz-Zimmerman *et al.* (2002) was a difference in mangrove floristics in areas closer to drainage channels compared to unaffected areas. Breitfuss (2003) proposed that runnelling altered habitat for saltmarsh taxa, including sesarmid crabs and found that small sesarmid burrows were less abundant close to drains. Instead, mid to large sized

burrows dominated in these areas. Lee *et al.* (2006) note that urbanisation both increases catchment imperviousness, which concentrates storm-water run-off, and modifies the quality of run-off by increasing loadings of sediment, nutrients and pollutants. However, changes in salinity as a result of hydrological change were not explicitly considered as an important water quality parameter. Strom and Thompson (2000), using the evidence of Spivak (1999) raised concern about the impacts on potential sesarmid recruits because of unstable salinity regimes within St Lucie Estuary in Florida (USA), as a result of increased urban storm-water run-off. However, the association between point discharge of urban storm-water into mangroves and a decline in sesarmid crab abundance has not been previously established. This is a noteworthy finding, because sesarmids are keystone species and a decline in their abundance is likely to have repercussions at the ecosystem level.

3.4.1 Relationship between storm-water input type and sesarmid burrow abundance

The magnitude of decline in soil core water salinity, and the decline in abundance of sesarmid burrows varied markedly amongst storm-water input sites. All sites were at similar tidal heights, had similar topographical relief, and were expected to experience similar flushing patterns by higher salinity, estuarine waters during high tides. Thus, differences in the extent of the decline in core water salinity were probably a consequence of the amount of storm-water entering the mangrove habitat from adjacent urban catchments. Unfortunately, there are considerable difficulties in directly measuring the volume and timing of storm-water run-off at any given site.

Further, Lee *et al.* (2006) noted that there are no suitable indices with which to assess urbanisation and changes in hydrological connectivity, and that appears to remain the case to date. This is a predicament because a calculation of the impact on sesarmid crabs from potential future urbanisation will include the requirement for a quantitative knowledge of the amount of storm-water input and the expected decline in sesarmid abundance. This study did, however, make note of features, notably the size of discharge outlets emptying to the mangroves, which may indicate the volume of storm-water entering each of the sites, so patterns in burrow abundance at storm-water input sites can be qualitatively related to these features. Both Slade Point storm-water input sites have been receiving inputs for at least 40 years. In both cases, and at any time, there were very few and often no burrows, of either *Neosarmatium trispinosum* or *Parasesarma erythrodactyla*. In contrast, storm-water input sites at Bucasia and Eimeo had been receiving urban storm-water input for a much shorter period (<10 years). At both locations, the storm-water input site with a smaller discharge pipe had a larger number of burrows of both taxa, at most times. For both these locations, there also appeared to be a consistent relationship between discharge pipe size and mean salinity, with the latter almost always being higher at sites with a smaller discharge pipe. These observations suggest that discharge of storm-water by smaller pipes at multiple points along the mangrove margin would have less site-specific impacts on sesarmid abundance than a single large discharge pipe. However, the combined effect on sesarmid abundance along the whole mangrove margin, by multiple, smaller discharge pipes, would also need to be assessed before a management recommendation could be made.

Monthly rainfall records for each location were compared to temporal changes in soil core water salinities. Notable events such as the large amount of rainfall received in February 2007 are reflected in the decrease in mean soil core water salinity at all locations. However, generally these comparisons did not provide any consistent insights, which is probably due to the difference in the size of discharge pipes amongst sites. Furthermore, the rainfall records are not location specific, but rather from a regional meteorological station located to the south of the study area. Future work should include a more quantitative analysis of catchment connectivity to the mangrove habitat, to better understand the impact of storm-water runoff.

3.4.2 Relationship between substratum characteristics and sesarmid burrow abundance

Of the habitat variables considered, neither soil core water pH, nor redox potential were useful measures in explaining sesarmid abundance. All study sites were located in very similar positions relative to the height of lowest astronomical tide. Thus no marked differences in the frequency or period of tidal inundation could be expected, so this factor was not likely to have any influence on sesarmid abundance. This study found that soil core water salinity was markedly lower at storm-water input sites compared to control sites during the wet season, although there was less difference during the dry season. However, the relationship between soil core water salinity and burrow numbers was complex. There was no correlation between either mean or minimum soil core water salinity and *N. trispinosum* burrow numbers. Nevertheless there was a threshold, at approximately 35‰, above which burrows were more

numerous. This may mean that habitats with a salinity of less than 35‰ were less suitable for *N. trispinosum*. Conversely, although areas where salinity was above 35‰ may have been more suitable, other influences may have been important determinants of *N. trispinosum* burrow abundance, and the magnitude of these differed amongst sites and times. From limited data from one storm-water input site, there was no correlation between either mean or minimum soil core water salinity and *N. fourmanoiri* burrow numbers.

For *P. erythrodactyla* there was also evidence of a threshold effect at about 35‰. This suggests that the soil core water salinity present within storm-water input sites was unsuitable for *P. erythrodactyla* for at least part of the time during the study, and even when it became higher in the dry season and reached levels more similar to control sites, this species did not recolonise to levels of abundance commensurate with that of control sites. Possible reasons are discussed below. At control sites (and therefore with higher salinity) there was a positive correlation between burrow numbers and both mean and minimum soil core water salinity. This suggests that this species preferred higher salinities within the range found in this study (to approximately 65‰).

Frusher *et al.* (1994) and Gillikin *et al.* (2004) provided data derived from laboratory tests of the salinity tolerances of some sesarmid species. Frusher *et al.* (1994) measured short-term survivorship (but not potential longer term declines in energy budgets) and found that four species of the genus *Perisesarma* showed greatest

survivorship at a salinity of 30‰ and significantly greater mortality at the extremes of 0‰ and 60‰. Gillikin *et al.* (2004) found that *Neosarmatium smithi* survived poorly in all salinities tested (16-65‰) except at 32‰. Conversely, *N. meinerti* survived well for up to a month at all salinities trialled. Empirical data describing the physiological tolerances of, and preferences for, differing salinities by *N. trispinosum*, *N. fourmanoiri*, and *P. erythrodactyla* are not available. Based on evidence provided by this current study, it appears that *N. trispinosum* and *P. erythrodactyla* may exhibit preferences for a specific salinity range (>35‰) but *N. fourmanoiri* may not. It should be noted that the estimates of soil core water salinity undertaken during this study were a relatively coarse way in which to measure the salinity of the sesarmid habitat.

Some burrows were present even when mean and minimum soil core water salinity was very low. This may be because the crabs were able to find and use micro-habitats with a higher salinity than that measured across the whole site; or they could persist for some period of time when salinity was lower than preferred. Frusher *et al.* (1994) also conducted some analyses based on comparisons between field observations of core water salinity and distribution of sesarmid species. However, observational studies are problematic as they may not take into account other determinants of distribution, which may obscure the observed relationship with salinity. These may include differences in mangrove species association within habitats as this influences availability of refugia (Lee & Kwok, 2002), and because crabs may have preferences for feeding on leaves and propagules of different species, as found for *P.*

erythrodactyla by Camilleri (1989), and for *N. trispinosum* by Giddins (1984) and Micheli (1993). Frusher *et al.* 1994 also found that in some cases, sediment type influenced the distribution of some taxa.

Testing for salinity tolerances in laboratory experiments would also be problematic. This would need to measure both short and long term survivorship as well as energy budgets in order to predict long-term persistence. In addition, laboratory studies should consider the rate at which salinity changes may affect taxa and their capacity to acclimatise. For example, in the vicinity of discharge pipes, heavy rainfall events could cause a large and rapid decrease in the salinity of the habitat when storm-water would flow into burrows. Alternatively, smaller rainfall events over the course of the wet season may result in a more gradual decrease in salinity to which crabs may acclimatise. Further, behavioural aspects should also be considered. Throughout the course of this study, individuals of *N. trispinosum* were regularly observed to plug their burrow entrances which would prevent storm-water from entering. Given that mangrove soils have a low porosity (Ridd, 1996; Stieglitz *et al.*, 2000) it is likely that storm-water would only slowly penetrate into a plugged burrow which may be an effective way for crabs to control the salinity within their burrows. For these reasons, development of hypotheses of salinity tolerances and preferences for testing in the laboratory, should be informed by a knowledge of the likely magnitude and rate of change of salinity in the habitat, and for some taxa, within their burrows. As noted above, it is important that future work include a more quantitative analysis of

catchment connectivity to the mangrove habitat, to better understand the impact of storm-water runoff on sesarmid crabs.

At storm-water input sites, there was no observed change in burrow abundance of either taxon as soil core water salinities increased from the late wet season to the late dry season. It may be possible that recruitment to those areas was inhibited by lack of adults, as settlement of sesarmid larvae has been demonstrated in some cases to be mediated by adult odour (Gebauer *et al.*, 1998; Gebauer *et al.*, 2002). This is discussed further below.

The potential transport of pollutants to the mangrove habitat also needs to be considered a possible factor in the observed decline in estimated sesarmid abundance. Other studies have investigated the potential impact on mangroves as a result of disposal of urban sewage) with focus on potential impacts of pollutants. Yu *et al.* (1997) made investigations within mangroves in China and found no significant differences in crustacean biomass between control and waste-water (settled municipal sewage) input sites during an 18-month long experiment. Cannicci *et al.* (2009), in a study that encompassed mangroves in both Kenya and Mozambique, concluded that crabs of the family Sesarmidae increased in biomass within sites receiving waste-water run-off for over a decade (primary municipal sewage and/or aquaculture pond outflows and/or solid waste). These results are consistent with Lee's (1998) assertion that sesarmid crabs are less vulnerable to pollution than other biota. Therefore, based on available data, a decline in soil core water salinity, and not increased pollutants, is

the most plausible explanation for the observed decline in estimated abundance of *N. trispinosum* and *P. erythrodactyla* in mangrove habitats receiving point discharge of urban storm-water.

3.4.3 Patterns of sesarmid recruitment

A prediction from this study was that burrows of both *N. trispinosum* and *P. erythrodactyla* would be more abundant when soil core water salinity is above 35‰. Most storm-water input sites had soil core water salinities that increased to this range for long periods after the wet season. However, there was no corresponding increase in abundance of small burrows of either *Neosarmatium* spp. or *P. erythrodactyla*.

This poses the question of whether habitat conditions in these areas were suitable for recruitment and, in particular, whether settlement of these taxa may be mediated by adult odour as found by Gebauer *et al.* (1998, 2002) for other species of crabs. If this were the case, the lack of adult crabs present might have influenced recruitment.

There is relatively little information about the life cycle of sesarmid crabs immediately after recruitment to the mangrove substratum. Skov *et al.* (2002), classified juveniles of *N. meinerti* as having a carapace width of <10mm and typically found those individuals living within chambers in adult burrows, as did Emmerson (2001). Schmidt and Diele (2009) noted that *Ucides cordatus* recruits were located in adult burrows with the carapace width of adult and co-inhabiting juvenile crabs being $38 \pm 2\text{mm}$ and $9 \pm 0.3\text{mm}$ respectively. In the case of this species, most recruits left the shared burrows after reaching 10mm carapace width although some stayed until reaching 25mm. Juvenile association with adult burrows is also known for other

species; *Neohelice granulata* (Luppi *et al.*, 2002) and *Cardisoma carnifex* (Vannini *et al.*, 2003), suggesting that juvenile co-habitation of adult burrows may be common in sesarmid crabs.

The first juvenile stage of *P. erythrodactyla* has been established as having a carapace width of 0.86mm (Guerao, *et al.*, 2004). Based on extensive field observations made during this study, it appears that this species does not need to use adult burrows.

Numerous burrows with very small apertures (as little as 2mm wide) were commonly observed at some sites, with the inhabitant often seen at the burrow entrance.

Burrows of juvenile *P. erythrodactyla* were classified as being in the 0-4.9mm and 5-9.9mm size classes and those of *N. trispinosum* were classified as being in the 0-9.9mm and 10-19.9mm size class. Whilst allocation to these size classes was to some degree arbitrary, it was necessary because as Salgado-Kent and McGuinness (2010) noted, before their recent contribution, no published information was available on either spatial or temporal patterns in the population structure of mangrove dwelling sesarmid crabs.

N. trispinosum and *N. fourmanoiri* burrows with an aperture width of <10mm were rarely present. This suggests that juveniles of these species may also co-inhabit within adult burrows in a similar way as does *N. meinerti*, and emerge to construct their own burrows at a similar size of 10mm carapace width, as described by Skov *et al.* (2002). It is notable that at BSW(a) where only *N. fourmanoiri* was present there was no clear difference in the number of burrows (10-19.9mm) between the storm-water input and control sites. At the other locations, with very few exceptions, there were more burrows at control sites than at storm-water sites, and notably, a complete

absence at the Slade Point storm-water sites. This suggests a species-specific difference in ability to recruit to storm-water influenced habitats. As discussed above, several species within the genus *Neosarmatium* have different salinity tolerances (Gillikin *et al.*, 2004) and it may be that *N. fourmanoiri* recruits can tolerate a lower salinity than those of *N. trispinosum*. For *N. trispinosum* there was no correlation between the number of adult burrows ($>19.9\text{mm}$) and smaller burrows at control sites. However, the number of burrows in the size class $\leq 19.9\text{mm}$ only estimated the number of recruits surviving to the point of emergence from adult burrows to construct their own, not the actual number of recruits. Given the potential importance of adult burrows as nursery habitat for recruits, there may be an advantage for pre-settlement recruits to be able to detect the presence of adults, so settlement may occur in response to cues from adults. Additional work is needed to clarify this. One useful approach would be excavation of adult burrows to determine actual numbers of recruits occurring in co-habitation with adult crabs, rather than counting small burrows.

The number of *P. erythrodactyla* burrows with an aperture of $<10\text{mm}$ was never greater at storm-water input sites than at controls, at any location over the three year period. Further, in virtually every comparison made, the number at control sites was much greater than at storm-water input sites. This is consistent with very few recruits of this species establishing within storm-water influenced habitats. There is a strong correlation between the number of recruits as estimated by counts of burrows with an aperture width up to 9.9mm width, and adult burrow numbers ($>9.9\text{mm}$ width). Given that this species rarely moves more than 1m away from its burrows (Guest, 2004) it is

likely that the recruits in small burrows did not migrate to the study sites post-settlement. These results suggest that the number of adults influenced settlement of this species, and lack of adults may explain why recruitment to storm-water input sites was reduced where few or no adults were present.

3.4.4 Summary and management implications

This study found fewer burrows of *Neosarmatium* spp. and *P. erythrodactyla* within storm-water input sites than at control sites. Of the factors investigated to date, the most plausible explanation for this was reduced soil core water salinity to levels outside of the tolerance of these taxa. The extent to which salinity and the abundance of sesarmid burrows declined, varied amongst different storm-water input types and this is probably related to the volume of storm-water discharge. However, more work is required to clarify the effects of different levels of hydrological connectivity of mangroves to urban catchments. Salinity alone did not fully explain the variability in sesarmid burrow abundance and, as such, further studies are required to gain a better understanding of other determinants. Some of these are the subjects of Chapters 4 & 5. It appeared that recruitment in storm-water influenced habitats was impeded compared to unaffected sites even in the dry season, when soil core water salinity increased. This may be because the presence of adults is a stimulus for settlement. Thus when adult crabs were absent (or in low numbers) settlement and consequent recruitment was decreased. These findings are important, because sesarmids are keystone species and a decline in abundance may have ecosystem level repercussions. In view of these findings, there seems justification for considering less ecologically

damaging ways of disposing of urban storm-water. Decreased crab recruitment, even when soil core water salinity recovers during the dry season, suggests that even if storm-water inputs were disposed of in other ways the sesarmid populations may not recover without interventions such as translocation of populations into affected areas.

4 A one-year regional comparison between mangroves receiving storm-water input and control sites

4.1 Introduction

The long-term comparisons described in Chapter 3 provided evidence that discharge of urban storm-water into mangrove communities resulted in a decline in abundance of both *Neosarmatium* spp. and *Parasesarma erythrodactyla*, as estimated by burrow counts. However, data were obtained from only three locations along a 10km section of coastline (Bucasia, Eimeo and Slade Point). Such limited replication may not reflect the natural variability of the mangrove habitat and/or the response of sesarmid crabs to storm-water input. Thus, a geographically larger study with greater replication, was undertaken to assess the effect of storm-water input at a broader regional scale.

Vegetation structure and floristics and soil core water characteristics may influence sesarmid abundance. However, since sesarmid abundance may also affect these features, the issue of causality must be carefully considered. These habitat features may also be changed by storm-water run-off, and measurements at a larger number of locations would assist in understanding the way any change may influence sesarmid abundance. These measurements would allow a number of predictions to be tested. Firstly burrow abundance can be compared among sites and related to vegetation type. If burrow abundance is similar among sites which also have similar vegetation, then some relationship could be drawn between these two variables, or *vice versa*.

Similarly, any relationship between presence of storm-water run-off and vegetation type can be examined by testing the prediction that vegetation at storm-water input sites is different to control sites. As for the long-term comparisons, the relationship between soil core water characteristics and both burrow abundance, and the presence of storm-water run-off, can also be examined. In this case, the prediction is that fewer burrows will be present at sites with lower soil core water salinity, and that these sites receive storm-water inputs.

4.2 Methods

4.2.0 Site selection

A paired design was used to make comparisons between storm-water input and control sites at 10 different locations, each of which contained a site receiving storm-water input, and the other a control located at least 120m away from any discharge. This distance was deemed sufficient as the mangrove forest floor sloped to seaward, and it was highly unlikely that any substantial amount of storm-water would have flowed obliquely across this gradient into the control sites. These included the six pairs used previously in long-term comparisons. Selection of additional sites was undertaken using the same methods as used previously. All sites were located in exactly the same upper intertidal area thus no substantial differences in their heights could be expected.

4.2.1 Sesarmid Burrow Abundance

At each site, ten 1m² quadrats were randomly placed on the substratum by haphazardly casting the quadrat backwards to an area out of sight as in section 3.2.1. As for the long-term comparisons, within each quadrat the number of burrows was recorded. Each burrow aperture was measured across its widest diameter and assigned to one of the two mutually exclusive morphological types; lateral (*Neosarmatium* spp.) or simple (*Parasesarma erythrodactyla*). Burrow counts were made in May 2007 (late in the tropical wet season) and in December 2007 (late in the dry season). These data were used to test the prediction that there would be fewer burrows at storm-water input sites than at control sites. Relationships were examined between burrow abundance and overall vegetation structure and floristics, the basal area of the most dominant species, soil core water pH and salinity.

4.2.2 Vegetation Descriptions

The floristics and structure of the mangrove community at each site were described by data collected from three 25m² randomly placed quadrats selected by haphazardly casting a marker out of sight. Within each quadrat, every mangrove was identified to species level and its diameter at breast height (DBH) recorded. For each mangrove species present, the mean density/ m² and mean DBH were used to calculate basal areas. These data were used to calculate a Bray-Curtis dissimilarity co-efficient for each quadrat. Analysis of similarity (ANOSIM) (Clarke & Gorley, 2001) was used to test the prediction that vegetation at storm-water input sites was different to that at control sites. ANOSIM cannot calculate interaction terms (Underwood *et al.*, 2003)

so cluster analysis was used to explore differences amongst sites. However, as Underwood *et al.* (2003) note, impacts may alter the variance rather than the mean, so within site variability was calculated by using measures of dissimilarity among ‘within site’ replicates (i.e. each of three quadrats used in each site), which then become independent univariate measures (Underwood and Chapman, 2000) and can be used in ANOVA to make comparisons of ‘within site’ and ‘among site’ variability.

The relationship between the vegetation community and burrow abundance was then examined using multi-dimensional scaling (MDS). Data were not transformed, so numerically dominant species had more influence on the calculation of the coefficient. Nor were the data standardized; the actual basal area of mangroves was used rather than relative proportions.

4.2.3 Substratum

At each site, five small pits were dug into the substratum at low tide, until soil core water flowed into the resulting hole. Within each, salinity and pH were recorded in both May and December.

4.3 Results

4.3.0 Site Selection

Paired sites were located at Mandalay, Cannonvale (two pairs), Bucasia (two pairs), Eimeo (two pairs), Slade Point (two pairs) and Armstrong’s Beach (Figure 4.1).

Details of each site including site code, name, location, type of storm-water input, and general description are in Table 4.1.

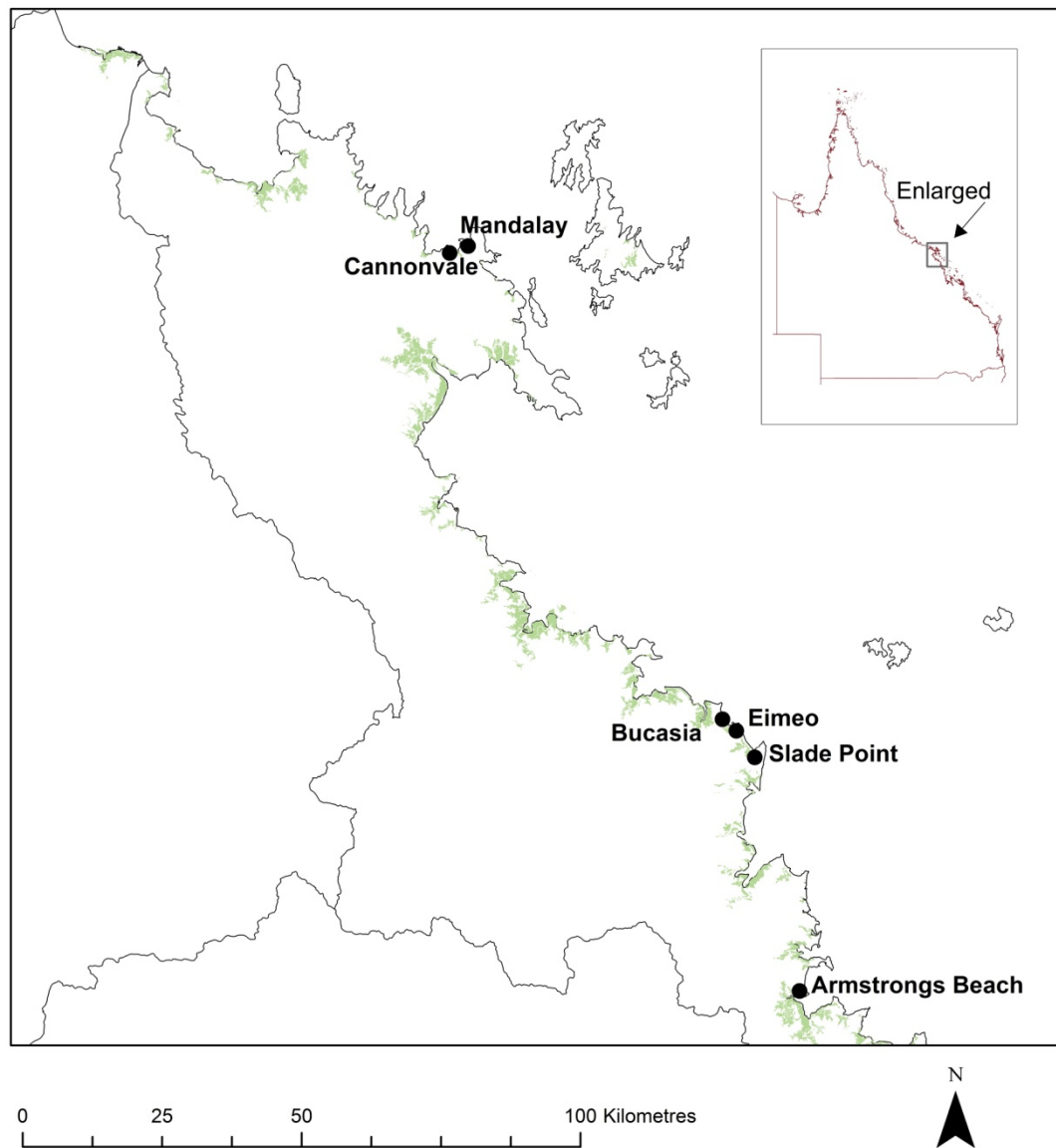


Figure 4.1 Study locations.

Table 4.1 Site codes, name, location and brief description of study sites (* denotes sites used in long-term comparisons).

Location	Site Name & Code	Site Description
Cannonvale (a)	Cannonvale Control (a) CC(a)	Located along the high intertidal margin app 15m seaward of the terrestrial vegetation margin. This site is located mid-way between CSW(a) and CSW(b) (120m away from each).
Cannonvale (a)	Cannonvale Storm-water (a) CSW(a)	The site lies along the high intertidal margin approximately 15m seaward of the terrestrial vegetation margin. Storm-water enters the site from a small earthen drain.
Cannonvale (b)	Cannonvale Control (b) CC(b)	Located along the high intertidal margin approximately 15m seaward of the terrestrial vegetation margin. This site is approximately 120m south-east from CSW(b).
Cannonvale (b)	Cannonvale Storm-water (b) CSW(b)	Located along the high intertidal margin approximately 15m seaward of an extensive stand of <i>Hibiscus tiliaceous</i> . Storm-water enters the site via a very large (app 5m wide by 1m deep) concrete drain. The end of the drain lies approximately 30m to landward of the site.

Location	Site Name & Code	Site Description
Mandalay	Mandalay Control MC	The site is located on the edge of a patch of mangroves which is surrounded by saltpan.
Mandalay	Mandalay Storm-water MSW	Located on the high intertidal margin of a linear strip of mangroves adjacent to Shute Harbour Road. Storm-water enters the site through a concrete pipe under the road that delivers storm-water from adjacent residential areas. The end of the pipe is located approximately 8m to landward of the site.
Bucasia (a)	Bucasia Control (a)* BC(a)	Located approximately 8m from the edge of the mangrove forest. An area of saltwater couch (<i>Sporobolus virginicus</i>) separates the mangroves from terrestrial vegetation (open fringing forest of <i>Melaleuca leucadendra</i>).
Bucasia (a)	Bucasia Storm-water (a)* BSW(a)	The site is located approximately 500m downstream from one storm-water outlet and approximately 20m to seaward of another large outlet. Mangrove forest of mixed species with a dense understorey of the holly mangrove (<i>Acanthus ilicifolius</i>) lies between the site and the latter storm-water outlet.

The effect of urban storm-water runoff on Sesarmid crabs

Location	Site Name & Code	Site Description
Bucasia (b)	Bucasia Control (b) BC(b)	Located approximately 300m from BC(a) within a linear strip (about 40m wide) of mangrove forest with saltpan on one side and a brackish lagoon with isolated trees of <i>Melaleuca leucadendra</i> on the other.
Bucasia (b)	Bucasia Storm-water (b)* BSW(b)	This site lies approximately 200m from BSW(a). Storm-water first flows into a large retention basin formed by bund walling along the edge of the mangrove forest. Storm-water flows into the site through a small 20cm diameter pipe running through the bund wall.
Eimeo (a)	Eimeo Control (a)* EC(a)	The site is located on the edge of a patch of mangroves that is surrounded by saltpan.
Eimeo (a)	Eimeo Storm-water (a)* ESW(a)	Storm-water is directly discharged into this site by a 50cm diameter pipe. The position of the site is approximately 8m downstream from the outlet and approximately 10m to seaward of fringing terrestrial vegetation.

Location	Site Name & Code	Site Description
Eimeo (b)	Eimeo Control (b) EC(b)	Located along the fringe of a mangrove forest in a slightly lower intertidal position from a low stunted thicket of <i>Ceriops tagal</i> .
Eimeo (b)	Eimeo Storm-water (b)* ESW(b)	Storm-water is discharged from a large concrete pipe into an earthen drain which travels for approximately 8m before entering the mangrove fringe. The site is located approximately 5m from the mangrove fringe.
Slade Point (a)	Slade Point Control (a)* SPC(a)	The site is located within a patch of mangrove forest that is surrounded by saltpan on three sides and an extension of the forest on the third.
Slade Point (a)	Slade Point Storm-water (a)* SPSW(a)	Storm-water enters the site via a gully through fringing terrestrial vegetation and saltwater couch (<i>Sporobolus virginicus</i>) grassland $\pm$ sedges (<i>Cyperus</i> spp.). The site is located within approximately 5m of the forest edge.

The effect of urban storm-water runoff on Sesarmid crabs

Location	Site Name & Code	Site Description
Slade Point (b)	Slade Point Control (b) SPC(b)	The site is located within a patch of mangroves that is surrounded by saltpan on two sides, an extension of the forest on a third and the lower intertidal area on the fourth.
Slade Point (b)	Slade Point Storm-water (b)* SPSW(b)	Storm-water enters the site via a gully through fringing terrestrial vegetation and saltwater couch (<i>Sporobolus virginicus</i>) grassland sometimes with sedges (<i>Cyperus</i> spp.). The site is located within approximately 5m of the forest edge.
Armstrong's Beach	Armstrong's Beach Control AC	Located approximately 150m away from its paired storm-water input site. The site lies approximately 10m from the mangrove fringe along which is remnants of terrestrial vegetation with a thick understorey of exotic grasses.
Armstrong's Beach	Armstrong's Beach Storm- water ASW	Storm-water enters the site from an earthen gully leading to storm-water drains in the directly adjacent residential area. The site lies approximately 10m from the mangrove fringe.

4.3.1 Sesarmid Burrow Abundance

Neosarmatium spp. burrows were fewer at every storm-water input site compared to the respective control site, at both times of sampling. The mean number of *Neosarmatium* spp. burrows/m² at each site, during the late wet season and late dry season, is shown in Figures 4.2 and 4.3 respectively.

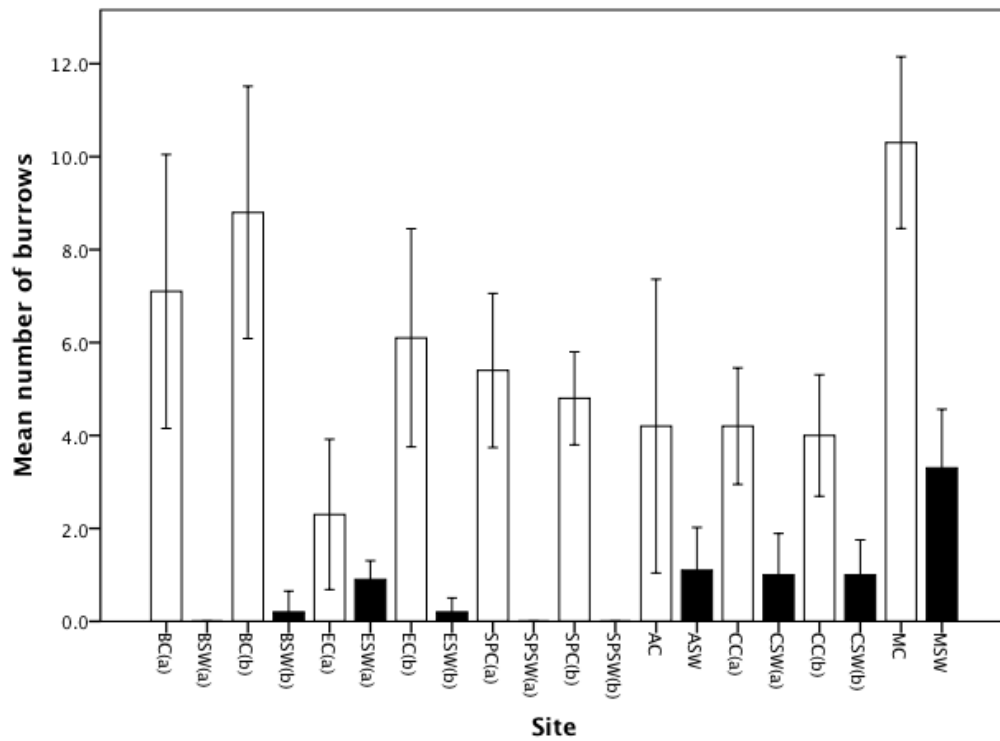


Figure 4.2 May 2007. Mean number of *Neosarmatium* spp. burrows at each site. Bars are the 95% confidence interval around the mean. No fill = control sites; dark fill = storm-water input sites.

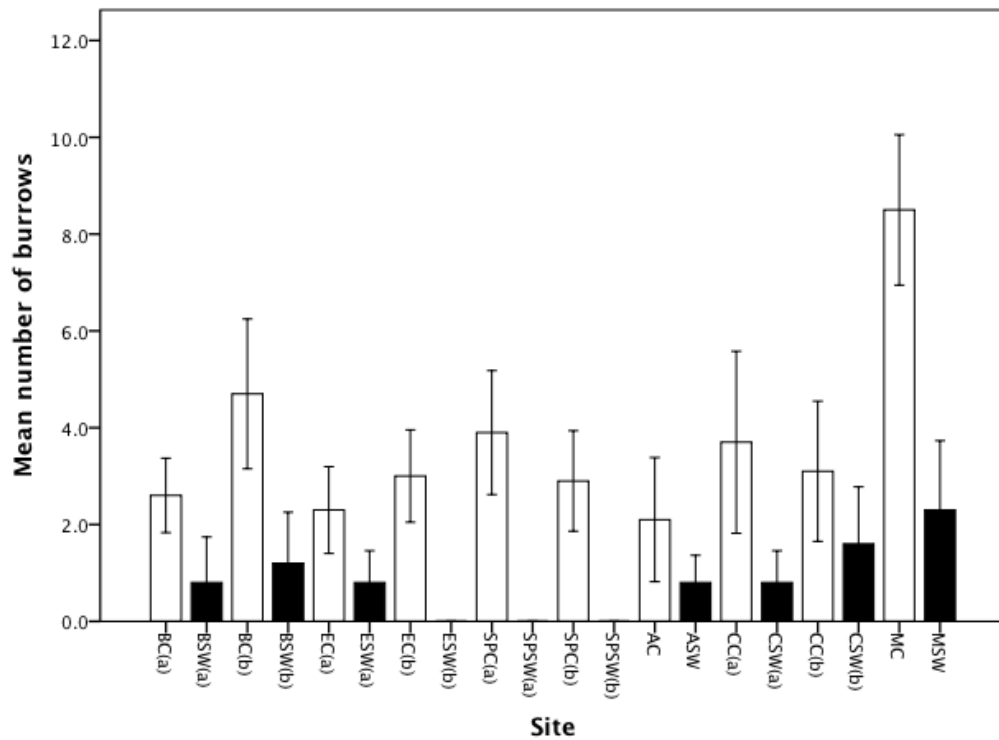


Figure 4.3. December 2007. Mean number of *Neosarmatium* spp. burrows at each site. Bars are the 95% confidence interval around the mean. No fill = control sites; dark fill = storm-water input sites.

As with the long-term comparisons, these data did not meet the assumptions of ANOVA and could not be adequately transformed. Instead, the mean numbers of *Neosarmatium* spp. burrows at the paired sites in each location were treated as matched pairs and a comparison made between control and storm-water input sites using a paired sample two-tailed *t*-test. Data were firstly transformed $[\log(x+1)]$ so that they met the assumptions of the *t*-test. There were significant fewer burrows at

storm-water input sites than at control sites in both May 2007 ($df = 9$, $t = 7.567$, $P < 0.001$) and December 2007 ($df = 9$, $t = 7.778$, $P < 0.001$).

The mean number of *P. erythrodactyla* burrows/m² at each site during the late wet season and late dry season is shown in Figures 4.4 and 4.5 respectively. There was a much larger difference in burrow numbers amongst sites in May than December so the May means are displayed on a log scale. A two-tailed *t*-test was used, as for *Neosarmatium* spp. burrow counts, again after firstly transforming the data in the same way. There were significantly fewer burrows at storm-water input sites than at control sites in both May 2007 ($df = 9$, $t = 6.275$, $P = 0.001$) and December 2007 ($df = 9$, $t = 4.349$, $P = 0.002$).

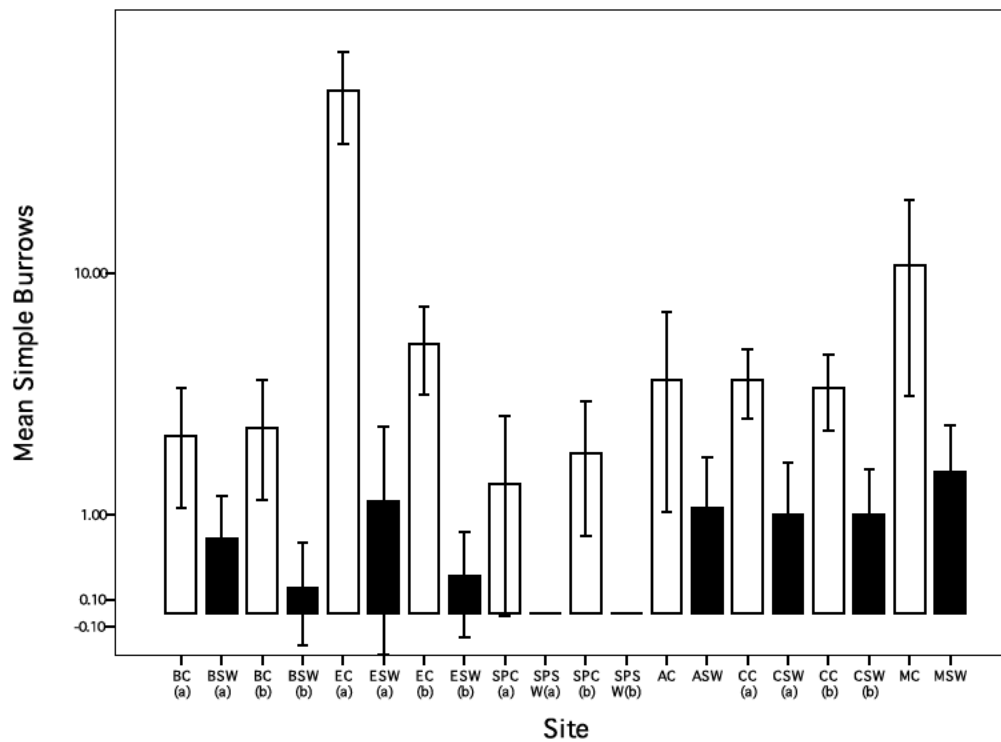


Figure 4.4 May 2007. The log of the mean number of *P. erythrodactyla* burrows at each site. Bars are the 95% confidence interval around the mean. No fill = control sites; dark fill = storm-water input sites.

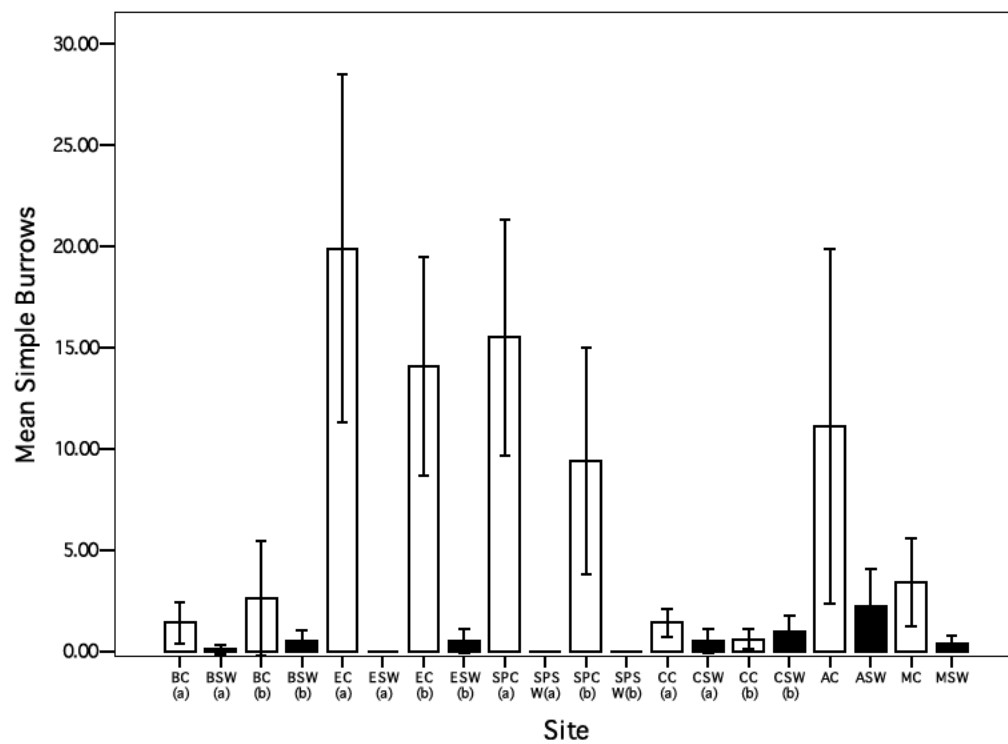


Figure 4.5 December 2007. The log of the mean number of *P. erythrodactyla* burrows at each site. Bars are the 95% confidence interval around the mean. No fill = control sites; dark fill = storm-water input sites.

4.3.2 Vegetation Descriptions

All control sites with the exception of CC(a) and five of the ten storm-water input sites were dominated by *Cerrops tagal*. Table 4.2 shows the mean basal area (from three quadrats) of each species within each site, as a measure of relative numerical dominance. Three sites were dominated by *Bruguiera exaristata* and this species was sub-dominant at six control sites and present within ten other sites. Two sites were somewhat different to the others; BSW(b) was dominated by *Lumnitzera racemosa*, and CSW(b) was dominated by *Excoecaria agallocha* and was the only site not containing *Cerrops tagal*.

Table 4.2 Basal area of each species within each site. Dark shading = dominant species in terms of basal area, light shading = sub-dominant species.

Site	<i>Cerrops tagal</i> Basal Area cm ²	<i>Bruguiera</i> <i>exaristata</i> Basal Area cm ²	<i>Bruguiera</i> <i>gymnorhiza</i> Basal Area cm ²	<i>Excoecaria</i> <i>agallocha</i> Basal Area cm ²	<i>Lumnitzera</i> <i>racemosa</i> Basal Area cm ²	<i>Avicennia marina</i> Basal Area cm ²	<i>Aegiceras</i> <i>corniculatum</i> Basal Area cm ²	<i>Aegiceras</i> <i>corniculatum</i> Basal Area cm ²	<i>Xylocarpus</i> <i>granatum</i> Basal Area cm ²
BC(a)	35.45	2.51	0	0.71	0	0.63	0	0	0
BC(b)	29.91	4.02	0	0	0	0	0	0	0
BSW(a)	1.23	15.55	0	3.62	4.83	1.77	0	0	0
BSW(b)	0.46	0.38	0	1.15	10.71	0	0	0	0
EC(a)	32.43	0.61	0	0	0	0	0	0	0
EC(b)	26.97	5.72	0	0	0	0	0	0	0
ESW(a)	49.11	0.25	0	0	0	0	0	0	0
ESW(b)	31.69	7.65	0	6.18	0	3.01	0	0	0
SPC(a)	45.53	1.06	0	0	0	0	0	0	0
SPC(b)	33.9	1.63	0	0	0	0	0	0	0
SPSW(a)	6.51	18.7	0	2.45	0	2.5	0	0	0
SPSW(b)	2.06	19.02	0	4.48	0	5.47	0	0	0

Table 4.2 Continued

Site	<i>Cerriops tagal</i> Basal Area cm ²	<i>Bruguiera</i> <i>exaristata</i> Basal Area cm ²	<i>Bruguiera</i> <i>gymnorhiza</i> Basal Area cm ²	<i>Excoecaria</i> <i>agallocha</i> Basal Area cm ²	<i>Lumnitzera</i> <i>racemosa</i> Basal Area cm ²	<i>Avicennia marina</i> Basal Area cm ²	<i>Aegiceras</i> <i>corniculatum</i> Basal Area cm ²	<i>Aegiceras</i> <i>corniculatum</i> Basal Area cm ²	<i>Xylocarpus</i> <i>granatum</i> Basal Area cm ²
AC	21.63	0	1.25	0	0	1.99	0.72	3.53	0
ASW	22.51	0	0	0	0	0	0	0	0
CC(a)	8.93	12.21	0	10.42	0	0	0	3.5	0
CC(b)	26.52	3.76	0	0.79	1.79	4.62	0	0	0
CSW(a)	22.56	0	0.57	12.36	2.96	0.21	0	0	0
CSW(b)	0	0	11.17	18.83	0	0	0	0	0
MC	32.31	0	0	0	0	0	0	0	0
MSW	17.65	0	0	0.09	1.11	0	0	0	1.32

Using the basal area for each species, within each three replicate quadrats at each site, a similarity matrix was developed by means of Bray-Curtis Dissimilarity measures within the software package 'Primer'. Using this matrix, a 2-way crossed layout design was selected, and analysis of similarity (ANOSIM) was utilised to test for differences in vegetation type between storm-water input and control sites. This design was chosen because it was unreasonable to assume that the vegetation type was the same at all sites prior to storm-water input, and in addition, storm-water sites may have had different times of exposure to storm-water input and thus may be in different states of response to that impact (i.e. the crossed design assumes there may be site differences). This detected a significant difference in vegetation type between storm-water input and control sites (Global $r = 0.57$, $P = 0.01$).

Sites containing more similar vegetation were identified by cluster analysis with the Bray-Curtis coefficient calculated using the basal area of each mangrove species present within each site (data from all three quadrats from each site were combined) (Figure 1.6). Two sites (CSW(b) & BSW(b)) were clearly dissimilar to all other sites and also to each other, which reflects that these sites were dominated by different species. The first cluster (from the left of Figure 4.6) contains ten sites of which eight were controls and two were storm-water input sites (ESW(a) & ESW(b)). These sites were dominated by *Ceriops tagal* with relatively high basal area (26.97 to 49.11 cm² m²) and typically sub-dominated by *Bruguiera exaristata*. The second cluster contains sites which were dominated by *Ceriops tagal* with moderate basal area (17.65 to 22.56 cm² m²) $\pm$ other species but not *Bruguiera exaristata*. This group

contains three storm-water input sites (CSW(a), MSW, ASW) and a single control sites (AC). The third cluster contains sites which were dominated by *Bruguiera exaristata* and includes three storm-water input sites (SPSW(a), SPSW(b), BSW(a)) and single control site (CC(a)).

A mixed model two-way ANOVA with control vs. storm-water input as a fixed factor and location as a random factor was used to test whether within site variability (i.e. the Bray-Curtis dissimilarity coefficient) differed between control and storm-water input sites or among locations. Calculation of the F value for the random factor was performed as advised by Quinn and Keogh (2002). Levene's test did not detect a significant difference among sample variances ($F_{19, 40} = 1.71, P = 0.076$). Although there was no significant difference between control and storm-water input sites ($F_{1, 9} = 0.896, P = 0.369$) there was a significant difference among locations ($F_{9, 9} = 5.598, P < 0.01$) and also a just significant interaction ($F_{9, 40} = 2.143, P = 0.048$) (Table 4.3). Consequently marginal means were calculated to clarify if any significant differences were present between storm-water input and control sites at any individual location (Table 4.4). The 95% confidence interval of the mean overlaps at all locations except at Slade Point (b) and so only at this location was there a significant difference in variability between the storm-water input and control site.

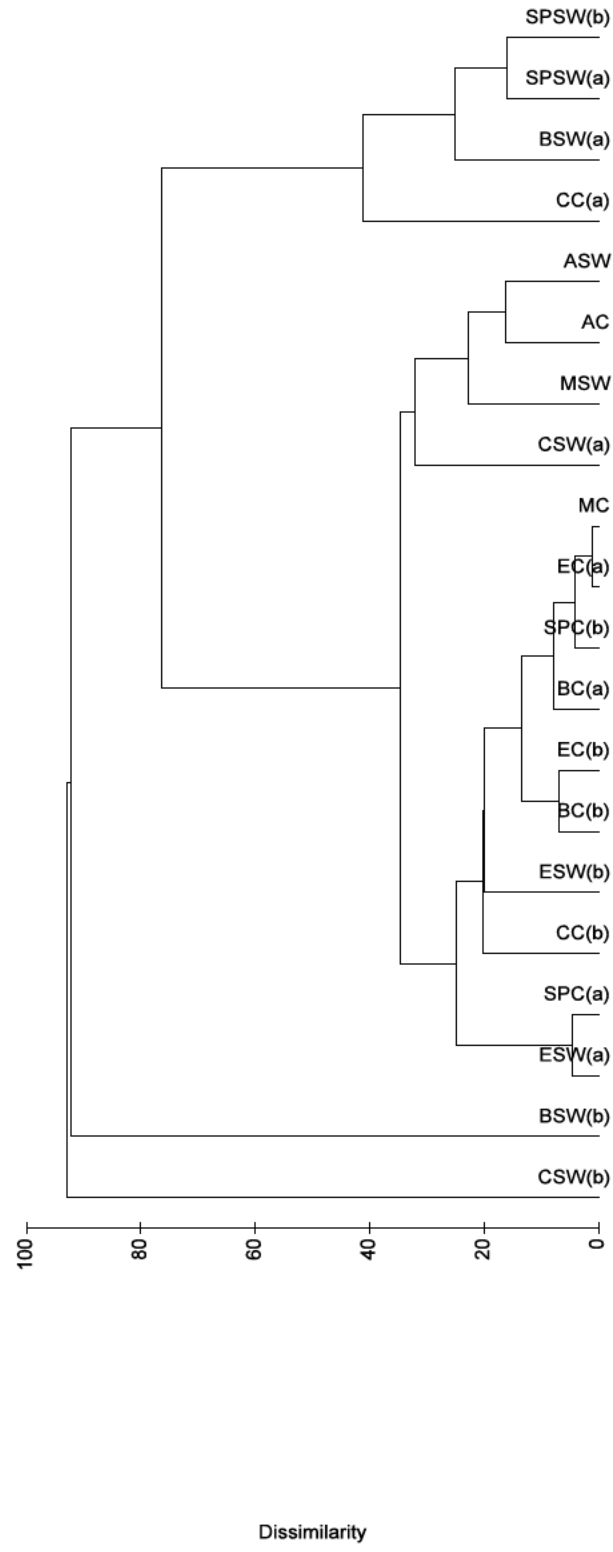


Figure 4.6 Cluster analysis groupings of sites with a more similar vegetation type.

Table 4.3 Results of ANOVA of the Bray-Curtis Dissimilarity Index between treatments and among locations.

		Type III				
		Sum of				
Source		Squares	df	Mean Square	F	Sig.
Treatment	Hypothesis	355.023	1	355.023	.896	.369
	Error	3565.072	9	396.119(b)		
Location	Hypothesis	9313.064	9	1034.785	5.598	< 0.01
	Error	3565.072	9	184.860(c)		
Treatment * Location	Hypothesis	3565.072	9	396.119	2.143	.048
	Error	7394.402	40	184.860(c)		

a MS(Location)

b MS(Treatment * Location)

c MS(Error)

**Table 4.4 Estimated marginal means of the Bray- Curtis dissimilarity index
for each site.**

Treatment	Location	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
Control	Armstrong's Beach	29.73	7.85	13.87	45.60
	Bucasia (a)	32.01	7.85	16.15	47.88
	Bucasia (b)	44.96	7.85	29.09	60.82
	Cannonvale (a)	65.02	7.85	49.15	80.89
	Cannonvale (b)	42.41	7.85	26.54	58.28
	Eimeo (a)	15.49	7.85	-0.38	31.36
	Eimeo (b)	28.75	7.85	12.88	44.62
	Mandalay	28.94	7.85	13.07	44.80
	Slade Point (a)	20.6	7.85	4.73	36.47
	Slade Point (b)	22.46	7.85	6.59	38.32
Storm-water	Armstrong's Beach	23.28	7.85	7.41	39.14
	Bucasia (a)	57.22	7.85	41.35	73.09
	Bucasia (b)	31.87	7.85	16.01	47.74
	Cannonvale (a)	51.71	7.85	35.85	67.58
	Cannonvale (b)	46.23	7.85	30.37	62.10
	Eimeo (a)	4.24	7.85	-11.63	20.11
	Eimeo (b)	35.18	7.85	19.31	51.05
	Mandalay	42.65	7.85	26.78	58.52
	Slade Point (a)	30.81	7.85	14.94	46.67
	Slade Point (b)	55.82	7.85	39.96	71.69

4.3.3 Relationship between burrow abundance and vegetation type

Figures 4.7 (a, b) are multidimensional scaling (MDS) plots of vegetation similarity with bubble size corresponding to the abundance of *Neosarmatium* spp. and *P. erythrodactyla* burrows respectively. In both cases, sites with similar vegetation types had markedly different burrow abundances, which suggest these variables are not related.

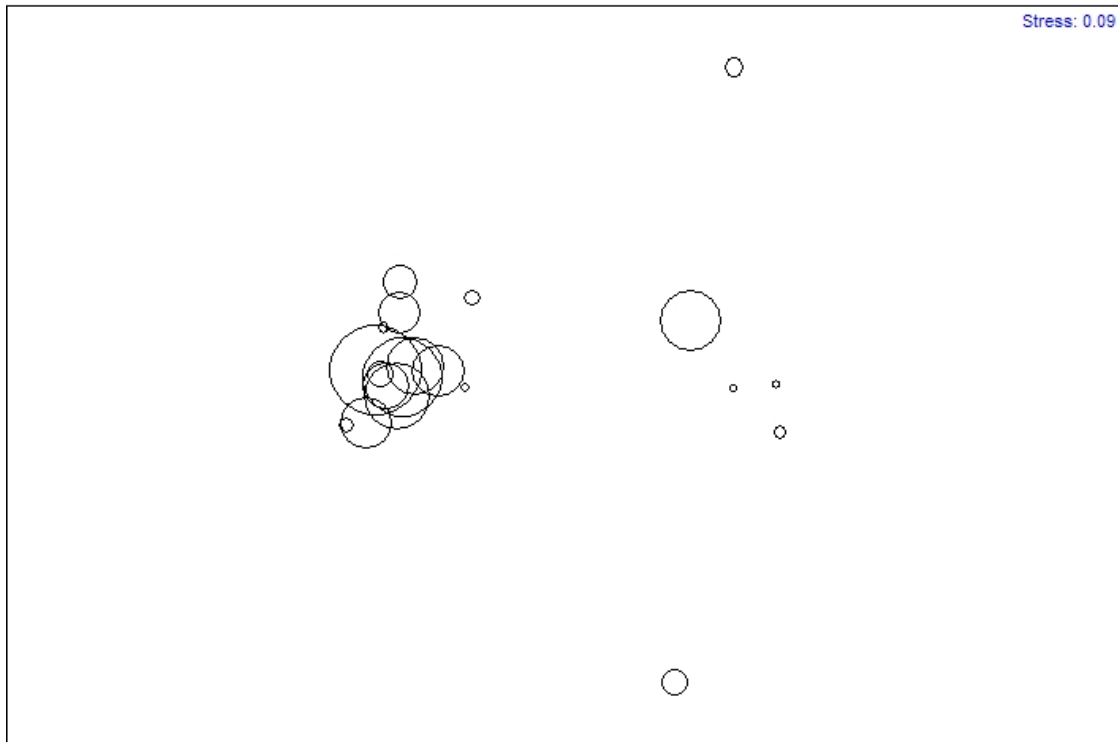


Figure 4.7(a) MDS plots of vegetation groups with bubble size relative to *Neosarmatium* spp. burrow density.

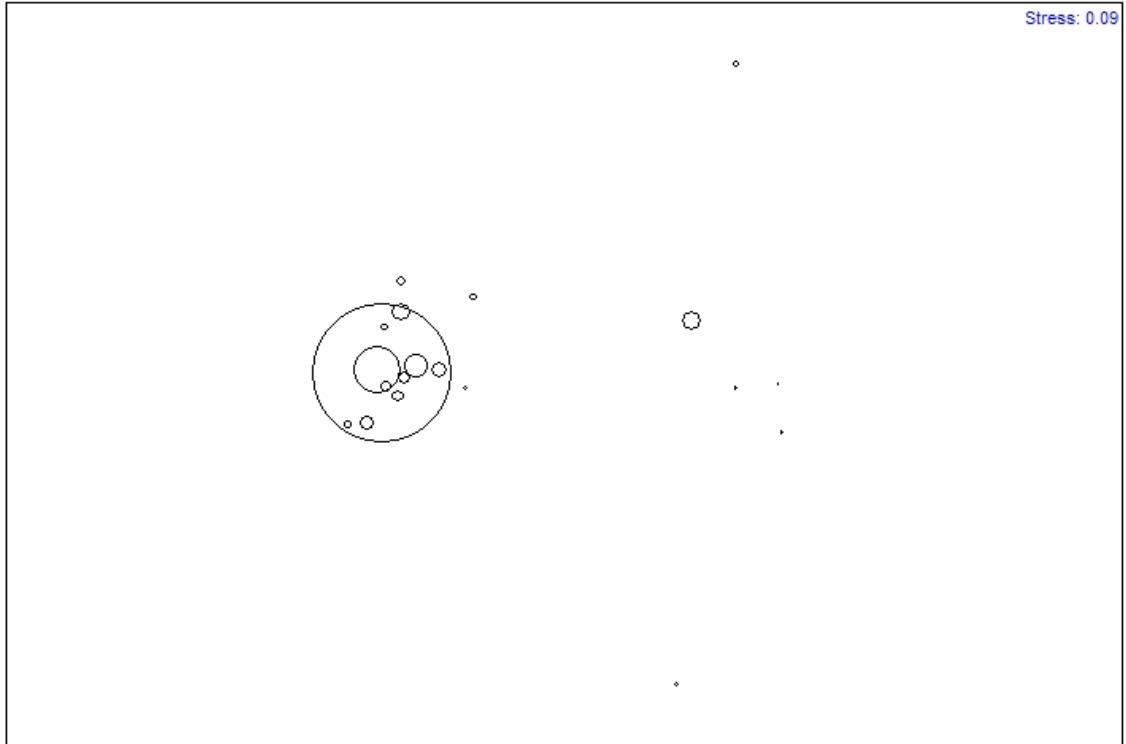


Figure 4.7(b) MDS plots of vegetation groups with bubble size relative to *P. erythrodactyla* burrow density.

4.3.4 Relationship between burrow abundance and *Ceriops tagal* dominance

Vegetation at control sites was dominated by *C. tagal* with the exception of CC(a) which differed in having more *B. exaristata*. Of the storm-water input sites, five were dominated by *C. tagal* and five by other mangrove species. Storm-water input sites were grouped on this basis and the number of *Neosarmatium* spp. and *P. erythrodactyla* burrows compared between them. There appeared to be more *Neosarmatium* spp. burrows at *C. tagal* dominated sites than at the others ($n = 10$, mean = 1.12 ± 0.7 95% CI vs. 0.48 ± 0.8 95% CI) and more burrows of *P.*

erythrodactyla ($n = 10$, mean = 0.89 ± 0.44 95% CI vs. 0.35 ± 3.00 95% CI).

However, these data could not be transformed to meet the assumptions of a t -test. Nor could a Mann-Whitney U test be used, as there was a marked difference between the sample distributions. Instead, a Fisher Exact test was used to determine if there were significant differences in the proportion of cases in which there were no burrows, and some burrows, in the two mutually exclusive groups. These tests did not detect a significant difference for *Neosarmatium* spp. burrows (Fisher Exact test $P = 0.141$) or for *P. erythrodactyla* burrows (Fisher Exact test $P = 0.303$). However, these results need to be interpreted with caution, as it is highly likely that salinity also affects burrow abundance as found in the long-term comparisons, and further discussed below.

4.3.5 Substratum

Mean salinity was lower at all storm-water input sites compared to the respective control site with the exception of ASW in May. Figures 4.8 and 4.9 show the mean soil core water salinity at each site in May and December 2007 respectively. These data did not meet the assumptions required by ANOVA and could not be adequately transformed. Nor were comparison of salinity between control and storm-water treatments at each time advisable using a paired t -test, because even after transformation there were large differences between sample variances, and the distribution of the differences were not normal. Instead, the non-parametric Mann Whitney U test (two-tailed) was used to compare the median salinity at storm-water input sites in May and in December. Data were first transformed ($\log x$) and

subsequently the sample distributions for May were very similar. There remained more difference between the sample distributions for December, and thus those results should be interpreted with caution. In both cases median salinity was significantly lower at storm-water input than control sites (May; Mann-Whitney $U = 7.5$, $n = 20$, $P = 0.001$; December; $U = 3$, $n = 20$, $P < 0.001$).

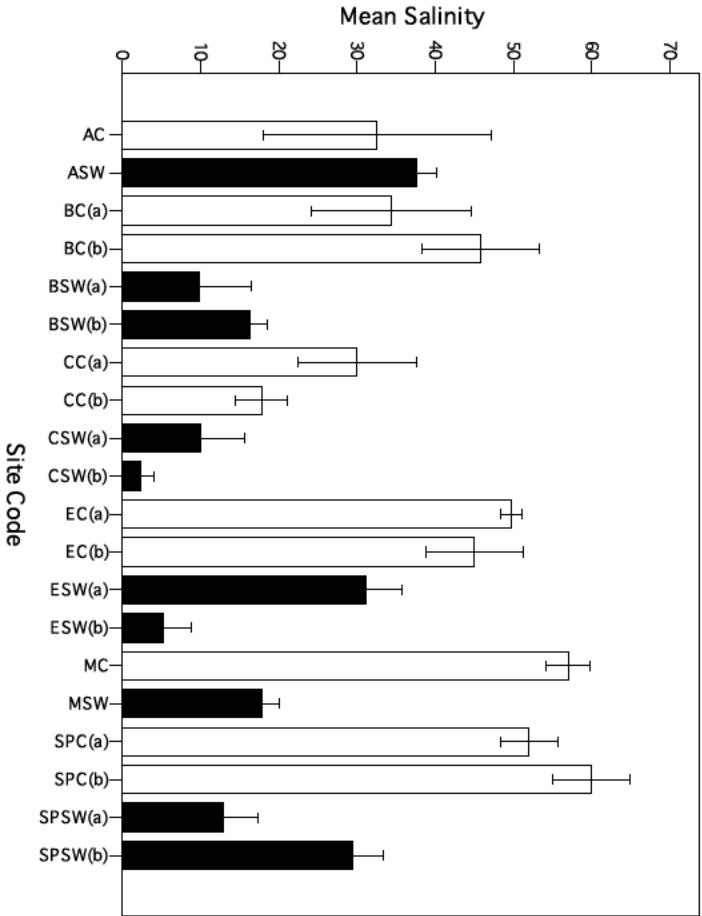


Figure 4.8 May 2007. Mean soil core water salinity at each site. Bars are the 95% confidence interval around the mean. No fill = control sites; dark fill = storm-water input sites.

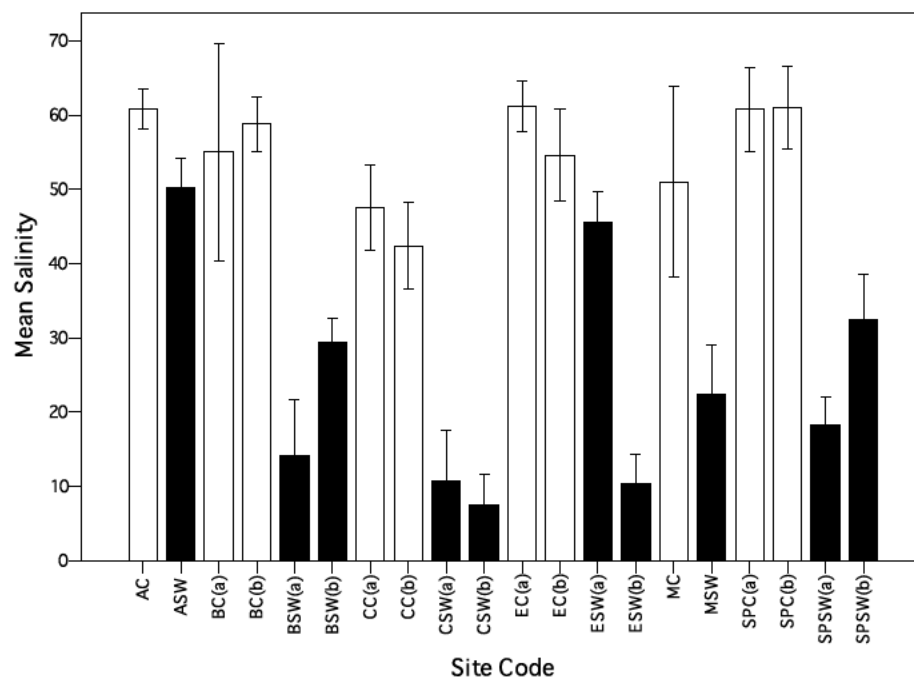


Figure 4.9 December 2007. Mean soil core water salinity at each site. Bars are the 95% confidence interval around the mean. No fill = control sites; dark fill = storm-water input sites.

Comparisons of mean pH between storm-water input and control sites are less clear. Figure 4.10 illustrates the pH at each site in May 2007. Within seven paired comparisons pH is higher at storm-water input sites; between one pair there is little difference; and pH is noticeably lower in two comparisons. As noted in the previous chapter, the December 2007 data are considered erroneous and are not considered further.

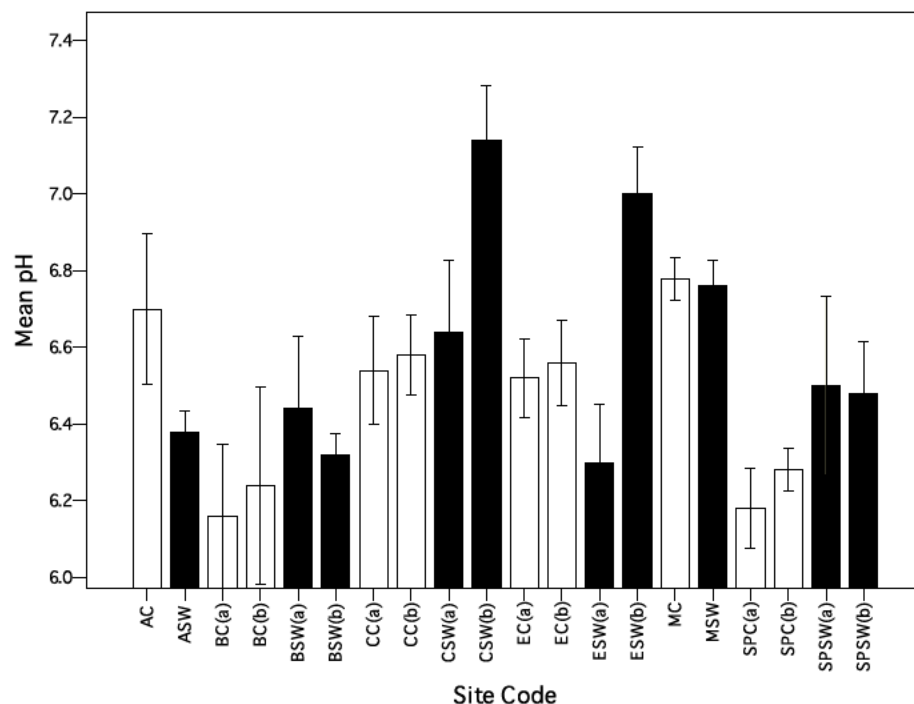


Figure 4.10 May 2007. Mean soil core water pH at each site. Bars are the 95% confidence interval around the mean. No fill = control sites; dark fill = storm-water input sites.

4.3.6 Relationship between burrow abundance and soil core water salinity

Figures 4.11 and 4.12 illustrate the relationship between mean soil core salinity and mean burrow abundance of *Neosarmatium* spp. and *P. erythrodactyla* burrows respectively (data are from May and December 2007 and are combined for illustrative purposes). In both cases the relationship is extremely similar to that found within the long-term comparison of fewer sites (Chapter 3). Considering all the data, there appears to be a threshold at a mean salinity approximating undiluted seawater, at

which larger numbers of burrows of both taxa were present. The possibility of a salinity threshold effect was examined using a Fisher Exact test to determine if there were significant differences in the number of cases in which there were no burrows, and some burrows, in the two mutually exclusive categories of core soil water salinity of (a) less than 35‰ and (b) equal or greater to 35‰. For *Neosarmatium* spp. there was a significant difference between the observed and expected frequencies of cases in each category (Fisher's Exact test; $P = 0.021$). However, for *P. erythrodactyla* there was no significant difference (Fisher's Exact test; $P = 0.345$).

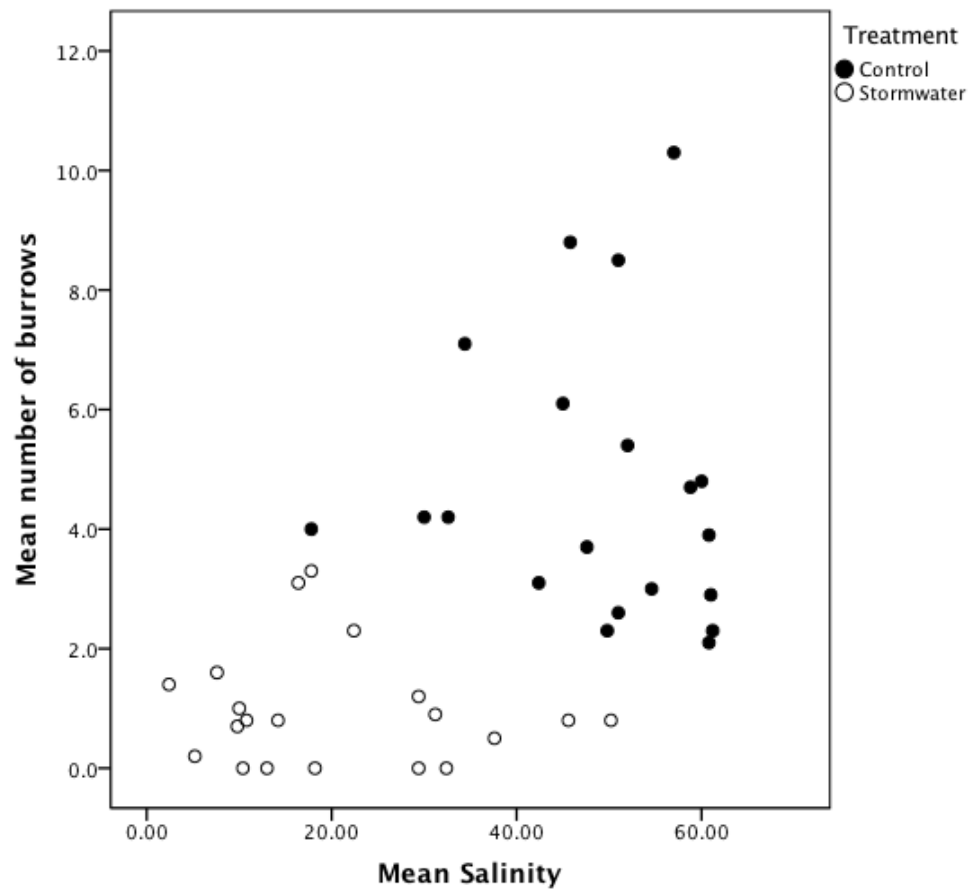


Figure 4.11 *Neosarmatium* spp. Mean soil core water salinity vs. abundance of burrows.

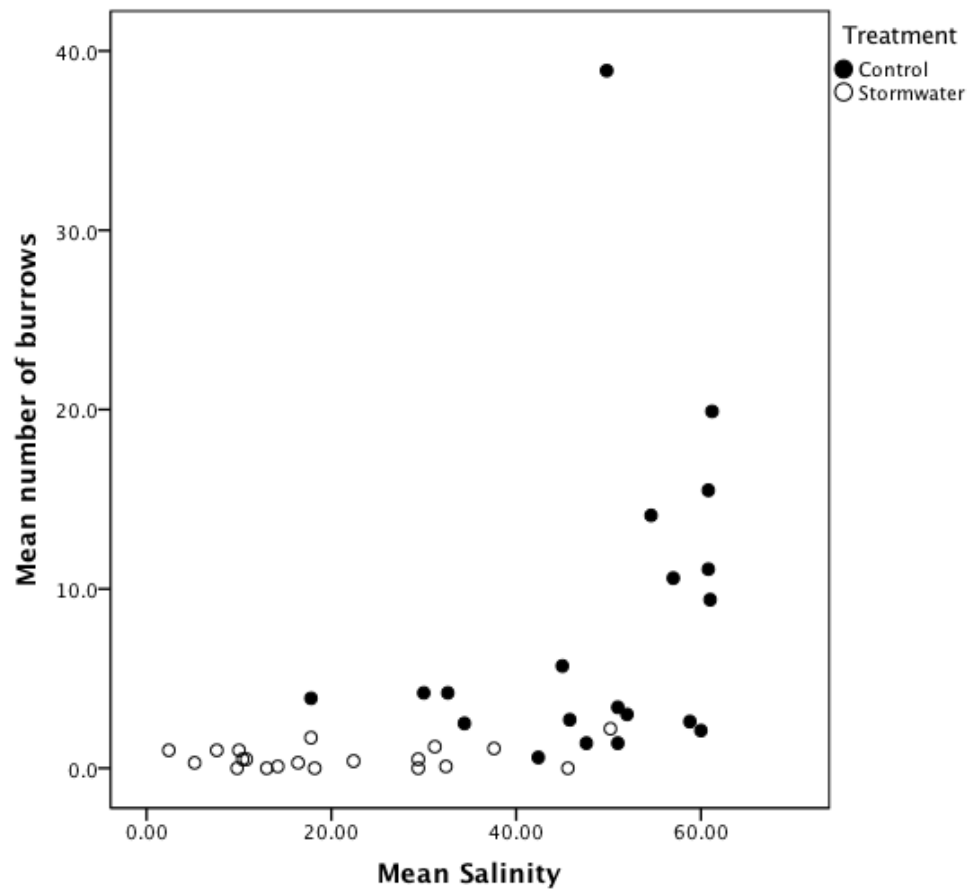


Figure 4.12 *P. erythrodactyla*. Mean soil core water salinity vs. abundance of burrows.

4.4 Discussion

4.4.0 Sesarmid burrow abundance

As for the long-term comparisons made in Chapter 3, the results of this study showing fewer burrows at storm-water input sites compared to control sites are consistent with discharge of urban storm-water into mangrove communities, resulting in a decline in abundance of both *Neosarmatium* spp. and *Parasesarma erythrodactyla*. This finding, from a larger geographical scale is consistent with discharge of urban storm-water runoff reducing the abundance of these two taxa in similar mangrove communities across the study region. Such communities occur along the entire eastern Queensland coast and, based on distribution records, are likely to be inhabited by *Neosarmatium trispinosum*, *N. fourmanoiri*, and *P. erythrodactyla* (Davie, 2002). Thus, storm-water runoff may be reducing the abundance of these species at a far larger scale than examined by this study, which is of considerable concern given their keystone role in mangroves. Duplication of this study in other areas would confirm if this was the case and if so, mapping of storm-water discharge points would be a useful way to estimate the geographical extent of the impact. In Chapter 6 I report upon the implications of a decline in abundance of *N. trispinosum* in terms of its role as a leaf remover in mangroves.

4.4.1 Vegetation comparisons between storm-water input and control sites

The vegetation at each site was described using the mean basal area of each mangrove species present. This allowed comparisons among sites, and between control sites and storm-water sites. Overall, Analysis of Similarity showed that in terms of mean basal area of each species present, there was a significant difference in the vegetation community at storm-water input and control sites. This dichotomy is broadly reflected in the groupings developed by cluster analysis although there are site-specific exceptions that may be related to the different time and magnitude of exposure to storm-water input as discussed below. Variability of the vegetation community differed significantly among locations but at only one site SP(b) was there a significant difference between a paired storm-water input and control site. In summary, there was a significant difference in mean measures of basal areas between storm-water input and control sites, but no significant within site variability for either storm-water input or control sites.

Across the regional study area, *Ceriops tagal* and *Bruguiera exaristata* were the most dominant species within the sites examined. All but one of the control sites was dominated by *C. tagal* and the exception, [CC(a)] also had *C. tagal* present. *C. tagal* dominated the vegetation at half the storm-water sites and the others were dominated by *B. exaristata* or *Excoecaria agallocha* or *Lumnitzera racemosa*. However, most of the storm-water input sites differed from controls in that they usually had a higher basal area of species other than *C. tagal* such as *B. exaristata*, *B. gymnorrhiza*, *E. agallocha*, and *L. racemosa*. This is important because these species are more

typically associated with the landward edge of mangroves (Bunt *et al.*, 1982; Lovelock, 1993, Duke *et al.*, 1998), which receive more freshwater influence. This finding is consistent with that of Moritz-Zimmerman (2002) who found that *Cerriops australis* was less prevalent, and species such as *L. racemosa* more common, adjacent to drainage channels carrying storm-water. It is also consistent with the known salinity preferences of seedlings of these species. For example, *B. exaristata* has optimal seedling growth in 5‰ seawater (Clarke *et al.*, 2001), *E. agallocha* has optimal growth at about 13‰ (Joshi & Ghose, 2003), young plants of *B. gymnorhiza* have an optimal growth rate at 22.5‰ (Takemura *et al.*, 2000), and germination of *L. racemosa* is restricted to salinities < 25‰ (Yong *et al.*, 2004). This suggests that these species may have been better able to colonise mangroves that received storm-water inputs and thus have lower soil core water salinities. The finding of a lower basal area of these species at some storm-water input sites (Eimeo and Armstrong's Beach) may be explained by the relatively recent input of storm-water compared to other sites.

4.4.2 Relationship between vegetation type and sesarmid burrow abundance

The finding that vegetation was different at storm-water input sites compared to control sites and the possible effect of this on sesarmid abundance needs to be interpreted with caution. Sesarmid distribution and abundance has been found to be influenced by vegetation characteristics (Lee & Kwok, 2002; Lui *et al.*, 2002) including different root and trunk types (Cantera *et al.*, 1999), or because they may have a preference for feeding on leaves and propagules of one mangrove species over

another (e.g. Ashton, 2002; Camilleri, 1989; Clarke & Kerrigan, 2002; Dahdouh-Guebas *et al.*, 1998; Smith, 1987). However, it has also been repeatedly proposed that sesarmids could influence the vegetation through the removal of propagules, especially considering they may have a preference for feeding on the propagules of one mangrove species over another (Clarke & Kerrigan, 2002; Clarke, 2004; Dahdouh-Guebas *et al.*, 1998; McGuinness, 1997b; Smith, 1987). Sesarmids may also influence soil biochemistry through their burrowing (Kristenson, 2008; Smith, *et al.*, 1991) and this in turn can change the amount of phytotoxins (such as sulphides) that are present in the soil. Within this study, the relationship between the abundance of both *Neosarmatium* spp. and *Parasesarma erythrodactyla* burrows and vegetation type was examined by multidimensional scaling. This found that even sites with very similar vegetation had marked differences in burrow abundance of both taxa, and thus shows that burrow abundance is not related to overall vegetation type or *vice versa*. Notwithstanding, burrow abundance may be related to single components of the vegetation community.

C. tagal dominated all control sites except at CC(a), but at that site it still made up 25% of the total basal area of the vegetation. Micheli (1993) found that in laboratory experiments *Sesarma smithii* (= *Neosarmatium trispinosum*) preferred to eat leaves of *Rhizophora stylosa* than those of *Avicennia marina*, *B. exaristata* and *C. tagal*. However, examination of burrows found that shredded *C. tagal* leaves were present in higher quantities than those of all other species indicating that *N. trispinosum* may have a preference for feeding on leaves of *C. tagal*. Micheli's (1993) study highlights

the risk of interpreting results of laboratory feeding experiments as accurate depictions of normal feeding behaviour. Storm-water input sites were divided into two groups, those that were dominated by *C. tagal* and those that were not. A comparison of *Neosarmatium* spp. and *P. erythrodactyla* burrow abundances between these groups was problematic because soil core water salinity varied markedly amongst sites, and this would have also influenced burrow abundance. However, it appeared that *C. tagal* dominated sites had more burrows of both taxa. Measures of presence or absence of burrows in each group were compared but there was no difference between the two vegetation groups. However, these results need to be interpreted with caution, as it is highly likely that salinity also affects burrow abundance as found in the long-term comparisons and this effect may have confounded these analyses. There is evidence that mangrove leaf chemistry changes with season and thus diet quality may also be influencing the abundance of crabs. For example, Kathireson & Ravi (1990) found that mangrove leaf tannins increased with the onset of the wet season and Basak *et al.* (1998) reported that both tannin and polyphenol concentrations were highest in the wet season, although there was significant temporal variation among species. Thus, leaves of mangroves growing in low salinity environments such as storm-water input sites may be less palatable to crabs and such changes may differ among mangrove species.

4.4.3 Influence of storm-water input on soil core water salinity

Storm-water input sites receive point discharge of large amounts of freshwater relative to control sites. Soil core water salinity was significantly lower at storm-

water input sites compared to controls during both the late wet season and late dry season. This is also consistent with observations made at a smaller number of sites over a longer period of time (Chapter 3). The differences in soil core water salinity amongst storm-water input sites were most likely due to differences in the quantity of storm-water input. Salinity amongst control sites was relatively consistent during the late dry season, but varied during the late wet season. This was not unexpected because rainfall was expected to vary across the region, and some sites may have received more overland flows due to topographical differences in the adjacent catchments.

4.4.4 Relationship between soil core water salinity and sesarmid burrow abundance

As for the long-term comparison study, there appeared to be a threshold at approximately 35‰ (the value of undiluted seawater) above which *Neosarmatium* spp. burrows were more abundant, and the overall pattern of higher burrow numbers at higher soil core water salinity was similar. However, it was again clear that above this threshold there were other factors that also influenced abundance. For *P. erythrodactyla* the overall relationship between burrow abundance and salinity was similar to that found in the long-term comparisons but in this geographically larger study there was no clear evidence of a threshold effect. This may be because mean soil core water salinity in this study was calculated from two measurements only, and thus was a less robust estimate than for that used in the long-term study.

4.4.5 Summary

This regional study corroborates the findings of the long-term comparisons at a local scale in that discharge of urban storm-water into mangrove communities appears to result in a decline in abundance of both *Neosarmatium* spp. and *P. erythrodactyla* as estimated by burrow counts. Soil core water salinity was higher at controls compared to storm-water input sites although the magnitude of this difference varied among locations. Declines in salinity were directly attributed to storm-water inputs, and the magnitude of the decline was proportional to the amount of storm-water input. Burrow abundance tended to be higher at sites with higher soil core water salinity, but there was no significant correlation between these factors. Instead, for *Neosarmatium* spp. at least, there was evidence of a threshold at about 35‰ where burrow abundance tends to increase, although it was clear that other factors had a marked influence. Overall, there was a difference between the mangrove vegetation at control sites compared to storm-water input sites with the latter tending to contain more mangroves species that recruit and survive better in lower salinity environments. However, this was not the case at all sites and the variation was attributed to the time and magnitude of exposure to storm-water inputs. Although burrow abundance was not related to overall vegetation type, it might be linked to the dominance of *C. tagal* within mangrove communities. At all sites where burrow abundance was high (i.e. controls), *C. tagal* was dominant or, in the case of the single exception, present as a high proportion of the vegetation. In addition, there may have been more crab burrows at storm-water input sites dominated by *C. tagal* than at those dominated by other mangroves. Based on these observations and evidence from

another study (Micheli, 1993), it was hypothesised that *C. tagal* leaves are preferred as a food source over leaves of other species. Other studies (Basak *et al.*, 1998; Kathireson & Ravi, 1990) found changes in the organic constituents in mangrove leaves during the wet season that may affect their palatability to crabs. Thus another hypothesis was that crabs will prefer to eat leaves from mangroves growing in high rather than low salinity environments. These hypotheses are examined in Chapter 5.

5 Selection of mangrove leaves from storm-water and control sites

5.1 Introduction

Previous investigations discussed in Chapter 4 found that *Cerriops tagal* typically dominated control sites and that sesarmid burrows were more abundant in these areas. Storm-water input sites were grouped into *C. tagal* dominated sites, and those that had a greater proportion of other mangrove species such as *Bruguiera exaristata*, *B. gymnorrhiza*, *Excoecaria agallocha* and *Lumnitzera racemosa*. The storm-water input sites dominated by *C. tagal* may have had more *Neosarmatium* spp. and *Parasesarma erythrodactyla* burrows. Based on these observations, and guided by the findings of another study (Micheli, 1993), it was proposed that sesarmids may have a preference for feeding on leaves of *C. tagal* over those of other species. In addition, it was proposed that crabs would prefer to eat leaves from mangroves growing in high rather than low salinity environments.

This chapter gives the results of experiments conducted to test two hypotheses.

Firstly, that sesarmids will prefer to eat leaves of *Cerriops tagal* to those of *Bruguiera exaristata*, the second most common mangrove species within the study sites.

Second, that regardless of species, leaves from sites unaffected by storm-water (high salinity environments) are preferred over those from storm-water sites (low salinity environments). If there is a preference for feeding on *C. tagal* then storm-water input may affect sesarmid abundance by causing a shift of species dominance within the

mangrove community from *Ceriops tagal* to *Bruguiera exaristata* or other species. Alternatively, storm-water run-off may affect sesarmid abundance by making their most consistently available food source of mangrove leaves less palatable. However, if such feeding preferences are demonstrated, they need to be carefully interpreted as sesarmids themselves may also have an influence on mangrove species distributions by selectively feeding on propagules of some species over others.

5.1.0 Experimental design

Leaf feeding preferences are often examined in laboratory experiments where captive crabs are offered a choice between or among equal quantities of leaves of different types. Such studies have been undertaken by Giddins *et al.* (1986) and Mitcheli (1993) for *Neosarmatium trispinosum*, by Camilleri (1989) for *Parasesarma erythrodactyla* and by Salgado-Kent & McGuinness (2008) for several northern Australian species. This technique has the benefits of ensuring that no other leaf consumers are present whose feeding may confound results, and the amount and type of food available can be effectively controlled. However, holding animals in captivity has the potential for changed behaviour that is difficult to quantify. This is a particularly important consideration for sesarmids such as *N. trispinosum*, which are known to store leaves within chambers in their burrows, possibly to improve their nutritional value (Giddins *et al.*, 1986). Many sesarmid studies have used *in situ* testing of feeding preferences (Smith, 1987; Mitcheli, 1993; Dahdouh-Guebas *et al.*, 1997; McGuinness, 1997; Clarke & Kerrigan, 2002; Clarke, 2004) particularly when an understanding of interactions between crabs and the mangrove community is

required. Techniques such as tethering of food items and exclusion caging do not appear to result in serious experimental artefacts (McGuinness, 1997b), but the design of *in situ* feeding preference experiments presents two challenges. Firstly, crab species may have different preferences for food items and areas may differ in the relative proportion of each crab species present. As such, and given the difficulty in quantifying actual crab abundance, it would be very difficult to achieve appropriate replication (i.e. identification of sufficient experimental units which support the same species assemblage with the same abundance of each species). Secondly, crabs should only be allowed access to equal quantities of each dietary item being investigated. The addition of other sources (e.g. from natural leaf litter drop) may increase availability of one or more items being tested with consequent experimental bias.

Within the study area, observations suggested that only one species of crab, *N. trispinosum*, removes leaves and further experiments confirmed this (see below). Therefore, experiments in the field at these sites can avoid complications resulting from replicate experimental units potentially containing different species of crabs, in different abundances, and with possible species-specific feeding preferences. The second complication requires more detailed consideration to develop experimental designs and techniques that isolate crabs from food sources other than that offered by the experiments. Outside of the mangrove fruiting period, *N. trispinosum* feeds almost exclusively on mangrove leaves with the only significant addition being crustaceans incidentally taken (Giddins *et al.*, 1986). Thus, a necessity of an appropriate experimental design was prevention of natural leaf litter and propagule

fall being accessible to the crabs. This was done by excluding leaf and propagule fall from the experimental units.

5.2 Methods

5.2.0 Identification of leaf removing species

Burrows of *Neosarmatium* spp. were readily identified by the presence of characteristic mounds at the entrance (see Chapter 3). Taxonomic keys use small morphological features of the dactyl to discriminate between *N. trispinosum* and *N. fourmanoiri* (Davie, pers comm), but these are difficult to discern unless the crab is captured and examined in detail. Within the study area, numerous such examinations showed that these species could also be readily identified in the field on the basis of the morphology of the dorsal carapace, at a distance of several metres (see Chapter 3). This showed that *N. fourmanoiri* is rare within the study area, occurring at only two sites; CC(a) and BSW(a). As such, its role as a leaf remover across the study site was considered minor, and leaf feeding preference experiments focused on the role of *N. trispinosum*. At all other sites any burrows with mounds could therefore be confidently identified as belonging to *N. trispinosum*, and it was within these areas that feeding preference studies were conducted. To confirm the role of *N. trispinosum* as the sole leaf remover at these sites, a preliminary experiment was done. This was carried out at each of three locations; Slade Point, Eimeo and Bucasia (close to existing control sites). Ten points were randomly selected along a transect running parallel to the shore and about 10m in from the landward mangrove margin. At each

point leaves from each of *C. tagal* and *B. exaristata* were tethered to an unmovable object (e.g. knee root, small sapling or stake made of a small mangrove branch) with one metre of coloured sewing cotton tied to the petiole. McGuiness (1997c) found that using one-metre long tethers with such small points of attachment did not alter normal feeding behaviour. Leaves of *B. exaristata* were tethered with blue cotton and those of *C. tagal* with maroon and the fate of each leaf was monitored daily for seven consecutive days. Every time a leaf was examined it was allocated to one of four categories; 1) left remaining uneaten on the forest floor, 2) partially eaten, 3) removed to a *N. trispinosum* burrow or 4) removed to another type of burrow. The latter two were easily discerned as the tether led down into a burrow.

5.2.1 Preliminary experiments

When conducting feeding preference experiments, leaves of different types or species offered to crabs need to be identifiable after nightly feeding periods, so that the number of each remaining can be determined. Large numbers of leaves were required for the experiments and these had to be placed under roofs made of trays to prevent natural leaf litter and propagule fall from being included in the experimental units (see below). Tethering, as previously described, is a common way of marking leaves but a pilot study found that this was unsatisfactory because large numbers of leaves placed closely together meant that tethers often became tangled, which was likely to interfere with natural feeding behaviour. Instead, the leaves were marked by using a paper punch to make a small (5mm diameter) hole through the leaf in a specific location for each leaf type (Figure 5.1).



Figure 5.1 **Method of marking leaves.**

To test whether any experimental artefacts resulted from this method of marking, a preliminary experiment was conducted adjacent to the Bucasia control site. Within the site, five square 2m² trays were randomly located and suspended approximately 50cm above the substratum so that natural leaf litter fall was prevented from reaching the substratum under the tray (i.e. the tray shadow). Trays were constructed of an outer frame of 20mm diameter PVC pipe, over which low shading grade shade cloth was attached with galvanised wire ties. To prevent crabs accessing natural leaf litter that had fallen outside of the tray, some prior knowledge of foraging patterns was required. At each of three locations (Slade Point, Eimeo, Bucasia; adjacent to existing control sites) 20 *N. trispinosum* burrows were randomly selected and the foraging trails leading from the burrow were observed. Trails were readily observable due to the indentations which the crabs' chelipeds had made in the soft soil surface. The

maximum distance between the burrow entrance and the furthestmost end of the trail was measured and taken as the maximum radius that the crab travelled each night. Whilst each tray was located randomly, its exact orientation was such that it covered at least four burrow entrances each of which was at least the maximum foraging distance inside the tray perimeter. Similarly, no burrow entrances outside the tray shadow were within the maximum foraging radius from the tray perimeter. In this way, it could be determined with some certainty that only crabs living under the tray shadow had access to leaves placed under the tray for the purpose of the experiment.

Six different types of leaves were placed under each tray; whole *Ceriops tagal* leaves, whole *Bruguiera exaristata* leaves, *Ceriops tagal* and *Bruguiera exaristata* leaves punched through the left hand side (looking down on the dorsal surface with the leaf petiole pointing towards the observer) and *Ceriops tagal* and *Bruguiera exaristata* leaves punched through the right hand side. The degree of leaf senescence is known to have a strong effect on leaf choice by *N. trispinosum* (Giddins *et al.*, 1986) but there was no practical way to accurately measure this in the field. To minimise variability among leaves, they were picked green from adjacent mangrove trees avoiding new growth, older nearly senescent leaves, or those with significant insect damage. For each species, collected leaves were as similar in size as possible to avoid confounding the results by any preference crabs may have for leaf size. Leaves were placed inside a calico bag from which they were randomly selected, marked (or left whole) and placed under each tray. The texture, colour and vein patterns differ between leaves of *C. tagal* and *B. exaristata* so these species could be readily

distinguished even when marked in the same way. Any leaves removed by crabs were replaced each day with others of the same type, so that equal numbers of leaves of each type were available each night. Initial experiments used four leaves of each type under each tray (21st, 22nd and 23rd March 2007) and then eight leaves (25th, 26th and 27th March 2007). These experiments were subsequent to a large spring tide period with a decline in tidal height commencing on the 20th March 2007. All experiments were conducted during periods when the study sites were not inundated by tides and thus there was no import or export of leaves by this means. In these experiments the number of leaves proved insufficient as all were consumed each night. The second experiment was conducted during a neap tide period (11th, 12th and 13th April) using ten leaves of each type which was sufficient as generally some leaves of each type remained each day, thereby allowing potential preferences to be examined.

5.2.2 Primary leaf feeding preference experiment

The primary experiment was conducted in areas adjacent to existing control sites at Slade Point, Eimeo and Bucasia, during the nightly periods 22nd to 26th April 2007 and four days subsequent to a spring tide period (maximum tidal height was reached on the 18th April 2007). Within each location, five leaf litter trays (1m²) were randomly placed and orientated in the manner described previously. Fifteen leaves of four different types were placed under each tray; *C. tagal* and *B. exaristata* from storm-water input sites marked with a hole punched on the leaf hand side as previously described, and *C. tagal* and *B. exaristata* from trees within the surrounding area (i.e. not affected by storm-water), marked with a hole punched on

the right hand side. Leaves were collected green and randomly allocated to trays. The number of each type of leaf remaining each day was recorded. Any leaves removed by crabs were replaced with others of the same type, so that an equal number of each was available each night.

On completion of the experiment (27th April 2007) the accumulated leaf litter on each tray was collected, dried at 60°C for 72 hours and weighed to the nearest 0.01g. The remainder of the leaves prepared for the experiment (*Cerriops tagal* $n = 58$; *Bruguiera exaristata* $n = 73$) were retained, dried in the same way, and the average leaf weight calculated. The dry weight of natural leaf litter accumulation on each tray was then compared to the estimated dry weight of leaves removed by the crabs.

5.3 Results

5.3.0 Identification of leaf removing species

The cumulative number of leaves for all locations combined over the period of the experiment in the categories; (a) left remaining on the forest floor (b) partially eaten or (c) removed to a burrow of either *N. trispinosum* or another crab are in Table 5.1.

No leaves were removed to any burrows other than those belonging to *N.*

trispinosum, and this species removed all but three leaves, two of which were untouched (one each of *C. tagal* and *B. exaristata*) at the end of the experiment. The third (*C. tagal*) was found partially eaten with the remainder left on the forest floor.

The tether connected to this leaf had become tangled and could not be extended any

further, so the remaining leaf portion could not be taken into any burrow. The tether was untangled and the next day it led into a *N. trispinosum* burrow. This suggests it is highly likely that the leaf was partially removed by *N. trispinosum* on the first night and, after the tether was untangled, the remainder was removed the following night.

5.3.1 Preliminary experiments

The maximum radius that *N. trispinosum* travelled from a burrow entrance was 29cm at Bucasia (mean = 20.6cm; 95% CI $\pm$ 1.75cm), 28cm at Eimeo (mean = 18cm; 95% CI $\pm$ 1.74cm) and 27cm at Slade Point (mean = 19.45cm; 95% CI $\pm$ 2.17). During the subsequent experiments, leaf litter trays were aligned so that no burrow entrance underneath the tray was within 35cm of the tray shadow perimeter and no burrow outside the tray shadow was within that distance from the perimeter.

On all occasions except one (tray five on the first night), one leaf of each type was left under each tray the next day. Table 5.2 shows the mean number of leaves of each type remaining after each night from the 11th to 13th April and over the whole period.

Table 5.1 **Fate of tethered *B. exaristata* and *C. tagal* leaves as cumulative totals for all locations combined** (n = 30 for each species tethered on the forest floor at the commencement of the experiment)

Remaining			Partially eaten		Removed to a <i>N. trispinosum</i> burrow		Removed to another burrow type	
Date	<i>Bruguiera exaristata</i>	<i>Cerriops tagal</i>	<i>Bruguiera exaristata</i>	<i>Cerriops tagal</i>	<i>Bruguiera exaristata</i>	<i>Cerriops tagal</i>	<i>Bruguiera exaristata</i>	<i>Cerriops tagal</i>
05/03/07	7	5	0	1*	23	25	0	0
06/03/07	2	4	0	0	28	26	0	0
07/03/07	2	3	0	0	28	27	0	0
08/03/07	1	3	0	0	29	27	0	0
09/03/07	1	2	0	0	29	28	0	0
10/03/07	1	1	0	0	29	29	0	0
11/03/07	1	1	0	0	29	29	0	0

*Approximately half eaten

Table 5.2 **Mean number of marked and unmarked *B. exaristata* and *C. tagal* leaves remaining after each night's feeding**

Date	<i>Bruguiera</i> <i>exaristata</i> ; left hole	<i>Bruguiera</i> <i>exaristata</i> ; right hole	<i>Bruguiera</i> <i>exaristata</i> ; whole leaf	<i>Ceriops</i> <i>tagal</i> ; left hole	<i>Ceriops</i> <i>tagal</i> ; right hole	<i>Ceriops</i> <i>tagal</i> ; whole leaf
11/04/07	2.4	3.0	4.0	5.4	5.2	3.6
12/04/07	6.4	5.4	6.4	6.2	7.2	7.0
13/04/07	5.8	5.2	6.2	7.4	6.2	6.2
Whole period	4.9	4.5	5.3	6.4	6.2	5.6

More leaves remained after the second and third night compared to the first.

However, the number of leaves of each species and mark type remaining did not appear to show any clear differences, except that fewer *Bruguiera exaristata* leaves were left in most cases. Feeding preferences and the effect of time were tested with a repeated measures ANOVA. A preliminary test for sphericity with Mauchly's Test was not significant ($df = 2$, $W = 0.198$, $P = 0.375$). There was a significant difference in the number of leaves remaining among nights ($F_{2, 48} = 17.747$, $P < 0.0001$) but no significant higher order interactions (Table 5.3). There was no significant difference in the numbers of differently marked leaves remaining ($F_{2, 24} = 0.026$, $P = 0.974$), nor between species ($F_{1, 24} = 1.41$, $P = 0.247$), and no significant interaction between

these factors ($F_{2, 24} = 0.314$, $P = 0.734$) (Table 5.4). These results show that there were no feeding preferences exhibited for differently marked leaves and thus it can be assumed that leaf marking would not result in any experimental artefacts.

Table 5.3 Tests of within-subjects effects of leaf removal for different times, for different treatments (marked and umarked) and species.

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
Time	Sphericity Assumed	113.09	2	56.54	17.747	< .001
Time * Mark	Sphericity Assumed	4.64	4	1.16	.364	.833
Time * Species	Sphericity Assumed	3.27	2	1.63	.513	.602
Time * Mark * Species	Sphericity Assumed	12.73	4	3.18	.999	.417
Error (time)	Sphericity Assumed	152.93	48	3.19		

Table 5.4. Tests of between-subjects effects of leaf removal for treatment (marked and unmarked) and species.

Source	Type III Sum	df	Mean		
	of Squares		Square	F	Sig.
Mark	.96	2	.48	.026	.974
Species	25.60	1	25.60	1.410	.247
Mark * Species	11.40	2	5.70	.314	.734
Error	435.87	24	18.16		

5.3.2 Primary leaf feeding preference experiment

The number of leaves of each species and from each source remaining was similar within locations. However, more leaves remained at Slade Point than at Eimeo and Bucasia and the latter two sites were more similar in this respect. Table 5.5 shows the mean number of leaves of each type remaining after each night from the 22nd to 26th April and over the whole period.

Table 5.5 **Mean number of *B. exaristata* and *C. tagal* leaves from storm-water input or control site remaining.**

Mean number of each leaf type remaining												
<i>Bruguiera exaristata</i> ; storm-water				<i>Bruguiera exaristata</i> ; control			<i>Ceriops tagal</i> ; storm-water			<i>Ceriops tagal</i> ; control		
Date	Slade Point	Eimeo	Bucasia	Slade Point	Eimeo	Bucasia	Slade Point	Eimeo	Bucasia	Slade Point	Eimeo	Bucasia
22nd	4.2	2.6	0.8	3.2	2.8	0.4	5.8	2.2	0.6	4.0	4.0	0.6
23rd	6.2	4.0	2.6	3.8	2.8	3.2	8.6	5.8	4.2	7.8	3.4	2.6
24th	6.8	5.6	1.4	8.0	3.8	2.2	8.2	6.0	2.4	9.2	5.2	4.2
25th	8.2	4.2	4.0	6.6	5.0	4.4	10.8	6.6	5.8	11.2	7.2	8.0
26th	11.6	6.8	10.6	10.0	5.8	9.2	12.4	6.4	10.4	12.4	8.2	9.2
Whole period	7.4	4.6	3.9	6.3	4.0	3.9	9.2	5.4	4.7	8.9	5.6	4.9

As in the preliminary experiment, feeding preferences were tested by a repeated measures ANOVA. Mauchly's Test was not significant and thus sphericity was assumed ($df = 9$, $W = 0.701$, $P = 0.057$). There was a significant difference in the number of leaves remaining among nights ($F_{4, 192} = 53.988$, $P < 0.001$) and a

significant interaction between times and location ($F_{8, 192} = 3.42, P = 0.001$). This shows that the numbers of leaves removed did not vary in the same way over time at different locations. Therefore, it was not unexpected that there was also a significant difference in the numbers of leaves remaining at each location ($F_{2, 48} = 6.899, P = 0.002$) (Table 5.6). There was no significant difference in the number of leaves of each species remaining ($F_{1, 48} = 2.41, P = 0.127$) or between the source of the leaves ($F_{1, 48} = 0.04, P = 0.842$), and no significant interactions (Table 5.6).

For the leaves used in the feeding experiments, the mean dry weight of a *C. tagal* leaf was 0.311g and 0.316g for a *B. exaristata* leaf. These data allowed an estimation of the dry weight of leaf litter removed each day at each location based on the number of leaves removed multiplied by the mean dry weight of each leaf type (Table 5.7). These were compared to the dry weight of actual leaf litter fall in each location collected from the tops of each of the five trays in each location.

Table 5.6 Tests of between-subjects effects of leaf removal for different locations, species and leaf source.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Location	778.687	2	389.343	6.899	0.002
Source	2.253	1	2.253	0.040	0.842
Species	136.013	1	136.013	2.410	0.127
Location * Source	12.007	2	6.003	0.106	0.899
Location * Species	28.247	2	14.123	0.250	0.780
Source * Species	10.453	1	10.453	0.185	0.669
Location * Source * Species	0.127	2	0.063	0.001	0.999
Error	2708.800	48	56.433		

Table 5.7 **Estimated dry weight of *B. exaristata* and *C. tagal* leaves removed**

<i>Bruguiera</i> <i>exaristata</i> ; Mean number of leaves removed				<i>Bruguiera</i> <i>exaristata</i> ; Estimated dry weight of leaves removed (g/m ²)			<i>Ceriops tagal</i> ; Mean number of leaves removed			<i>Ceriops tagal</i> ; Estimated dry weight of leaves removed (g/m ²)			Total Estimated dry weight of leaves removed (g/m²)		
Date	Slade Point	Eimeo	Bucasia	Slade Point	Eimeo	Bucasia	Slade Point	Eimeo	Bucasia	Slade Point	Eimeo	Bucasia	Slade Point	Eimeo	Bucasia
22nd	22.6	24.6	28.8	7.14	7.77	9.10	20.2	23.8	28.8	6.28	7.40	8.96	28.88	15.17	18.06
23rd	20.0	23.2	24.2	6.32	7.33	7.65	13.6	20.8	23.2	4.23	6.47	7.22	10.55	13.80	14.87
24th	15.2	20.6	26.4	4.80	6.51	8.34	12.6	18.8	23.4	3.92	5.85	7.28	8.72	12.36	15.62
25th	15.2	20.8	21.6	4.80	6.57	6.83	7.0	16.2	16.2	2.18	5.04	5.04	6.98	11.61	11.87
26th	9.4	17.4	10.2	2.97	5.50	3.22	5.2	15.4	10.4	1.62	2.55	3.23	4.59	12.64	6.45

Over this period of time, the mean amount of leaf litter (dry weight) removed at Slade Point was 11.94 ± 8.52 g/m² and the actual leaf litter fall during this period was 9.48 ± 2.27 g/m². At Eimeo 13.12 ± 1.22 g/m² was removed and the actual leaf litter fall

was $6.90 \pm 1.60 \text{ g/m}^2$. At Bucasia $13.37 \pm 3.91 \text{ g/m}^2$ was removed and the actual leaf litter fall was $8.41 \pm 2.23 \text{ g/m}^2$. These data show that during the period of time measurements were taken, crabs would have removed all naturally available leaf litter from the substratum. However, this observation needs to be interpreted with caution because leaves offered to crabs were fresh and those that made up the litter fall were senescent.

5.4 Discussion

These experiments were aimed to determine if *N. trispinosum* prefers to eat leaves of *Cerriops tagal* over those of *Bruguiera exaristata*, and that regardless of species, leaves from sites unaffected by storm-water (high salinity environments) are preferred over those from storm-water sites (low salinity environments).

5.4.0 Identification of leaf removers

The results of preliminary studies guided the design of this experiment, but also provided interesting insights into sesarmid feeding ecology. Sesarmids have been considered as important consumers of mangrove leaf litter (Lee, 1998) and leaves form the most important part of their diet. More recently, this generalisation has been questioned through use of techniques such as stable isotope analysis (Bouillon, *et al.*, 2008) and fatty acid profiling (Meziane *et al.*, 2006; Mchenga & Tsuchiya, 2011). An important finding of this study was that *N. trispinosum* was the only species in the study area that removed leaves from the substratum, even though *P. erythrodactyla*

was also present and abundant. However, the experiment did have a limitation in that only green leaves were used and whether this species would remove senescent leaves requires investigation. *P. erythrodactyla* is found in both mangrove and saltmarsh habitats (Mazumder *et al.*, 2008; Guest & Connolly, 2004). Laboratory experiments conducted by Camilleri (1989) demonstrated the capacity of this species to process large amounts of mangrove leaves. Oakes, (2007) using stable isotope analysis, found that in a southeast Queensland mangrove forest, 88% of the diet of *P. erythrodactyla* was composed of mangrove detritus with the remainder being microphytobenthos. However, within the same region, Guest & Connolly (2004) found that $\delta^{13}\text{C}$ values for *P. erythrodactyla* varied according to whether they inhabited mangroves, or adjacent saltmarsh, suggesting that its diet varied with habitat. Further, Mazumder & Saintilan (2010) found that in temperate mangroves, leaf litter was an insignificant component of the diet of *P. erythrodactyla*. Importantly, Nerot *et al.* (2009) in a mesocosm study, found that *P. erythrodactyla* adjusted its diet to different food sources. Only mangrove leaves were available at sites used in the present study but Meziane *et al.* (2006) note that *P. erythrodactyla* may also utilise fungal biomass. Thus it seems more likely that in this study area this species consumed microphytobenthos and possibly associated fungi from the mangrove forest substratum. These findings further support the growing evidence that the role of *P. erythrodactyla* as a mangrove leaf litter remover cannot be assumed across the range of its distribution at both local scales and across climatic gradients.

5.4.1 Foraging ecology of *N. trispinosum*

The mean radius that *N. trispinosum* travelled from a burrow entrance was extremely similar at each site (18 - 20.6cm), and suggests that *N. trispinosum* individuals removed leaves from only a small area of the available foraging habitat (0.10 – 0.13m² per crab burrow). From estimates of *Neosarmatium* spp. abundance made in this study (i.e. from long-term comparisons described in Chapter 3 and wider comparisons in Chapter 4) the mean density was $4.87 \pm 0.28/\text{m}^2$. Thus the density of *Neosarmatium* spp. was such that the total available foraging habitat was not fully exploited. The reasons for this may have included predator avoidance limiting the distance travelled from the burrow refuge, competition with crabs from adjacent burrows or limited availability of suitable areas in which to construct burrows.

Within the study area, *Neosarmatium trispinosum* was observed to be cryptic and upon disturbance individuals immediately retreated into their burrows. In addition, these crabs are principally nocturnal and forage at low tide when the substratum is exposed. These observations are suggestive of predator avoidance but the identity of potential predators remains unknown. Sasekumar (1984) found sesarmid remains in the gut contents of estuarine fishes and Sheaves & Molony (2000), in a north Queensland study, found that sesarmid crabs comprised a high proportion of the gut contents of large estuarine fishes, although *Neosarmatium* spp. (misnamed in their report as *Neosesarma* sp.) were a minor component compared to crab species that inhabit lower tidal areas. Thus, predation by fishes may be less important for *N. trispinosum* than other crabs. Some sesarmids are known to prey on other sesarmid

species including *Metopograpsus thukuhar* (Fratini *et al.*, 2000) and *Epixanthus dentatus* (Cannicci *et al.*, 2002). These species were not present within the study area, although a congener *M. frontalis* was frequently encountered. However, it is unlikely that this latter species (which is relatively small) would feed on *N. trispinosum*. The mangrove mouse *Xeromys myoides* preys heavily on sesarmid crabs (Ball, 2004; Van Dyck, 1996) but is typically very rare within the study sites (pers obs) and would therefore be unlikely to be a significant predator of *N. trispinosum*. It is considered much more likely that birds such as herons and owls prey on *N. trispinosum* as they have the capacity to feed at night on the exposed substratum and are common components of the mangrove fauna assemblage. However, if this is the case, the role of such predation in regulating foraging behaviour requires testing.

The mangrove leaf consumer *Ucides cordatus* (Ucididae) occupies a very similar habitat to *N. trispinosum* and also has a limited foraging radius averaging 19cm (Nordaus *et al.*, 2009). These authors observed agonistic interactions between individual crabs and concluded that the species was territorial and that there was a high level of competition. Piou *et al.* (2009) noted that *Ucides cordatus* had an affinity for burrowing close to mangrove roots, but still maintained a regular distance between burrows of between 10-15cm, so occurred at densities that would result in overlap of foraging radii. The relationship between the foraging radius of *N. trispinosum* and the distance between burrow entrances is examined in Chapter 7.

Far greater emphasis has been placed on the way that sesarmid burrows influence substratum biogeochemical processes (reviewed by Kristensen, 2008) than on the way in which substratum characteristics influence burrowing behaviour, and the burrowing ecology of sesarmids is generally not well known (Gillikin & Chomba, 2005). McKillup & Butler (1979) proposed that substrate types differed in their structural capacity to support varying densities of crab burrows. Piou *et al.* (2009) observed that *Ucides cordatus* had an affinity for constructing burrows close to mangrove roots and it was proposed by Lee and Kwok (2002) that the habitat value of mangrove forests differ because root types offer different quality of refugia. The observed density of *N. trispinosum* within the study site varied considerably even at small spatial scales (i.e. metres). Visually, the substratum was homogenous and it was considered unlikely that changes in its composition (e.g. particle size, moisture and organic content) influenced the distribution of burrows. However, qualitative observations indicated that more burrows were located close to mangrove roots than in intervening areas. Further examination of burrow distribution in relation to presence of mangrove roots may provide important insights into their role in influencing the small-scale distribution of *N. trispinosum*.

Giddins (1984) determined that leaf litter represents the major (mean 90%) component of the diet of *N. trispinosum*. For the duration of the present experiment, *N. trispinosum* removed more of the provided leaf litter than would have naturally fallen to the substratum. This suggests that during the time of measurement, natural leaf litter fall may have been a limiting dietary resource and that larger foraging radii

would have been an advantage to *N. trispinosum*. However, the experiment was conducted for only a short period, with fresh not senescent leaves, and further study will be required to examine longer term, seasonal availability of leaf litter fall. In addition, the placement of leaf litter trays over the burrow entrances may have excluded some predators such as birds, which could have affected foraging behaviour.

5.4.2 Feeding preferences of *N. trispinosum*

Two previous studies have examined the dietary preferences of *N. trispinosum*; Giddins (1984) by laboratory experiments, and Micheli (1993) by both laboratory experiments and in the field using leaves tethered to the substratum. As previously noted, holding animals in captivity may affect their behaviour. Also, presenting leaf choices to crabs by tethering leaves to the mangrove substratum without excluding leaf inputs from natural leaf litter drop, potentially results in experimental bias. Thus the results of these studies should be interpreted with caution. Micheli (1993) reported that within laboratory experiments *Sesarma smithii* (= *N. trispinosum*) preferred *Rhizophora stylosa* to *Avicennia marina*, *Bruguiera exaristata*, or *Ceriops tagal* but displayed no preferences amongst the last three. However, no preferences were shown for any mangrove species during field experiments, although examination of burrows found more leaves of *C. tagal* than other species. Giddins (1984) reported that *N. smithi* (= *N. trispinosum*) did not show preferences for feeding on leaves of *Rhizophora stylosa* over *Ceriops tagal* when these were provided in similar states of decomposition. The final experiment in the present study showed

that *N. trispinosum* did not have a preference for feeding on leaves of *Ceriops tagal* over *Bruguiera exaristata*, the two most common species within its habitat in the study area; when feeding within its natural environment and with the amount of leaves presented in each experimental unit strictly controlled to avoid experimental bias.

N. trispinosum did not show feeding preferences for leaves of either species sourced from areas unaffected by storm-water over those from sites receiving storm-water. This suggests that if the dietary quality of leaves sourced from storm-water affected areas was lower than those from unaffected sites as hypothesised, than *N. trispinosum* did not detect this, or the change was within dietary acceptability. Nevertheless, the experiment has not eliminated the possibility that crabs might remove both types of leaves to their burrows and then preferentially feed on one type. *N. trispinosum* stores leaves in chambers within its burrows (Giddins *et al.*, 1986; Neilson *et al.*, 1986; Micheli, 1993) as do other *Neosarmatium* spp. such as *N. meinerti* (Emmerson & McGwynne, 1992; Skov & Hartnoll, 2002). Giddins (1984) demonstrated that as leaves of *Ceriops tagal* aged over a ten week period the protein content increased, flavolans (condensed tannins) decreased and the carbon to nitrogen ratio (C:N) decreased. Thus it was proposed that storage of leaves by sesarmids allows them to become more nutritious with age; a hypothesis referred to by Skov & Hartnoll (2002) as the 'leaf aging hypothesis'. This hypothesis has been rejected by Skov & Hartnoll (2002) and Thongtham & Kristensen (2005) based on experiments that showed crabs would not have been able to meet their nitrogen needs from aged leaves alone.

Nevertheless, leaf aging may still be utilised by *N. trispinosum* to improve the dietary quality of collected leaves by reducing their polyphenol and tannin content. Thus if these compounds were present in higher quantities in leaves sourced from mangroves subject to storm-water inputs, they might need to be aged for longer before becoming palatable to crabs. It is also important to note that if the dietary value of leaves from storm-water affected sites was less than non affected leaves, but they were nonetheless removed by *N. trispinosum*, crabs in storm-water affected sites may not be able to meet their long term energy requirements.

5.4.3 Leaf litter removal rates

The number of leaves removed by *N. trispinosum* varied amongst the locations in which the experiments were conducted. The most plausible explanation is that there were different densities of crabs present in each location. The number removed also varied amongst nights with a decline observed as the experiment progressed. This may have been due to decreasing activity levels associated with different tidal patterns as found in experiments described in Chapter 2. However, it may also be that because a relatively large amount of leaf litter was provided to the crabs (higher than natural leaf fall) they were able to store a surplus of leaves within their burrow chambers and were thus not stimulated to collect as much in subsequent nights. These observations are important in that they suggest that foraging behaviour is not consistent over time and experiments designed to estimate leaf litter removal rates should be cognisant of temporal and spatial variability.

6 Leaf Litter Processing

6.1 Introduction

Within many mangrove ecosystems one of the major roles attributed to sesarmids is the removal of mangrove leaf litter from the substratum, and subsequent processing (Alongi, 2009), thus these crabs create an important link between primary and secondary producers (Lee, 1998). However, there is considerable geographical variation and sesarmids may play a less important role in temperate mangroves (Imgraben & Dittmann, 2008). This study (Chapters 3 & 4) provided evidence that sesarmids, including *Neosarmatium trispinosum*, are less abundant in mangroves affected by urban storm-water run-off, than in unaffected areas. Subsequently, studies discussed in Chapter 5 found that *N. trispinosum* is the sole leaf remover within the study area. Therefore, a reduction in the abundance of *N. trispinosum* may result in decreased leaf litter removal in storm-water affected habitats, with consequent impacts on ecosystem level processes. Alternatively, if leaf litter availability is a limiting factor for *N. trispinosum* as it is for *Neosarmatium meinerti* in east Africa (Olafsson *et al.*, 2002), then a reduction in numbers of *N. trispinosum* may not necessarily equate to reduced leaf litter processing, as the remaining individuals may remove more leaves when competition is less. The potential impact of storm-water run-off on leaf litter processing cannot be assessed without first determining the amount of available leaf litter that is actually removed by *N. trispinosum* and comparing that to what is naturally available.

It is estimated that sesarmids remove between 30 and 90% of the available leaf litter (Kristenson 2008). Within the study area, preliminary estimates of potential leaf removal rates by *N. trispinosum* were made over a five-day period in the late wet season during which large quantities of leaf litter were supplied (22-26th April 2007; Chapter 5). Removal varied between $11.94 \pm 8.52 \text{ g/m}^2$ and $13.37 \pm 3.91 \text{ g/m}^2$ compared to actual leaf litter drop which varied from $6.90 \pm 1.6 \text{ g/m}^2$ to $9.48 \pm 2.27 \text{ g/m}^2$. Thus, leaf litter removed exceeded the amount available from natural falls to the substratum, and the crabs would have potentially removed 100% of the available leaf litter. However, these measurements need to be interpreted with caution as the study was only conducted during one season and for a limited period of time. Also the leaves offered to crabs were fresh, but those that made up the litter fall were senescent, and crabs might have preferences for feeding on leaves of one condition over another. In addition, crabs were offered a high density of leaves, close to their burrows, so removal rates might have been increased as an artefact of this. Lee (1998) noted that due to problems in estimating the density of sesarmid crabs, it is difficult to relate the amount of leaf litter removed to actual crab numbers. Therefore, leaf litter removal rates provided above should be considered estimates which will be affected by differences in crab densities.

An additional experiment was undertaken to determine with more confidence the leaf removing capacity of sesarmids within the study area, and to determine if it was related to sesarmid density as estimated by burrow numbers. This experiment was designed to sample over a greater period of time, within two different seasons, in

order to develop a more accurate depiction of sesarmid leaf removing activity. It is possible that different species of sesarmids will vary in their ability to remove leaf litter. However, it was established by experiments described in Chapter 5 that *N. trispinosum* is the sole leaf removing sesarmid within the mangrove community in the study locations. This provides the opportunity to determine how much leaf litter this species removes, if removal is variable over time, and if it can be related to burrow abundance as an estimate of actual sesarmid abundance.

6.2 Methods

To estimate the amount of natural leaf litter fall, five collection trays (0.5m²) were constructed of heavy gauge wire over which lightweight cloth was loosely sewn to create a concave collection bag of 10cm depth. These were randomly located by haphazardly throwing a marker out of sight and suspended 30cm above the substratum by wooden stakes. Leaf litter intercepted by these trays was not available for removal by *N. trispinosum*. Next to each tray, an area (ground unit) of the same size and shape was outlined on the substratum using a metal scribe. Any leaf litter falling into this area was available for removal by *N. trispinosum*. Whilst each ground unit was located randomly, its exact orientation was such that no burrow entrances outside the unit were within the maximum foraging radius (defined in Chapter 5) from its perimeter. In this way, it could be determined with some certainty that only crabs living within the ground unit had access to leaf litter within it. The number of burrows within each ground unit, and the aperture width of each, was measured at the beginning of each sampling period. Five paired trays and ground units were installed

in each of three locations; Eimeo, Bucasia and Slade Point.

This experiment was conducted during both the dry season (2nd – 11th August) and wet season (17th – 26th December). During each season, at three separate intervals, of three days duration and corresponding to different phases of the tidal cycle (early, mid and late) all remaining leaf litter remaining in the suspended collection trays and in the ground units was collected. Leaf litter samples were dried at 60°C for 72 hours and weighed to the nearest 0.01g and measures expressed as g/m²/day dry weight.

High tides during these times did not inundate the substratum and thus there was no import, export or spatial redistribution of leaf litter by tidal flows. In addition, there was no evidence of the presence of non-sesarmid leaf removers such as the snail *Terebralia palustris*, so the difference in the amount of leaf litter between the ground and the trays could be solely attributed related to removal by *N. trispinosum*.

Numerous field observations throughout this study showed that the size of the crab was very similar to the width of its burrow aperture. This relationship has been observed previously (Breitfuss, 2003b; Dunham & Gilchrist, 1988; Emmerson, 2001; Piou *et al.*, 2009; Prosser, 2004). Relating leaf litter removal to burrow density alone was considered inappropriate as larger burrows housed larger crabs and it was reasonably likely that larger crabs had the capacity to remove more leaf litter than smaller ones. The *N. trispinosum* body shape is strongly quadrilateral and slightly depressed; 1.1 times broader than it is long, with a body depth of approximately 0.8 of the width (Davie, 2002). Estimated body volume (EBV) was calculated from the burrow aperture width, noting that because crabs move in and out of burrows in a

lateral direction, burrow aperture width (BAW) would have best estimated crab body length rather than width:

$$EBV = BAW \times (1.1 \times BAW) \times (0.8 \times BAW)$$

$$EBV = BAW \times 0.88BAW^2$$

$$EBV = 0.88 BAW^3$$

The Estimated Body Volumes of all crabs residing in each ground unit were then combined and related to leaf litter removal, taking into account that increases in body length (i.e. burrow aperture) result in disproportionately larger increases in body volume.

6.3 Results

The dry weight of leaf litter falling to the substratum, as measured using the suspended trays, was similar amongst locations (Table 6.1) in the dry season. Leaf litter weights in the ground units (areas in which leaves could be removed by crabs) were less than in trays in all cases. Estimated removal of leaf litter by *N. trispinosum* ranged from 1.07 to 1.58 g/m²/day representing between 37-63% of the total leaf litter fall.

Table 6.1 Leaf litter fall and estimated removal in the dry season.

Location	Leaf Litter Fall	Leaf Litter Fall	Removal*	Removal*
	g/m ² /day ±	t/ha/year ±	g/m ² /day	t/ha/year
	95% CI of	95% CI of		
	mean	mean		
Bucasia	2.82 ± 0.50	10.30 ± 1.83	1.12	4.10
Eimeo	2.52 ± 0.55	9.20 ± 2.00	1.58	5.76
Slade Point	2.89 ± 0.43	10.56 ± 1.58	1.07	3.90

* Mean leaf litter weight in trays minus mean leaf litter weight in areas available for removal.

During the wet season the results were not as consistent (Table 6.2). The dry weight of leaf litter falling to the substratum varied more amongst sites, however, leaf litter weights in the ground units were still less than in the trays at all locations. Results from Eimeo during the wet season sampling period were similar to results obtained during the dry season in terms of both leaf litter fall and removal rates (42% of the available litter). At both Bucasia and Slade Point, leaf litter fall was more than double that during the dry season. There was less removal of leaves from the substratum at Eimeo than in the dry season but removal at Slade Point was higher in the wet season than the dry season.

Table 6.2 Leaf litter fall and estimated removal in the wet season.

Location	Leaf Litter Fall	Leaf Litter Fall	Removal*	Removal*
	g/m ² /day $\pm$	t/ha/year $\pm$	g/m ² /day	t/ha/year
	95% CI of	95% CI of		
	mean	mean		
Bucasia	2.71 $\pm$ 0.57	9.91 $\pm$ 1.83	1.15	4.21
Eimeo	6.32 $\pm$ 1.45	23.08 $\pm$ 5.29	0.54	1.96
Slade Point	4.98 $\pm$ 0.82	18.16 $\pm$ 2.98	1.74	6.35

* Mean leaf litter in trays minus mean leaf litter in areas available for removal.

The difference in leaf litter weights between trays and ground units at each time, in each season and at different locations were examined by a repeated measures ANOVA after first testing for sphericity with Mauchly's Test. Data were square root transformed to reduce heteroscedasticity, but there remained a significant deviation from sphericity ($df = 2$, $W = 0.338$, $P < 0.001$) and thus Greenhouse-Geisser and Huynh-Feldt adjusted degrees of freedom were used for tests of significance. There was a significant difference in leaf litter amongst periods of sampling (Greenhouse-Geisser; $df = 1.203/41.964$, $F = 10.256$, $P = 0.001$; Huynh-Feldt; $df = 1.527/41.964$, $F = 10.256$, $P < 0.001$) and a significant interaction between time and season (Greenhouse-Geisser; $df = 1.203/41.964$, $F = 8.254$, $P = 0.004$; Huynh-Feldt; $df =$

1.527/ 41.964, $F = 8.254$, $P = 0.002$). There were no other significant within-subject effects (Table 6.3). Test of between-subject effects detected significant differences amongst locations ($F_{2, 44} = 6.653$, $P = 0.003$), season ($F_{1, 44} = 29.496$, $P < 0.001$), treatment (leaf litter weight in trays vs. ground units) ($F_{1, 44} = 12.451$, $P = 0.001$), and a significant interaction between location and season ($F_{2, 44} = 10.540$, $P < 0.001$) (Table 6.4). These results can be further interpreted with the aid of Figures 6.1 and 6.2, which show the mean dry, leaf litter weights ($\text{g/m}^2/\text{day}$) in trays and ground units in the dry and wet seasons respectively. Leaf litter removal varied during the sampling periods and was probably related to differing crab activity levels, which differed with season. Leaf litter removal varied amongst locations and compared to what was available, there was less removal of leaf litter by crabs in the wet than the dry season. However, the magnitude of difference between seasons varied amongst locations.

Table 6.3 Tests of within-subjects effects for leaf removal at different times, locations and seasons.

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
Time	Greenhouse-Geisser	9.782	1.203	8.131	10.256	.001
	Huynh-Feldt	9.782	1.527	6.404	10.256	.000
	Lower-bound	9.782	1.000	9.782	10.256	.003
Time*Location	Greenhouse-Geisser	.617	2.406	.257	.324	.764
	Huynh-Feldt	.617	3.055	.202	.324	.812
	Lower-bound	.617	2.000	.309	.324	.725
Time*Season	Greenhouse-Geisser	7.872	1.203	6.543	8.254	.004
	Huynh-Feldt	7.872	1.527	5.154	8.254	.002
	Lower-bound	7.872	1.000	7.872	8.254	.006
Time*Treatment	Greenhouse-Geisser	2.014	1.203	1.674	2.112	.149
	Huynh-Feldt	2.014	1.527	1.319	2.112	.140
	Lower-bound	2.014	1.000	2.014	2.112	.153
Time*Location *Season	Greenhouse-Geisser	1.390	2.406	.578	.729	.511
	Huynh-Feldt	1.390	3.055	.455	.729	.541
	Lower-bound	1.390	2.000	.695	.729	.488
Time*Location *Treatment	Greenhouse-Geisser	.723	2.406	.301	.379	.724
	Huynh-Feldt	.723	3.055	.237	.379	.772
	Lower-bound	.723	2.000	.362	.379	.687

		Type III Sum of Squares	df	Mean Square	F	Sig.
Time*Season* Treatment	Greenhouse- Geisser	.633	1.203	.526	.663	.446
	Huynh-Feldt	.633	1.527	.414	.663	.479
	Lower-bound	.633	1.000	.633	.663	.420
Time*Location *Season* Treatment	Greenhouse- Geisser	1.631	2.406	.678	.855	.449
	Huynh-Feldt	1.631	3.055	.534	.855	.471
	Lower-bound	1.631	2.000	.815	.855	.432
Error (Time)	Greenhouse- Geisser	41.964	52.933	.793		
	Huynh-Feldt	41.964	67.206	.624		
	Lower-bound	41.964	44.000	.954		

Table 6.4 Tests of between-subjects effects for different locations, seasons and treatments (trays and ground units).

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Location	9.717	2	4.859	6.653	.003
Season	21.540	1	21.540	29.496	.000
Treatment	9.093	1	9.093	12.451	.001
Location * Season	15.394	2	7.697	10.540	.000
Location * Treatment	.932	2	.466	.638	.533
Season * Treatment	.681	1	.681	.933	.339
Location * Season * Treatment	.597	2	.299	.409	.667
Error	32.132	44	.730		

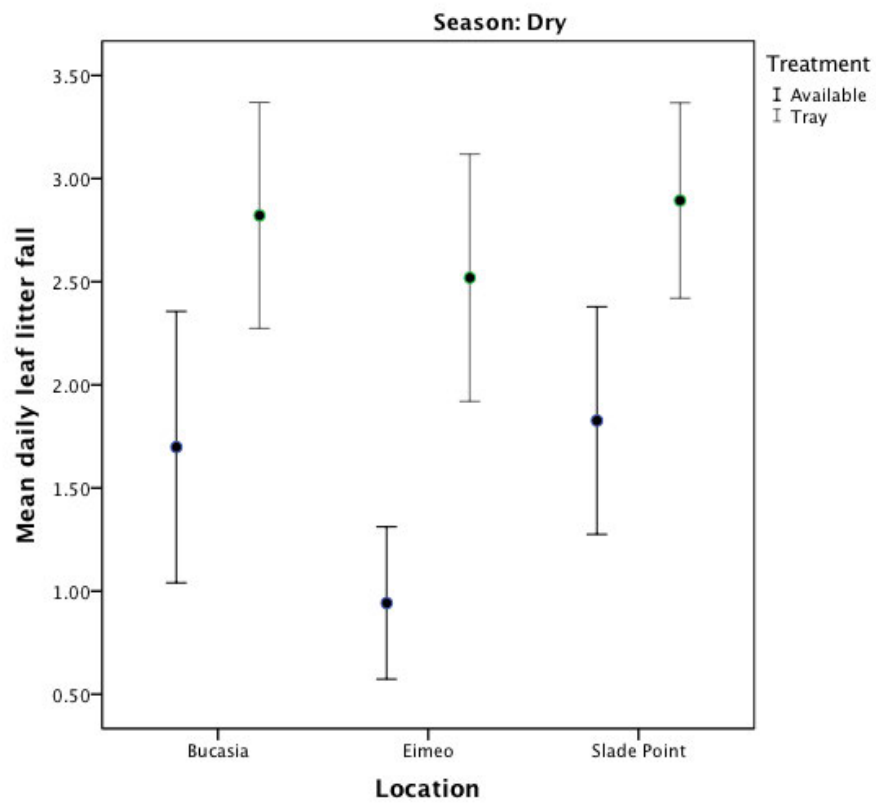


Figure 6.1 Mean dry leaf weight ($\text{g/m}^2/\text{day}$) in trays and ground units during the dry season (bars are the 95% confidence interval of the mean).

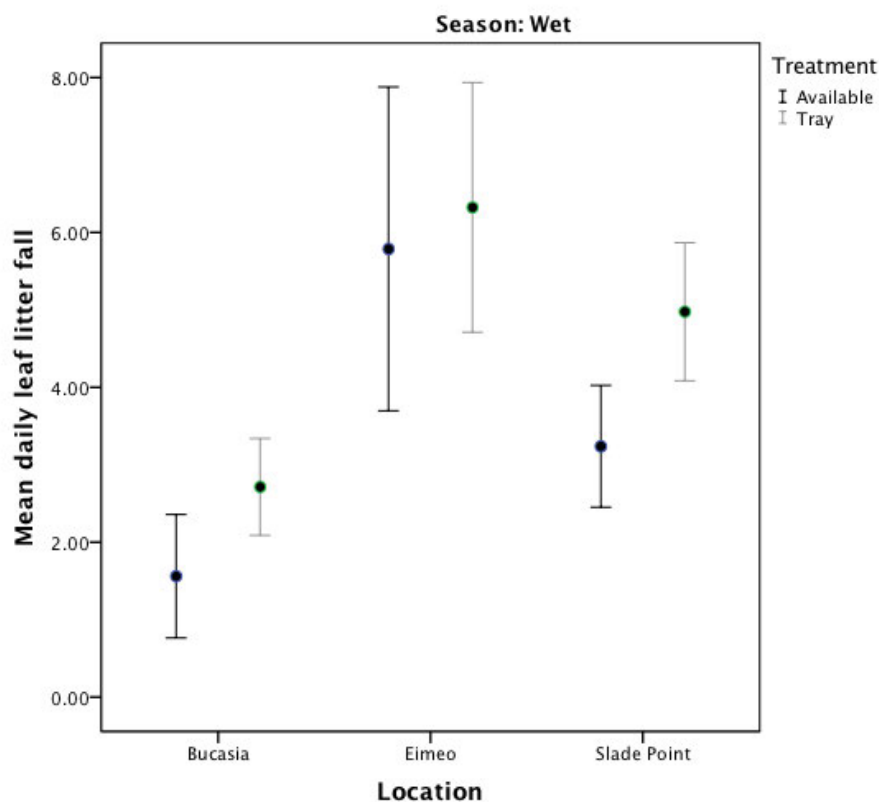


Figure 6.2 Mean dry leaf weight ($\text{g/m}^2/\text{day}$) in trays and ground units during the wet season (bars are the 95% confidence interval of the mean).

There was a minimum of two burrows within each ground unit and the Estimated Body Volume (EBV) in these cases varied from 135267.44 to 161307.52 mm^3 . The maximum number of burrows was 10 and the EBV in this case was 641488.32 mm^3 . The highest EBV was 729512.96 mm^3 (for nine burrows). Mean leaf litter removal of the three samples collected within each nine day sampling period, for each of the dry

season and wet season, was calculated for each of the 15 comparisons (i.e. dry weight of leaf litter within trays minus dry weight of leaf litter left remaining within the adjacent ground unit) and related to the combined Estimated Body Volume (EBV) of crabs inhabiting the ground units. Figures 6.3 and 6.4 illustrate these comparisons for the dry season and wet season respectively. Within the range of combined EBV encountered, there is no apparent relationship in either season.

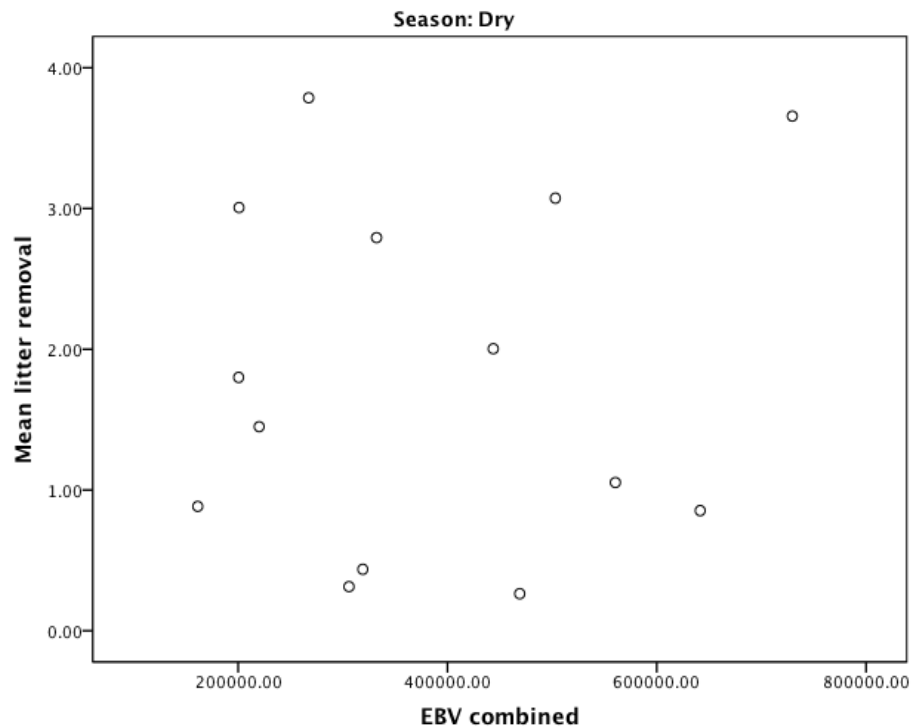


Figure 6.3 Mean leaf litter removal (grams) vs. Total Estimated Body Volume in the dry season.

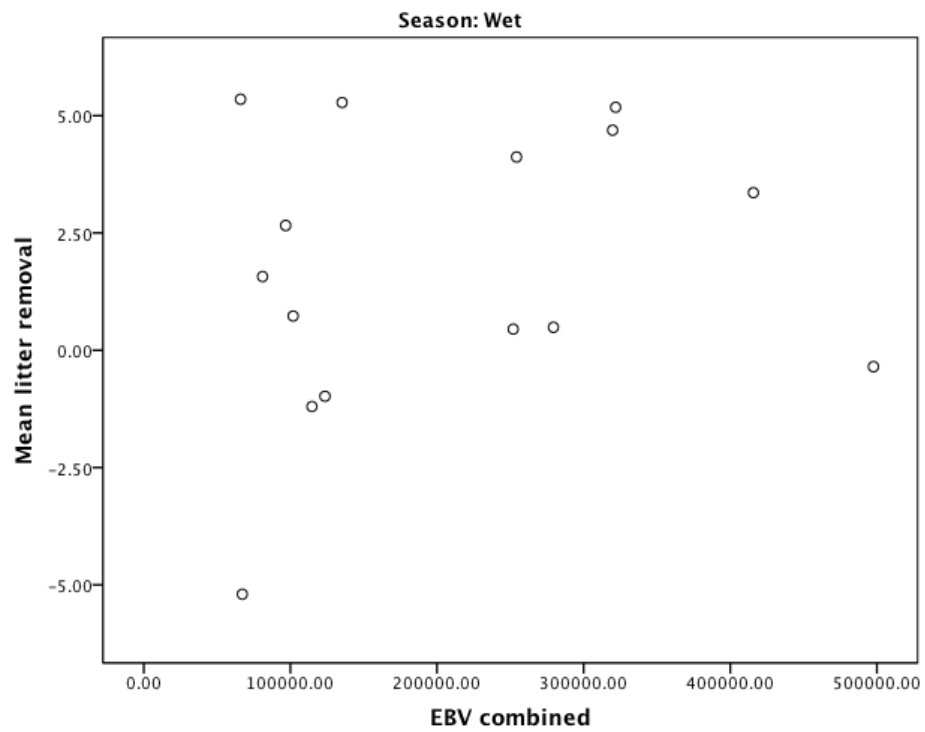


Figure 6.4 Mean leaf litter removal (grams) vs. Total Estimated Body Volume in the wet season.

6.4 Discussion

6.4.0 Estimates of natural leaf litter fall

Mangrove leaf litter production varies considerably geographically, within different habitats, and seasonally (Utrera-López & Moreno-Casasola, 2008). Within the study area, *Ceriops tagal* dominated the mangrove community but *Bruguiera exaristata* was always present. The estimated amount of leaf litter falling to the substratum within the study sites varied from a minimum of 9.20 ± 2.00 t/ha/year in the dry season to a maximum of 23.08 ± 5.29 t/ha/year in the wet season. These figures are higher than those of Woodroffe *et al.* (1988) who studied a mixed *Ceriops tagal* and *Bruguiera exaristata* community in Darwin Harbour and reported greater leaf litter fall during the wet season, but only recorded an annual average leaf litter fall of 7.45 t/ha/year. Similarly, Robinson & Daniel (1989) measured leaf litter fall within communities dominated by *Ceriops tagal* and by *Bruguiera exaristata* (separately) and reported leaf litter fall of 8.22 t/ha/year and 10.22 t/ha/year respectively. Leaf litter fall recorded in the study area is within the medium to high range estimated for other mangrove systems worldwide (the latter reviewed by Utrera-López & Moreno-Casasola, 2008) and concurs with the seasonality of fall described by Gwada & Kairo (2001), Twilley *et al.* (1986), and Twilley *et al.* (1997).

6.4.1 Variation in natural leaf litter fall

There was a significant difference in leaf litter fall at two time scales; amongst times of sampling, and between seasons (dry and wet). There was also a significant difference in leaf litter fall amongst locations, but, the magnitude of difference varied between the two seasons. These findings are important because they demonstrate temporal variability in leaf litter available to *N. trispinosum*, which may influence its foraging behaviour. They also demonstrate that the amount of leaf litter available varied spatially, which may mean that different mangrove communities have a different capacity to support populations of *N. trispinosum*. Importantly, these findings reinforce the need for careful design of experiments aimed at estimating litter fall in mangrove forests, including the imperative of appropriate spatial and temporal replication. Results presented in Chapter 5 demonstrated that removal of leaves by *N. trispinosum* varied significantly on a nightly basis as the tidal cycle progressed from spring to neap tides, despite a constant over-abundance of leaves available. This reduction in removal over time may have been because the crabs were able to store a surplus of leaves within burrow chambers and were thus not stimulated to collect as much in subsequent nights. Storage of leaves within burrow chambers has, to date, usually been considered as a means in which to improve their nutritional value. However, it may also be that this represents a ‘stockpiling’ strategy to ensure continuity of food supply during periods when they are restricted to their burrows (e.g. within periods of moisture stress during neaps tides when their habitat is not regularly inundated) or during periods of lesser leaf litter availability.

6.4.2 Removal of leaf litter by *N. trispinosum*

There was a significant difference in leaf litter between trays and ground units, which demonstrated removal of leaf litter by *N. trispinosum*. During the dry season crabs removed 4.10 to 5.76 t/ha/year (37-63% of leaf litter fall) and in the wet season 1.96 to 6.35 t/ha/year (8-42% of leaf litter fall). Although this removal was substantial, it was less than that found by Robinson & Daniel (1989) who reported that in communities dominated by *Ceriops tagal* and by *Bruguiera exaristata*, leaf litter removal by crabs was 5.80 t/ha/year (71%) and 8.03 t/ha/year (79%) respectively. Thus, within the study area, it appears that leaf litter fall was not limiting to *N. trispinosum* and in other communities it was not limiting to the sesarmid assemblage present. This finding is in contrast to the results presented in Chapter 5, which found that when offered fresh leaves, crabs removed more than the equivalent amount of leaf litter fall. However, that previous study was conducted for only five nights and during a period that coincided with a peak in activity levels. Thus crabs might remove all leaf litter, but only during periods of high foraging activity, and these are followed by periods of less removal during which leaf litter accumulates.

A previous observation reported in Chapter 5, was that *N. trispinosum* under-exploited the total available foraging habitat because it had a limited foraging radius from its burrow entrance and this was very similar amongst different mangrove habitats. Thus, a reduction in *N. trispinosum* abundance due to storm-water run-off may result in reduced leaf litter removal because remaining crabs may not forage more widely, and more leaf litter would be left on the substratum. However, this

hypothesis remains untested and the relationship between foraging distance from burrow entrances, and factors such as predation, competition and preferred burrowing micro-habitat, as discussed in Chapter 5, will be required to better understand the likely impact of fewer crabs on leaf litter removal. In particular it would be useful to determine if burrows are only constructed in certain micro-habitats, because this would then influence the amount of the total available foraging habitat that can be utilized. If this were the case, a decline in *N. trispinosum* would be expected to result in less leaf litter removal. In addition, although the mean distance that crabs foraged from burrow entrances was similar, it would be useful to determine if the foraging distances of individual crabs was related to the proximity of other burrow entrances.

6.4.3 Relationship between leaf litter removal and *N. trispinosum* biomass

No relationship was found between mean leaf litter removal and estimated *N. trispinosum* biomass. There may be several explanations. Burrows counts may be an unreliable method of estimating actual crab density, even if great care is taken to only consider active burrows, as a given burrow may have a different number of inhabitants. This may lead to underestimation of the number of crabs present and thus overall biomass in a given area. In addition, the estimation of biomass from burrow measurements and crab morphological characteristics may be relatively coarse. Alternatively, or in combination with the above, the lack of a relationship between estimated biomass and leaf removal might reflect a periodically fluctuating foraging effort that was not accurately estimated by the time of sampling. For example, during

the study period, not all crabs present may have been removing leaves, or for only a part of the time that sampling took place.

6.4.4 Summary

Leaf litter fall recorded in the study area was within the medium to high range estimated for other mangrove systems worldwide and higher than for previous estimates for similar mangrove communities in northern Australia. Leaf litter falls ranged from 9.20 ± 2.00 t/ha/year in the dry season and 23.08 ± 5.29 t/ha/year in the wet season of which 37-63% and 8-42% was removed respectively. Therefore it appeared that leaf litter was not a limiting resource for *N. trispinosum*. However, *N. trispinosum* under exploits the total available foraging habitat and it is hypothesised that this may be because of a micro-habitat preference for burrowing. Therefore, a decline in *N. trispinosum* may result in less leaf litter removal. However, if a micro-habitat preference exists, another hypothesis is that crabs may increase their spatial foraging effort when other crab burrows are not in close proximity. In this case, some decline in crab abundance may not translate to less leaf litter removal. These hypotheses are the subject of further studies presented in Chapter 7.

7 Micro-distribution of *Neosarmatium trispinosum*

7.1 Introduction

Of the roles that sesarmid crabs play in mangrove ecosystems, propagule and leaf litter consumption have been considered by many studies. Smith (1987) proposed that the distribution of mangrove species along the tidal gradient was not fully explained by their physiological capacity to colonise different habitats, but that differential predation on their propagules by sesarmids also influenced their distribution, and impacts of predation were dependant on the relative dominance of the mangrove species present (the Predator-Dominance model). Subsequent studies (Smith *et al.*, 1989) found that this model did not hold true for all mangroves tested, which might be due to differences in the sesarmid assemblage. Similarly, the model was not supported by studies in Belize (McKee, 1995), north Queensland (Clarke & Kerrigan, 2002) and northern Australia (McGuinness, 1997a). McGuinness (1997b) noted that small-scale changes in sesarmid abundance may influence propagule predation on a local scale and regional differences in predation might be attributed to the presence of different sesarmid assemblages. However, the latter might also be true for local scales. In the initial study that proposed the Predator-Dominance model, Smith (1987) noted that there were five sesarmid species present in the study location and all were considered predators of propagules, but, there was no consideration that the abundance of each species may have differed amongst the study sites, and each species may have had different feeding preferences. As such, the results of that study showing that propagule predation was related to mangrove species dominance may

have been confounded by the presence of different sesarmid assemblages. This potential for experimental bias was also discussed within the context of *in-situ* leaf feeding preference experiments in Section 5.1.0 above. Further complicating this situation, in Chapter 5 it was reported that the only species (*N. trispinosum*) that removed leaves from this study area did not fully exploit the available foraging habitat and thus its impact as a leaf remover was highly unlikely to be spatially uniform within the mangrove community. Levin (1992) noted that an effort to understand the variability or predictability of the environment could not be made without an understanding of the organisms or processes at the range of scales that are relevant to them. Piou *et al.* (2009) reinforced this and made the observation that despite the numerous studies of mangrove crabs undertaken to date, none have examined their small-scale spatial distribution. It is argued that without such studies, the way in which sesarmids contribute to larger scale ecological processes will remain unclear.

The purpose of this chapter is to develop a better understanding of the smaller scale spatial distribution of *Neosarmatium trispinosum* within its habitat and specifically to test the hypotheses that:

1. *N. trispinosum* burrows are contagiously dispersed within the mangrove habitat
and,
2. *N. trispinosum* has a preferred micro-habitat for burrowing within the mangrove community *and,*

3. The distance between burrow entrances is related to foraging radii of resident crabs away from burrow entrances *and*,
4. If the small-scale spatial distribution of *N. trispinosum* would influence the way it removes leaves and propagules.

The results of these tests will allow a better understanding of the way in which this species utilizes its habitat and of the spatial application of its function as a keystone species within the mangrove community.

7.2 Methods

The study was undertaken within the Bucasia Control (a) site and was typical of the broader study area, being dominated by *Cerriops tagal* with smaller numbers of *Bruguiera exaristata*. Data collection was undertaken subsequent to spring high tides (maximum height 5.99m) so that active burrows could be readily identified by the presence of foraging trails extending away from the entrances.

The distance between mangrove stems was measured using the Nearest Neighbour technique, whereby a mangrove stem was selected at random by haphazardly throwing a marker out of sight and choosing the stem closest to it. The distance to the nearest stem was then measured. From this second stem the distance to the next nearest stem was measured and so on, for a total of 80 measurements. The same process was used to measure the distance between knee root structures. These

measures were used to calculate the frequency distributions of the distances between stems and between knee roots, and the dispersion index for each.

The frequencies of the measures of distance between stems were grouped into percentage quartiles and in each, the range of the distances between stems identified.

The percentage of burrow to stem measures occurring within each of these ranges was then determined. The range of distances were treated as mutually exclusive categories, and a Chi Square test used to compare the proportion of stem to stem measures, and burrow to stem measures within each category. The same analysis was performed for the root to root, and burrow to root measures.

Within the site, 60 1m² quadrats were placed randomly on the substratum by haphazardly throwing a marker out of sight. The numbers of active *N. trispinosum* burrows were counted and sample statistics from these data used to calculate dispersion indices. For each quadrat, the centremost burrow entrance was selected and three measurements made: the distance to (a) the nearest living mangrove stem (b) the nearest knee root structure, and (c) the next nearest active burrow entrance. These data were used to examine whether the crabs had any preference for constructing burrows near mangrove stems or knee root structures, and to examine the relationship between the known foraging radii of this species and the distance to other burrows. Next, 30 burrows were chosen at random by haphazardly throwing a marker out of sight and choosing the burrow closest to it. Both the foraging radii of

the resident crab and the distance to the nearest burrow were measured. These data were used to determine if foraging radii were related to distances between burrows.

7.3 Results

7.3.0 Distribution of mangrove stems and knee roots

The mean distance between mangrove stems was 43.5cm (95% CI $\pm$ 6.3) and the Dispersion Index (Fowler & Cohen, 1997) was 19.12, which showed a strongly contagious dispersion (i.e. >1). The mean distance between knee roots was 25.2cm (95% CI $\pm$ 3.2) and the Dispersion Index 8.44, also showing a strongly contagious dispersion.

7.3.1 Burrow dispersal

For the 60 quadrats, the mean number of burrows was 5.03 and the variance 11.05 giving a Dispersion Index of 2.20, which shows a contagious burrow dispersion.

Figure 7.1 shows that the frequency distribution for burrow counts for the 1m² quadrat data was bimodal with peaks at the values of one to two burrows and five and six burrows per quadrat. Morisita's Index of Dispersion I_δ (Schuh *et al.*, 1986), calculated as

$$I_\delta = [\sum (x^2) - \sum x / (\sum x)^2 - \sum x] n$$

also showed a contagious dispersion ($I_\delta = 1.23$ where values over > 1.0 indicate a contagious dispersion). This index was used because re-combination of the data could then examine the effect of increasing quadrat size on I_δ (Schuh *et al.*, 1986). The burrow count data for the first and second quadrats were combined, then the third and fourth, and so on, to give burrow counts for 2m^2 . These were combined again to create a sample of burrow counts for 4m^2 , and again for burrow counts at a quadrat size of 15m^2 . For these datasets, Morisita's Index of Dispersion was again calculated and then plotted against the size of the quadrat (Figure 7.2). This shows a declining dispersion index as quadrat size increased suggesting that burrows were clumped more at a scale of 1m^2 than at the others.

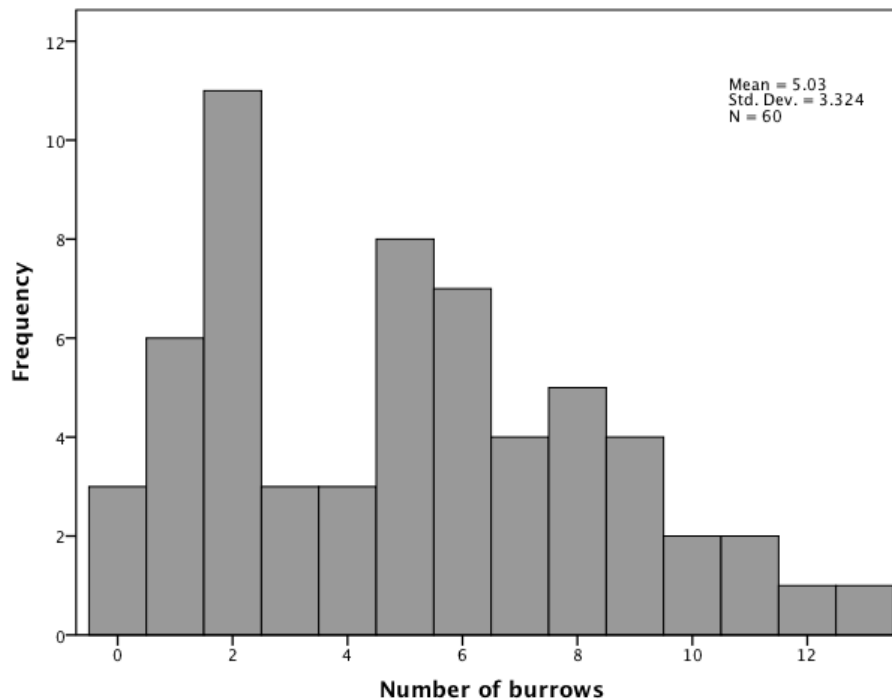


Figure 7.1 Burrow frequency distribution for counts in 1m^2 quadrats.

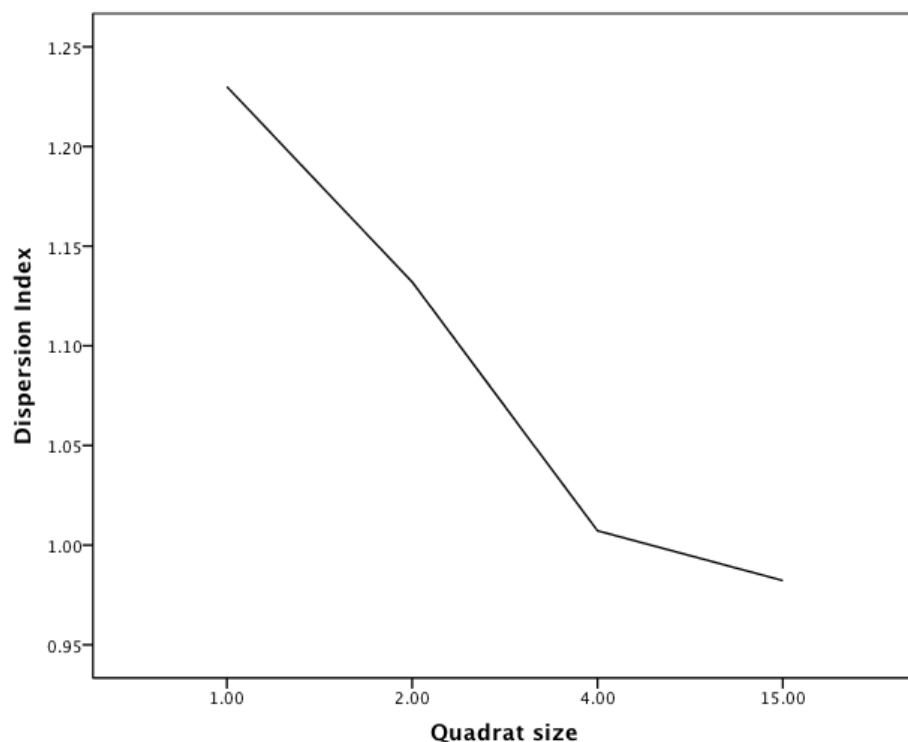


Figure 7.2 The value of Morisita's Index of Dispersion vs. quadrat size for burrow counts.

7.3.2 Burrow micro-distribution

The mean distance of burrows to the nearest stem was 62.6cm (95% CI $\pm$ 8.2), and the distribution was not significantly different to a normal distribution (Kolmogorov-Smirnov one-sample test; $Z = 0.823$, $P = 0.507$). In comparison, the mean distance between mangrove stems was 43.5cm (95% CI $\pm$ 6.3). The frequencies of the measures of distance between stems were grouped into percentage quartiles (Table 7.1) and in each, the range of the distances between stems identified. These data showed that most stems (75%) were within 52cm of another stem and this is

consistent with the finding that stem dispersal is strongly contagious. The percentage of burrow to stem measures occurring within each of these ranges was then determined, and this showed that most burrows (59.6%) were more than 52cm away from stems (and 75.4% more than 38cm). These data are consistent with burrows being more abundant in gaps amongst clumps of stems. To test this, the range of distances were treated as mutually exclusive categories, and a Chi Square test used to compare the proportion of stem to stem measures, and burrow to stem measures within each category. This was done because if crabs did not have a spatial preference for constructing burrows, then there should have been similar numbers of stem to stem, and burrow to stem measures in each category. The test found that there was a significant difference ($\chi^2 = 17.33$, $df = 3$, $P = 0.001$).

Table 7.1 Frequency distributions of distances between stems and burrows to stems. Figures in brackets are number of measures in each category.

Range of distances between stems	Quartiles			
	$\leq 26\text{cm}$	$> 26 - \leq 38\text{cm}$	$> 38 - 52\text{cm}$	$> 52\text{cm}$
Percentage of stem to stem measures	25% (20)	25% (19)	25% (20)	25% (21)
Percentage of burrow to stem measures within the distance between stems range	7% (4)	17.5% (10)	15.8% (9)	59.6% (34)

The mean distance from burrow entrances to roots was 17.0 cm (95% CI ± 3.1), and the distribution was not significantly different to a normal distribution (Kolmogorov-

Smirnov one-sample test; $Z = 1.354$, $P = 0.051$). In comparison the mean distance between roots was 25.2cm (95% CI ± 3.2). As for the distances between stems, the frequencies of the measures of distance between roots were grouped into percentage quartiles (Table 7.2) and in each, the range of the distances between stems identified. In this case the quartile divisions are approximate because there were multiple measures of the same distance that overlapped the 50% and 75% divisions. These data show that 75% of the distances between roots were more than 14cm, but most burrows (59.6%) were within 14cm of roots, which is consistent with crabs preferring to construct burrows close to roots. This was tested using the same procedure as for stem to stem, and burrow to stem distances and there was a significant difference ($\chi^2 = 17.58$, $df = 3$, $P = 0.001$).

Overall, these results are consistent with burrows being preferentially constructed away from stems and closer to roots. For illustrative purposes Figure 7.3 shows, for each burrow, the distance to the nearest stem minus the distance to the nearest root. Therefore, negative values show that the burrow was closest to a stem, whilst positive values show the burrow was closest to a root. With very few exceptions, burrows were closer to roots than stems.

Table 7.2 **Frequency distributions of distances between roots, and burrows to roots. Figures in brackets are number of measures in each category.**

	Quartiles			
Range of distances between roots	$\leq 14\text{cm}$	$> 14 - \leq 22\text{cm}$	$> 22 - 33\text{cm}$	$> 33\text{cm}$
Percentage of root to root measures	25% (20)	27.5% (22)	23.8% (19)	23.8% (19)
Percentage of burrow to root measures within the distance between roots range	59.6% (34)	12.3% (7)	10.6% (6)	17.5% (10)

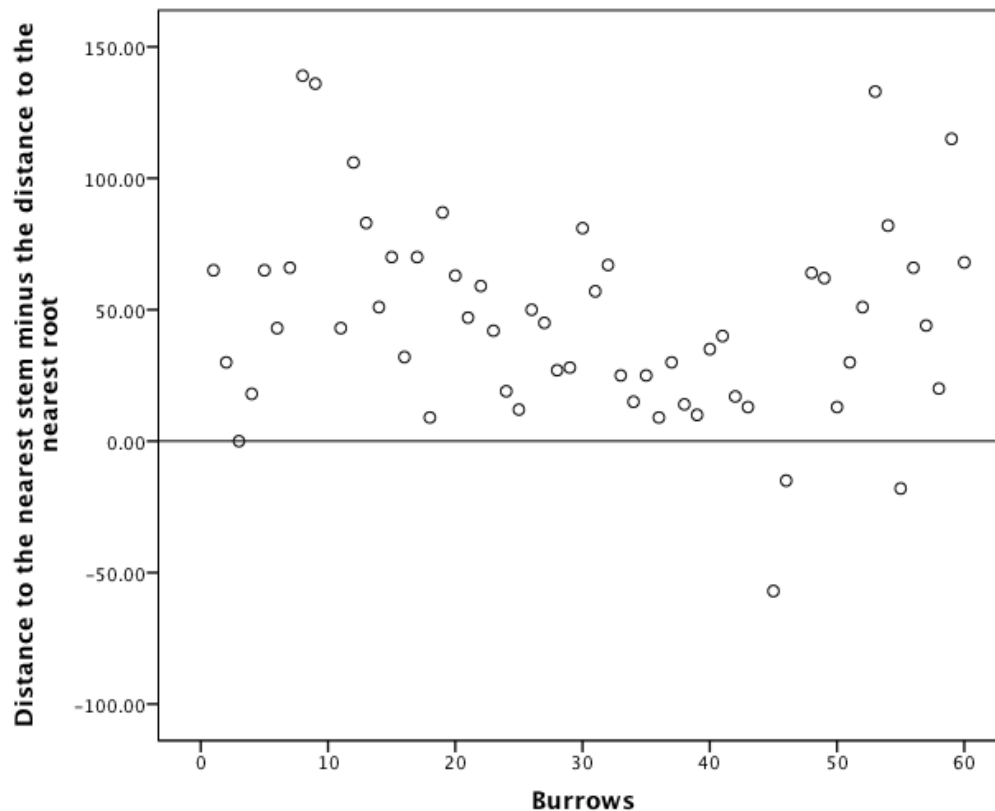


Figure 7.3 Distance of each burrow to the measure of distance to the nearest stem minus the distance to the nearest root. Positive values show when burrows were closer to roots than stems.

7.3.3 Relationship between foraging distance and distance between burrows

In Chapter 5 it was reported that the maximum radius that *N. trispinosum* foraged away from its burrow entrance was 29cm at Bucasia (mean = 20.60cm; 95% CI $\pm$ 1.75cm), 28cm at Eimeo (mean = 18cm; 95% CI $\pm$ 1.74cm) and 27cm at Slade Point (mean = 19.45cm; 95% CI $\pm$ 2.17). Within this study the mean distance between

burrow entrances was 30.50cm (95% CI $\pm$ 3.07) (Figure 7.4), which suggests that the spatial distribution of burrows was such that foraging radii would overlap, although on average there was an area close to each burrow which was likely to be used exclusively by the inhabitant. These data could not be analysed using ANOVA as there were large differences amongst sample variances that could not be reduced by transformation, so instead a Friedman test was used. This test cannot be performed on unequal sample sizes. Data for foraging radii at each of the three locations consisted of 20 measures whilst those for distances between burrows had 57 measures. To complete the analysis 20 measures of distance between burrows were randomly selected using a random number table and used within the Friedman test, and this procedure was repeated five times. There was a significant difference amongst foraging radii and distances between burrows for all five tests [$(n = 20, df = 3) \chi^2 = 18.497, P < 0.001$; $\chi^2 = 21.365, P < 0.001$; $\chi^2 = 24.879, P < 0.001$; $\chi^2 = 19.974, P < 0.001$; $\chi^2 = 29.593, P < 0.001$]. Because a Friedman test can only examine differences of one factor, the test was also applied to the foraging radii data alone. This found that there was no significant difference in foraging radii amongst location ($n = 20, df = 2, \chi^2 = 2.810, P = 0.245$) and thus it is reasonable to assume that the difference found in the previous test was because the mean distance between burrows was greater than the mean foraging radii.

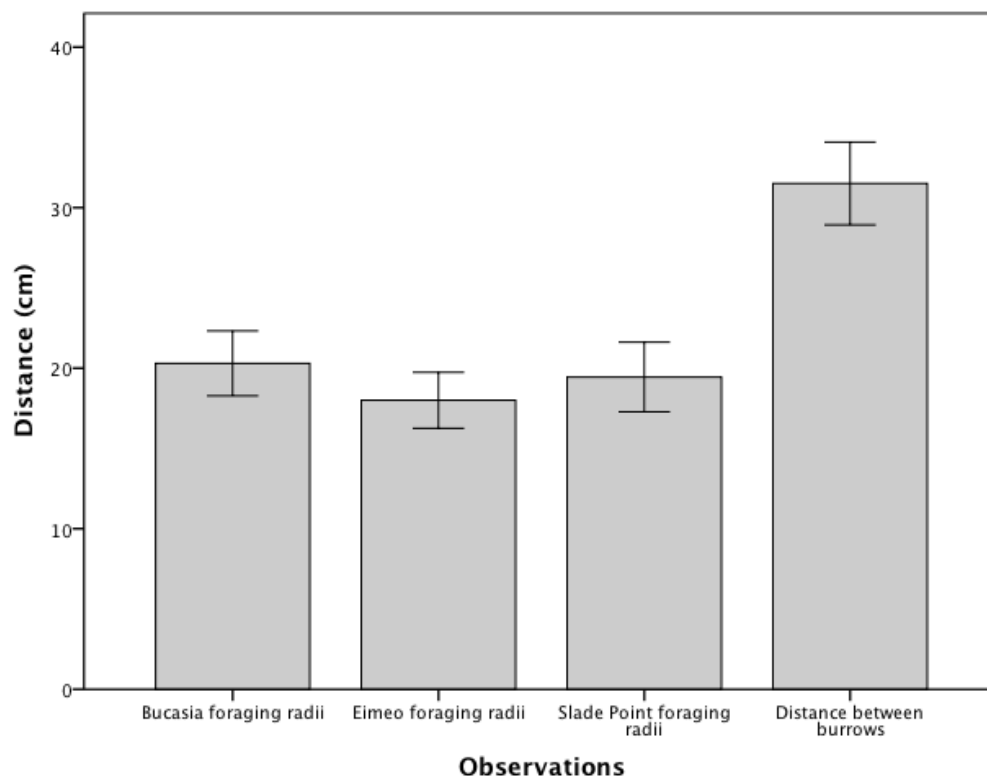


Figure 7.4 Difference between observed foraging radii at Bucasia, Eimeo and Slade Point and distance between burrows (bars are 95% confidence intervals of the mean).

Measurements taken in this study ($n = 30$) showed that the mean foraging radii away from burrow entrances was 20.40cm (95% CI ± 1.61) and the maximum was 30cm, which was very similar to results presented in Chapter 5 (20.60cm; 95% CI ± 1.75 cm; maximum 29cm). The measures of foraging radii away from each burrow were related to the distance to the nearest burrow, using a two-tailed Pearson's Correlation (the data were bivariate normal). This found a significant positive correlation between

these variables ($r^2 = 0.41$, $P < 0.001$); foraging radius increased as distance between burrows increased (Figure 7.5).

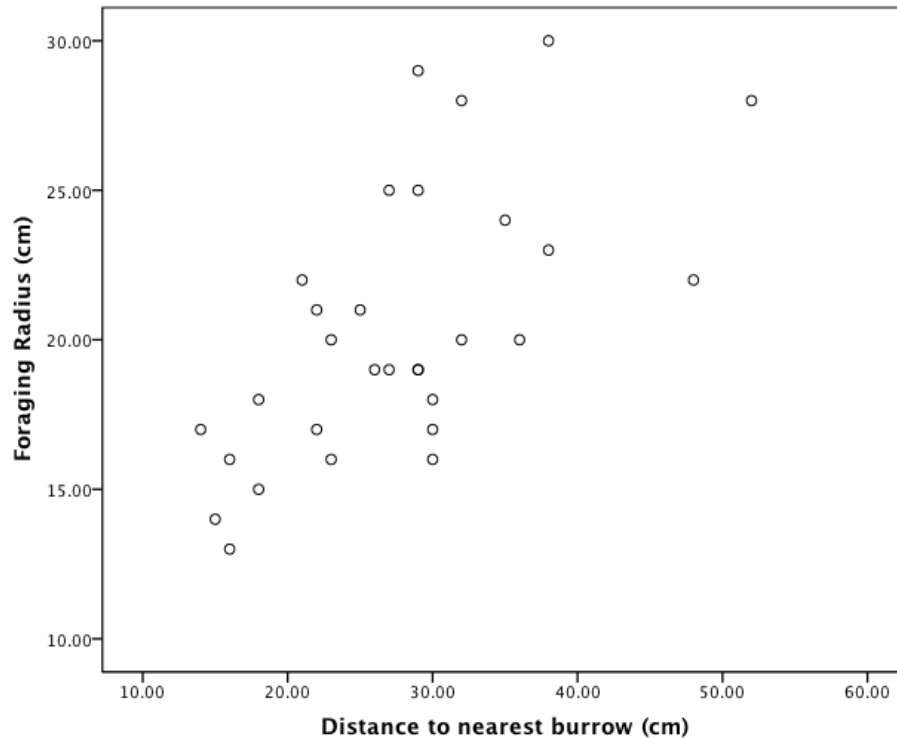


Figure 7.5 The relationship between the distance between burrows and the foraging radii

The data were divided into groups where the distances between burrows were at or below the maximum foraging radii (30cm) and those that were above this value. A two-tailed Pearson's Correlation found a significant positive correlation for the first group and r^2 was greater than in the previous case ($n = 19$, $r^2 = 0.50$, $P = 0.001$).

There was no significant correlation for the second group of data ($n = 11$, $r^2 = 0.28$, $P = 0.097$). These results show that when the distance between burrows was more than

the maximum foraging radii, there was no comparable increase in foraging radii with increased distance between burrows.

7.4 Discussion

7.4.0 Distribution of mangrove stems and roots

The purpose of this study was to develop a better understanding of the smaller scale spatial distribution of *Neosarmatium trispinosum* within its habitat. In first describing the mangrove habitat (a forest dominated by *Ceriops tagal*), the results show that major structural components of the mangrove community, stems and roots, were contagiously dispersed. Most stems (75%) occurred within 52cm of another stem, and most roots (76.3%) were within 33cm of another root. These results are consistent with a pattern of clumps of trees and roots separated by gaps. Clarke and Kerrigan (2000) noted that studies of patterns in the distribution of tropical mangroves have focussed on patterns across environmental gradients, rather than variation within forest types. However, the presence of gaps in mangrove forests has been noted by numerous studies and is a commonly accepted feature of these communities (e.g. Feller & McKee, 1999; Duke, 2001; Clarke & Kerrigan, 2002; Clarke, 2004; Gladstone & Schreider, 2003; Ellis & Bell, 2004). Gaps have been attributed to the occurrence of a mosaic of successional stages co-existing within a particular mangrove stand, as a result of small-scale disturbances (Alongi, 2009). Therefore, clumping of mangroves found in the present study is not unexpected. Nevertheless, it may not be universal because Bosire *et al.* (2008) found that stems were evenly dispersed in a Kenyan mangrove forest dominated by *Ceriops tagal*. The potential

consequence of different mangrove stem dispersion to *N. trispinosum* is discussed further below.

7.4.1 Burrow dispersal and micro-distribution

Burrows of *N. trispinosum* were contagiously dispersed within the habitat and were more clumped at the scale of 1m² than at larger dimensions. Most burrows (59.6%) were more than 52cm away from stems, which is consistent with burrows being constructed in gaps amongst clumps of stems. Of the spaces measured between roots, 75% were more than 14cm, however most burrows (59.6%) were within 14cm of roots. This is consistent with burrows being constructed close to roots. The mangrove habitat within the study site was numerically dominated by *C. tagal* stems with occasional *Bruguiera exaristata* trees. Both these species have knee roots (Lovelock, 1993) that are formed by lateral roots that radiate away from the stems (Hutchings & Saenger, 1987) and generally occur away from the tree stem. Therefore, the results of this study need to be interpreted with caution, because the area away from stems and the area close to roots, is largely mutually inclusive. If crabs construct burrows in this micro-habitat it may be because of the distance from stems, or proximity to roots, or a combination of both.

Piou *et al.* (2009) noted that there appeared to be no previous investigations of the small-scale spatial distribution of burrowing decapod crabs. This appears to remain the case. Although Piou *et al.* (2009) studied *Ucides cordatus*, which is not a sesarmid, it nevertheless performed an analogous role as a leaf remover in Brazilian mangroves. Piou *et al.* (2009) found that *U. cordatus* constructed burrows so that they

were clustered around *Rhizophora mangle*, and close to its roots. Based on the evidence of Diele *et al.* (2005) and Nordhaus *et al.* (2009), that *U. cordatus* had a preference for feeding on leaves of *R. mangle*, the aggregation of burrows around this mangrove was explained as a means to better access preferred food. The results of Chapter 5 showed that *N. trispinosum* did not have a preference for feeding on leaves of *C. tagal* over those of *B. exaristata*, and these were the only mangroves found within the current study area. Whilst gaps were present between stems, they were not so large (a maximum of 148cm), that there were noticeable gaps in the canopy. Therefore, crabs that constructed burrows within these gaps would still have had access to similar amounts of leaf litter fall, as crabs with burrows closer to stems. Therefore, it seems unlikely that the distance of burrows to stems would have had any influence on the crabs' access to food. Piou *et al.* (2009) suggested that burrowing close to roots would improve burrow stability in soft sediments and offer protection against predators. Many mangrove habitats have soft sediments and this was the case within the current study site. Chapter 5 discussed the observation that *N. trispinosum* shows cryptic and nocturnal behaviour that is consistent with the need to avoid predators. Therefore, the finding that *N. trispinosum* has a preferred micro-habitat is best explained by the advantages of constructing burrows close to roots, those being enhanced burrow stability and better protection from predators.

7.4.2 Spatial distribution of *N. trispinosum* burrows within the micro-habitat

The results of this study show that within the micro-habitat in which crabs preferred to burrow, their foraging radii away from burrow entrances overlapped. However,

there was an area close to each burrow which was used exclusively by the inhabitant. This spatial distribution was consistent with habitat partitioning, which would minimise competitive interactions. The results also showed that foraging radii increased as distance between burrows increased. This is consistent with an expansion of spatial foraging effort, with a reduction in overlap with the foraging space of neighbouring crabs, which would be expected if competition influenced burrow distribution. Piou *et al.* (2009) also proposed that the small-scale spatial distribution of *Ucides cordatus* was determined by intraspecific competition. For *N. trispinosum*, this effect was only observed when the distance between burrows was the same, or less, than the maximum foraging radii (approximately 30cm). This result showed that there was a spatial limit to which crabs foraged, which is relevant to interpretation of results presented in Chapter 6. Combined, these findings suggest a small reduction in sesarmid abundance may not result in reduced leaf litter removal, as foraging radii would increase as distance between burrows increased. However, if crab abundance was reduced so that the distance between burrows became greater than 30cm, then less leaf litter removal would be expected, because crabs would not continue to expand their foraging radii. Within a similar mangrove community, Robinson & Daniel (1989) measured a higher rate of leaf litter removal than this study. The most plausible explanation for this difference is that in their study site, there were more crabs.

7.4.3 Influence of the small-scale spatial distribution of *N. trispinosum* on leaf and propagule removal.

The results of studies presented in Chapter 5 showed that *N. trispinosum* underexploited the total available foraging habitat. A finding of this present study was that *N. trispinosum* had a preferred micro-habitat in gaps between mangrove stems, and thus a prediction is that this crab would remove more leaves and propagules in these gaps. This is similar to the results obtained by McGuiness (1997b) who found in a *C. tagal* forest, more propagules were removed in gaps, although in this case by *Neosarmatium meinerti*. The findings of this present study are also useful in interpreting existing data that describes sesarmid ecology. A landmark study by Clarke and Kerrigan (2002) compared the numbers of propagules removed by sesarmids firstly, to different canopy gap sizes and shading, and secondly, to floristics of the mangrove forest as a test of the Predator-Dominance model. One of the three most important propagule predators within their study sites was *N. trispinosum* (identified by them as *Sesarma smithii*). They found that more than 50% of the variances in predation were associated with random spatial factors (i.e. among replicates within the fixed treatments), and this was attributed to idiosyncratic patterns of crab foraging. Considering the results of this present study, showing a strongly contagious dispersion of *N. trispinosum* burrows and thus foraging effort, it seems more likely that in Clarke and Kerrigan's study (2002) the small numbers (three) of replicates were placed in areas with markedly different numbers of crabs, and thus they obtained large variations in measures of propagule predation. Studies designed to test the Predator-Dominance model have used

replicated experimental units with four levels; replicate plots within sites, within vegetation types, within intertidal zones (i.e. Smith *et al.*, 1989; Clarke and Kerrigan, 2002) with replication at the plot level varying from three to five units. Thus, the within site variability in propagule predation may not have been estimated equally well, may have obscured the results of comparisons among higher levels, and this may be another reason why tests of the Predator-Dominance model have yielded inconsistent results. Therefore it is proposed that better measurement of the variability of sesarmid abundance at small scales, may assist in a better understanding of ecological processes at larger scales.

7.4.4 Summary

Both tree stems and above ground root structures were contagiously dispersed within the mangrove community, which is consistent with the co-existence of a mosaic of successional stages as described by Alongi (2009). The results of this study showed that the distribution of *N. trispinosum* burrows was also contagiously dispersed, with more burrows being found in close association with root structures, which occurred in gaps between clumps of tree stems. The likely advantages of burrowing within this micro-habitat were proposed to be enhanced burrow stability and better protection from predators. Within the micro-habitat, the spatial distribution of burrows was consistent with habitat partitioning, which would minimise competitive interactions. Foraging radii of crabs increased with distance to the nearest burrow. This is consistent with an expansion of spatial foraging effort when the overlap with the foraging space of neighbouring crabs is reduced. This finding further supports the

proposal that burrows were positioned to minimise competition. However, the results show that when the distance between burrows exceeded 30cm, there was no corresponding increase in foraging radii. These findings mean that leaf litter removal rates may remain similar after a small decrease in *N. trispinosum* abundance, but a larger decrease is predicted to result in less removal. *N. trispinosum* underexploited the total available foraging habitat and was predicted to remove more leaves and propagules in gaps between mangroves. It is proposed that more studies are required to better understand the smaller scale distribution of sesarmids, in order to improve knowledge of their role in ecological processes at larger scales.

8 General Discussion

8.1 The impact of urban storm-water runoff on sesarmid crabs

This thesis has described the impact of urban storm-water runoff on abundance of the sesarmid crabs *Neosarmatium trispinosum*, *N. fourmanoiri* and *Parasesarma erythrodactyla*. Obtaining reliable estimates of the abundance of sesarmid crabs for use in ecological studies remains problematic. A series of pilot studies was conducted and these tested the efficacy of different methods commonly used to estimate the abundance of sesarmids. Within the study area, burrow counts were most useful in providing estimates of relative abundance and thus were used to compare the relative abundance of *Neosarmatium* spp. and *P. erythrodactyla* among paired storm-water input and control sites at two scales; a three year study in mangroves close to Mackay City, and a one year study at a larger geographical scale.

The results of both studies were similar and consistent with discharge of urban storm-water into mangrove communities resulting in a decline in abundance of both *Neosarmatium* spp. and *Parasesarma erythrodactyla*. This is the first report of an association between urban storm-water runoff and a decline in the abundance of sesarmid crabs. It is important because sesarmids are considered to be keystone species so a decline in their abundance may have effects at ecosystem level.

8.1.0 Likely causes of a decline in sesarmid abundance

Soil core water salinity was found to be significantly lower at storm-water input sites than at control sites. The magnitude of this decline varied markedly amongst storm-water input sites, which was attributed to differences in the volume of storm-water discharge amongst sites. The relationship between soil core water salinity and the abundance of sesarmid burrows was complex. There was no correlation between either the mean or minimum soil core water salinity and burrow abundance of either *N. trispinosum*, or *N. fourmanoiri*. However, for *N. trispinosum* there was evidence of a threshold effect at a salinity of 35‰ (approximately the value of undiluted seawater), above which burrows were more numerous. This suggested that habitats with a salinity below 35‰ were less suitable for *N. trispinosum*. Whilst habitats with a salinity above this level may have been more suitable, there were considerable differences in burrow abundance among sites with similar salinities, so other factors may also affect burrow abundance. There was no threshold effect observed for *N. fourmanoiri*, which suggested that this species is more tolerant of low salinities. For *P. erythrodactyla* there was also evidence of a threshold effect at 35‰. Importantly, within control sites (i.e. those with a higher salinity), there was a positive correlation between the burrow abundance of *P. erythrodactyla* and both mean and minimum salinity, within the range measured (to approximately 60‰).

These findings are consistent with a decline in abundance of both *N. trispinosum* and *P. erythrodactyla* because of reduced soil core water salinity, as a result of storm-water discharge into the mangrove habitat. Nevertheless, changes in salinity did not

fully explain the variation in burrow abundance of either species and thus other factors may also have had an influence.

The difference in soil core water salinity between storm-water input and control sites was less in the dry season than in the wet season, and the salinity at most storm-water input sites increased to above the threshold level of 35‰ during the dry season.

However, this was not accompanied by an increase in abundance of small burrows of either *Neosarmatium trispinosum* or *P. erythrodactyla* which may be because habitat conditions remained unsuitable for recruits. It was proposed that these species might exhibit adult odour mediated settlement, as has been shown for some other sesarmids.

For *P. erythrodactyla*, there was a strong positive correlation between numbers of small and large burrows, which is consistent with recruitment occurring in response to the presence of adults. There was no correlation between numbers of small and large burrows for *N. trispinosum*, but juveniles may inhabit adult burrows and thus the presence of adults could also be an important habitat condition required for recruitment. These findings may explain some of the variations in burrow abundances, which do not appear to be related to soil core water salinity.

The study conducted at a larger geographical scale made comparisons between sesarmid burrow abundance and characteristics of the mangrove vegetation occurring at each site. Within each site, mean measures of the basal area of each mangrove species were used to describe the vegetation community. There was a significant difference between the vegetation present at storm-water input sites compared to

controls. However, sites with very similar vegetation had markedly different burrow abundances of both *Neosarmatium* spp. and *P. erythrodactyla*. This finding is not consistent with burrow abundance being related to overall vegetation type or *vice versa*. Notwithstanding, there did appear to be more burrows of both taxa at sites where the vegetation was dominated by *Ceriops tagal*. Although not conclusive, this observation warranted further consideration because results of a previous study (Mitcheli, 1993) suggested that *N. trispinosum* might have a preference for feeding on leaves of *C. tagal* to those of other mangroves. In addition, previous studies (Kathireson & Ravi, 1990; Basak *et al.*, 1998) found that tannin and polyphenol concentrations in mangrove leaves were highest in the wet season. This suggested that leaves from mangroves growing in storm-water input sites might have been less palatable than those from controls, because the former received more freshwater.

It was hypothesised that sesarmids might prefer to eat leaves of *Ceriops tagal* to those of other species, and that leaves from mangroves at storm-water input sites may be less palatable than those from control sites. These hypotheses might have helped to explain some of the observed differences in sesarmid burrow abundance and were experimentally tested within mangroves where the only known leaf removing sesarmids were *N. trispinosum* and *P. erythrodactyla*. An important preliminary finding was that within these areas, *P. erythrodactyla* did not remove leaves as had been previously reported for this species (Camilleri, 1989; Guest & Connolly, 2004; Oakes, 2007). Conversely, this finding supports the results of Mazumder & Saintilan (2010) who found that in temperate mangroves, *P. erythrodactyla* does not remove

significant amounts of mangrove leaves, and another study which found that the diet of this species is variable (Nerot *et al.*, 2009). Another notable finding was that *N. trispinosum*, as the sole leaf remover, took leaves from only a small area of the total available foraging habitat. Feeding experiments found that *N. trispinosum* did not show a preference for feeding on leaves of *C. tagal* to those of *Bruguiera exaristata*, the second most common mangrove in the study area. Neither was there any preference shown for feeding on leaves of either species from control sites compared to those from storm-water input sites. Therefore, based on these findings, there was no evidence that either *P. erythrodactyla* or *N. trispinosum* preferred to inhabit mangroves dominated by *C. tagal* because of feeding preferences, nor that they preferred to inhabit control sites to storm-water sites because of different leaf palatability.

N. trispinosum preferred to construct burrows in gaps between mangroves stems, in close association with mangrove roots. A study by Piou *et al.* (2009) found that another leaf removing crab, *Ucides cordatus*, also preferred to burrow close to mangrove roots. The advantages for crabs burrowing within this micro-habitat are most likely enhanced burrow stability and better protection from predators. This study was conducted within a mangrove community dominated by *C. tagal* with occasional *B. exaristata* trees so comparisons could not be made of the proximity of burrows to roots of other mangrove species. Both *C. tagal* and *B. exaristata* have knee roots and these species were common at control sites and sometimes storm-water input sites. At storm-water input sites, however, other mangroves were also

common, particularly at sites with a longer history of storm-water input. Empirical data from other studies (Joshi & Gosh, 2003; Yong *et al.* 2004) suggested that the presence of *Excoecaria agallocha*, and *Lumnitzera racemosa* at storm-water sites, might be because these species are better able to colonise habitats with a lower salinity. Generally these species do not have above ground root structures (Lovelock, 1993). *Avicennia marina* was also more common in storm-water input sites than controls, and has peg like roots which are much less substantial than the knee roots of *C. tagal* and *B. exaristata*. Therefore, the observation that *N. trispinosum* burrows appeared more common at sites dominated by *C. tagal* might be because this mangrove offered larger areas of a preferred micro-habitat. Another study found that sesarmids had a preference for using habitats with a particular root type (Lee & Kwok, 2002) but for *N. trispinosum* this remains to be tested.

In describing and comparing the mangrove vegetation present at different sites, this study used the commonly measured features (e.g. English, *et al.*, 1994) of stem density, diameter at breast height and the calculated basal area of each mangrove species. However, sites with similar measures of these may have had markedly different dispersal of the mangrove stems, which would have influenced dispersal of roots. Therefore, sites with similar vegetation, as defined by the methods used in this study, might have offered different quality habitat to *N. trispinosum* and this may help explain why some sites that had very similar vegetation types (as described), had different numbers of burrows.

8.1.1 The ecological consequences of a decline in sesarmid abundance

One of the major roles attributed to sesarmid crabs in mangrove ecosystems is the removal and processing of leaf litter, which creates an important link between primary and secondary producers. The results of studies described in this thesis have shown that in mangroves receiving urban storm-water discharge, the abundance of *N. trispinosum* is lower. The results have also shown that *N. trispinosum* is the only leaf remover within most of the landward mangrove community in the study area.

Therefore, the decline in abundance of this species might result in less leaf litter removal, with consequent effects at ecosystem level. Further experiments were conducted to estimate the amount of leaf litter falling within the mangrove habitat, and compare that to the amount of leaf litter removed by crabs. The results of these experiments showed that leaf litter fall varied from 9.2 ± 2.0 t/ha/year (95% confidence interval) in the dry season to 23.08 ± 5.29 t/ha/year in the wet season. In contrast, *N. trispinosum* removed only 4.10 to 5.76 t/ha/year in the dry season (37-63% of the leaf litter fall), and 1.96 to 6.35 t/ha/year in the wet season (8-42%). At a smaller temporal scale, the results also showed a significant difference in the amount of leaf removal over time, with most occurring during higher amplitude tides. This periodicity in crab activity was a consistent finding among the studies conducted. Therefore, it appeared that leaf litter was not limiting to *N. trispinosum*, which was consistent with a study of a similar mangrove forest by Robinson & Daniel (1989). These results need to be interpreted in the context of the way in which *N. trispinosum* utilises the foraging habitat. Results of experiments described in this thesis showed that this species had a restricted foraging radius away from its burrow, and the

assemblage of crabs present did not fully exploit the total available foraging habitat. If the abundance of *N. trispinosum* were to decrease, two responses could potentially occur; one, that foraging radius will increase as the distance between neighbouring crabs increases; and two, that the foraging radius will not increase. In the former case, total leaf litter removal may remain similar, and in the latter, leaf litter removal may decrease.

Within the preferred burrowing habitat of *N. trispinosum*, the spatial distribution of burrows was consistent with habitat partitioning, which would minimise competitive interactions and this was similar to the findings of Piou *et al.* (2009). The foraging radii of crabs were found to be larger as the distance to the nearest burrow increased, however when the distance between burrows exceeded 30cm, this did not appear to influence foraging radii. These findings are important as they mean that leaf litter removal rates may remain similar after a small decrease in the abundance of *N. trispinosum*, but a larger decrease may result in less removal. Therefore, at storm-water input sites that had few *N. trispinosum* burrows, leaf litter removal would be less than at controls. Studies described in this thesis did not investigate the removal of propagules by *N. trispinosum* although it is known to do so (Clarke & Kerrigan, 2002). However, a decrease in the number of crabs at storm-water input sites would have also reduced propagule removal, because many of these would have been located outside of areas in which crabs foraged. These findings support the proposition that discharge of urban storm-water into mangroves disrupts two major roles attributed to sesarmids as keystone species: leaf and propagule removal.

Sesarmids also influence the mangrove ecosystem because their burrowing activity aerates the soil (Kristensen, 2008), decreasing the concentration of phytotoxins such as sulphide and ammonia (Smith *et al.*, 1991) and this could result in increased primary production within mangrove ecosystems (Lee, 1998). The finding that *N. trispinosum* burrows close to mangrove roots through which biochemical exchanges take place, may mean that the results of burrowing activity benefit mangroves more than previously considered. Therefore, at storm-water sites with few burrows, soil conditions may have been less favourable for mangrove growth. This suggests that discharge of storm-water into mangroves disrupts a third important role attributed to sesarmids.

N. trispinosum does not fully exploit the total available foraging habitat, and there are temporal differences in activity where it does forage. This behaviour, which creates spatial and temporal variation in foraging pressure, may have implications at ecosystem level. Firstly, because *N. trispinosum* also consumes propagules (Lee, 1998), there are areas within the mangrove habitat where removal of mangrove propagules will be less, and these are likely to be closer to mangrove stems. This is consistent with the results of McGuinness (1997a) who found greater mortality of propagules through predation, in gaps within a *C. tagal* forest in northern Australia. This would mean that *N. trispinosum* might maintain gaps within the mangrove habitat, but in the case of reduced crab abundance (due to for example storm-water input), these gaps may close. Secondly, where *N. trispinosum* does forage, there is evidence that there will be not only spaces, but also times when propagule removal

will be more restricted. Dispersal of *C. tagal* propagules within the mangrove forest is restricted (McGuinness, 2007b) and primarily occurs through tidal flows. Because the mangrove habitat of *N. trispinosum* is very high relative to tidal datum, dispersal of mangrove propagules close to the supralittoral margin would only occur during high amplitude tides, when crabs are actively foraging. In contrast, propagules may be carried to the lower intertidal area during tides of smaller amplitudes, when crabs are not actively foraging. Therefore, propagules in lower intertidal areas would have more time to establish before being predated upon, than those in higher areas. This too may mean that *N. trispinosum* influences vegetation structure across the tidal gradient and a reduced abundance of this crab may result in changes. The potential presence of spatial and temporal refuges from propagule predation should be considered when designing experiments to investigate the reasons for variation in vegetation within mangrove stands.

It appears that the most comprehensive model of the impacts of urbanisation on coastal wetlands is the one developed by Lee *et al.* (2006). It recognises urban runoff as being an important impact that carries increased loads of sediment, nutrients and contaminants to wetland systems. Also considered is the potential for changes in salinity due to sedimentation and subsequent modification to hydrological flows. However, it does not recognise that point discharge of freshwater, such as urban storm-water into estuarine systems, could also have a direct impact on biota and in turn, on the ecological roles they play. In the case of sesarmids, these include roles

that have ecosystem level consequences. As such, the findings presented in this thesis may help further refine this model.

8.2 The broader relevance of this study to seascape ecology

This study has investigated the response of sesarmid crabs to urban storm-water runoff, within a high littoral mangrove habitat. The results have been discussed in terms of potential changes to keystone roles undertaken by these crabs and possible ramifications to this habitat. In doing so, this study has contributed knowledge about an ecological ‘patch’ within the coastal seascape. Urban storm-water runoff has created patches where sesarmid crab numbers are very low, and in these, it is likely that their activities such as leaf litter processing have reduced. This has made the upper littoral mangrove margin more spatially heterogeneous. These patches may be quite small and restricted to areas directly adjacent to stormwater runoff, but ongoing urbanisation along the coastline will result in more of these patches, and a growth in their overall spatial area. Within the context of seascape ecology, it is important to consider how this knowledge might improve understanding of the broader ecological ramifications to the coastal zone. This is because “Most coastal biogenic habitats exist as components of functionally connected mosaics, so loss or degradation of a particular habitat is likely to impair the integrity of neighbouring patches and disrupt links in the ecosystem as a whole” (Bostrom *et al.*, 2011).

8.2.0 Structural and functional fragmentation

The mangrove habitat studied was dominated by open to closed forest of *Ceriops tagal* ± *Bruguiera* spp. (mapped by Winter & Wild, 1995) and geographically represented 25% of the total estuarine vegetation within the region. This type of forest occurs as a broadly contiguous band around estuarine margins; it occurs below patches of supratidal saltpan and salt marsh (23% of the estuarine vegetation), and above the lower intertidal zone, which was dominated by contiguous areas of *Rhizophora stylosa* forest (31% of the estuarine vegetation). The results of this study showed that there is potential for these anthropogenic foci of freshwater runoff to increase both structural and functional fragmentation within the *Ceriops tagal* ± *Bruguiera* spp. band. Comparison of vegetation between control and storm-water input sites found a significant difference in floristics between the two groups, although the magnitude of this difference varied amongst paired sites. The development of different mangrove communities at storm-water input nodes along the *Ceriops tagal* ± *Bruguiera* spp. band is likely to cause structural fragmentation along its length. That is, different mangroves trees provide different habitat conditions for biota, i.e. micro-habitats associated with root structures (e.g. Lee & Kwok, 2002). Changes in the presence or abundance of biota could subsequently result in modification of food chains and the interactions between the biota and their physical and chemical environments.

This study also found that it was likely that at these storm-water input nodes, there would be a decline in leaf litter processing, alterations in mangrove propagule

removal patterns and in crab burrowing activity resulting in functional fragmentation as well as structural fragmentation.

The development and likely lateral expansion of these nodes, with different structure and function may lead to: (a) a decrease in the overall geographical extent of the original *Cerriops tagal* ± *Bruguiera* spp. habitat (i.e. a decrease in patch size) (b) increased fragmentation and (c) a decrease in contributions that it makes to neighbouring ecological patches and/or the broader seascape. The ramifications of this are difficult to quantify. There are deficiencies in knowledge of distributional patterns of mangrove fauna, and their capacity (and need) to move amongst areas of suitable habitat. There also remain gaps in knowledge about how organic carbon and other materials are produced by different mangrove communities and flow to other ecological patches.

8.2.1 Fragmentation and habitat loss

The distribution of mangrove fauna, including crabs is of great interest to ecologists. Distributional studies on crabs have been conducted in some areas (e.g. Dadhouh-Guebas *et al.*, 2002; Frusher *et al.*, 1994; Ravichandran *et al.*, 2001; Snelling, 1959; Warner, 1969) and also for other taxa (e.g. Ball, 2004; Clay & Anderson, 1996; Noske, 1995; Noske, 1996). A review of the literature found few references to any species of crab or other fauna that might be restricted to a particular mangrove habitat such as the *Cerriops tagal* ± *Bruguiera* spp. zone, for part or all of their life cycle. For crabs, characteristics of the mangrove vegetation appear to be but one of several

factors that influence distribution patterns, and others notably include substrate type, inundation period, and salinity (reviewed in Chapter 1). Clay & Anderson *et al.* (1996) found that some ants occurred in distinct zones along the tidal gradient but this did not appear to be regulated by floristic patterns. For birds, however, Noske (1995, 1996) found that the distribution of several bird species corresponded to the zonation of mangroves both at Peninsula Malaysia and Darwin Harbor. Ball (2004) also found that the false water rat (*Xeromys myoides*) was largely restricted to the *Ceriops tagal* ± *Bruguiera* spp. habitat within central coastal Queensland. Thus for this species the fragmentation and loss of this mangrove community may have deleterious effects, although there is no evidence that its movement through the forest would be impeded by patches of stormwater affected habitat of the size reported in this study.

Notwithstanding the above distribution studies, there is a marked absence of knowledge of the habitat requirements of mangrove biota, how they might move amongst suitable patches of habitat, and what they might consequently contribute to the ecological links amongst habitat patches. The reduction and/or fragmentation of any particular habitat may be a concern within the broader seascape because it could (a) reduce the abundance of some biota and the ecological roles they play within storm-water modified patches and (b) limit the movement of species amongst patches that may be required to complete their life cycle. Both these changes may be exacerbated by an increased number of storm-water modified patches and, in particular, by the potential development of larger contiguous strips of storm-water affected habitat as a result of ongoing coastal urbanisation.

8.2.2 Production and flows of organic carbon and other materials

Leaf litter fall measured by this study within the *Ceriods tagal* ± *Bruguiera* spp. community was higher than for similar communities investigated by Woodroffe *et al.* (1988) and Robinson & Daniel (1989), higher than other communities measured by Woodroffe *et al.* (1988), and within the medium to high range estimated for other mangrove communities globally (reviewed by Utrera-López & Moreno-Casasola, 2008). Leaf litter fall was not measured at storm-water input sites, but it is possible that the mangroves within these areas may not produce as much leaf litter that would in turn be available to the seascape in some form.

With few exceptions (e.g. the whelk *Terabralia* spp.) sesarmid crabs are the principal taxon that processes leaf litter and thus a decline in their abundance may result in less organic carbon being available through the coprophagous food chain. Although not yet well replicated within tropical systems, studies in temperate areas found that sesarmid larvae exports (e.g. *Parasesarma erythroclaylai*) were important contributors to the diet of estuarine fish (Mazumder *et al.*, 2009) and that fish actively move between seagrass beds and adjacent mangroves and saltmarsh to feed during spring high tides (Saintilan *et al.*, 2007). Thus, a decline in sesarmid crabs within the *Ceriods tagal* ± *Bruguiera* spp. community may result not only in decreased organic carbon flows through the coprophagous food chain within habitat patches, but also decreased food supply to the estuarine nekton, and also organic carbon flows to the seagrass component of the seascape. These disruptions would be expected to increase,

as storm-water affected patches increased in number and overall spatial extent as coastal urbanisation expands.

Another consideration is the fate of leaf litter that is not processed by Sesarmids.

Figure 8.1 shows the substratum of the *Ceriops tagal* ± *Bruguiera* spp. habitat when sesarmids were present and Figure 8.2, a very similar habitat where there were very few sesarmids. Both images were captured during a neap tide period when the substratum had not been inundated for several weeks.



Figure 8.1 **Appearance of the mangrove substratum when sesarmids are present (Eimeo Control Site).**



**Figure 8.2 Appearance of the mangrove substratum when sesarmids are rare
(Eimeo storm-water input site).**

These images illustrate a substantial accumulation of leaf litter when there were few sesarmids. During inundation by spring tides, this accumulation of leaf litter was available for transport out of the mangrove habitat, to downstream mangroves, the estuarine water body and to offshore coastal areas. Given that it was demonstrated by this study that this habitat could produce up to 23.08 ± 5.29 t/ha of leaf litter, potential tidal export of this material may be significant, and have affects on other systems. For example, Lee (2005) using a microcosm experiment on a non-mangrove substrate, found a decrease in species richness after enrichment with mangrove leaf litter, which was suggested to be due to higher concentrations of tannins. Alongi &

Christoffersen (1992) found that deposition of mangrove detritus in non-mangrove inshore areas caused a decrease of both species richness and diversity of the free-living nematode community and for most of the meiofauna.

The movement, or change in movement of other materials from the *Cerriops tagal* ± *Bruguiera* spp. habitat to other ecological patches should also be considered. The burrowing activity of sesarmids has been noted as being important in decreasing phytotoxins such as sulphide and ammonia through aeration of the substrate (Kristensen, 2008; Smith *et al.*, 1991). Thus in the absence of burrowing, these phytotoxins would be expected to occur in higher concentrations within the mangrove soil. Whilst mangrove soils have a very low porosity (Ridd, 1996), movement of dissolved materials will still occur through processes such as lateral diffusion (Hollins *et al.*, 2000). In addition, this process might be increased by flushing with urban storm-water runoff. This might mean, that the altered *Cerriops tagal* ± *Bruguiera* spp. substratum becomes a larger exporter of pulses of phytotoxins to adjacent and especially downstream habitats.

In summary, release of urban storm-water at point sources has created patches of mangrove habitat that are ecologically different to the remainder of the high littoral mangrove strip and may result in both structural and functional fragmentation of this habitat. Important differences in storm-water modified patches are a reduction in sesarmid crabs, and structural changes that might lead to functional changes within the mangrove habitat. These may include modification of food chains and of the

interactions between the biota and their physical and chemical environments. These disruptions may have ramifications for other systems to which mangroves are ecologically linked and may increase as urbanisation continues along mangrove margins.

8.3 Future studies

8.3.0 Implications of urban storm-water run-off in other areas

Storm-water runoff may be reducing the abundance of sesarmid crabs at a far larger scale than examined in this study. I have made qualitative observations in other parts of Queensland and the south-west Pacific region (e.g. Fiji, Tonga, the east Kalimantan region of the Indonesian island of Borneo, and the central Philippine island of Bohol), and found low numbers of sesarmid crabs in areas of urban storm-water runoff. Studies in other areas of Australia and the broader region, would be useful to determine if sesarmid species present elsewhere are also susceptible to urban storm-water runoff. This may be especially important to mangroves in shallow gulfs and embayements within restricted drainage to the open ocean.

In addition to studies of other sesarmids, it would also be useful to examine the response of other mangrove taxa to storm-water, particularly those that also have significant roles such as the leaf removing snail *Terebralia palustris*. In addition, longer term studies would be important in determining the change in the floristics and structure of mangrove vegetation with time since exposure to storm-water discharge.

The findings of these studies might provide additional insights into other determinants of sesarmid distribution.

8.3.1 Management responses

Considering the findings presented in this thesis, there is justification for considering less ecologically damaging ways of urban storm-water disposal. For example, discharge by smaller pipes at multiple points along the mangrove margin may have less site-specific impacts on sesarmid abundance than a single large discharge pipe. However, the net effect of multiple smaller discharge pipes needs to be assessed before such a management recommendation can be made.

A calculation of the impact on sesarmid crabs from both current and future urbanisation will require a quantitative knowledge of the amount and timing of storm-water input at any location. Whilst mapping of storm-water discharge points would be a useful way to estimate the broad geographical extent of the impact, quantitative analysis of catchment connectivity to the mangrove habitat is also required in order to clarify the effects of different levels of hydrological connectivity of mangroves to urban catchments.

8.3.2 Sesarmid salinity tolerances

A decline in soil core water salinity was the most plausible explanation for the decreased sesarmid abundance described by this thesis. There is very little known

about the salinity tolerances of most sesarmids. Studies that improve this knowledge will be required for all stages of the sesarmid life cycle, in order to assess impacts on their populations that may result through hydrological change. Development of hypotheses of salinity tolerances should be informed by knowledge of the likely magnitude and rate of change of salinity in the habitat, and for some taxa, within their burrows. Further, testing of hypotheses in the laboratory needs to be complemented by field studies that aim to detect behavioural adaptations that crabs might use to control their burrow environments.

8.3.3 Response of sesarmids to pollutants

A decline in soil core water salinity, and not increased pollutants, was considered the most plausible explanation for the decline in sesarmid abundance. Other studies have shown sesarmids to be tolerant to pollutants within urban run-off, including municipal sewage. Nevertheless, the role of pollutants needs further investigation, as there may be some that occur in higher concentrations than found in areas previously studied.

8.3.4 Sesarmid ecology

There is a notable paucity of knowledge of sesarmid ecology and behaviour. Further studies are required to gain a better understanding of the determinants of distribution patterns such as vegetation and substrate types, and location across the tidal gradient. For studies on sesarmids, commonly used descriptors of vegetation communities such

as stem density, diameter at breast height, and basal areas, may not be adequate alone in describing the habitat in a way which is ecologically meaningful. Further studies should also consider the importance of mangrove tree dispersion and relate that to the consequent patterns of micro-habitats within the mangrove community.

Piou *et al.* (2009) noted that there had been no previous investigations of the small-scale spatial distribution of burrowing decapod crabs. Apart from findings presented in this thesis, this appears to remain the case. Further studies are needed to develop a better understanding of the spatial and temporal application of the functions that sesarmids perform, at a range of scales.

The presence of adults has been demonstrated to be important for settlement of some species of sesarmids, and other studies have shown that small crabs rely on adult burrows for habitat. Additional studies are required to determine if these strategies are utilised by sesarmids more widely. One useful field based approach, for *Neosarmatium* spp., would be excavation of adult burrows to determine the actual number of recruits occurring in co-habitation with adult crabs.

The implications of ‘within habitat’ ecological changes, to the broader seascape through changes in organic carbon production and flows are unclear. Direct measurement of the production of organic carbon within habitats influenced by urban storm-water, and those not so affected, and the way in which this carbon flows out of the habitat, would provide some clarity.

8.3.5 Paradigms in sesarmid ecological research: leaf storage, grapsid vs. sesarmid, the unequal role of species

There are a number of paradigms that have become established within the literature that should be tested further, before becoming more broadly accepted:

1. Giddens *et al.* (1986) first proposed that sesarmids store leaves within burrows for a period of time, during which the leaves become more nutritious. Whilst studies have shown that leaves do become more nutritious over time, this is only indirect evidence that sesarmids store leaves for this purpose. Nevertheless, the ‘leaf ageing’ hypothesis appears to have received broader acceptance than the evidence warrants. Other hypotheses, including that storage of leaves is a ‘stockpiling’ strategy for when they are not available, should be further investigated.
2. In the majority of cases, the literature refers to grapsids as keystone species. Previous taxonomic arrangements considered the sesarmids (i.e. Sesarminae) as a Sub-Family within the Grapsidae. However, grapsids (i.e. those species now confined to the current Family Grapsidae) found in mangroves are generalists in habitat, non-burrowers, and are not known to feed on either mangrove leaves or propagules. Within Australian and many other mangroves, these roles are more often undertaken by species of the Family Sesarmidae. Thus it is more appropriate for the literature to specifically recognise sesarmids as keystone species to reflect current taxonomic arrangements.
3. Since the last comprehensive review of the literature (Lee, 1998), it has become clear that in addition to the above, not every sesarmid performs all roles attributed

to the group. For example, *Parasesarma erythrodactyla* does not always remove leaf litter, although it does burrow. Thus different species will have a different type and magnitude of influence on the ecosystem. Further studies are required to clarify the roles of different crab species within mangroves, and these should be cognisant that a species may perform different roles across its distributional range.

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