The ecology of the mud crab (*Scylla serrata*):
their colonisation of estuaries and role as scavengers in ecosystem processes

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Abstract

*Scylla serrata* is a portunid crab which can attain a weight of over 2 kg and a carapace width exceeding 250 mm. It is distributed throughout the Indo-West Pacific extending down the east coast of Africa, and both the east and west coasts of Australia. In Australia it is commonly known as the mud crab because it occurs within muddy, mangrove-lined bays and estuaries. Mud crabs are generalist predators eating most small, slow moving animals which they can catch, but they are also vigorous scavengers. Being scavengers, they are readily caught in baited traps set by commercial and recreational fishers, and are the stock for these popular fisheries.

Female crabs spawn offshore and larvae spend a period in the plankton where they develop into postlarvae or megalopae. The megalopae settle to the substratum and metamorphose into crablets (carapace width (CW) < 30 mm). Mud crab megalopae and crablets are rarely found, however, the larger juvenile crabs (CW > 30 mm) can be found in muddy mangrove habitat within bays and estuaries. Little is known about how mud crabs recruit to estuaries, where the megalopae settle, whether the megalopae or crablets colonise the estuaries, and their early use of different estuarine habitats. The first aim of this thesis was to contribute to our understanding of the mechanism utilised by mud crabs to recruit to estuaries.

The megalopae of several crab species use selective tidal-streaming to colonise estuaries. The ability of these megalopae to move vertically in the water column to selectively ride flooding tidal currents and maintain ground gained is critical to this process. The well-studied blue crab (*Callinectes sapidus*) of North America has an endogenous circadian rhythm, swimming upward during the day in offshore water, to utilise onshore, wind-generated currents to remain close to shore. Once in estuarine water, they descend to the substratum during daylight and rise during night-time flooding tides, presumably to avoid visual predators and move further upstream. I examined the vertical displacement response of mud crab megalopae to illumination in estuarine and offshore water during both the day and the night. In laboratory experiments mud crab megalopae swam higher in the water column when illuminated than when in darkness and this behaviour was maintained in both offshore and estuarine water. The apparent indifference to water type together with the fact that
mud crab megalopae are rarely caught in estuaries, led me to propose the model that for mud crabs, the megalopae tend not to colonise estuaries, as they do not appear to have developed a strategy to avoid visual predators once inside estuaries. Instead, I propose a new model of recruitment for mud crabs suggesting that they settle to the nearshore region of the coast and metamorphose into small crablets, and it is this life stage that tends to colonise estuaries.

Megalopae of many species actively select particular habitats when settling. Usually they select structurally complex habitats which may provide refuge from predators and sufficient food for growth. If mud crab megalopae do colonise estuaries, then it is likely that they would express similar selectivity for structurally complex habitats, where they can shelter from predators and metamorphose into crablets. If mud crab megalopae tend not to colonise estuaries, then this trait of selective behaviour among estuarine habitats is unlikely to have been derived. In an experiment however, the megalopae may still exhibit an ancestral selective trait even though it is not exhibited in nature, because megalopae rarely encounter estuarine habitats.

I used two laboratory experiments to determine whether megalopae and early stage crablets are selective among three estuarine habitats which they would likely encounter when colonising estuaries in southeast Queensland. Using circular choice arenas, I compared the selective behaviour of the megalopae and crablets within treatments where they had a choice: seagrass, mud or sand, and arenas where they had no choice: only seagrass, mud or sand. Contrary to the associations exhibited by other portunid crab megalopae, mud crab megalopae showed no selectivity among these estuarine habitats. Crablets, however, strongly selected seagrass over mud and sand. In the megalopae experiments, the number of individuals recovered was low overall, and uneven across the different habitats of the arenas without choice. This made interpretation of the results difficult and the effects of inefficient recovery, density-dependent mortality and post-settlement migration are discussed.

The selection exhibited by crablets shows an evolved behaviour for selecting seagrass, whereas the lack of selectivity by megalopae indicates that there is no evolved behaviour for selecting among these three habitats at this life stage. I argue that this selectivity has not evolved in mud crab megalopae because they tend not to encounter estuarine habitats. Whilst not rejecting other possibilities, I suggest that
these results support the coastal settlement model. I describe this conceptual model, showing the benefits for mud crab megalopae to settle on the coastal shelf, in the near shore region, colonising estuaries as crablets rather than megalopae, and remaining close to the substratum.

The second aim of the thesis was to investigate the role of mud crabs in the ecosystem process of scavenging. Scavenging, defined as the location and intentional consumption of carrion, recycles nutrients within the higher trophic levels of the food web, rather than allowing those nutrients to fall to the decomposers. Opportunistic scavenging is done by a broad range of taxa; not many species pass up an easy meal. In this section of the thesis, I explain how scavenging potential is a function of an ecosystem process and its organisation, being competition for food and the assemblage of opportunistic scavengers. I assess scavenging across a range of estuaries of varying condition and show that scavenging is a prospectively useful component of a metric for assessing ecosystem function or health.

Whilst many animals are opportunistic scavengers and readily eat fresh carrion, few are obligate scavengers. The spatial and temporal abundance of carrion is often too sporadic for the vast majority of animals to rely on as their sole source of nutrition. Vultures are a notable exception. In vigorous ecosystems animals rarely die a peaceful death; if they become sick or weak they are quickly killed and eaten. Therefore, the actual occurrence of scavenging is much less than the potential for scavenging, explaining why scavenging is rarely observed and little carrion found. I tested methods to quantify scavenging potential in estuaries of southeast Queensland. Scavenging potential was quantified by calculating the proportion of carrion consumed from carrion platters. The scavenging assemblage was determined using baited remote underwater videos (BRUVs). Initially, three questions relating to the methodology for measuring scavenging potential and the scavenging assemblage were asked: (1) is there a difference in scavenging potential between day and night and the duration that carrion is available, (2) is scavenging potential greater during times of tidal flow, and (3) is there a difference in scavenging potential between day and night, sites and dates and did these factors interact? The experiments determined that scavenging potential was greater during the night but there was no interaction between day/night and any other factor. During the day, flow had no effect on scavenging potential. The
scavenging assemblage was similar in the day and night. The results demonstrated that using carrion platters and BRUVs during the day is an appropriate method for determining the scavenging potential and scavenging assemblage within estuaries of southeast Queensland.

Having developed an appropriate method to measure scavenging potential and assemblages, I used this method to examine how scavenging related to ecosystem health. The concept of ecosystem health encompasses the organisation, vigour and resilience of an ecosystem. Scavenging is embedded within two of these key components of ecosystem health, the organisation of the ecosystem (the assemblage) and the vigour of its processes, for example the vigour of competition for food. As the magnitude and diversity of the assemblage increases, and the vigour of competition increases, scavenging potential should increase because many species are opportunistic scavengers. Healthier ecosystems tend to have a greater diversity and abundance of organisms for extended periods of time, therefore I predicted that scavenging potential would be greater in healthier estuaries. The Queensland government monitors the health of 19 estuaries in southeast Queensland using an index of water quality called the Ecosystem Health Index (EHI). Using carrion platters and BRUVs, I measured scavenging potential across nine estuaries in southeast Queensland spanning a spatial scale greater than 200 km. A significant negative relationship was found between the water quality (EHI) of an estuary and scavenging potential, the opposite to my prediction. The BRUVs showed that scavenging assemblages were not significantly different among healthy and unhealthy estuaries. Observations from this field work and the literature suggest that within urbanised regions, fishing pressure tends to be greater in places which are visually pleasing, have high water quality and are accessible. The unexpected relationship between water quality and scavenging potential is explained in terms of greater fishing pressure in estuaries with better water quality.

Fishing with baited traps and hooks selectively removes those animals with a propensity to scavenge, possibly depressing scavenging potential in heavily fished places. In southeast Queensland, mud crabs are more abundant in estuaries and bays where fishing is prohibited. Because they are a major scavenger, their removal from fished estuaries may affect the scavenging process there. However, many other
animals such as amphipods, snails, teleost fish, rays and sharks are also opportunistic scavengers and may maintain the scavenging normally done by the mud crabs and other species removed by fishing.

In addition to the desire to catch fish, recreational anglers are motivated to fish by other non-economic factors, for example the enjoyment of being outdoors. The visual appeal of a fishing site ranks highly among factors affecting the choice of sites by anglers. In populated places, where many anglers have easy access to waterways, fishing pressure in places of good water quality is likely to be greater. These non-economic factors mean that recreational fishers may fish in places that commercial operators find unprofitable, thereby maintaining high fishing pressure and a ‘press’ impact on populations of fished opportunistic scavengers, such as mud crabs.

Importantly, recreational fishing has little impact on water quality. I tested whether fishing pressure in southeast Queensland is sufficient to depress scavenging potential and alter the assemblage of scavengers by measuring scavenging inside and outside five visually appealing zones closed to fishing. Scavenging potential was significantly greater inside these No-Take zones and the assemblages scavenging inside were different to those scavenging outside. Therefore it is likely that fishing pressure in southeast Queensland is significant and able to depress scavenging activity. Because scavenging potential is embedded within two of the key components of ecosystem health, it is likely that where scavenging potential is altered, ecosystem health is also altered. Therefore, whilst important, measures of water quality may not be sufficient to monitor ecosystem health in places subject to fishing pressure of magnitudes occurring in southeast Queensland.
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Declaration

The material presented in this thesis has not been previously submitted for degree or diploma in any university, and to the best of my knowledge contains no material previously published or written by another person except where due acknowledgement is made in the thesis itself.

James Webley
Chapter 1: General introduction

1.1 The mud crab (Scylla serrata), and thesis rationale

The mud crab, Scylla serrata, is a large portunid crab which can attain a weight of over 2 kg and a carapace width exceeding 250 mm (Heasman 1980). There are four species within the genus Scylla, and they are distributed throughout the Indo-West Pacific (Keenan et al. 1998). Whilst the other three species tend to be restricted to the warmer regions, S. serrata has an extended distribution down the east coast of Africa, and both the east and west coasts of Australia (Ryan 2003, Anon 2005).

Scylla serrata is the only member of the genus found in southeast Queensland. Adults tend to occur in muddy, mangrove-lined bays and estuaries throughout this region (Heasman et al. 1985), which is the location for the research presented in this thesis. Mud crabs are generalist predators eating gastropods, bivalves and most other small animals that they can catch (Hill 1976), but they are also vigorous scavengers. Being scavengers, they are readily caught in baited traps set by commercial and recreational fishers. They are highly sought after and have attained an ‘icon’ status, appearing as features on many seafood restaurant menus (Hill 2007).

Ovigerous mud crabs tend to move offshore to spawn. The larvae spend a period in the plankton where they grow through five zoeal stages before becoming megalopae (Hill 1994, Rabbani & Zeng 2005). In portunid crabs, the megalopa is the transitional stage which settles to benthic habitats and subsequently moults into a true crab. Mud crab megalopae and crablets (carapace width (CW) < 30 mm) are cryptic and rarely found, however, juvenile crabs (CW > 30 mm) can be found in mangrove habitats in bays and estuaries. Because of difficulties in finding mud crab megalopae and crablets, little is known about their mechanism of recruitment to estuaries, or their use of different estuarine habitats.

This thesis has two aims. The first aim was to provide new insights into the recruitment mechanism of the mud crab. Previous research has made considerable efforts searching for mud crab megalopae and crablets in an attempt to understand the recruitment process (e.g. Moser & Macintosh 2001). However, because they have not been consistently captured, it has been difficult to test the models explaining this process. Properly testing models that comprehensively explain recruitment and larval
supply in the field, requires large temporal scales (e.g. Pile et al. 1996). Unfortunately, projects of this duration are beyond the three year funding window of many PhD programs. For this reason, I used two laboratory experiments to test whether or not the mud crab conformed to selected components of the general model of estuarine recruitment for similar crabs (Forward et al. 1997, Tankersley et al. 2002). Specifically I tested whether: (1) megalopae behave in a manner consistent with models using selective tidal streaming to explain how crabs colonise estuaries, and (2) megalopae and crablets settle to preferred benthic estuarine habitats.

Mud crabs are scavengers, rapidly locating and consuming carrion. Many other animals are opportunistic scavengers and it is likely that scavenging is driven by fundamental ecosystem processes such as competition for food and the organisation of the assemblage. The second aim of the thesis was to investigate the role of mud crabs in the ecosystem process of scavenging. This work has led to a prospective method to evaluate ‘ecosystem health’ by measuring a latent process, scavenging potential.

1.2 Part I: Mud crabs: recruitment and nursery habitats

1.2.1 General model for colonising estuaries

Many estuarine crabs migrate seaward or move out onto the coastal shelf to spawn (Hill 1994, Forward et al. 2003b). This behaviour is likely to provide evolutionary fitness benefits. Fitness may be enhanced because the physical environment of the coastal shelf is often more thermostatically and chemically stable than within estuaries. Smaller estuarine water bodies are less able to buffer the effects of events such as the large freshwater inputs from a storm, which can lead to rapid changes in temperature and salinity. In a fluctuating environment, the energy used by larvae to maintain cell homeostasis is energy that is lost to development and growth. Fluctuating salinity and temperature increases mortality of laboratory reared mud crab larvae; in early zoeal stages (Z1 – Z2) oceanic salinity and stable temperatures (27 – 30°C) optimise survival (Hill 1974, Fielder & Heasman 1999). The buffering effect of a large water body provides a more stable environment, enhancing larval development. Fitness may also be improved because larval dispersal and thus genetic mixing occur across a larger spatial scale on the coastal shelf than within isolated estuaries (Pechenik 1999, Gopurenko & Hughes 2002). One cost of these benefits is, however,
the journey of finding and recruiting to the estuarine habitats in which mud crabs are found as adults.

1.2.2 **Selective tidal streaming**

Recruiting to coastal habitats from the coastal shelf is a transitional stage marking the end of the pelagic period. Many species of crabs throughout the world recruit to coastal habitats when they are postlarval megalopae or early juveniles (Queiroga et al. 2002, Lee et al. 2005, Giménez & Dick 2007). Although crab larvae are relatively strong swimmers, they are usually unable to swim upstream against the flows commonly found in tidal estuaries (Luckenbach & Orth 1992, Lee et al. 2004). Research into the blue crab (*Callinectes sapidus*), a North American portunid, has revealed that their megalopae colonise estuaries by using selective tidal streaming (Tankersley et al. 2002, Forward et al. 2003b).

This general model predicts that offshore, blue crab megalopae are more abundant in surface waters during the day. Here, they use onshore, wind-generated surface currents to remain near the coast, and are thus able to enter estuaries during flooding tides (Goodrich et al. 1989, Etherington & Eggleston 2000). Inside the estuary, they rise into the water column during night-time flooding tides and ride the current to move farther upstream. As slack water approaches and turbulence increases with the changing tide, the megalopae descend to the substratum and remain there where the ebbing current is reduced by drag from the substratum. They remain near the substratum during daylight, possibly to reduce their exposure to visual estuarine predators (Tankersley et al. 2002). When the megalopae find suitable estuarine habitat, such as seagrass beds or oyster reefs, they settle to the benthos and moult into juvenile crabs (van Montfrans et al. 2003). The colonisation of estuaries by these megalopae is characterised by episodic bursts against a continuous background of minor influx (Forward et al. 2004). Various estuarine stimuli, for example turbulence at slack tide, light and changes to pressure and salinity, interact in complex ways with the swimming patterns of megalopae to generate this selective tidal streaming (Forward & Rittschof 1994, Forward et al. 2003b).

Whether or not mud crab megalopae colonise estuaries in a similar manner has not been tested. Earlier researchers made substantial efforts to develop an estuarine recruitment model for mud crabs, but difficulties in consistently finding megalopae
and crablets (CW < 30 mm) prevented them from testing such models (Heasman 1980, Hill et al. 1982, Knuckey 1999, Moser & Macintosh 2001).

Mud crab megalopae and crablets are rarely found. In my review of the literature, there was one report of mud crab megalopae and crablets being found within an estuary in South Africa (Forbes & Hay 1988), and a second from the Philippines, reporting that megalopae were found in coastal waters but not in estuaries or ponds within mangroves (Arriola 1940). An extensive experiment in Moreton Bay, Queensland, placed artificial habitats (roof tiles) within a mangrove habitat (Hill et al. 1982). Over the 17 month duration of this experiment, fewer than 20 crablets were found under the 99 tiles sampled every 2 – 4 weeks (> 1600 tile lifts). Other researchers have searched mangrove habitats and used tiles in a similar manner in estuaries in the Northern Territory without success (I. Knuckey, Fishwell Consulting Pty Ltd, pers. comm.). There have been other anecdotal reports of sporadic sightings of mud crab crablets in other estuarine habitats, including sandy beaches, saltmarsh and seagrass. Observations as sporadic as these prevent us from determining if these crablet-habitat associations are representative or exceptional.

There are a number of possible explanations for the lack of success in finding mud crab megalopae within estuaries. Not finding megalopae is not evidence of their absence, so one explanation may be that their recruitment to estuaries may be very temporally sporadic, making them difficult to detect. The blue crab (C. sapidus) has large episodic recruitment events and megalopae of the velvet swimming crab (Necora puber) tend to be scarce, but long term data sets show that these sporadic events punctuate a low but measurable background level of recruitment (Pile et al. 1996, Forward et al. 2004, Lee et al. 2005). This background level of recruitment appears to be absent for mud crabs. Mud crab megalopae may also settle and grow rapidly once entering estuaries, leaving very little time in which they can be sampled. Given that the efforts of many researchers (Heasman 1980, Hill et al. 1982, Knuckey 1999), at different times and places, have failed to consistently find mud crab megalopae and crablets within estuaries, a more likely explanation is that the recruitment mechanism for mud crabs into estuaries is different to the general model that megalopae tend to be the life stage which colonises estuarine or coastal habitats. Mud crab megalopae may not be the life stage that colonises estuaries and, therefore, are rarely caught there.
If mud crab megalopae do colonise estuaries however, then it is likely they, like the blue crab, use selective tidal streaming to move upstream against the net outward estuarine flow. Blue crab megalopae alter their swimming behaviour in response to light and the presence of estuarine stimuli (Tankersley et al. 2002, Forward et al. 2003b). Using laboratory experiments, presented in Chapter 2, I tested whether mud crab megalopae behave in a manner consistent with the general blue crab selective tidal streaming model. Specifically, I tested whether the vertical migration behaviour of megalopae, the key behaviour in selective tidal streaming, was different to that predicted by the general blue crab estuarine colonisation model.

1.2.3 **Habitat selectivity of mud crab megalopae and crablets**

Organisms are rarely randomly distributed spatially, and instead tend to be associated with particular habitats, physical conditions, or other variables (Condit et al. 2000, Bertness et al. 2001). This non-random distribution can be, but is not necessarily, the result of previous choices or preferences. Animals are constantly faced with choices, such as what to eat, where to live and who to mate with. The consequences of these choices may affect their survival and therefore enhance the fitness of future generations (Gould & Lewontin 1979, Krebs & Davies 1997). These choices are most important and therefore, probably most pronounced, when the animal’s life or potential reproductive success is at greatest risk. For many marine organisms, this period is the settlement and early juvenile stages. During these stages the probability of mortality is very high (Hunt & Scheibling 1997).

1.2.3.1 Evolutionary benefits of selectivity

Rather than remaining in hostile places, the postlarvae of several decapod species choose to settle in, or move to, habitats which provide refuge or abundant food (Dionne et al. 2003, Moksnes et al. 2003, van Montfrans et al. 2003). This behaviour increases the potential reproductive fitness of the individuals making such a choice, over those that do not. Understanding the behavioural choices made among different habitats that they are likely to encounter, enables us to rank those habitats according to the likelihood that the move to those habitats increases the fitness of populations.

Places which increase the probability of an individual juvenile contributing to future generations can be considered nursery habitats (Beck et al. 2001, Dahlgren et al.
Preference behaviours are only likely to evolve where the behaviour increases reproductive fitness. Therefore, selectivity for a particular habitat is evidence that the characteristics of that habitat increased the reproductive fitness of the juvenile’s ancestors. This does not necessarily mean, however, that the selected habitat is optimal. Novel habitats could have been created which provide better refuge or food, thereby increasing fitness. However, these novel habitats may not have been encountered frequently enough for preferences to have evolved.

Structurally complex habitats such as seagrass beds, saltmarsh and mangroves are often cited as nursery habitats for juvenile animals including crabs (Jackson et al. 2001a, Minello et al. 2003, Mumby et al. 2004). The complex structure of these habitats provides refuge from predation and stable surfaces which can enhance primary production (epiphytic algae) and trap nutrients and food (Agawin & Duarte 2002). Paradoxically, the greater abundance of small animals consuming this food and seeking shelter attracts predatory fish and crustaceans, which seek to eat them (Connolly 1994, Franco et al. 2006).

The megalopae and juveniles of the blue crab (*C. sapidus*) and an Indo-Pacific portunid, the blue swimmer crab (*Portunus pelagicus*), are associated with seagrass (Kenyon et al. 1999, van Montfrans et al. 2003). Blue crab megalopae have been shown to alter their swimming behaviour and settle in greater densities to seagrass than other habitats (Forward et al. 2003a). If the general estuarine colonisation model applies to mud crabs, then their megalopae and crablets are likely to also select for structurally complex estuarine habitats such as seagrass, over other less complex habitats.

I tested the model that mud crab megalopae and crablets strongly select seagrass over other commonly occurring, less complex estuarine habitats using laboratory experiments (Chapter 3). These results were congruent with those of Chapter 2 and are used to develop a new coastal settlement model explaining how mud crabs recruit to estuaries in southeast Queensland.

1.3 Part II: The role of mud crabs in the ecosystem: neither engineer nor keystone

This second part of my thesis investigated the role of the mud crab in the scavenging process. Scavenging is a process embedded in the ecosystem, involving a
broad range of taxa, and driven by fundamental ecological factors such as competition for food. As such, it is a process of the ecosystem as opposed to the activity of a single functional group. This research developed a simple and effective way to measure the potential for scavenging. Using the concept of ‘ecosystem health’, it demonstrated that measures of water quality alone are insufficient for determining estuarine health in places accessible to large human populations.

1.3.1 **Many small links make an ecosystem**

1.3.1.1 Few organisms are keystones, the small links are important

By definition, few organisms within an ecosystem can be classified as foundation species, ecosystem engineers, or keystone species (Paine 1969, Dayton 1972, Hurlbert 1997). These organisms contribute spectacularly to the functions and structure of ecosystems, in magnitudes which are disproportionate to their relative abundance. They are exceptional species and because of their uniqueness and influence, or the ecologists examining them, they attract considerable research interest (Underwood & Fairweather 1986, Bond 2001). For every such exceptional species, though, there are many others within the ecosystem whose contributions appear less critical for ecosystem processes, and they might even be considered functionally redundant (Walker 1992, Johnson et al. 1996).

Recent evidence suggests, however, that the numerous unexceptional species make a considerable hidden contribution to the ecosystem. By providing multiple predator-prey pathways and functional interactions, they bestow stability (McCann et al. 1998, Walker et al. 1999, Neutel et al. 2007). Paradoxically, complexity within systems is predicted to lead to instability where species are randomly included within assemblages (May 1972), yet empirical observations of ecosystems appear to show that complexity begets stability (Polis 1994). This paradox can be explained in part because species within ecosystems are unlikely to be randomly selected. Neutel et al. (2007) propose that species within an ecosystem are incorporated, or rejected, over a progressive pattern of increasing and decreasing stability during the development of the ecosystem based on their ability to persist. Using mathematical models and case studies, they show that numerous weak interactions between species buffer the ecosystem against perturbations, increasing its resilience and stability. Therefore, in
diverse systems, it is likely that the unexceptional species help to underpin the stability of ecosystems by providing a variety of alternative trophic pathways and service providers.

Within an ecosystem, several taxa may perform similar functions but differ in their ability to respond to environmental perturbations. For a given set of environmental conditions, one of these species may be dominant. When conditions change, however, this species may decline, but can be replaced by one of the less abundant species more suited to the new conditions (Walker et al. 1999). This 'switching' of the dominant provider after disturbances helps maintain ecosystem services. In addition, some of these apparently redundant species may have latent functions, which provide pivotal services under different environmental conditions (Bellwood et al. 2006).

Mud crabs are unlikely to be an ecosystem engineer, or a keystone species, but they are one of the many unexceptional species contributing to vital ecosystem processes. Mud crabs are bioturbators, digging burrows and foraging for gastropods and bivalves (Hill 1979). They are voracious scavengers, quickly locating and consuming carrion within turbid estuaries and mangroves (J. Webley, pers. obs.). At different stages of their life, from larvae to adults, they are also a source of nutrition for planktivores, other macro-crustaceans, teleost fish, sharks, rays, birds and humans. Many other species within estuaries do similar things, and it is unlikely that the loss of mud crabs from estuaries would lead to a dramatic phase shift, or a collapse of the estuarine ecosystem. Instead, it is likely, as Walker et al. (1999) hypothesise, that other species doing similar services would effectively fill the functional void.

1.3.1.2 Ecosystem services

Ecosystems are not static entities; rather, they encompass the organisms and the environment which continually interact with each other, performing a variety of essential and valuable functions while maintaining a degree of stability. This description does not go so far as the Gaia hypothesis, which suggests that ecosystems are superorganisms (Lovelock 1979), but rather aims to emphasise the functions and processes of an ecosystem instead of its constituent taxa. Ecosystems also deliver services which benefit or sustain the lives of humans; examples are the provision of food and the purification of water (Costanza et al. 1997). From an anthropocentric
perspective, and putting aside our emotional attachment to particular species, the maintenance of ecosystem services is more important than the maintenance of particular species that happen to be involved in the processes at any one time. Because ecosystem processes deliver the services, managing ecosystems should therefore primarily entail maintaining and conserving ecosystem processes as well as the assemblage of organisms (Lindenmayer et al. 2008).

Good management requires that ecosystems also have resilience to recover from the inevitable perturbations which will impact them over time (Hughes et al. 2005, Lindenmayer et al. 2008). Complexity, through an intricate network of species interactions and apparent redundancy, adds to stability. Measuring ecosystem processes and understanding the mechanisms that generate rate changes and affect resilience will provide the foundations for better ecosystem management practices.

1.3.2 ‘Ecosystem health’: words for management

1.3.2.1 What is ‘ecosystem health’?

Definitions of ‘health’ conjure ideas of homeostasis, but not stagnancy; vitality, but with stability (e.g. cell growth but not cancer; economic growth but not housing booms) (Karr 1999). In allopathic medicine, doctors measure numerous specific indicators for example, core body temperature, blood pressure, lipid levels and then tell patients whether they consider them to be ‘healthy’ or not. Health itself is not directly measurable, but the word is used to communicate succinctly the condition or integrity of a person. Using the metaphor with human health, Rapport (1985) defined health in ecosystems to mean an absence of disease or dysfunction and an ability to recover from perturbation. Importantly, anthropocentric values are incorporated into what it means to be ‘healthy’, for example in nature; a productive fishery, clear water in an estuary, and stability through time. Definitions of health, including ecosystem health therefore, are to some extent subjective. They invariably incorporate anthropocentric perceptions of how an ecosystem should appear and function (Rapport 1998, Fairweather 1999a, Fairweather 1999b, Karr 1999, Vugteveen et al. 2006). Rather than being a real character of an ecosystem, ‘healthy’ is an anthropocentrically desired state space.
Science will always have difficulty incorporating subjective definitions into research programs (Peters 1991). Subjectivity does not fit the scientific process and because of this, the validity of ‘ecosystem health’ as a measurable characteristic generated vigorous debate (Wicklum & Davies 1995, Rapport et al. 1999, Wilkins 1999). Scientists may never settle on an objective definition of ecosystem health because of its implied subjectivity however, science can report the metrics of ecosystem characters and processes, and develop mechanistic models describing their function. This data and theory can be used to judge whether an ecosystem is functioning within the bounds of what society considers being ‘healthy’, i.e. a socially acceptable state space.

Natural resources and ecosystem processes are vital for human survival; we need ecosystems to continue to provide benefits for humans into the future (Costanza et al. 1997). Managers are expected to preserve ecosystem productivity and function, and maintaining ecosystem health or integrity has become the public goal of many environmental management agencies (for international examples see Karr (1999)). Given that it is likely that ecologists understand ecosystems better than other members of society, it is important that they contribute to subjective definitions such as ecosystem health and integrity, especially if these definitions form the benchmarks managers strive for. By having input into the definitions of these subjective terms, ecologists may be able to better direct them to objective measurements of ecosystem characteristics and processes, for example; biodiversity, productivity, and recruitment.

1.3.2.2 Organisation, vigour and resilience

Development of the ecosystem health concept has led to three overarching components of ecosystem health: organisation, vigour and resilience (Rapport et al. 1998). These three components deal with the constituents, the processes and the ability of the ecosystem to recover from disturbance, respectively.

The organisation of the ecosystem reveals its complexity (Rapport 1998). In many cases, increasing species richness promotes interactions between species, and creates additional opportunities for redundancy and facilitation (Hooper et al. 2005). Food webs become more complex, and additional trophic pathways are generated. Importantly, with more complex organisation and greater species richness, the probability that energy flows are dominated by a few simple pathways is reduced.
Many alternative pathways or weaker links are generated, increasing stability (Polis 1994, McCann et al. 1998, Neutel et al. 2002).

The vigour of an ecosystem is a rate term referring to ecosystem processes (Rapport 1998). Within an ecosystem, the rates of these processes vary naturally through time but can also change when ecosystems are disturbed by humans. For example, rates of primary production become excessive when limiting nutrients are added (Cloern 2001, Baird et al. 2004). These rates can be greater than or less than the ideal healthy condition. These rate processes, therefore, should be compared to representative ‘healthy’ ideal systems, such as a representative ecosystem considered undisturbed.

Resilience is the ability of an ecosystem to absorb natural or human-generated disturbance and recover to essentially the pre-disturbed, but naturally variable state (the ‘basin of attraction’ Walker et al. 2004), instead of degrading or flipping to an alternate state (Holling 1973, Beisner et al. 2003, Hughes et al. 2005, Thrush et al. 2008). This interesting characteristic is perhaps the most difficult to study because it is a latent property of the undisturbed ecosystem.

Resilience has evolved into an important component of adaption to climate change and is central to maintaining social-ecological systems (Walker et al. 2004, Adger et al. 2005, Nelson et al. 2007). Resilience and its mechanisms can only be observed after the ecosystem has been disturbed. Testing resilience hypotheses, therefore, requires manipulative or opportunistic disturbance of ecosystems, followed by careful monitoring of the recovery processes (e.g. Thrush et al. 2008). This approach has led to surprising discoveries in coral reefs.

The recovery of a coral reef from a macroalgae-dominated state was primarily driven by a single species of batfish (*Platax pinnatus*) rapidly clearing the reef of macroalgae (Bellwood et al. 2006). What is interesting is that in less disturbed coral reefs, this batfish is scarce and regarded as a predator of invertebrates, not a voracious grazer. The batfish’s function in resilience was latent and was only revealed after a manipulative experiment disturbing the coral reef ecosystem. Latent effects such as resilience will not be evident until natural or anthropogenic disturbances occur. Manipulative experiments at the ecosystem scale are logistically and financially
difficult (Carpenter et al. 1995), but the knowledge gained from these experiments is a prerequisite for better management of ecosystems.

Different types of ecosystems can have fundamentally different degrees of organisation, vigour and resilience. A pristine desert community, for example, is no less healthy than a pristine rainforest simply because biodiversity, primary production and biomass are lower in desert communities (Rapport 1998). The health of an ecosystem should be assessed against a suitable benchmark, posing questions such as: (1) Is this the healthiest assemblage that we can expect in this place?, and (2) Are these processes occurring at the rates we expect for this place (Fairweather 1999a)? This requires a good understanding of how assemblages interact with the physical environment and each other to drive ecosystem processes. We need to have a scientific model of what we expect the magnitude and range of services and processes to be in undisturbed, resilient ecosystems.

1.3.3 Scavenging potential: a latent ecosystem process

Scavenging can be defined as the intentional consumption of carrion (Britton & Morton 1994, DeVault et al. 2003). Many omnivorous and carnivorous animals will eat fresh carrion if they find it because it is just as nutritious as live prey. When carrion is abundant or consistently available, it can be a significant source of energy and ultimately increases the abundance of individuals, or provides stability to populations of opportunistic scavengers (Garthe et al. 1996). Despite the ubiquity of scavenging and its potential importance for understanding ecosystem processes, it has been little studied, especially in the coastal marine environment (Britton & Morton 1994, DeVault et al. 2003). Reasons for this are speculative, but may include a general distain by researchers for the odours and sights of putrefying carcasses or, more importantly, that carrion is rarely observed in the environment and therefore considered insignificant.

1.3.3.1 Scavenging effects on food webs and populations

By consuming carrion, scavengers deprive biomass and energy from the microbes which would otherwise decompose the corpse (Putman 1983). Scavenging, therefore, can be considered to recycle nutrients within higher trophic levels (Figure 1.1). This consumption of carrion may supplement food supplies and lead to an
increase in the biomass of scavengers and subsequently their predators, as well as generating alternative food web pathways. This is especially the case where carrion is delivered to an otherwise energy-limited or nutrient-limited environment. For example, coastal populations of coyotes foraging on the Baja California peninsula consume marine carrion washed onto beaches. This additional supply of food supports the greater densities of coyote populations found along the coast than in the adjacent inland regions (Rose & Polis 1998). Many seabirds and crabs scavenge the discards from trawlers; this carrion is thought to have increased their populations and altered food webs (Wassenberg & Hill 1987, Garthe et al. 1996). The great skua (Stercorarius skua), a predator of other seabirds, scavenges a considerable amount of trawler discards. Should the availability of this carrion be reduced, and the great skua’s foraging activities switch to hunting seabirds rather than scavenging discards, then effects are likely to be seen in food webs and seabird populations (Votier et al. 2004).

![Simplified food web showing the scavenging process recycling nutrients and energy at higher trophic levels, whereas energy falls to lower trophic levels when it is decomposed.](image)

**Figure 1.1** Simplified food web showing the scavenging process recycling nutrients and energy at higher trophic levels, whereas energy falls to lower trophic levels when it is decomposed.

1.3.3.2 Energetics of scavenging: opportunistic vs obligate

Scavenging involves a degree of searching to locate carrion, so the principles of foraging theory are likely to apply (Perry & Pianka 1997). Upon finding a piece of unclaimed fresh carrion, either by an intentional search as a vulture does, or by a chance discovery, there is little additional energetic cost incurred in eating it. Compare this with the detection of live prey, after which additional energy must be expended to
catch and subdue the prey. Predators which have to hunt and subdue their prey can also be injured, which may result in a loss of fitness or, in the extreme, their own demise. Therefore, once found, eating fresh carrion is usually energetically beneficial, explaining why many omnivores will eat fresh carrion.

Although many animals are opportunistic scavengers, few are obligate scavengers. Initially this appears paradoxical considering the beneficial energetics of consuming fresh carrion once found. Obligate scavengers derive all of their energy from carrion but they must search for it; few animals will die right in front of a scavenger’s nose. Locating carrion is a function of its abundance, distribution, ease of detection, and competition for it. These factors are less important for the opportunistic scavenger, which uses carrion only as a supplement for other sources of food.

Carrion is patchily distributed through space and time. Large pieces of carrion, such as whale falls and the remains of elk from wolf kills, may be separated by many kilometres and occur sporadically through time (Smith & Baco 2003, Wilmers et al. 2003). The abundance of carrion tends to be less than the abundance of prey, except in the short term case of mass mortality events, such as fish kills in lakes. Obligate scavengers may lose potential meals of carrion to opportunistic scavengers or the carrion may decompose and become unpalatable. Carrion is likely to be scarce and only available for short periods before it is either eaten or spoilt (Putman 1983). Obligate scavengers therefore need to locate carrion quickly, with a minimum energetic cost. These criteria restrict the viability of obligate scavengers. In the terrestrial realm, obligate scavengers are restricted to the vultures (DeVault et al. 2003). Old world vultures are able to exploit this lifestyle because their searching method of soaring high above the savanna uses little energy and provides an excellent vantage for locating carrion quickly (DeVault et al. 2003).

In the abyssal plains, however, things may be different where carrion such as whale falls may have substantially contributed nutrients to a dark oligotrophic ecosystem (Smith & Baco 2003). Although no large obligate marine scavengers have yet been discovered, Ruxton and Houston (2004) demonstrate that scavenging in the deep sea is a feasible life strategy. In time, as the deep is explored, deep sea metazoan may be discovered that depend almost entirely on carrion.
Smaller items of carrion, for example the remains of shore crabs, may be more abundant than larger items. Oystercatchers (*Haematopus palliatus*) forage for the intertidal crab *Cystograpsus angulatus*. These crabs tend to have a carapace width of 17 – 30 mm. The oystercatchers rarely eat the entire crab, leaving significant portions for scavengers such as other birds and snails (Daleo et al. 2005). Calculations from predation rates showed that the oystercatchers generated 0.23 pieces of crab carrion per m² per day and that scavenging snails arrived at this carrion within 2 minutes (Daleo et al. 2005). In terrestrial systems, ants have been observed to find and remove small carrion items within five minutes (Retana et al. 1991). Generally, accessible carrion tends to be quickly scavenged by a broad range of opportunists, thereby reducing the carrion standing crop and the viability of obligate scavengers.

Scavengers also compete with the microbial community for carrion (Burkepile et al. 2006). Bacteria and fungi decompose carrion and in the process exude metabolites. Initially, the volatile metabolites may be a signal, helping scavengers to locate the carrion. Turkey vultures (*Cathartes aura*) locate carrion within forests by smell, finding one-day old carrion faster than recently killed animals (Houston 1986). However, as microbial decomposition progresses, the carrion putrefies, becoming unpalatable and toxic, and loses its nutritional value to scavengers (Janzen 1977).

Obligate scavengers compete with many organisms because carrion is easily consumed by a broad range of opportunistic species. The natural abundance of carrion, therefore, is likely to influence the success of obligate scavengers in highly competitive environments.

### 1.3.3.3 The natural abundance of carrion and scavenging

Although predation tends to be the major killer, animals die from causes other than predation (DeAngelis 1992). Factors such as starvation, disease, exposure, accident and environmental extremes can also take a substantial toll (Oksanen & Oksanen 2000). For the copepods that dominate the plankton of Chesapeake Bay, for example, up to 29% die from causes other than predation (Tang et al. 2006). Predation itself also generates carrion when all of the prey is not consumed (Wilmers et al. 2003). However, despite the many non-predatory causes of death and the availability of carrion as by-product from predation events, carrion is not readily
observed in the field, and this might be explained by the speed with which carrion is consumed (i.e. its turnover rate, (DeVault et al. 2003).

Observations and experiments have shown that carrion can be consumed quickly. For example, dead slugs placed in wheat fields are scavenged by beetles within six hours (Foltan et al. 2005). Arthropod corpses placed in a temperate grassland are scavenged within five minutes (Retana et al. 1991). In shallow coastal environments, sharks, birds, fish, dolphins and crabs arrive within minutes to feed on carrion discarded from trawlers, and the majority of the carrion is completely consumed within 24 to 48 hours (Wassenberg & Hill 1987, Bergmann et al. 2002). If the standing crop of carrion does turn over rapidly, then the low abundance at any point in time may hide the importance of carrion in trophic dynamics.

1.3.3.4 Scavenging potential: a latent process embedded in the ecosystem

A latent process is a process which does not manifest itself until the right conditions occur. Opportunistic scavenging is such a process. For example, on a pristine coral reef, where a diverse range of fish and crustaceans are abundant, very little scavenging activity may be observed, yet if carrion is added, many of these animals quickly move to consume it. In this scenario, scavenging potential always existed, but was only manifested by the addition of carrion.

In the subtidal estuarine environment, which is often turbid, it is logistically difficult for researchers to locate naturally-occurring carrion. This makes testing models about the natural scavenging rates or abundance of carrion problematic. However, understanding the potential for scavenging may be just as valuable as understanding actual scavenging activity.

Scavenging is a process within the ecosystem. It is affected by the composition of the assemblage of animals and the vigour of competition. It is a process embedded within two of the key components of ecosystem health, organisation and vigour. Therefore, it might be a useful component of a broader ecoassay. Animals in vigorous ecosystems rarely die a peaceful death, because the sick and weak are quickly preyed upon. However, if an animal dies from causes other than predation, it is likely that its carcass would be quickly scavenged. In an ecosystem in which competition for food is vigorous and the assemblage of organisms is diverse, the natural occurrence of scavenging may be low, but latent scavenging potential is high. Therefore, measuring
and understanding this latent scavenging potential may provide insights into the health of ecosystems, because it samples both the assemblage and vigour of the ecosystem.

1.4 Structure of the thesis

The remainder of this thesis is presented as a series of discrete chapters describing experiments on mud crab ecology and behaviour, and the role of scavengers more broadly.

Chapter 2 tests the model that the vertical migration of megalopae in response to light in both offshore and estuarine water is different to that predicted by the general selective tidal streaming model. This research has been published as Webley and Connolly (2007) and is presented here as published, except for changes to formatting for consistency with the thesis style.

Chapter 3 presents a laboratory habitat preference experiment. This experiment tested whether or not mud crab megalopae and crablets had similar preferences for commonly occurring estuarine habitats.

Chapter 4 presents initial experiments done to develop a method to investigate the scavenging processes across estuaries in southeast Queensland. Models about the effect of day and night, site, date and tidal flow on scavenging potential and interactions among the factors were tested. The results of this chapter were used in the experimental designs testing hypotheses presented in Chapters 5 and 6.

Chapter 5 examined the relationship between water quality, as a proxy for estuarine health, and scavenging potential. I predicted that scavenging potential would be positively correlated with water quality. The Moreton Bay Waterways and Catchment Partnership, a Queensland government organisation responsible for assessing estuarine ecosystem health, uses a metric of water quality, the Ecosystem Health Index, to assess the health of estuaries in southeast Queensland. This research rejected the hypothesis and showed that scavenging potential decreased as water quality increased.

Chapter 6 tested the effect of current levels of fishing pressure on scavenging potential, and related this result to the conclusions drawn from the experiment in Chapter 5.
Chapter 7 summarises the experimental work and discusses the implications for mud crab recruitment models and the role of mud crabs and the scavenging process in assessing estuarine ecosystem health.
Chapter 2: Vertical movement of mud crab megalopae (*Scylla serrata*) in response to light: doing it differently down under

2.1 Abstract

Selective tidal-streaming is a model frequently used to explain how planktonic larvae colonise estuaries. The ability of larvae to move vertically in the water column to selectively ride favourable currents and maintain ground gained is critical to this process. The mud crab (*Scylla serrata*) is a widely distributed, commercially and recreationally important portunid crab but little is known about its estuarine recruitment mechanisms or the vertical migration behaviour of its megalopae. In studies of the blue crab (*Callinectes sapidus*), important factors identified in the recruitment mechanism include altered vertical swimming behaviours in estuarine and offshore water and an endogenous circadian rhythm. Using laboratory experiments we examined the vertical displacement response of mud crab megalopae to illumination in estuarine and offshore water during the day and the night. Mud crab megalopae released into 1 m high towers swam higher when illuminated than when in darkness. This behaviour was repeated during the day and the night and in offshore and estuarine water. Given the apparent indifference to water type and the fact that mud crab megalopae are rarely caught in estuaries, we propose the model that these crabs do not colonise estuaries as megalopae, but settle and metamorphose into small crabs on the coastal shelf before moving along the sea bed into estuarine habitats.
2.2 Introduction

Many marine animals have broadly dispersed pelagic larvae associated with large variations in recruitment, which in turn can lead to large fluctuations in population size. Differences in transport whilst in the pelagic larval stage have explained much of the variation in recruitment (Gaines & Bertness 1992, Hughes et al. 2000). Therefore, understanding the mechanisms of the transport process will help us to understand recruitment and make predictions of future population sizes.

Many adult portunid crabs associated with estuaries migrate seaward to spawn, increasing the chance that their larvae develop in the open coastal region (Hill 1994, Forward et al. 2003b). Seaward transport of larvae may be beneficial as conditions are more thermostatically and chemically stable, providing a more consistent environment for development. Seaward transport would also increase mixing within the population, increase genetic heterogeneity and reduce the risk of total failure of an entire cohort (Pechenik 1999, Gopurenko & Hughes 2002). The new generation of crabs must, however, return to the estuary at some stage.

Despite being relatively strong swimmers for invertebrate larvae, crab megalopae tend to be unable to maintain swim speeds exceeding flow rates commonly found in tidal estuaries (Luckenbach & Orth 1992, Lee et al. 2004). Models using selective tidal-stream transport have been used to explain how larvae with an apparent swimming deficit are able to colonise estuaries (Forward et al. 2003b, Queiroga & Blanton 2005). The spawning and recruitment characteristics of the portunid crab, Callinectes sapidus (the blue crab) have been the focus of considerable research in the USA (e.g. van Montfrans et al. 1995, Pile et al. 1996). The female crabs migrate to the lower estuary to spawn, with subsequent larval development occurring on the coastal shelf through to megalopal stage. Offshore, blue crab megalopae are more abundant in surface waters during the day, utilising wind-generated surface currents to remain near the coast and enter estuaries (Goodrich et al. 1989, Etherington & Eggleston 2000). In estuaries they ascend into the water column during night-time flood tides and descend during both the daytime and ebb tides. This behaviour reduces their exposure to visual planktivores and allows them to ride the flooding tide to migrate upstream. Upon finding suitable estuarine habitat they settle to the benthos and moult into juvenile crabs (van Montfrans et al. 2003). Stimuli including light, turbulence, salinity and
estuary derived chemical cues interact in complex ways with the circadian swimming rhythm of the megalopae to generate this selective tidal streaming behaviour (Forward & Rittschof 1994, Forward et al. 2003b).

The mud crab (*Scylla serrata*) is a portunid crab distributed throughout the Indo-West Pacific region and is generally found in muddy mangrove habitats during adulthood. Like the blue crab, female mud crabs are thought to migrate to the coastal shelf to spawn (Hill 1994). Their zoea cannot survive low salinities (Hill 1974) and their megalopae have been caught in offshore waters but rarely within estuaries (Arriola 1940). Despite a substantial research effort, difficulties in finding significant numbers of megalopae and early-stage crabs (< 30 mm carapace width (CW)) have hampered investigations into the mechanisms of their recruitment into estuaries (Heasman 1980, Hill et al. 1982, Moser & Macintosh 2001).

For much of the mud crab recruitment season, Australian estuary mouths within the distribution of the crabs, tend to have similar or in some cases greater salinities than offshore waters (e.g. Wolanski 1986). Penaeid prawns, which have a similar distribution to the mud crab, also develop offshore before recruiting to estuaries as postlarvae. Falling salinity gradients are not thought to stimulate these postlarvae to colonise estuaries in the wild because in some African and Australian estuaries, postlarvae have colonised inverse estuaries (Rothlisberg et al. 1995). Instead, alternative stimuli have been proposed e.g. changes in pressure due to increasing water depth on flooding tides, the presence of other estuarine plant or animal-derived chemical cues.

There are a number of possible explanations for the lack of success in finding mud crab megalopae and/or early-stage mud crabs in estuaries. Their recruitment to estuaries may be temporally sporadic, making it difficult to detect them. This is the case for the blue crab, however, long term data sets have successfully detected sporadic blue crab recruitment events (Pile et al. 1996, Forward et al. 2004). Mud crabs may also grow rapidly once in estuaries, leaving very little time in which they can be sampled. These are unconvincing reasons, however, given that the efforts of many researchers at different times and places have failed to find significant numbers of mud crab megalopae within estuaries.
Nearly all observations of mud crab megalopae have been made on larvae reared in aquaculture tanks because they are rarely found in the wild. In rearing tanks, mud crab megalopae tend to adopt a benthic habit when observed during the day or under illuminated conditions (Rabbani & Zeng 2005). This behaviour is consistent with the selective tidal streaming model and similar to field observations of blue crab megalopae in estuaries, which tend to be absent from estuarine surface waters during the day but present during night (De Vries et al. 1994). In offshore waters, however, blue crab (C. sapidus) megalopae are found near the surface during the day (Etherington & Eggleston 2000). Megalopae of Portunus pelagicus, another Indo-Pacific portunid, have also been observed to be photopositive and more active when illuminated in offshore water (Bryars 1997).

Using two laboratory experiments, we tested the model that mud crab megalopae behave in a manner consistent with the field observations of blue crab megalopae and aspects of the selective tidal-streaming model. Specifically, three hypotheses were tested: 1) that megalopae tend to be higher in a water column of offshore water when illuminated than when not and this pattern would be reversed in estuarine water, 2) that megalopae in a column of offshore water tend to ascend after the lighting switches from dark to light but the reverse occurs when in estuarine water, and 3) that the effect of the above treatments will be suppressed or enhanced when exercised during daytime or night-time.
2.3 Methods

2.3.1 Water towers and lightproof rooms

Two lightproof rooms were used for both experiments. Inside each room, straight-sided glass water towers (H×W×D; 100×10×9 cm) were arranged such that the top of the towers were 10 cm below an unfiltered fluorescent light (2 × Osram 35 W Daylight tubes). These lights emit a spectrum with peaks between 400 – 500 nm, 530 – 560 nm and 580 – 640 nm. Light intensity at the water’s surface was 193 $\mu$mol.m$^{-2}$.s$^{-1}$ ± 1.53 (SE). This spectrum is not equivalent to daylight but the intensity is brighter than during dawn or dusk and includes the 400 – 500 nm region to which adult $S$. serrata and the larvae of other crab species have been shown to be sensitive (Forward & Cronin 1979, Leggett 1979). We considered filtering the light to the 400 – 500 nm region, however, in the wild megalopae are exposed to a wider range of wavelengths and we saw no detriment in exposing these megalopae to a broad spectrum. The towers were opaque on three vertical sides and arranged such that animals in one tower were not able to see animals in another. Towers were graduated at 10 cm intervals from bottom to top. A small amount of beach sand was added to each tower to cover the glass bottom and reduce light reflection. Although not tested, it was likely that the brightest source of light as seen from inside the towers would be from directly above. We consider that this mimicked the position of the sun at its zenith in a similar manner to that described by Forward et al. (1984).

2.3.2 Megalopae: Rearing and selection

Bribie Island Aquaculture Research Centre, Queensland Department of Primary Industries & Fisheries provided the megalopae used in both experiments. Two experiments were completed and the megalopae used were reared from two female mud crabs collected from Pumicestone Passage. Pumicestone Passage is a narrow waterway separated from the Pacific Ocean by Bribie Island, Queensland (153° 11’ 55” E, 27° 03’ 04” S). The passage is flanked by intertidal mudflats, seagrass beds and mangroves along most of its length. The rearing protocol followed the ambient day:night cycle (12:12) at temperatures between 27 - 29°C and salinities between 35 - 36 ppt. Larvae were fed twice per day, generally in the early morning and mid-
afternoon. Megalopae were collected from incubation tanks by lifting a bucket (25 cm diameter, 1 mm mesh base) vertically through the water column, sampling a range of swimming and benthic megalopae. The sample (∼100 megalopae) was placed into a container partially filled with water. Individual megalopae were haphazardly collected using a pipette and randomly allocated to a vial within an array of vials that corresponded to the number of towers used until each vial contained 10 live megalopae. These megalopae were added to their respective tower at the start of each experiment.

2.3.3 **Experimental design**

Experiment 1 used three towers per room, all were filled with offshore water collected 100 m offshore from the ocean side of Bribie Island. In the second experiment an additional factor being Water Type (2 levels, offshore and estuarine; salinities 36.0 ppt and 35.7 ppt respectively) was introduced. Experiment 2 used 6 towers per room, three with offshore water and three with estuarine water collected from the seagrass beds of Pumicestone Passage (153° 07’ 45” E, 27° 03’ 52” S). In both experiments, the lights in one room were turned off (Dark) whilst they were turned on (Light) in the other. Ten megalopae were added to each tower and after 2 hr, the position of each megalopa within each tower was recorded. For towers in darkness, observations were made using a dim incandescent torch covered with red cellophane because crab larvae are less responsive to far-red light (Cronin & Forward 1988). Position recordings were completed within 1 min per tower. After collecting these data, the light within the rooms were reversed (Light → Dark and Dark → Light). Megalopae were left for a further 2 hr to adjust to the new lighting conditions after which their positions were recorded again before they were discarded. This 4 hour protocol was completed during day and night (Factor: Time of day, 2 levels) on two days (Factor: Date, 2 levels) for both experiments. The experiments were started at different times during the day and the night so that the potentially confounding effects of the larval rearing protocol or lighting regimes were reduced. Water temperatures (25.8°C ± 0.1 SE) were similar for all treatments during both experiments.
2.3.4 **Data analyses**

The data for hypothesis 1 were the mean vertical position of all megalopae within a tower after 2 hrs. Data for hypothesis 2 were the change in mean vertical position 2 hrs after changing the light regime (mean position after 2 hrs – mean position after 4 hrs). These variables provided independent data and equal sample sizes across all treatments (refer to Tables 1-4 for relevant df for tests of different factors). The hypotheses were tested using ANOVA (GMAV, Underwood & Chapman 2001). For hypothesis 1, data were arcsine transformed as values were constrained between 0 and 100. We examined heterogeneity of variance using plots of the data and Cochran’s test. After the initial ANOVA, terms were pooled if they were not significant at $\alpha = 0.25$ and pooling provided a more powerful test of higher terms (Quinn & Keough 2002).
2.4 Results

In the first experiment using only offshore water, megalopae tended to be higher in the water towers when the lights were on (Figure 2.1). The factors Light Regime and Time of Day had a significant effect ($p < 0.001$, $df = 1,18$ and $p < 0.035$, $df = 1,18$ respectively; Table 2.1). There were no significant interactions. This supported the hypothesis that megalopae tend to be higher in the water column when illuminated, however, they tend to be higher during the night than the day.

Changing the factor Lighting, from dark to light, caused the megalopae to ascend while changing from light to dark elicited the reverse behaviour ($p < 0.006$, $df = 1,11$; Table 2.2). There was no significant effect of Time of Day and no interactions.

![Figure 2.1: Mean (SE) vertical position of megalopae in towers filled with offshore water (Experiment 1), for treatments Light to Dark, Dark to Light during both day and night.](image)
Table 2.1 ANOVA results for Experiment 1, testing the effects of treatments on the vertical position of megalopae in towers filled with offshore water, 2 hr after being subjected to illumination or darkness. Data transformed to arc-sine, Cochran test = ns. Some terms were pooled (●) where \( p > 0.25 \) and pooling resulted in a more powerful test.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>MS</th>
<th>( p )</th>
<th>( F \text{ versus} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Light Regime (LR)</td>
<td>1</td>
<td>3247.2</td>
<td>&lt;0.05*</td>
<td>Pooled</td>
</tr>
<tr>
<td>Time of day (Ti)</td>
<td>1</td>
<td>353.9</td>
<td>&lt;0.05*</td>
<td>Pooled</td>
</tr>
<tr>
<td>Date (Da)</td>
<td>1</td>
<td>21.7</td>
<td>&gt;0.575</td>
<td>Pooled</td>
</tr>
<tr>
<td>LR × Ti</td>
<td>1</td>
<td>7.8</td>
<td>&gt;0.850</td>
<td></td>
</tr>
<tr>
<td>● LR × Da</td>
<td>1</td>
<td>78.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>● Ti × Da</td>
<td>1</td>
<td>84.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>LR × Ti × Da</td>
<td>1</td>
<td>141.9</td>
<td>&gt;0.160</td>
<td>Pooled</td>
</tr>
<tr>
<td>Pooled Terms</td>
<td>18</td>
<td>67.6</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 2.2: ANOVA results for Experiment 1, testing the effects of treatments on the vertical displacement of megalopae, 2 hr after the lighting was changed from Off → On or On → Off. Water columns were filled with offshore water. Cochran test = ns. Terms were pooled (●) where \( p > 0.25 \) and pooling resulted in a more powerful test.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>MS</th>
<th>( p )</th>
<th>( F \text{ versus} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lighting (L)</td>
<td>1</td>
<td>2.075</td>
<td>&lt;0.05*</td>
<td>L × Da</td>
</tr>
<tr>
<td>Time of day (Ti)</td>
<td>1</td>
<td>0.003</td>
<td>&gt;0.725</td>
<td>Pooled</td>
</tr>
<tr>
<td>Date (Da)</td>
<td>1</td>
<td>0.008</td>
<td>&gt;0.605</td>
<td>Pooled</td>
</tr>
<tr>
<td>L × Ti</td>
<td>1</td>
<td>0.073</td>
<td>&gt;0.555</td>
<td>L × Ti × Da</td>
</tr>
<tr>
<td>L × Da</td>
<td>1</td>
<td>0.000</td>
<td>&gt;0.935</td>
<td>Pooled</td>
</tr>
<tr>
<td>● Ti × Da</td>
<td>1</td>
<td>0.002</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L × Ti × Da</td>
<td>1</td>
<td>0.109</td>
<td>&gt;0.080</td>
<td>Pooled</td>
</tr>
<tr>
<td>Pooled Terms</td>
<td>17</td>
<td>0.030</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

In the second experiment, megalopae tended to be higher in the illuminated water columns for both estuarine and offshore water (Figure 2.2). The ANOVA to test hypothesis 1 showed a significant three-way interaction between Lighting Regime, Time of Day, and Date \( (p < 0.029, df = 1,35): \) Table 2.3). A series of pairwise SNK tests found a complex pattern of interaction among levels of the three terms, without a clearly discernible trend. These differences were, in any case, considerably smaller than changing the lighting regime (Figure 2.2). Lighting Regime and Date, were also
significant \((p < 0.001, df = 1.35\) and \(p < 0.006, df = 1.35\) respectively: Table 2.3), but Time of Day was not. There was no main effect of Water Type (estuarine, offshore), nor did this factor interact with any other (Table 2.3). The hypothesis that megalopae tend to be higher in a water column of offshore water when illuminated than when not and that this pattern would be reversed in estuarine water was rejected.

The data for hypothesis 2 showed that where the factor Lighting was changed from dark to light, megalopae tended to ascend the water column. When changed from light to dark megalopae tended to descend (Figure 2.3). There were significant three-way and two-way interactions (Table 2.4, Figure 2.3), however the factor Water Type was not significant and did not interact with any other factor (Table 2.4). Therefore the hypothesis that megalopae in a column of offshore water tend to ascend after the lighting changes from dark to light but the reverse occurs in estuarine water was rejected. Time of Day was not significant but interacted with Lighting and Date (Table 2.4).

![Figure 2.2: Mean (SE) vertical position of megalopae in towers after 2 hr of darkness or illumination, on two different days during both the daytime and night-time (Experiment 2).](image)
Figure 2.3: Mean (SE) vertical displacement after changing the lighting (ON → OFF, OFF → ON) on two days, during daytime and night-time, for towers filled with estuarine (E) or offshore (O) water (Experiment 2).
Table 2.3: ANOVA results for Experiment 2, testing the effects of treatments on the vertical position of megalopae, 2 hr after being subjected to illumination or darkness. Data transformed to arc-sine, Cochran test = ns. Some terms were pooled (●) where $p > 0.25$ and pooling resulted in a more powerful test.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>MS</th>
<th>$p$</th>
<th>$F$ versus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Light Regime (LR)</td>
<td>1</td>
<td>14232.3</td>
<td>&lt;0.05*</td>
<td>Pooled</td>
</tr>
<tr>
<td>Water type (WT)</td>
<td>1</td>
<td>352.3</td>
<td>&gt;0.070</td>
<td>Pooled</td>
</tr>
<tr>
<td>Time of day (Ti)</td>
<td>1</td>
<td>398.8</td>
<td>&gt;0.055</td>
<td>Pooled</td>
</tr>
<tr>
<td>Date (Da)</td>
<td>1</td>
<td>863.8</td>
<td>&lt;0.05*</td>
<td>Pooled</td>
</tr>
<tr>
<td>LR × WT</td>
<td>1</td>
<td>26.8</td>
<td>&gt;0.500</td>
<td>LR × WT × Da</td>
</tr>
<tr>
<td>LR × Ti</td>
<td>1</td>
<td>2.2</td>
<td>&gt;0.955</td>
<td>LR × Ti × Da</td>
</tr>
<tr>
<td>●LR × Da</td>
<td>1</td>
<td>20.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>WT × Ti</td>
<td>1</td>
<td>81.3</td>
<td>&gt;0.540</td>
<td>WT × Ti × Da</td>
</tr>
<tr>
<td>●WT × Da</td>
<td>1</td>
<td>60.5</td>
<td></td>
<td>-</td>
</tr>
<tr>
<td>●Ti × Da</td>
<td>1</td>
<td>9.9</td>
<td></td>
<td>-</td>
</tr>
<tr>
<td>LR × WT × Ti</td>
<td>1</td>
<td>53.3</td>
<td>&gt;0.685</td>
<td>LR × WT × Ti × Da</td>
</tr>
<tr>
<td>LR × WT × Da</td>
<td>1</td>
<td>26.9</td>
<td>&gt;0.610</td>
<td>Pooled</td>
</tr>
<tr>
<td>LR × Ti × Da</td>
<td>1</td>
<td>524.3</td>
<td>&lt;0.05*</td>
<td>Pooled</td>
</tr>
<tr>
<td>WT × Ti × Da</td>
<td>1</td>
<td>105.7</td>
<td>&gt;0.310</td>
<td>Pooled</td>
</tr>
<tr>
<td>LR × WT × Ti × Da</td>
<td>1</td>
<td>184.3</td>
<td>&gt;0.185</td>
<td>Pooled</td>
</tr>
<tr>
<td>Pooled Terms</td>
<td>35</td>
<td>101.4</td>
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<td></td>
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Table 2.4: ANOVA results for Experiment 2, testing the effects of treatments on the vertical displacement of megalopae, 2 hr after the lighting was changed from Off → On or On → Off. Cochran test = ns. Terms were pooled where $p > 0.25$ and pooling resulted in a more powerful test.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>MS</th>
<th>$p$</th>
<th>$F$ versus</th>
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<tr>
<td>Lighting (L)</td>
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<td>L × Da</td>
</tr>
<tr>
<td>Water type (WT)</td>
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<td>Pooled</td>
</tr>
<tr>
<td>Time of day (Ti)</td>
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<td>0.527</td>
<td>&gt;0.180</td>
<td>Ti × Da</td>
</tr>
<tr>
<td>Date (Da)</td>
<td>1</td>
<td>0.028</td>
<td>&gt;0.300</td>
<td>Pooled</td>
</tr>
<tr>
<td>L × WT</td>
<td>1</td>
<td>0.000</td>
<td>&gt;0.905</td>
<td>L × WT × Da</td>
</tr>
<tr>
<td>L × Ti</td>
<td>1</td>
<td>0.009</td>
<td>&gt;0.850</td>
<td>L × Ti × Da</td>
</tr>
<tr>
<td>L × Da</td>
<td>1</td>
<td>0.254</td>
<td>&lt;0.05*</td>
<td>Pooled</td>
</tr>
<tr>
<td>WT × Ti</td>
<td>1</td>
<td>0.003</td>
<td>&gt;0.825</td>
<td>WT × Ti × Da</td>
</tr>
<tr>
<td>★WT × Da</td>
<td></td>
<td>0.003</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Ti × Da</td>
<td>1</td>
<td>0.047</td>
<td>&gt;0.180</td>
<td>Pooled</td>
</tr>
<tr>
<td>L × WT × Ti</td>
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<td>0.001</td>
<td>&gt;0.895</td>
<td>L × WT × Ti × Da</td>
</tr>
<tr>
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<td>0.020</td>
<td>&gt;0.375</td>
<td>Pooled</td>
</tr>
<tr>
<td>L × Ti × Da</td>
<td>1</td>
<td>0.169</td>
<td>&lt;0.05*</td>
<td>Pooled</td>
</tr>
<tr>
<td>WT × Ti × Da</td>
<td>1</td>
<td>0.004</td>
<td>&gt;0.705</td>
<td>Pooled</td>
</tr>
<tr>
<td>L × WT × Ti × Da</td>
<td>1</td>
<td>0.026</td>
<td>&gt;0.310</td>
<td>Pooled</td>
</tr>
<tr>
<td>Pooled Terms</td>
<td></td>
<td>33</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>


2.5 Discussion

In offshore and estuarine water, during the daytime and night-time, mud crab megalopae tended to swim higher in the water towers when illuminated. For offshore water, this was consistent with the hypothesis, however the ascent in illuminated estuarine water was not predicted. Contrary to the results obtained here, swimming was suppressed in estuarine water for fiddler crab (*Uca* spp.) and blue crab (*C. sapidus*) megalopae (Forward & Rittschof 1994).

It is possible that the mud crab megalopae had the capacity to, but did not distinguish between the two water types. This is unlikely as the estuarine water was collected over seagrass beds and no doubt contained many chemical cues associated with an estuary. Salinity of the estuarine water was only slightly lower than offshore water. This was expected as salinities at the mouth of Pumicestone Passage are usually within this range (EPA Qld, pers. comm.). Mud crab megalopae are rarely caught in estuaries and if this is because they are rarely there, rather than the result of ineffective sampling, mud crab megalopae in offshore or coastal waters would rarely encounter estuarine salinity gradients, ruling out salinity as a natural stimulus (Rothlisberg et al. 1995). The offshore water may have contained small traces of estuarine derived chemicals, however the behaviour exhibited by the megalopae in our experiment is consistent with the behaviour of other portunid megalopae in offshore waters. This behaviour would be beneficial in maintaining them close to the coast during their pelagic larval phase. Surface currents generated by on-shore winds assist the ingress of blue crab megalopae to estuaries. In offshore waters, migrating to the surface during the day enhances the utilisation of these currents, thus increasing the probability of remaining near or penetrating estuaries (Goodrich et al. 1989, Morgan et al. 1996). Exhibiting this behaviour inside estuaries would expose megalopae to a suite of estuarine visual predators (Forward & Rittschof 1994). For these reasons, we consider that the megalopae behaved as expected in offshore waters and the combined differences between the water types were sufficient to elicit any natural behavioural response due to water type if one was forthcoming.

Blue crab megalopae are found in significant numbers in estuaries and complex models have been developed to explain their upstream migration (Forward et al. 2003b). Mud crab megalopae, however, have proved difficult to find in estuarine
surveys (Macintosh et al. 1999, Moser & Macintosh 2001). Given the extensive efforts to collect mud crab megalopae from estuaries, the most parsimonious alternative model explaining their apparent absence is that mud crab megalopae tend not to occur within estuaries. This model explains why estuarine water did not suppress their swimming activity. In the wild, mud crab megalopae may rarely occur in estuaries and therefore have not evolved an alternative swimming behaviour more suited to the estuarine environment as the blue crab has. If the megalopae tend not to enter estuaries they must settle out of the plankton along the coast before metamorphosing into small crabs. This settlement process may be controlled ontogenetically or stimulated by coastal cues. Migration to estuarine habitats would occur shortly after settlement, since juveniles found in estuaries and mangroves are typically > 30 mm CW (Hill et al. 1982). This new model requires mud crabs to settle out of the plankton on the coastal shelf and colonise estuaries, not as planktonic larvae, but as small, benthic juvenile crabs. This coastal settlement model is analogous with the mechanism of estuarine colonisation by the prawn Penaeus plebejus (Rothlisberg et al. 1995). In their model, the postlarval prawns become epibenthic on the coastal shelf before colonising estuaries during flooding tides. Water pressure changes, generated by increasing depth on flooding tides, stimulates the epibenthic prawn postlarvae to selectively ride tidal currents and opportunistically colonise estuaries whilst being swept along the coast by alongshore drift.

Megalopae in Experiment 1, but not experiment 2, swam significantly higher in water towers during the night than the day, and in either case the effect was small compared to the effect of light. Blue crab megalopae have been shown to have an endogenous circadian rhythm (Tankersley & Forward 1994) and this may also be the case for mud crab megalopae, although it was not tested here. The experiment could have been improved by using a gradient of light intensities. The intensities used here were greater than at dawn and dusk, spanning the time at which we considered changes to the swimming behaviour of megalopae most likely to occur.

We used hatchery-reared megalopae because collecting them from the wild is rarely successful. Whether the behaviour exhibited by hatchery-reared mud crab megalopae can be generalised to wild populations is not known. Behaviours exhibited by hatchery-reared animals are not always consistent with their wild conspecifics. For
example, hatchery-reared blue crabs are preyed upon at higher rates than wild crabs (Davis et al. 2004). The behaviour of larvae can also vary spatially (Manuel et al. 1996), therefore all of these factors should be considered when generalising to wild populations.

Whilst laboratory experiments can be useful, by their nature they remove many potentially interactive factors (Carpenter 1996) and perhaps the most obvious issue in the current experiment is that the water depth was limited by the height of the tower. These mud crab megalopae could swim from the bottom to the top in a single burst. They then tended to swim at the surface for a short period before sinking 30 - 60 cm after which they resumed swimming back to the top. The stimuli for this swimming/sinking pattern are unknown, however, blue crab megalopae respond to changes in pressure (Tankersley et al. 1995). The resumption of swimming may be a response to exceeding a pressure threshold whilst sinking. If this is the case, then it is important to ensure that the water column is deep enough to trigger this response. In shorter towers, megalopae may be inactive and benthic, not because they are exhibiting their natural behaviour, but because they have not crossed the pressure/depth threshold and consider themselves to be in surface waters. The fact that the sinking megalopae observed here tended to resume swimming before reaching the bottom of the tower indicates that the towers were tall enough.

The blue crab recruitment model is unlikely to be wholly applicable to mud crabs as the swimming behaviour of the mud crab megalopae does not change in estuarine water and they have rarely been found in estuaries. The combination of (1) the apparent absence of mud crab megalopae from estuaries, (2) the consistency in vertical swimming behaviour in offshore and estuarine water and (3) that mud crabs smaller than 30 mm CW are rarely found in estuaries prompts us to propose an alternative model to explain how mud crabs colonise estuaries. We postulate that mud crab megalopae tend to settle from the plankton on the coastal shelf and colonise estuaries by moving along the sea bed as early-stage crabs, before migrating further upstream and inhabiting the intertidal shallow estuarine habitats.
Chapter 3: Habitat selection by megalopae and juvenile mud crabs (*Scylla serrata*): tastes change with age

3.1 Abstract

The megalopae of several crab species exhibit active habitat selection when settling from the plankton. These megalopae usually select structurally complex habitats that can provide refuge and food during this vulnerable stage in their life. The portunid mud crab *Scylla serrata* is commonly found within the muddy estuaries of the Indo-West Pacific after attaining a carapace width > 40 mm. Ovigerous mud crabs migrate offshore to spawn but, despite substantial efforts, the recruitment mechanism of juvenile mud crabs to estuaries is not understood because their megalopae and early stage crablets (carapace width < 30 mm) are rarely found. I used laboratory experiments to determine whether megalopae and early stage crablets exhibit any selectivity among three estuarine habitats which commonly occur in southeast Queensland. These animals were placed in arenas where they had a choice of habitats: seagrass, mud or sand, and arenas where they had no choice: only seagrass, mud or sand to determine their selectivity among habitats. Contrary to the associations exhibited by other portunid crab megalopae, *S. serrata* megalopae show no selectivity among these estuarine habitats. Crablets, however, strongly selected seagrass over sand and mud. The selection exhibited by crablets indicates that there is an adaptive advantage for the behaviour. The lack of a selective behaviour by megalopae indicates that there is no adaptive advantage for selecting among these three habitats at this life stage. In Chapter 2 I proposed that for *S. serrata*, it is the crablets and not the megalopae which tend to colonise estuaries. These results support this model because the crablets have evolved a behaviour which selects among commonly occurring estuarine habitats, selecting the structurally complex habitat, whereas the megalopae have not, indicating that megalopae tend not to encounter these habitats, or derive no fitness benefit from them.
3.2 Introduction

Organisms are rarely randomly distributed throughout the environment (Condit et al. 2000, Bertness et al. 2001). For animals, this non-random distribution is generated by mechanisms that may or may not involve habitat choice. Mortality is one mechanism; animals which recruit randomly and subsequently die in inhospitable places but survive elsewhere will be non-randomly distributed. They will be associated with the hospitable habitats (Crowe & Underwood 1998). This mechanism does not require the exercise of choice or selection, yet still generates habitat associations.

Alternatively, animals may make choices about where they live. For pelagic larvae competent to settle, choices among settlement habitats may initially establish a non-random distribution (Orth & van Montfrans 1987, Moksnes 2002). Post-settlement movements of individuals towards particular chosen habitat types can redistribute the population (Moksnes 2002, Lecchini et al. 2007). These latter mechanisms involve the selection of particular habitats to create non-random distributions of animals.

Organisms are constantly faced with choices, for example about feeding, habitat and breeding. It is a tenet of evolution that, collectively, these choices or selections serve to enhance the fitness of future generations (Gould & Lewontin 1979, Krebs & Davies 1997). These selections are likely to be most important and therefore most pronounced during the period of an animal’s life when its potential reproductive success is at greatest risk. For many marine organisms, this period is the settlement and early juvenile stage, because the probability of mortality is high (Hunt & Scheibling 1997). The postlarvae of several decapod species actively choose to settle, or move to habitats which provide refuge or abundant food, rather than remaining in hostile places (Dionne et al. 2003, Moksnes et al. 2003, van Montfrans et al. 2003). This behaviour is likely to increase the reproductive fitness of these individuals over those not making such a choice. Understanding selectivity by individuals among different habitats enables us to rank those habitats according to the likelihood that they enhance the survival of that species.

Selectivity among different habitats may be a dormant ancestral trait rather than a utilised derived trait. For example, the megalopae of ancestral mud crabs may have colonised estuaries and evolved selectivity among different habitats but today’s mud crab megalopae may no longer enter estuaries. Despite not entering estuaries they may
still posses the ancestral trait of selectivity. When confronted with a choice of estuarine habitats, for example in an experiment, they may exhibit selectivity. Obviously this is not evidence that they enter estuaries. An absence of selectivity suggests however, that the selective trait, either ancestral or derived, is truly absent which is consistent with the hypothesis that in nature they rarely enter estuaries.

Places that increase the probability of an individual juvenile surviving and subsequently contributing to future generations can be considered nursery habitats (Beck et al. 2001). Nursery habitats might not, however, be the dominant contributor to future adult populations. Their area may be small compared to other habitats and therefore, despite being relatively more productive, they could contribute a smaller proportion of the future adults compared to the larger habitats (Dahlgren et al. 2006). However, the intense productivity of the nursery habitats may provide the population a degree of reproductive resilience, which is important during periods of disturbance (Mumby et al. 2004). Nursery habitats, therefore, can contribute subtly to the persistence of populations over an evolutionary timescale by providing a more stable source of larval production in times of more variable disturbance.

Seagrass beds are often cited as nursery habitats for small juvenile animals because they provide refuge from predators and a greater abundance of food (Jackson et al. 2001a). The complex structure of seagrass beds provides refuge in the form of hiding places. It can also restrict the movement of larger animals which potentially prey on the small juveniles. Paradoxically, the abundance of small animals is also considered to attract slightly larger animals, such as predatory fish and crustaceans, which seek to prey on those seeking shelter (Connolly 1994, Franco et al. 2006). Postlarvae and juveniles of the portunid crabs *Callinectes sapidus* (blue crab) and *Portunus pelagicus* (blue swimmer crab) are strongly associated with seagrass (Orth & van Montfrans 1987, Kenyon et al. 1999, van Montfrans et al. 2003). Although many settling animals do select structurally complex habitats, there are exceptions. For example, the megalopae of the crab *Cancer irroratus* are not selective among habitats, settling in large numbers on both cobbles and sand (Palma et al. 1998).

The mud crab (*Scylla serrata*) is an economically and recreationally important portunid crab distributed throughout the coasts of the Indo-West Pacific. Adult mud crabs are generally found in muddy, mangrove-lined estuaries, and ovigerous females
move offshore to spawn (Hill 1994). Despite considerable efforts, mud crab megalopae and crablets (carapace width (CW) < 30 mm) are rarely found within estuaries (Arriola 1940, Heasman 1980, Forbes & Hay 1988, Knuckey 1999, Moser & Macintosh 2001, Hay et al. 2005). In Australia, crablets have been found in seagrass at a river mouth (D. Mann, Queensland Department of Primary Industries and Fisheries, pers. comm.), under debris and stones in bayside patches of sheltered mangroves (Heasman 1980), on sand bars near a river mouth (Mounsey 1990) and in baited traps in shallow saltmarsh creeks (L. Anderson, University of Central Queensland, pers. comm.). Observations as sporadic as these prevent us from determining if these crablet-habitat associations are representative or exceptional. Other crab megalopae are found within estuaries. For example, *C. sapidus* colonises estuaries as megalopae where they encounter and settle to estuarine habitats (Tankersley et al. 2002), and I have collected blue swimmer crab megalopae from the estuaries of southeast Queensland.

Many postlarvae of decapod species exhibit habitat selectivity among settlement habitats, selecting habitats with complex three dimensional structure. Where this selectivity has been demonstrated, it has been strongly exhibited. For example, the number of *Carcinus maenas* postlarvae settling to structurally complex habitats such as mussel, algae and eelgrass patches was more than an order of magnitude greater than that settling to sand (Moksnes 2002). For *C. sapidus*, the number of postlarvae settling to *Zostera marina* was more than twice the number settling to other less complex habitats such as mud and sand, in both laboratory and field experiments (van Montfrans et al. 2003, Moksnes & Heck 2006). The selectivity is strong and likely to have evolved because their ancestors regularly encountered these habitats and obtained significant evolutionary fitness benefits by utilising them. These benefits include refuge from predation and enhanced growth (Perkins-Visser et al. 1996, Moksnes et al. 1998). If mud crab megalopae have regularly encountered estuarine habitats and the benefits derived by being selective are of similar magnitude, then I contend that similar strong selection behaviours would be exhibited and an effect size of two to three times or greater difference in the number of settlers among habitats should be observed.
Webley and Connolly (2007) proposed a coastal settlement model that pelagic mud crab megalopae settle on the coastal shelf in the nearshore region, possibly behind the surf zone, as is suggested for the prawn *Peneaus plebejus* (Rothlisberg et al. 1995). There, the megalopae metamorphose into benthic crablets which utilise along-shore currents and flooding tides to colonise estuaries, keeping close to the substratum. At the mouths of estuaries in southeast Queensland, the subtidal substratum tends to be dominated by a mosaic of sandy or muddy habitats with patches of seagrass. As crablets colonise estuaries from the nearshore region they likely encounter these habitats before moving upstream to stands of mangroves. This conceptual model is controversial because it predicts that for mud crabs, the crablets and not the megalopae tend to colonise estuaries, whereas for several other portunids, the megalopae is the colonising stage (Moksnes 2002, Tankersley et al. 2002).

The coastal settlement model implies that mud crab megalopae tend not to encounter estuarine habitats and have therefore not evolved selectivity among habitats in the estuaries of southeast Queensland. Mud crab crablets, however, are predicted to colonise estuaries and therefore encounter and utilise the benefits of the structurally complex habitats such as seagrass. Specifically I predicted that: (1) *S. serrata* crablets would select seagrass habitats over mud or sand, and (2) megalopae would show no selectivity among the estuarine habitats: seagrass, mud, and sand. This second hypothesis is a demanding test for the coastal settlement model to pass, because many other portunid megalopae selectively settle to structurally complex habitats, with more than twice the number settling to complex habitats.

Active selection intrinsically involves an active choice by the organism. In contrast to acceptability or electivity, it is a characteristic of the organism and cannot be determined from simple assessments of association (Singer 2000, Underwood & Clarke 2006). Here, I use a commonly accepted and testable definition that active selection is demonstrated when animals select an option to a greater extent when offered a choice than could be predicted from observations of the behaviour in the absence of a choice (Barbeau & Scheibling 1994, Olabarria et al. 2002, Haughland & Larsen 2004). I tested the hypotheses with laboratory experiments because these animals are small and cryptic, making it difficult to complete these experiments in the
field. In the absence of field experiments, the results of carefully designed laboratory experiments can infer processes in nature and focus subsequent field research.
3.3 Methods

3.3.1 Rearing

*Scylla serrata* megalopae and crablets were provided by Bribie Island Aquaculture Research Centre, Queensland Department of Primary Industries and Fisheries. All were reared from a single batch of eggs extruded by a wild female crab collected from Pumicestone Passage, Queensland (153°11'55"E, 27°03'04"S). Larvae from multiple females would have been preferable; unfortunately mud crabs are difficult to culture and only one batch was available. Pumicestone Passage is a sheltered waterway flanked by a mosaic of sandy beaches, intertidal mudflats, seagrass beds and mangroves. The larval rearing protocol followed the ambient day:night cycle (12:12) with temperatures between 27 - 29°C and salinities between 35 – 36. Larvae were fed twice per day, generally in the early morning and mid-afternoon.

The selection experiment was done twice, once using megalopae and once using crablets (CW < 8 mm). The animals were randomly selected from the rearing facility, allocated to 18 batches of 100 (megalopae) or 10 (crablets) and then randomly allocated to an arena. Mud crab megalopae can metamorphose to crablets after 6-7 days (Baylon & Failaman 1999, Holme et al. 2007). The megalopae used here were 2-3 days old and therefore likely to be competent to settle before the experiment finished.

I used arenas similar to those described by van Montfrans et al. (2003). These circular plastic arenas (H = 450 mm, dia. = 1 100 mm, area = 0.95 m²) held ca. 320 l of filtered seawater (salinity 35.4). An air stone was placed inside a standpipe (6 cm dia.) positioned in the centre of the arena. Water intake and outlet holes at the top and bottom of the standpipe were covered with mesh (800 μm). These holes permitted a slow circulation of water in the vertical plane when air was released from the air stone. Both the megalopae and the crablets were easily able to move against the current. The arenas were divided into three equal segments by inserting dividers between the standpipe and the arena wall. Combinations of different habitats, sand (S), mud (M) and seagrass (G), were added to the segments (Figure 3.1). All habitats were collected locally, sand from a beach, mud from mangroves and seagrass from an estuary. The seagrass was predominantly *Zostera capricorni* with a three dimensional structure (determined from seven haphazardly placed 900 cm² quadrats) as follows: mean (SE)
shoots per quadrat 129 (11.8), with 3 (0.1) blades per shoot, a blade length of 103 (6.1) mm and width of 2.4 (0.1) mm.

The 18 arenas were haphazardly arranged in a shed with a translucent roof providing a natural day:night cycle. The experiment was completed indoors to reduce temperature fluctuations and thus reduce crab mortality. Water temperature varied little during the course of the experiment (21.6°C, 0.03 SE). The arenas were filled with seawater, dividers inserted and habitats added. Infauna were not removed from habitats because it may contribute to cues causing habitat selection. Sods of seagrass and mud habitats were carefully transported and placed within the arenas. Beach sand was unable to be collected intact. After adding the habitats to arenas in segment combinations described below, the arenas were left to settle for 3 days before the megalopae or crablets were added to the arenas start segment only (denoted by a subscript ‘s’ in Figure 3.1). At this point the dividers were removed.

![Diagram of arenas](image)

**Figure 3.1:** One replicate of the experiment showing arenas with a choice (Choice: 1 – 3) and arenas without a choice (No-Choice: 4 – 6). Each arena was divided into 3 segments; each segment contained only sand (S), mud (M) or seagrass (G). The Habitat Starting Segments are identified with a subscript s (e.g. Gs). There were three replicates of each arena, 18 in total.

The animals were free to roam for 3 days, then the dividers were reinserted and the arenas drained by puncturing the bottom of the standpipe. The habitat of each segment was washed and sieved (salt water, 2 mm mesh) and the retained material placed in 70% ethanol for later sorting and counting. From the total megalopae or
crablets recovered from each arena, I calculated the proportion found in each of the three segments.

3.3.2 Experimental design and analysis

To determine habitat selectivity, it is necessary to compare an animal’s behaviour in the presence and absence of choice. Animals were considered to select seagrass if the proportion found in seagrass where they had a choice of habitats was greater than would have been predicted from their distribution in the absence of choice (Olabarria et al. 2002, Underwood et al. 2004).

The experiment had 2 factors: Choice (2 levels; Choice and No-Choice) and Habitat Start Segment (3 levels; Start in Seagrass, Mud or Sand) and was replicated 3 times (Figure 3.1). Megalopae and crablets data were analysed separately and to obtain independent data, only the proportions of animals found within the start segment of each arena were analysed. A selectivity for seagrass was demonstrated if a significantly greater proportion of animals occurred in the seagrass start segments within Choice arenas (Gₐ, Arenas 1; n = 3) than in the seagrass start segments within No-Choice arenas (Gₐ, Arenas 4, n = 3). Likewise, the proportion that occurred in the start segments for mud (Mₐ, Arenas 2, n = 3) and sand (Sₐ, Arenas 3, n = 3) within Choice arenas would be less than in start segments within the respective No-Choice arenas (Mₐ, Arenas 5 and Sₐ Arenas 6; n = 3). Because the data were proportions, they were arc-sine transformed and Cochran’s test was used to test for heterogeneity of variance. The selectivity hypothesis was tested using ANOVA, where a significant Choice × Habitat Start Segment interaction (C × Hₛ) would support selectivity. Student-Newman-Keuls (SNK) tests followed significant interaction effects to determine which habitats the megalopae or crablets selected. The main factors do not test the hypothesis of a difference in behaviour in the presence or absence of choice, therefore SNK tests were not done for these terms.

For the megalopae experiment, it is possible that the recovery of megalopae from seagrass segments was inefficient (Table 3.1). If this was solely due to my ability to recover megalopae from seagrass then it is likely that a similar loss of megalopae occurred within the seagrass segments within Choice arenas. To compensate for this possibility, the data were adjusted as follows. The number of megalopae found within
the seagrass segments of the Choice arenas were multiplied by the deficiency between the mean recovery rates of megalopae from the seagrass No-Choice arenas and the mud and sand No-Choice arenas (2.43 times). The adjusted data were reanalysed using the same ANOVA procedures outlined above. I assume that the lower recovery of megalopae from seagrass is not due to post-settlement mortality or movement.

To determine if there was a difference in the recovery of animals from different habitat types the animals recovered from each replicate of the No-Choice arenas (Arenas 4, 5 and 6: Figure 3.1) were compared using ANOVA after testing for heterogeneity of variance using Cochran’s test (Single factor: Habitat, 3 levels, \( n = 3 \)).

To determine if the animals had sufficient time and ability to disperse through the entire arena, their distribution through the different segments of the No-Choice treatments was analysed. For each segment, the proportion of the total number of animals recovered from the respective No-Choice arena was calculated. These data were arc-sine transformed, and Cochran’s test was used to assess heterogeneity of variance. ANOVA tested the factors, Habitat (3 levels: Seagrass, Mud and Sand, Fixed), Segment (3 levels: Start segment and segment 1 & 2, Fixed) and their interaction.

3.3.3 **Power analysis**

The postlarvae of many decapods that select among potential settlement habitats are found in greater abundance within structurally complex habitats; a 2 – 10 fold difference has been found (e.g. Moksnes 2002). Support for the second hypothesis, that megalopae show no selectivity among the habitats, requires that no significant \( \text{C} \times \text{H} \) interaction be found, which is a statistical null hypothesis (Underwood 1991). Therefore a power analysis of the experiment must be done to interpret the results of the hypothesis test. Two power analyses were done, one with an effect size of 1 – 2 fold more megalopae in seagrass segments and the other with a 2 – 3 fold effect which I consider to be a conservative range of possible effect sizes. The data sets were generated using the data from the megalopae choice experiment. The numbers of megalopae found within the seagrass segments for each Choice replicate (Arenas 1, 2 and 3: \( n = 3 \) each) were replaced with an ‘expected abundance’. This expected abundance was calculated by multiplying the average abundance of megalopae found
within the respective mud and sand segments of the arena by a random number between either 1 and 2 or 2 and 3. This process provided two data sets with a variable effect size ranging from 1 – 2 times and 2 – 3 times greater abundance in seagrass. This method of applying the effect generates a more variable (and possibly more realistic) data set than would be obtained by multiplying by a fixed effect size (e.g. 2 or 3). Abundance data were converted to proportions, arc-sine transformed, tested for heterogeneity of variance using Cochran’s test and the power to detect a C × H interaction calculated using PiFace Ver 1.65 software (Lenth 2007).

Mud crab larvae are not easily cultured and I was fortunate to have the ones used here. It was impractical to do a pilot experiment and *a priori* power analysis, to aid in the experimental design. This *post-hoc* power analysis was completed to assist in interpreting the non-significant results and cannot be used to justify the effect sizes.
3.4 Results

A total of 346 megalopae (19%) were recovered from the arenas at the end of the experiment and at least 5 molted to first instar crablets, all of which were found within the seagrass. Within the No-Choice arenas, the mean number of megalopae recovered from seagrass arenas was less than half that recovered from either the mud or the sand arenas, however the difference was not significant (Cochran’s test = ns: ANOVA df 2,6; \( P > 0.17 \): Table 3.1). A total of 144 crablets (80%) was recovered from the arenas at the end of the experiment. Within the No-Choice arenas, all the crablets were recovered from seagrass arenas and almost all were recovered from the mud and sand arenas. These were not tested using ANOVA because there was no variance within the seagrass No-Choice arenas and large proportions of the crablets were recovered in all habitat types (Table 3.1).

Table 3.1: Number of megalopae and crablets recovered from all segments within the No-Choice arenas (mean (SE)).

<table>
<thead>
<tr>
<th>No-Choice Arena</th>
<th>Mean (SE) of animals recovered</th>
<th>Megalopae</th>
<th>Crablets</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seagrass</td>
<td>10.0 (6.0)</td>
<td>10.0 (0.0)</td>
<td></td>
</tr>
<tr>
<td>Mud</td>
<td>24.3 (5.2)</td>
<td>7.3 (0.9)</td>
<td></td>
</tr>
<tr>
<td>Sand</td>
<td>24.3 (4.8)</td>
<td>9.7 (0.3)</td>
<td></td>
</tr>
</tbody>
</table>

3.4.1 Megalopae

The megalopae showed no selectivity among the habitats offered. There was no significant interaction (C \( \times \) H\(_s\)) between the presence or absence of Choice and Habitat Start Segment nor any significant main effect (Table 3.2, Figure 3.2). There was no significant effect of the habitat type among the No-Choice arenas, nor any significant difference in the distribution of megalopae among segments within the No-Choice arenas (Table 3.3).

The selectivity hypothesis was retested using adjusted megalopae data. The data were adjusted for the recovery deficiency of 2.43 times and arc-sine transformed.
These adjusted data also showed no selectivity among the habitats offered; the \((C \times H)\) interaction was not significant (Table 3.4).

### 3.4.2 Crablets

The crablets showed a strong preference for seagrass. There was a significant Choice × Habitat Start Segment interaction (Table 3.2; Figure 3.2). Significantly more crablets were found in seagrass within Choice arenas than could be predicted from the No-Choice arenas, demonstrating preference for seagrass (Table 3.2). Significantly fewer crablets were found in sand within Choice arenas than predicted from the No-Choice arenas, demonstrating a bias against sand (Table 3.2). The proportion of crabs found in mud within Choice arenas was consistent with that predicted from the No-Choice arenas, demonstrating an indifference to mud (Table 3.2). In the Choice arenas, the proportion of crablets found in seagrass segments was always greater than for either mud or sand, regardless of the habitat in which they started (Figure 3.3). Within the No-Choice arenas, there was no significant difference in the distribution of crablets either within or among habitat types, nor any interaction (Table 3.3, Figure 3.4).

### 3.4.3 Power Analysis

The power of the experimental design to detect selectivity \((C \times H)\) when there was a 1-2 or a 2-3 fold greater abundance of megalopae within seagrass than in mud and sand was 0.72 and 0.98 respectively (Table 3.5). As the effect size increased the power to detect an effect of the factor Habitat Start Segment reduced. This occurred because increasing the selectivity of the animals increases the variance within this factor because, in the presence of choice, animals leave undesirable start segments (e.g. mud or sand), but remain in or return to desirable start segments (e.g. seagrass). In arenas without choice, however, animals distribute evenly among the three segments within each arena.
Table 3.2: ANOVA (megalopae and crablets) and SNK tests (crablets only) for the hypothesis that there is a significant interaction between presence or absence of Choice (C) and Habitat Start Segment (Hs). Cochran’s test = ns.

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>df</th>
<th>Megalopae</th>
<th>Crablets</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td>Choice</td>
<td>1</td>
<td>0.82</td>
<td>0.382</td>
</tr>
<tr>
<td>Habitat Start Segment</td>
<td>2</td>
<td>3.73</td>
<td>0.055</td>
</tr>
<tr>
<td>C × Hs</td>
<td>2</td>
<td>0.18</td>
<td>0.834</td>
</tr>
<tr>
<td>Residual</td>
<td>12</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

SNK comparisons for C × Hs interaction for crablets

<table>
<thead>
<tr>
<th>Habitat Start Segment</th>
<th>P</th>
<th>Direction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seagrass</td>
<td>&lt; 0.01</td>
<td>Choice &gt; No Choice</td>
</tr>
<tr>
<td>Mud</td>
<td>ns</td>
<td>na</td>
</tr>
<tr>
<td>Sand</td>
<td>&lt; 0.05</td>
<td>Choice &lt; No Choice</td>
</tr>
</tbody>
</table>

Table 3.3: ANOVA test for an effect of Habitat or Segment on the distribution of megalopae and crablets within No-Choice arenas. Cochran’s test = ns.

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>df</th>
<th>Megalopae</th>
<th>Crablets</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>0.03</td>
<td>0.968</td>
</tr>
<tr>
<td>Segment</td>
<td>2</td>
<td>0.01</td>
<td>0.992</td>
</tr>
<tr>
<td>Habitat × Segment</td>
<td>4</td>
<td>1.01</td>
<td>0.426</td>
</tr>
<tr>
<td>Residual</td>
<td>18</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 3.4: ANOVA for megalopae adjusted for lower recovery rates from seagrass segments to test the hypothesis that there is a significant interaction between presence or absence of Choice (C) and Habitat Start Segment (Hₛ). Cochran’s test = ns.

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choice</td>
<td>1</td>
<td>0.77</td>
<td>0.398</td>
</tr>
<tr>
<td>Habitat Start Segment</td>
<td>2</td>
<td>0.79</td>
<td>0.477</td>
</tr>
<tr>
<td>C × Hₛ</td>
<td>2</td>
<td>2.06</td>
<td>0.170</td>
</tr>
<tr>
<td>Residual</td>
<td>12</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 3.5: Two power analyses of the experimental design testing the hypothesis that there is a significant interaction between the presence or absence of Choice (C) and Habitat start segment (Hₛ) for two effect sizes, being 1-2 and 2-3 times greater abundance of megalopae within seagrass segments. Cochran’s test = ns.

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>df</th>
<th>Effect size</th>
<th>Effect size</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>1-2 times</td>
<td>2-3 times</td>
</tr>
<tr>
<td>Choice</td>
<td>1, 2</td>
<td>0.32</td>
<td>0.57</td>
</tr>
<tr>
<td>Habitat Start Segment</td>
<td>2, 2</td>
<td>0.63</td>
<td>0.06</td>
</tr>
<tr>
<td>C × Hₛ</td>
<td>2, 12</td>
<td>0.72</td>
<td>0.98</td>
</tr>
<tr>
<td>Residual</td>
<td>12</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 3.2: The interaction between the presence or absence of Choice and the Habitat start segment ($C \times H_s$) for megalopae (a) and crablets (b). Data are the mean proportion (SE) of animals found within the start segment for the different habitat types within No-Choice and Choice arenas ($n = 3$). Data points offset for clarity.
Figure 3.3: Mean (SE) proportion of crablets found in each of the habitat segments within the Choice arenas (Arenas 1–3, n = 3) where crablets started in seagrass, mud or sand.

Figure 3.4: Mean (SE) proportion of crablets found within the segments of the No-Choice arenas (Arenas 4–6, n = 3) for seagrass, mud and sand.
3.5 Discussion

3.5.1 Megalopae

No significant C × H, interaction was detected in the megalopae experiment, supporting the model that megalopae are not selective among the habitats offered. The power analysis shows that if habitat selection by mud crab megalopae is as pronounced as for other portunid species, then the experimental design had reasonable power to detect it (power ranged between 0.72 and 0.98). The low overall recovery of megalopae and the different recovery rates from the seagrass, sand and mud No-Choice arenas does, however, complicate the interpretation of these results.

Although not significantly different, the mean number of megalopae recovered from the seagrass No-Choice arenas was less than half that recovered from the sand or mud arenas. If this was solely due to my ability to recover megalopae from seagrass then it is likely that a similar loss of megalopae occurred within the seagrass segments within Choice arenas. Adjusting the data for this artefact increases the proportion of megalopae found in seagrass segments and reduces the proportion found elsewhere, but even these adjusted data showed no significant C × H, interaction, supporting the hypothesis of lack of selectivity among habitats.

Mud crab megalopae are delicate, and washing them from seagrass blades and collecting them over a sieve was a difficult task. The recovery rates of megalopae from seagrass may have been improved by using a gentler method. Submerging the seagrass into dense, hypersaline water and agitating can cause the megalopae to float from the seagrass based on differential densities. Alternatively, submerging the seagrass in freshwater and agitating can cause live megalopae to separate from the seagrass, possibly because of osmotic shock, allowing them to be collected from the water column in a gentler manner (Forward et al. 2004).

An alternative explanation for the lower recovery of megalopae from seagrass is that it resulted from post-settlement mortality or movement. Post-settlement mortality may be due to many factors including predation and cannibalism and these processes may have different rates in different habitats. Mud crab megalopae, like many other megalopae, are cannibalistic and may have eaten each other and those
metamorphosing into first instar crablets (Rabbani & Zeng 2005). Blue crab megalopae are cannibalistic at high densities, but generally only over unvegetated habitats (Moksnes et al. 1997). The initial megalopal densities used in our experiment were high (greater than 100 megalopae.m\(^{-2}\)), but the recovered densities were much smaller (mean density was 20.2 megalopae.m\(^{-2}\)). If cannibalism or predation is the reason for lower numbers of megalopae in seagrass, then mortality due to these processes must be greater within seagrass because fewer were found there. This is contrary to other studies which indicate that the structural complexity of seagrass provides refuge from predation and cannibalism (Moksnes et al. 1997, Moksnes et al. 1998). If mortality, for any reason, explains why fewer megalopae were found within the seagrass segments, then it is difficult to argue that seagrass is a beneficial refuge for mud crab megalopae.

As animals grow, the potential benefits of a particular habitat can change, and it may become advantageous for those animals to migrate to different habitats (Moksnes & Heck 2006, Lecchini et al. 2007). These post-settlement migrations can disguise initial settlement patterns, including which habitat was selected at settlement. The early stage juveniles of several crab species have been shown to undertake post-settlement migrations away from the initial settlement habitat (Etherington & Eggleston 2000, Pardo et al. 2007). In the current experiment I reduced the possibility of ontogenetic post-settlement migrations confounding the results by examining megalopae and crablets separately and running the experiment for only 3 days.

Competition for space can also drive animals from favourable habitats. For example, juvenile *Carcinus maenas* (J5 – J7) start to compete for space and subsequently migrate to less populated places when densities of conspecifics approach 25 individuals.m\(^{2}\), yet this pattern was not evident for smaller J2 – J3 crablets. In the field, densities of J2 – J3 *C. maenas* have exceeded 170 individuals.m\(^{2}\) (Moksnes 2004). In my experiment, initial megalopae densities were high (105 individuals.m\(^{-2}\)), but at the end of the experiment the mean density of megalopae recovered from the arenas was 20.2 individuals.m\(^{2}\). With fewer megalopae recovered from seagrass segments than mud or sand, competition for space should have been driving megalopae into seagrass segments, not out of them. Whether mud crab megalopae
undergo post-settlement density-dependent migrations prior to moulting is an issue for future testing.

These considerations potentially confound the interpretation of the results, but all suggest a greater number of megalopae within the structured habitat, which did not occur. However, whether or not the low numbers of megalopae recovered from seagrass were due to any or a combination of inefficient recovery, differential mortality or post-settlement migration, the results remain. The hypothesised significant C × Hs interaction was absent. Whilst it is possible that these megalopae may have a less pronounced selectivity for complex habitats than other species, there was no large effect and there tended to be fewer megalopae found within the seagrass segments. Therefore, it is unlikely that megalopae strongly select seagrass over mud or sand to an extent exhibited by other species of crab. Undoubtedly, the interpretation of these results would be simpler had the recovery rate of megalopae been greater and similar across all habitat types within the No-Choice arenas as was the case for crablets.

As with all laboratory experiments, these results should be interpreted with caution because the animals were subject to artificial conditions within the arenas. The megalopae and crablets used, although from wild stock, were reared in aquaculture facilities. I used one brood of crabs, presumably all with the same parents. Therefore genetic diversity was limited to the diversity of the gene pool of those parents. Also, mobile predators such as large fish (TL > 5 cm) were absent from the arenas. These artefacts may have caused these crabs to behave differently to the wild population and this should be considered when interpreting these results.

The facilities did not allow me to test settlement patterns under flow conditions (for example, Lee et al. 2004). Within estuaries and bays, flow may tend to be laminar or turbulent depending on such factors as, stage of the tide, winds, and strength of the tides. The blue crab is thought to use the turbulence of strong flooding tide currents as a cue to swim, thereby maximising upstream transport, settling when flow reduces at slack water before the ebb (Tankersley et al. 2002). For this reason I consider that settlement behaviours are more likely to be exhibited in the more stable conditions I used rather than in an annular flume.
3.5.2 **Crablets**

The recovery rate of crablets was high, at 80%, and similar across the different habitats of the No-Choice arenas, making interpretation of the results simpler. The crablets strongly selected seagrass, were indifferent towards mud but disliked sand. Where crablets had a choice, more were found within the seagrass segments than within mud or sand, regardless of which habitat they started in. Crablets tended to either remain in or move to seagrass.

3.5.3 **Coastal settlement model**

Together, these results support the coastal settlement model proposed by Webley and Connolly (2007), which states that mud crab megalopae tend to settle on the nearshore coastal shelf before colonising estuaries as crablets (CW < 30 mm). Had the megalopae exhibited a strong selection for either the seagrass or mud, as other species do, then the coastal settlement model would likely be rejected. The coastal shelf adjacent to estuaries in southeast Queensland is dominated by a sandy, unvegetated substrate (Stevens & Connolly 2005). I would expect, therefore, that if megalopae do not colonise estuaries then their ancestors were unlikely to have encountered estuarine habitats, and therefore would not have evolved selectivity among the habitats as other species have (Moksnes & Heck 2006). The crablets, however, would have encountered estuarine habitats, and if benefits were available, selectivity would likely have evolved.

If, when colonising estuaries, crablets are less likely to be eaten than megalopae, then a fitness benefit may exist for nearshore settlement of megalopae and subsequent metamorphosis into crablets before colonising estuaries. The total length of a mud crab megalopa is approximately 4 - 5 mm; this relatively large size, together with its propensity to rise into the water column when illuminated (Webley & Connolly 2007), suggests that it will be exposed to substantial predation pressure if it were to colonise estuaries. Predation by juvenile fish is cited as a reason for suppression of megalopal swimming activity in illuminated estuarine water (Tankersley et al. 1995, Forward et al. 1997). However, if the crablets colonise estuaries, predation risks may be lower because of their cryptic nature and ability to bury in the substrate (J. Webley pers. obs.).
Adult mud crabs are associated with estuarine mangroves, but despite considerable search effort in several countries the crablets and megalopae are rarely found. Few mud crab megalopae are reported to be caught within bays or estuaries using plankton tows or 'hogs hair' style larvae collectors (Arriola 1940, Moser & Macintosh 2001, Sumpton et al. 2003, J. Webley pers. obs.). Only two reports of crablets occurring within mangroves or estuaries were found in my review of the literature. One instance is from a prawn sampling program in a South African estuary (Forbes & Hay 1988) and the other from an extensive experiment where artificial habitats (roof tiles) were placed within the mangrove habitat lining a bay (Hill et al. 1982). Over the 17 month duration of the latter experiment, fewer than 20 crablets were found under the tiles, a very small number compared to that required to maintain the adult population. It is also unclear whether the crablets would have occurred within the mangroves in the absence of the tiles. Other researchers have searched mangrove habitats and used tiles in a similar manner along other mangrove-lined estuaries without success (I. Knuckey, Fishwell Consulting Pty Ltd, personal communication). Mangroves were excluded from this experiment because, despite being the most thoroughly searched estuarine habitat, mud crab crablets are rarely found within it. There are no reports in the literature of mud crab megalopae occurring within estuaries in southeast Queensland, despite considerable field sampling. Although absence of evidence is not evidence of absence, it suggests that they are unlikely to settle directly to mangroves within estuaries. The first habitats that crablets are likely to encounter if they colonise estuaries in southeast Queensland are seagrass, mud or sand.

One likely reason that the crablets prefer seagrass is the benefits provided by the structural complexity of the habitat. Many other crustacea have been shown to recruit to substrates that offer a complex structure (Stevens 2003, van Montfrans et al. 2003, Lee et al. 2004). This complexity can provide a refuge from predation and a greater abundance of food compared to the more two-dimensional mud and sand substrates. This food can be live prey such as small crustacea, bivalves and polychaetes found within the seagrass, but it can also be carrion delivered to the seagrass from elsewhere. The drag and turbulence around seagrass beds makes them effective traps for particles in the seston (Agawin & Duarte 2002), and tiny pieces of carrion are likely to be delivered to and trapped in seagrass beds. Many portunid crabs scavenge carrion and
the mud crab crablets have been observed to feed on carrion within traps (Wassenberg & Hill 1987). Scavenging is energetically beneficial, especially when consumers are able to utilise the “sit and wait” strategy by residing within a carrion trap such as seagrass (Ruxton & Houston 2004).

Since habitats such as seagrass extend into the water column and create an above-ground structure the possibility that the seagrass itself restricts the movement of crablets should be carefully considered in the current experiment. If crablets are thought of as simple clockwork toys, randomly moving around the arenas with their velocity reduced within seagrass segments, then they would tend to accumulate within the seagrass. Whilst theoretically possible, this scenario is unrealistic. In this experiment the crablets had sufficient time to sample the other habitats, as demonstrated by their distribution throughout the seagrass No-Choice arenas. They were also observed several times to simply swim over or around the seagrass segment whilst exploring the arenas. Therefore the simplest explanation is that they selected the seagrass and tended to choose to remain there.

Many coastal marine organisms have a pelagic life stage. For these organisms, the chaotic nature of their recruitment makes testing mechanistic models difficult. Studies need to encompass large temporal and spatial scales to discern general patterns in the apparent chaos (Gaines & Bertness 1992). Where recruitment events are witnessed sporadically, such as with mud crabs, it is difficult to use these occasional observations to test among competing recruitment models. Carefully designed laboratory experiments are needed to provide insights into the biology and behaviour of these animals. They allow us to test hypotheses about evolved behaviours, thus contributing to our understanding of nature (Underwood et al. 2004). The evolved behaviour, in this case, is a selection for seagrass over mud and sand. It suggests that there are fitness benefits in selecting seagrass (Krebs & Davies 1997) and defines seagrass habitat as a nursery for mud crab crablets amongst those tested (Beck et al. 2001).

This experiment did not reject the hypothesis that megalopae select among different estuarine habitats, but rather it supported the hypothesis that they do not. Therefore the power of the test and the effect size considered relevant are important when interpreting the results. Generally, the results obtained here are what would be
expected if the coastal settlement model explains how mud crabs colonise estuaries. In Australia, management of harvested species is increasingly taking an ecosystem-based approach. Our experiment suggests that because of the behaviour exhibited by the crablets, seagrass beds are a likely nursery habitat for mud crabs, and as such, management of this habitat is important to maintain the resilience of the population. To quantify the importance of seagrass beds to the mud crab, experiments investigating abundance, survival and residence time within this habitat are required.
Chapter 4: Development of a method to assess scavenging potential within the estuaries of southeast Queensland

4.1 Abstract

This chapter introduces the ecosystem process of scavenging and the role of mud crabs in this process. Scavenging is the process of finding and intentionally consuming carrion. Mud crabs, like many other omnivorous animals, are opportunistic scavengers. Few animals though are obligate scavengers. Animals in vigorous systems rarely die a peaceful death. Instead, if they become sick or weak they are quickly preyed upon rather than scavenged. Therefore, the actual act of scavenging is likely much less than the potential for scavenging. This concept of scavenging potential is developed here, along with methods used to detect it. Scavenging potential was determined by calculating the proportion of carrion consumed from carrion platters during a fixed period of emersion in an estuary (Soak time). The scavenging assemblage was determined using baited remote underwater videos (BRUVs). Three hypotheses were tested: (1) there was a difference in scavenging potential between day and night and soak times, (2) scavenging potential was greater during times of tidal flow, and (3) there was a difference in scavenging potential between day and night, sites and dates and that these factors did not interact. The experiments determined that scavenging potential was greater during the night than the day but there was no interaction between day/night and any other factor. During the day, flow had no effect on scavenging potential. The assemblage of scavengers consuming carrion during the day was similar to that at night. Carrion platters and BRUVs deployed during the day are appropriate methods for determining the scavenging potential and assemblage of scavengers within estuaries of southeast Queensland.
4.2 Introduction

An important part of the life strategy for all animals is how they obtain sufficient food. To balance their energy and nutrient budgets, carnivorous and omnivorous animals often hunt and catch their prey. An alternative and less appreciated source of nutrition for these animals is fresh carrion, the flesh of dead animals.

Fresh carrion is nutritious but tends to be patchily distributed through time and space. In the marine environment, carrion can be locally massive but extremely patchy, as is the case for the mega-carrion provided by whale falls in the oceans (biomass > 100 kg, Britton & Morton 1994). For example, a 40 tonne whale falling to the abyssal sea floor is estimated to be similar to the amount of carbon that falls from the eutrophic zone onto a hectare of sea floor over 100 – 200 years (Smith & Baco 2003). Because carrion is generally patchily distributed, scavengers need to be able to locate and move towards it, or opportunistically consume it when they discover it by chance.

Scavenging is defined as a process of being able to detect carrion, move towards it and consume part or all of it (Britton & Morton 1994). Scavenging therefore requires intent to consume the carrion. The passive consumption of carrion by animals such as detritivores is not considered to be scavenging, although the broader ecosystem effect may be similar.

4.2.1 An ecosystem perspective of the scavenging process

Scavenging is not a rare phenomenon. It occurs in a variety of ecosystems, and has been described for example from terrestrial grasslands (Bestelmeyer & Wiens 2003), the deep sea (Smith & Baco 2003), and the intertidal zone (Rose & Polis 1998). A huge variety of animals, from ants to killer whales, scavenge. It would probably be rare for a hungry omnivore to forego a meal of fresh carrion (Retana et al. 1991, Whitehead & Reeves 2005). The diversity of taxa which scavenge means that within an ecosystem, scavenging is a process of the assemblage rather than of a single species.

Scavenging transfers energy and nutrients from carrion to scavengers, but although many animals scavenge, as a process within food webs, scavenging is unlikely to transfer as much energy as predation does (Britton & Morton 1994).
Predation undoubtedly accounts for the bulk of energy flux through food webs (DeAngelis 1992). Whilst fresh carrion has many nutritional benefits, it is an unreliable food source because the place and time it occurs tends to be unpredictable. It is also easily and often rapidly eaten, ensuring it is only available for a short time. This makes it difficult to use as an exclusive source of food, and carrion is therefore generally utilised opportunistically, as a supplement for the usual predation based diet (Britton & Morton 1994).

Animals can die because of injury, sickness and old age among other things (DeVault et al. 2003). Injury, sickness and old age, however, often increase the animal’s risk of being preyed upon before becoming carrion. An injured fish, for example, is less able to avoid predators. In ecosystems where predation pressure is high, the actual occurrence of scavenging may be low, because animals which potentially could become carrion are eaten before they die. Although actual scavenging activity may be low, the potential for scavenging is high, because many of the predators would readily eat fresh carrion if available.

The factors which drive predation pressure and scavenging potential are similar. Competition for food and the composition of the scavenging assemblage will influence scavenging potential. The propensity to scavenge is likely to be different among species, with changes to the assemblage of scavengers expected to enhance or depress scavenging potential. Therefore, scavenging potential is the result of interactions between the assemblage of animals and the competition for food within the ecosystem.

Understanding how scavenging potential varies through time and space may provide useful insights into the condition of ecosystems. Because potential scavengers are represented by a broad range of taxa, scavenging has the potential to reveal information about the organisation of the assemblage, and the vigour of competition for food at the ecosystem scale. For example, stressed ecosystems may have fewer species of opportunistic scavengers, and carrion may take longer to be consumed than in reference systems. Ecosystem organisation and the vigour of its processes are key components of ecosystem health (Rapport et al. 1998). Because scavenging potential simultaneously samples the assemblage of opportunistic scavengers and the rate of the process, it may be a useful biotic indicator for comparing ecosystems of interest to reference systems i.e. contributing to an assessment of an ecosystem’s health.
Other questions about the significance of scavenging activities in ecosystems are being asked. Bestelmeyer and Wiens (2003) ask whether the foraging activities of ants, which are opportunistic scavengers, retain nutrients within ecosystems? DeVault et al. (2003) suggest that scavenging ecology is “rich with the potential to advance our understanding of energy flow dynamics”.

4.2.2 **Methods and energetics of scavenging**

The biggest advantage to an individual animal gained from scavenging is that the energetic costs and risks associated with catching and killing live prey are avoided. Despite these hunting costs being absent, scavenging is not without expense. Before carrion can be eaten it must be found, and found quickly. Scavengers are competing with other scavenging animals as well as microbes (Janzen 1977). Microbes can render carrion unpalatable through decomposition. Therefore, quickly locating carrion, which is patchily distributed through time and space, is both necessary and challenging.

I propose that individual scavenging strategies lie on a continuum, with the extremes being the constant search strategy and the sit and wait strategy (Figure 4.1). The constant search strategy requires scavengers to have an efficient means of locomotion together with an ability to detect carrion over large areas. The most successful vertebrate scavengers to adopt the search strategy are the Old and New World vultures (DeVault et al. 2003). These birds are obligate scavengers, deriving all of their nutrition from carrion. Their ability to soar combined with good vision or sense of smell allows them to search large areas quickly and efficiently (Houston 1986). In turbid or dark marine environments, vision is unlikely to be useful in finding carrion. Chemoreception is more useful and is a method utilised by many estuarine gastropods and crustaceans (Ferner & Weissburg 2005). Within tidal estuaries, chemical metabolites from the carrion can be carried downstream in odour plumes. As flow rates increase, these plumes are likely to be dispersed over greater areas and potentially be detected by more scavengers. However, the distinctiveness of plume boundaries and gradients are reduced in turbulent flows, subsequently reducing the ability of scavengers to locate carrion (Weissburg & Zimmerfaust 1994). Turbulence within estuaries tends to be greatest during the changing tide. Animals which rely
extensively on scavenging need to locate carrion shortly after it becomes available, so as not to lose it to other animals and microbial competitors.

![Figure 4.1: The scavenging strategy continuum showing the two extremes; “Constant search” and “Sit and wait” strategies. Scavengers with different strategies can be placed somewhere along the continuum depending on the effort expended on searching. Examples given: Vultures (Houston 1986), Dolphins (Wassenberg & Hill 1990), Coyotes (Rose & Polis 1998).](image)

An alternative to searching for carrion is to sit and wait. Animals adopting the sit and wait strategy are generally opportunistic scavengers. They subsidise other sources of energy with carrion which has either died near them, or, is delivered to them by physical vectors such as tides and currents. These scavengers can enhance the probability of finding carrion by residing within or near a carrion trap. I define a carrion trap as a place where carrion accumulates in greater abundance than expected by chance. These places are generally edges of juxtaposed habitats, for example coast lines (Polis & Hurd 1996) or the edges of submerged aquatic vegetation (Hori 2006). Physical processes such as wind and currents transport carrion to these habitat borders where it can be trapped. These places can dramatically increase the abundance and reduce the variability of carrion. Along the Baja California peninsula, for example, the carcasses of birds, marine mammals and fish wash ashore frequently and regularly (Polis & Hurd 1996). Animals which frequent or reside within these carrion traps increase their chances of discovering carrion without expending the energy required to search for it. The coyotes of the Baja California peninsula have adopted the sit and wait strategy by residing near the coast, which acts as a carrion trap for dead marine animals that are washed ashore. The additional food from carrion maintains a greater population of coyotes near the coast than in the less productive inland areas (Rose & Polis 1998).
Bacteria and fungi (the microbes) gain energy by decomposing carrion. In doing so they release metabolites which are toxic, or at best unpalatable for many scavengers (Janzen 1977, Sherratt et al. 2006). At low concentrations, during the early stage of decay, volatile metabolites produced by microbes can act as cues for scavengers, informing them of the presence of carrion (Shivik 2006). However, during the later stages of decay, the increased concentration of toxic metabolites discourages scavengers from consuming the putrefying carrion (Burkepile et al. 2006). Scavengers that consume putrefied carrion expend additional energy detoxifying the microbial metabolites. In subtropical climates, carrion putrefies within days and it will no longer be available to scavengers, it will be the property of the microbes (Burkepile et al. 2006).

If fresh carrion is found then scavengers may have to compete with other animals (Houston 1986). This competition can lead to aggressive interactions consuming additional energy and possibly resulting in injury. A severe injury could easily outweigh the nutritional benefits of the carrion and place the scavenger at increased risk of predation (e.g. red fox and wolverine, Samelius et al. 2002).

4.2.3 Potential insight to ecosystem health

Scavenging potential, when combined with other indicators, may make a useful contribution to assessments of ecosystem health because it is directly influenced by the vigour of competition for food, and the organisation of the scavenging assemblage. The vigour, organisation and resilience of an ecosystem are key indicators of an ecosystems integrity or health (Rapport et al. 1998, Hewitt et al. 2005, Vugtveen et al. 2006, Thrush et al. 2008). In vigorous ecosystems, carrion is probably rare and scavenging uncommon, because sick, weak or injured animals are quickly consumed. But, if an animal was to die and become available as carrion, it is likely that its carcass would be quickly eaten because so many omnivorous animals are opportunistic scavengers. In an ecosystem in which competition for food is vigorous and the assemblage of organisms diverse, the natural occurrence of scavenging may be low, but latent scavenging potential high. Therefore, scavenging potential may be a useful component of a suite of indicators for ecosystem health assessments, because it samples both the assemblage and vigour of an ecosystem process.
Mud crabs (*Scylla serrata*) are known scavengers and are regularly captured by fishers using traps baited with carrion. These crabs are abundant within unfished muddy estuarine habitats (Pillans et al. 2005) and occur throughout the Indo-West Pacific. They are likely to be a major participant in the scavenging process within these ecosystems. I wanted to determine the relationship between current ratings of ecosystem health and scavenging potential, and the role that the mud crabs play in this ecosystem process.

4.2.4 **Developing a method to measure scavenging activity**

Before testing hypotheses about scavenging potential in estuarine ecosystems, a method to measure the key characteristics of scavenging is needed. The properties of scavenging potential that are likely to provide the most useful information about ecosystem health are the scavenging rate and the scavenging assemblage. Ideally, the method needs to be easy to use, allow sufficient replicates and be relatively inexpensive.

To measure scavenging potential, known amounts of carrion were secured to submersible platters which allowed scavengers open access to the carrion. These platters were submerged in the estuaries for fixed periods of time (soak time). This allowed the proportion of carrion scavenged during the soak times to be calculated. This measure of scavenging rate is a direct measure of the potential for carrion to be scavenged when available within the estuaries. To determine the composition of the scavenging assemblage, baited remote underwater videos (BRUVs) were used.

I completed three experiments which tested the hypotheses that: 1) there is a difference in scavenging potential between day and night and soak time, 2) during daylight, scavenging is greater during times of tidal flow (ebb and flood) than during slack water and was different between sites, and 3) that scavenging potential does not interact among the factors date, day/night and site. During the second and third experiments, BRUVs were used to test the models that scavenging assemblage was different between different tidal flows and between day and night.
4.3 Methods

4.3.1 Platters and baited remote underwater videos

Platters were used to measure scavenging rates. They were made from steel wire bent into a ring (400 mm dia.). Honeycomb mesh netting (holes: 4 mm) was threaded onto the ring such that a cone was formed when a 220g weight was attached to the centre of the netting. A spherical float was attached to the ring in three places so that the platters remained perpendicular to the float line when retrieved but lay flat on the substratum whilst soaking (Figure 4.2).

The assemblage of scavengers was recorded using baited remote underwater videos (BRUVs). Water proof camera housings were made from PVC gas pressure pipe and clear acrylic. A water proof seal was achieved by applying pressure to a single O-ring (5 mm dia.) which separated the two parts of the housing. Snap locks held the two parts in place. The housing was mounted on a plywood platform. A PVC tube extended 500 mm from the platform and terminated with a 200 × 200 mm carrion platter (4 mm mesh). This platter was raised 60 mm above the level of the platform so that it did not bury in the sediment when the platform was resting on the substratum (Figure 4.2). A Sony Mini-DV camcorder (DCR-HC26e) was placed inside the housing and recorded activity in the field of view for 60 – 90 minutes. In clear water, the horizontal field of view was 60 cm at the carrion net. When deployed at night, the carrion platter was illuminated with an 8 LED torch, which was covered with red cellophane (peak transmittance $\lambda > 680$ nm) because many fish and crustacea are unresponsive to red and far red light (Cronin & Forward 1988, Cappo et al. 2004). The torch was positioned to minimise backscatter.
Two undamaged pilchards (*Sardinops sagax*) were used as carrion for each platter and BRUV. Pilchards were used because these fish tended to be of a similar size which enabled similar quantities to be allocated to each platter without having to break or damage them. Breaking or damaging individual pilchards may have released significantly different quantities of attractive cues into the water column, confounding interpretations of the results. Preliminary trials with other carrion types (e.g. mullet) showed that pilchards were of a consistency which allowed scavengers to break distinct sections (e.g. mid section, head) off the platters rather than tearing off indistinct pieces. This enabled me to more easily estimate the proportion of carrion scavenged though time from the BRUV tapes.

The pilchard carrion was weighed [Mean (SE): 55.6 (1.0) g], placed in numbered bags and frozen in the laboratory. In the field the two pilchards were secured to each platter using 2 zip ties (100 × 3 mm zip-ties) per pilchard. Ties were placed just posterior to the gill slit and 15 mm anterior to the caudal peduncle. Tightening of the ties was standardised such that pilchards were undamaged and secured to the net, but could be removed by determined scavengers. Excess tie was trimmed close to the carrion allowing all scavengers easy access. On retrieval of the platters from the estuary, any remaining carrion was collected and weighed. For each platter, the proportion of carrion scavenged during the soak time was calculated. Platters and BRUVs were separated from each other by at least 60 m to increase independence of samples.
These platters and BRUVs were used in three experiments testing hypotheses 1), 2) and 3).

### 4.3.2 Experiment 1: Testing effects of Day/Night and Soak Time

Platters were set during the flood tide during the day or night (Factor: Day/Night, Fixed, 2 levels) for either 90 or 120 min soak time (Factor: Soak Time, Fixed, 2 levels). Platters were set on four different days: Dec 13 and 14 (T1 and T2) and Dec 20 and 21 (T3 and T4) (Factor: Trial, Random, 4 levels nested in Soak time: Figure 4.3). Each trial was done at one of three haphazardly chosen sites in the Coomera or Coombabah estuarine systems. Eleven to fifteen platters were set during each trial. Not all platters could be retrieved, so to maintain a balanced design, only the first 11 platters from each trial were used in the analysis. At the same time, I deployed three BRUVs for 90 min during each trial. There were recording and visibility problems with these BRUVs which prevented sufficient data from being collected to justify statistical analysis.

After arc-sine transforming the platter data (proportion scavenged), Cochran’s test was used to test for significant heterogeneity of variance before ANOVA was used to test for significant effects.

![Figure 4.3: Experiment 1: Hierarchical experimental design testing the factors: Day/Night (Fixed, 2 levels), Soak Time (Fixed, 2 levels) and Trial (Soak Time) (Random, 4 levels nested in Soak time) with 11 platters per trial.](image)

### 4.3.3 Experiment 2: Testing the effects of Tide and Site

This experiment tested whether the flow of the tides affected scavenging potential and whether scavenging varied from place to place within a river. Three
stages of the tide were sampled (Fixed factor: flooding, slack high and ebb). Sampling was restricted to the northern branch of the Coomera River to reduce travel time so that platters and BRUVs could be deployed at the correct times. Three sites separated by more than 1000 m were sampled (Random factor: 2A, 2B and 2C, Figure 4.4). Sampling was done over the one period of three consecutive days (7 – 9 Jan 2007) with each stage of the tide sampled at only one site on each day (Table 4.1). The experiment was completed over consecutive days to minimise the potential confounding effects of weather, tidal amplitude and time of the tide. These days are considered as one continuous temporal period and therefore are not a factor of this experiment.

Table 4.1: Experiment 2: The sampling events were interspersed across sites and the different stages of the tide during the period (● indicates sampling event).

<table>
<thead>
<tr>
<th>Site</th>
<th>Tide</th>
<th>2A</th>
<th>2B</th>
<th>2C</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Flood</td>
<td>Slack</td>
<td>Ebb</td>
<td>Flood</td>
</tr>
<tr>
<td>7-Jan</td>
<td>♦</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8-Jan</td>
<td></td>
<td>♦</td>
<td></td>
<td></td>
</tr>
<tr>
<td>9-Jan</td>
<td>♦</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Before doing the experiment a bootstrapped power analysis was done to determine the power of the design to detect different effect sizes. Two effect sizes, 30% and 40%, were chosen for the bootstrap analysis, because the intention of the experiment was to detect a large effect. Replication of the platters was limited to 7 per Site, using all available platters (total = 21). Bootstrap data were randomly selected with replacement from a pool of scavenging platter data (n = 84) collected earlier. Data in this pool used the same soak time (90 min) as this experiment. The selected data were allocated to the different Sites and Tides. Data for one level of Tide (i.e. slack high) were multiplied by the effect size (30% or 40% reductions) to represent scavenging activity during slack high water. These data were arc-sine transformed then analysed using ANOVA, testing the factors Tide (Fixed, 3 levels) and Site (Random, 3 levels) with 7 replicate platters. This procedure was repeated 20 times for each effect size to determine the probability of generating significant results.
In the field, scavenging rates and assemblages were sampled using platters and BRUVs during daylight hours. Slack high tide was between 10 am and midday during this period. The three BRUVs were deployed only at site 2B, removing site as a factor from the BRUV analysis. Platter data were arc-sine transformed before Cochran’s test was used to determine heterogeneity of variance. Hypotheses were tested using ANOVA. Student-Newman-Keuls (SNK) tests were used to determine differences among Sites or Tides.

BRUVs provided multivariate data of the proportion of carrion consumed by different taxa. When a scavenger removed a pilchard, the pilchard often broke at specific places e.g. the location of the zip ties or at the anal fin. To estimate the proportion of the whole pilchard that these commonly observed sections were, I quartered 10 pilchards in the laboratory. Pilchards were severed just posterior to the gills, at the anal fin and 15 mm anterior to the caudal peduncle. The whole and the parts were weighed and mean proportions calculated. The videos were used to estimate the proportion of carrion scavenged by individual scavenging species to generate a multivariate data set. A Bray-Curtis dissimilarity matrix was made from these untransformed proportions. This matrix was used to create nMDS plots and analysed using ANOSIM within the PRIMER package.
4.3.4 Experiment 3: Testing for interactions between: Date, Day/Night and Site

This experiment tested hypothesis 3) that scavenging potential did not interact among the factors Date (Random, 3 levels), Day/Night (Fixed, 2 levels) and Site (Random, 3 levels), and was done between 25 Jan – 5 Feb 2007. Seven platters were set at sites 3A, 3B, and 3C during both the day and the night time flooding tide (n = 126) over three haphazardly chosen non-consecutive days within the period. Platters were soaked for 90 min before being retrieved. Three BRUVs were deployed at site 2B during the day and the night over the period and recorded scavenging activity for 90 min. Site 2B was randomly selected from the four designated sites (Figure 4.4).
Data were arc-sine transformed and Cochran’s test checked for heterogeneity of variance. A three factor ANOVA tested for significant differences in scavenging activity. To provide a more powerful test of the main factors, interactions were pooled where $P > 0.25$ and the contribution to variance was considered to be negligible (Underwood 1997). For significant factors, SNK tests determined which levels were significantly different from each other. A Bray-Curtis dissimilarity matrix was made from these untransformed proportions. This matrix was used to create nMDS plots and was analysed using ANOSIM within the PRIMER package.
4.4 Results

4.4.1 Experiment 1: Day/Night and Soak Time

The univariate results of the three experiments are summarised in Table 4.2 and presented in more detail below.

Table 4.2: Summary of experiments done, factors tested, significant results and interpretations

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Factors Tested</th>
<th>Significant factors</th>
<th>Interpretation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Exp 1</td>
<td>Day/Night</td>
<td>Trial (Soak Time)</td>
<td>Trial encompassed date and site, therefore these components individually or together affected scavenging.</td>
</tr>
<tr>
<td></td>
<td>Soak Time</td>
<td>Trial (Soak Time)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Trial (Soak Time)</td>
<td>Trial (Soak Time)</td>
<td></td>
</tr>
<tr>
<td>Exp 2</td>
<td>Tide</td>
<td>Site</td>
<td>Scavenging was not affected by the stages of the tide but varied among sites.</td>
</tr>
<tr>
<td></td>
<td>Site</td>
<td>Site</td>
<td></td>
</tr>
<tr>
<td>Exp 3</td>
<td>Date</td>
<td>Day/Night</td>
<td>Scavenging was greater at night and varied across sites. No interactions.</td>
</tr>
<tr>
<td></td>
<td>Day/Night</td>
<td>Day/Night</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Site</td>
<td>Site</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Interactions</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

During the day time of Trial 4 (soak time = 90 min), scavenging only occurred on one platter out of the 11 deployed. During the night of Trial 3 (soak time = 90 min), the proportion scavenged on all platters was greater than 0.99. For the other trials the mean proportion of carrion scavenged ranged from 0.54 to 0.76 (Figure 4.5). Trials 3 and 4 introduce a degree of heterogeneity of variance among treatments and may have increased the Type I error. Cochran’s test, however, was not significant. The analysis of variance found a significant effect for Trial (Soak Time) only (Table 4.3).
Table 4.3: Experiment 1: ANOVA testing for a difference in the amount of carrion scavenged during the Day/Night, Soak time and Trial nested in Soak. Data were arc-sine transformed and Cochran’s test was not significant.

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Day/Night</td>
<td>1</td>
<td>11227</td>
<td>7.37</td>
<td>0.113</td>
</tr>
<tr>
<td>Soak time</td>
<td>1</td>
<td>839</td>
<td>0.08</td>
<td>0.810</td>
</tr>
<tr>
<td>Trial (Soak)</td>
<td>2</td>
<td>11167</td>
<td>19.67</td>
<td><strong>0.001</strong></td>
</tr>
<tr>
<td>Day/Night × Soak</td>
<td>1</td>
<td>9536</td>
<td>6.26</td>
<td>0.129</td>
</tr>
<tr>
<td>Day/Night × Trial(Soak)</td>
<td>2</td>
<td>1522</td>
<td>2.68</td>
<td>0.075</td>
</tr>
<tr>
<td>Residual</td>
<td>80</td>
<td>567</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>87</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 4.5: Experiment 1: Mean (SE) proportion of carrion scavenged during the day and the night using 120 and 90 min soak times with two trials nested in each soak time. Each trial was done on a different date at one of three haphazardly chosen sections of the Coomera/Coombabah estuarine system.
4.4.2 **Experiment 2: Tide and Site**

The results of the bootstrap analysis showed that the experimental design had a power of 0.3 to detect a 30% reduction in scavenging pressure at slack high water and a power of 0.7 to detect a 40% reduction. This was considered sufficient to warrant doing the experiment because I was testing for large differences in scavenging potential.

Cochran’s test was not significant and the ANOVA showed that Sites were significantly different ($P < 0.018$) but Tide was not. The Tide × Site interaction was also not significant (Table 4.4). The post-hoc SNK test of the factor Site showed that scavenging pressure at Site 2C was significantly lower than sites 2A and 2B which were similar (Figure 4.6).

Table 4.4: Experiment 2: ANOVA testing the difference between states of the Tide (Ti) at three Sites (Si) within the Coomera River during one sampling period spanning three days.

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tide</td>
<td>2</td>
<td>448</td>
<td>0.36</td>
<td>0.715</td>
</tr>
<tr>
<td>Site</td>
<td>2</td>
<td>2675</td>
<td>4.35</td>
<td>0.018</td>
</tr>
<tr>
<td>Tide × Site</td>
<td>4</td>
<td>1228</td>
<td>2.00</td>
<td>0.108</td>
</tr>
<tr>
<td>Residual</td>
<td>54</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Seven different species were recorded scavenging at the BRUVs during daytime tidal phases. Five of the species occurred during just one phase of the tide and two during all three phases (Table 4.5). Carrion was scavenged at all BRUVs except one and there was no significant difference in the proportion of carrion consumed by the various species of the scavenging assemblage among Tides (ANOSIM: Global R = -0.173, \( P = ns \), Figure 4.7).
Table 4.5: Experiment 2: Scavenging activity recorded on BRUVs set during the ebbing, flooding and slack high tides in the Coomera River. The proportion scavenged is the mean proportion of the carrion consumed by the scavenger observed on the BRUV tapes. The number of observations is the number of tapes which recorded this group.

<table>
<thead>
<tr>
<th>Taxonomic group</th>
<th>Mean proportion scavenged</th>
<th>Ebb, Flood or Slack High</th>
<th>Number of observations</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acanthopagrus australis</em> - Teleostei</td>
<td>0.84</td>
<td>All</td>
<td>4</td>
</tr>
<tr>
<td>Dasyatidae - Elasmobranchii</td>
<td>0.40</td>
<td>All</td>
<td>4</td>
</tr>
<tr>
<td><em>Tetractenos hamiltoni</em> - Teleostei</td>
<td>0.25</td>
<td>Ebb</td>
<td>1</td>
</tr>
<tr>
<td><em>Terapon theraps</em> - Teleostei</td>
<td>0.06</td>
<td>Flood</td>
<td>2</td>
</tr>
<tr>
<td>Muraenidae - Teleostei</td>
<td>0.05</td>
<td>Flood</td>
<td>1</td>
</tr>
<tr>
<td><em>Nassarius pullus</em> - Gastropoda</td>
<td>0.01</td>
<td>Slack High</td>
<td>1</td>
</tr>
<tr>
<td><em>Scylla serrata</em> - Decapoda</td>
<td>0.01</td>
<td>Flood</td>
<td>1</td>
</tr>
</tbody>
</table>

*▲* = Ebbing tide  
*▽* = Flooding tide  
*○* = Slack high water

*Stress* = 0.00

Figure 4.7: Experiment 2: nMDS plot for the proportion of carrion consumed by the scavenging assemblage during different stages of the tide.
4.4.3 **Experiment 3: Date, Day/Night and Site**

More carrion was scavenged during the night than the day (Figure 4.8). There was a difference between sites, with less scavenging occurring at site 3C than at sites 3A and 3B which were similar (Table 4.6: SNK: $P < 0.05$: Figure 4.9). There was no effect of date and none of the interactions were significant, which allowed the Day/Night × Site × Date and the Day/Night × Date interactions to be pooled.

**Figure 4.8: Experiment 3: Mean (SE) proportion of carrion scavenged during the day and night at three sites within the Coomera River over three non-consecutive days.**

Seven different species were recorded scavenging at these BRUVs. Three of the species occurred only at night and one occurred only during the day (Table 4.7). Carrion was scavenged at all BRUVs except one. Despite this apparent segregation between day and night, there was no significant difference in the proportion of carrion consumed by the various species of the scavenging assemblage between the day and the night (ANOSIM: Global $R = -0.06$, $P = ns$, Figure 4.10).
Figure 4.9: Experiment 3: Mean (SE) proportion of carrion scavenged at three sites within the Coomera River during the day and the night over three non-consecutive days. Different letters indicate a significant difference (SNK test: $P < 0.05$).

Table 4.6: Experiment 3: ANOVA testing for interactions in scavenging potential between Day/Night, three Sites and three Dates during flooding tides within the Coomera River. * denotes pooled terms where $P > 0.25$.

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Date</td>
<td>2</td>
<td>751</td>
<td>3.4</td>
<td>0.136</td>
</tr>
<tr>
<td>Day/Night</td>
<td>1</td>
<td>17660</td>
<td>23.9</td>
<td><strong>0.039</strong></td>
</tr>
<tr>
<td>Site</td>
<td>2</td>
<td>3893</td>
<td>17.7</td>
<td><strong>0.010</strong></td>
</tr>
<tr>
<td>* Day/Night × Date</td>
<td>2</td>
<td>363</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Date × Site</td>
<td>4</td>
<td>219</td>
<td>0.5</td>
<td>0.722</td>
</tr>
<tr>
<td>Day/Night × Site</td>
<td>2</td>
<td>739</td>
<td>2.1</td>
<td>0.209</td>
</tr>
<tr>
<td>* Day/Night × Site × Date</td>
<td>4</td>
<td>359</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Residual</td>
<td>108</td>
<td>423</td>
<td></td>
<td></td>
</tr>
<tr>
<td>*Pooled Terms</td>
<td>6</td>
<td>360</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 4.7: Experiment 3: Scavenging activity recorded on BRUVs set during the night and the day in the Coomera River during a flooding tide. The proportion scavenged is the mean proportion of the carrion consumed by the scavenger when observed on the BRUV tapes. The number of observations is the number of tapes which recorded this group.

<table>
<thead>
<tr>
<th>Taxonomic group</th>
<th>Mean Proportion scavenged</th>
<th>Day or Night or Both</th>
<th>Number of observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dasyatidae - Elasmobranchii</td>
<td>0.74</td>
<td>Both</td>
<td>3</td>
</tr>
<tr>
<td>Muraenesocidae - Teleostei</td>
<td>0.58</td>
<td>Both</td>
<td>3</td>
</tr>
<tr>
<td><em>Portunus pelagicus</em> - Decapoda</td>
<td>0.50</td>
<td>Night</td>
<td>1</td>
</tr>
<tr>
<td><em>Scylla serrata</em> - Decapoda</td>
<td>0.43</td>
<td>Both</td>
<td>3</td>
</tr>
<tr>
<td><em>Lutjanus russelli</em> - Teleostei</td>
<td>0.31</td>
<td>Day</td>
<td>2</td>
</tr>
<tr>
<td>Tetraodontidae - Teleostei</td>
<td>0.25</td>
<td>Night</td>
<td>1</td>
</tr>
<tr>
<td>Gammaridae - Amphipoda</td>
<td>0.01</td>
<td>Night</td>
<td>2</td>
</tr>
</tbody>
</table>

Figure 4.10: Experiment 3: nMDS plot for the proportion of carrion consumed by the species of an assemblage during the day and night.
4.5 Discussion

4.5.1 Day vs Night

The first experiment showed that scavenging pressure was greater during the night than the day but not significantly so. However, in the third experiment significantly more carrion was scavenged during the night. Together these results show that while scavenging potential is likely to be greater at night, substantial scavenging potential exists during the day.

4.5.2 Soak time and Trial nested in Soak time

Soak time was tested in the first experiment and was not significant. Similar proportions of carrion were scavenged over 90 and 120 minutes. This was unexpected because the longer carrion is available the more likely it will be consumed. The significant factor, Trial nested in Soak time, reveals that almost nothing was scavenged during the day of Trial 4 and almost everything was scavenged during the night of Trial 3. Both of these Trials soaked for 90 min (Figure 4.5). This increases the variance of Soak time, reducing the power of the test. Preliminary trials in these estuaries never resulted in a complete absence of scavenging as almost occurred during the day in Trial 4. The factor Trial also incorporated the natural variability of scavenging pressure between different sites and dates and the effects or interactions of these two factors could not be separated in this experiment. They are discussed below.

4.5.3 Site

Both experiment 2 and 3 showed that scavenging potential was different among sites. Scavenging potential was lower at sites 2C and 3C, which were both closer to the mouth of the Coomera River (Figure 4.4). Apart from their distance from the mouth, all sites appeared similar, with turbid waters over a muddy substratum and mangrove lined banks.

4.5.4 Tide

The second experiment showed that the flow of the tide did not affect scavenging potential. I predicted that scavenging would be greater during times of
flow than during slack water. In turbid estuaries, such as the system used here, scavengers are likely to locate prey by following odour plumes, moving against the flow towards the carrion (Weissburg et al. 2002, Keller et al. 2003). In estuaries during the flooding or ebbing tide, flow tends to be relatively laminar, generating odour plumes with distinct boundaries; during the slack period, as flow changes direction, turbulence increases (Tankersley et al. 2002). Animals such as crabs that move relatively quickly sample plumes on a coarse scale and are less efficient at following odour plumes in turbulent flows (Weissburg & Zimmerfaust 1994, Ferner & Weissburg 2005). During the flood or ebbing tide, the flow will extend the odour plume over a larger area, possibly reaching more scavengers than during slack high water. The plume is also likely to have a more defined gradient and distinct boundaries compared to the diffuse gradient generated in turbulent slack water. The results have shown that in this place and for this period, if this switch between laminar and turbulent flow occurs in these estuaries, it had no large effect on scavenging at the platters. The experiment was, however, completed over one continuous period of 3 days and as such is not temporally replicated and results may be different at other times.

There are a number of possibilities why there was no effect of tide. It may be that tidal flow was too turbulent and mobile scavengers obtained no advantage in the increased dispersal of the odour plume or, alternatively, they were not disadvantaged in turbulent flows. Soak time may have been insufficient for scavengers some distance away to be able locate the carrion before the platters were removed. There may also have been sufficient carrion or other food between the distant mobile scavengers and the platters, such that they found other food before encountering the platter. Or, there may have simply been too few scavengers.

4.5.5 Date

Experiment 3 resolved that there was no effect of date on scavenging potential. The three sampling dates were haphazardly selected and separated by 3 and 6 days. Over longer periods, date may have an effect but I was interested in the effect of short separation periods because I expected to complete future experiments within similar periods of a few days.
4.5.6 **Interactions among Date × Day/Night × Site**

Scavenging potential did not interact among the factors Date, Day/Night and Site suggesting that scavenging potential, although occurring in different degrees, behaved consistently and in a similar pattern among combinations of these factors. This experiment did not test for interactions of these factors with the stage of the tidal cycle. Scavenging potential may be different during spring and neap tides, and it may interact with these factors.

4.5.7 **Independence and normality of data**

The sites were separated by at least a kilometre and individual platters by at least 60 metres. The platters and BRUVs presented the carrion so that any type of scavenger, small or large, could access it. Large, highly mobile scavengers such as stingrays were observed at the BRUVs and could conceivably have moved between platters and sites consuming all of the carrion on several platters. Smaller mobile animals such as yellowfin bream (*Acanthopagrus australis*) were also observed scavenging at the BRUVs, however, the two pilchards on a platter would likely satiate a bream for over 90 minutes. Mud crabs (*S. serrata*) can move an average of about 500 m over a 24 hr period within similar-sized estuaries, although tend to be less active after feeding (Hill 1976, 1978). It is unlikely then, that individual mud crabs and fish of a similar size (weight < 2 kg) would detect, locate and scavenge on one platter, and then move to a second platter more than 60 m away, to again scavenge the carrion there. Support for this assumption was obtained from the BRUV data. Individually identifiable mud crabs were only ever seen at one BRUV during one sampling period, and individual yellowfin bream were never observed to consume more than one pilchard. For animals no more mobile than mud crabs, or animals that would be satiated after eating two pilchards, it is reasonable to assume that the platters and BRUVs were independent replicates for soak times of less than 120 minutes. However, to improve the independence of platters, a soak time of 90 minutes was used in the second and third experiment.

The data collected were proportions and therefore bounded at 0 and 1. To be able to detect differences in means between treatments, it is important not to have the distribution of data compressed against these limits. If the platters are left to soak for
too long, then much of the carrion is scavenged and data tend to be compressed around 1 (see Night, Trial 3 in Figure 4.5). This can make data non-normal and may introduce heterogeneity of variance, which breaches the assumptions of analysis of variance tests, making results difficult to interpret (Quinn & Keough 2002). Therefore, reducing soak times, completing experiments during the day and using more carrion all contribute to reducing the number of platters which are completely scavenged. This shifts data to a more central distribution, away from the upper limit.

All carrion missing from the platters was considered to have been scavenged. Whilst it is possible that carrion was carried away from the platters and not consumed, video evidence from the BRUVs showed that where carrion was removed from the platters in the field of view, it was consumed quickly. I never observed broken pieces of carrion on platters being swept away by currents.

4.5.8 The assemblage of scavengers

The assemblages of scavengers observed during the day and the night were not significantly different. The night time BRUVs were illuminated using red light and this could potentially have confounded these results. However, crabs and fish tend to be less sensitive to light in the red and infrared region of the spectrum compared to white light (Cronin & Forward 1988, Cappo et al. 2004). The effect of the light used here on scavenger behaviour appeared minimal because the caution exhibited by scavengers approaching the BRUVs during the day and the night was not noticeably different.

The assemblage of scavengers during the different stages of the tide were also similar to each other. These experiments aimed to detect large differences in the assemblages rather than subtle alterations to the mix of species scavenging. As with most studies, increased replication and power may have detected a difference between assemblages. My results show, nevertheless, that mud crabs, in particular, scavenge during the day and the night and during flooding tides.

In turbid estuaries where visibility is limited, as is the case here, visual predators are considered to be disadvantaged compared to those which locate food using chemoreception or electroreception. The mud crab uses chemoreception to locate food (Hill 1979). Mud crabs were observed on BRUVs scavenging twice during the day and twice at night. Rays are considered to locate food primarily using senses other than
vision and were successful scavengers in these experiments during both the day and the night. The turbidity may have reduced the ability of opportunistic scavengers more dependent on vision, to locate the carrion platters. This may not be the case during the day in less turbid estuaries when visual predators are likely to have a greater chance of finding and consuming the carrion, possibly increasing scavenging potential.

4.5.9 **Conclusions**

These experiments demonstrate that this method of using platters and BRUVs is simple and efficient and provides quality data about scavenging potential within an estuary. Platters should be left to soak for no more than 90 minutes to improve independence and to reduce the probability that carrion on all platters is completely scavenged. Sampling can be completed during the day or the night without site and date interactions confounding interpretations, and scavenging potential within a site does not significantly vary over a period of 12 days. This method can be used to test many models about scavenging potential including differences between estuaries, estuarine habitats or management regimes.
Chapter 5: Scavenging potential: a potential ‘ecoassay’ for measuring the health of estuaries

5.1 Abstract

Many environmental authorities are tasked with maintaining the integrity or ‘health’ of ecosystems. Defining what constitutes a healthy ecosystem is to some extent subjective, but definitions tend to refer to characteristics such as the organisation, vigour and resilience of an ecosystem. Scavenging potential is driven by the structure of the assemblage of scavengers, and the vigour of competition for food: it is a function of two key components of ecosystem health. As diversity of the assemblage of scavengers increases and the vigour of competition for food increases, scavenging potential should increase. Generally, healthier ecosystems should be associated with a greater diversity and abundance of organisms, and I therefore predicted that scavenging potential would be greater in healthier estuaries. The health of 19 estuaries in southeast Queensland is assessed using an index of water quality called the Ecosystem Health Index (EHI). I used this index to rank the health of estuaries. Using carrion platters and BRUVs (Chapter 4), I measured scavenging potential across a gradient of the EHI using nine estuaries in southeast Queensland spanning 200 km of coastline. A significant negative relationship ($R^2 = 0.70$) was found between the water quality of an estuary (its EHI or assessment of its health) and scavenging potential, the opposite to my prediction. To analyse the multivariate, baited remote underwater video data, estuaries were grouped into ‘unhealthy’ and ‘healthy’ groups. The scavenging assemblages were not significantly different among these two groups. Observations from the field work and literature suggest that fishing pressure in urbanised regions is greater in places which are visually pleasing and have good water quality. The unexpected relationship between water quality and scavenging potential is explained in terms of greater fishing pressure in estuaries with better water quality.
5.2 Introduction

5.2.1 Ecosystem health: organisation, vigour and resilience

Natural resources and ecosystem processes are vital for human survival (Costanza et al. 1997). Environmental management agencies are expected to preserve ecosystem productivity and function, and maintain ecosystem health or integrity. What represents ‘healthy’ is subjective and usually based around anthropocentric ideals such as stability, productivity and continuity. In Australia, this concept underlies environmental legislation such as the Environment Protection and Biodiversity Conservation Act 1999 – “…that the present generation should ensure that the health, diversity and productivity of the environment is maintained…for the benefit of future generations;”.

Healthy estuaries provide human societies with significant ecological services. Some juvenile fish and crustaceans use the structurally complex habitats found within healthy estuaries as nurseries. An example is reef fish and mangroves (Beck et al. 2001, Mumby et al. 2004, Dahlgren et al. 2006). Several of these species are the target of commercial and recreational fisheries as adults. The presence of coastal vegetation also reduces the loss of land and property by decreasing erosion during storms (Granek & Ruttenberg 2007). Healthy estuaries can also provide an aesthetically pleasing environment which is conducive to recreational activities such as boating and fishing. These are valuable services provided by healthy estuaries to urbanised coastal regions and they require effective management if they are to be conserved (Alongi 2002, Harborne et al. 2006, Duke et al. 2007).

Effective management is a constant loop of assessment and action. Ideally, management policies are implemented and their effectiveness evaluated; lessons learned are incorporated into future management actions. To judge the effectiveness of any management strategy, we need to measure variables that relate directly to the management goals.

When the goal is to manage and conserve ecosystem health, the fundamental characters of ecosystem health or their best proxies should be measured. A critical issue therefore is choosing the best ‘ecoassay’ that is representative of ecosystem health (Fairweather 1999a). Development of the ecosystem health concept has led to
three overarching components of ecosystem health: organisation, vigour and resilience (Rapport et al. 1998). These three components deal with the constituents, the processes and the ability of the ecosystem to recover from disturbance, respectively. A good ecoassay will be a multivariate combination of both the physical and biological characteristics and the processes of the ecosystem.

5.2.2 Scavenging: a process embedded in the ecosystem

Scavenging potential is driven by the structure of the assemblage of scavengers, and the vigour of competition for food: it is a function of two key components of ecosystem health. Changes to the assemblage of animals and the vigour of competition for food are likely to affect scavenging potential. In vigorous ecosystems, animals rarely die from old age because the sick and weak are quickly preyed upon (Britton & Morton 1994). Whilst the ambient occurrence of scavenging may be low compared to predation, the potential for scavenging may be high because a broad range of species opportunistically scavenge carrion. Therefore, I suggest that latent scavenging potential may be a useful component to assess the health of an ecosystem because it samples both the vigour of competition for food, and the opportunistic scavenging assemblage of the ecosystem.

The mud crab (Scylla serrata) is an omnivore with a strong propensity to scavenge fresh carrion. In southeast Queensland, the mud crab tends to inhabit muddy mangrove-lined estuaries (Hill et al. 1982). It is frequently caught in traps baited with carrion and was observed on baited remote underwater video (BRUV) tapes in Chapter 4. This crab locates carrion by chemoreception, following odour plumes to their source (Hill 1979). During a flowing tide, odour plumes in estuaries have more distinct boundaries and cover a larger area than during the more turbulent periods of slack tides. The time during which an odour plume is available affects the probability that the source will be located by animals which follow the plume. The longer the odour plume is available, the greater the probability that the carrion will be scavenged.
5.2.3  

**Water quality, air quality and physical properties**

Estuarine assemblages live in a variable physicochemical environment. Tidal flushing and freshwater flows from storm events can alter factors such as the salinity and turbidity of the estuary, both regularly and stochastically. However, there are limits to these physicochemical conditions which, when exceeded, increase the probability of undesirable events such as hypoxia, fish kills and algal blooms. Managing physicochemical variables is therefore an important component in the maintenance of ecosystem health. Effective management of the physicochemical environment provides the foundations for the assemblage to persist but it does not guarantee stability or function.

5.2.4  

**The Ecosystem Health Index**

The Ecosystem Health Monitoring Program (EHMP 2007) collects monthly data on five water quality variables from eighteen estuaries across southeast Queensland. The variables measured are: chlorophyll a, dissolved oxygen, total nitrogen, total phosphorous and turbidity. These data are used to calculate the physicochemical Ecosystem Health Index (EHI) for each estuary. The EHI ranges from 0 (‘unhealthy’) to 1 (‘healthy’) and is derived from a spatial interpolation of the compliance of the medians of the five water quality variables relative to the targets of the Southeast Queensland Regional Water Quality Monitoring Strategy (MBWCP 2001). It uses variables that are familiar to managers, may affect ecosystem processes and assemblages (e.g. dissolved oxygen, total nitrogen), and can be directly affected by management actions. For example, within some estuaries receiving sewage treatment discharges, total nitrogen has been reduced by engineering upgrades to the respective wastewater treatment plants (EHMP 2007). The EHI is the current government metric of estuarine ecosystem health and, importantly, the EHI’s for the estuaries within the region are published and available publicly.

The EHI does not directly measure the key biological components of estuarine ecosystems, namely the organisation of the assemblage, the vigour of processes and the resilience of the system to perturbations. If these biological components of the ecosystem are degraded whilst water quality remains within the ‘healthy’ range, the EHI will fail to detect the broader decline in ecosystem health. For example, pollutants
other than those measured may alter the assemblage without affecting the EHI. Overfishing with carrion baits, too, can degrade estuarine health without altering the water quality. Managers may therefore be oblivious to potential reductions in estuarine health and take no remedial action. Expenditure on water quality enhancements could continue, whilst the ecosystem health and services within the estuaries wane. A broader ecoassay that also measures the assemblage of organisms and the vigour of ecosystem processes, may provide a better assessment of estuarine health.

5.2.5 Models

Estuaries subjected to the pressures of urbanisation and poor water quality are expected to have a lower abundance and poorer diversity of species. In such estuaries the ecosystem processes, especially those involving higher trophic level organisms such as fish and large crustaceans, are expected to be less vigorous. The healthy estuaries of southeast Queensland are perceived to have an abundant and diverse assemblage of organisms, spanning several trophic levels (Stewart 1993). The water quality within healthy estuaries is expected to be high in dissolved oxygen and to have low to moderate levels of total nitrogen, phosphorous, chlorophyll a and turbidity (EHMP 2007). The EHI is a published assessment of estuarine health and is utilised by State and Local governments. I predicted that for estuaries in southeast Queensland, there would be a positive relationship between scavenging potential during 2007 and published 2006 EHI scores.

As in Chapter 4, scavenging potential was measured using carrion platters. The longer these platters are available to scavengers the more likely it is that carrion will be completely consumed, reducing the ability to resolve any relationship between scavenging potential and EHI scores. I therefore also tested this relationship using two different soak times, predicting that the shorter soak time will resolve this relationship better.

Estuaries with worse EHI scores are characterised by low dissolved oxygen and higher nitrogen, phosphorous, chlorophyll a and turbidity. Active organisms intolerant to low levels of oxygen are likely to be less abundant, or less active in these types of estuaries. Therefore, I predicted that the assemblage of scavengers would be different in estuaries with better EHI scores (‘healthy’) compared to those with worse EHI scores (‘less healthy’).
5.3 Methods

5.3.1 Sites

The scavenging potential was measured and the assemblage was sampled in nine estuaries in southeast Queensland, spanning 200 km of coastline (Figure 5.1). The EHI is calculated for 19 estuaries within this region (EHMP 2007). The estuaries were haphazardly selected so that they spanned the region and represented the full range of EHI values, from 0.2 to 1.0. To reduce spatial confounding among estuaries, the sites selected within each estuary were restricted to being within 7 km of the mouth and having extensive sections of muddy mangrove habitat.

<table>
<thead>
<tr>
<th>Estuary</th>
<th>EHI</th>
<th>Condition Group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Noosa River</td>
<td>0.91</td>
<td>Healthy</td>
</tr>
<tr>
<td>Maroochy River</td>
<td>0.64</td>
<td>Unhealthy</td>
</tr>
<tr>
<td>Mooloolah River</td>
<td>0.94</td>
<td>Healthy</td>
</tr>
<tr>
<td>North Pine River</td>
<td>0.52</td>
<td>Unhealthy</td>
</tr>
<tr>
<td>Oxley Creek</td>
<td>0.20</td>
<td>No data</td>
</tr>
<tr>
<td>Tingalpa Creek</td>
<td>0.54</td>
<td>Unhealthy</td>
</tr>
<tr>
<td>Albert River</td>
<td>0.22</td>
<td>No data</td>
</tr>
<tr>
<td>Coomera River</td>
<td>1.00</td>
<td>Healthy</td>
</tr>
<tr>
<td>Currumbin Creek</td>
<td>0.93</td>
<td>Healthy</td>
</tr>
</tbody>
</table>

Figure 5.1: Map of southeast Queensland showing the locations of the nine estuaries sampled, their 2006 EHI scores and their allocated Condition group for analysis of the BRUV data.
5.3.2 **Platters and BRUVs**

The scavenging potential and the scavenging assemblage were sampled using the same platters and BRUVs described in Chapter 4.

5.3.3 **Experimental design**

Over six days (9 – 15 Mar 2007), sampling was done once in each of the nine estuaries. It was not possible to sample all estuaries on the same day because of the large spatial scale. Platters were deployed during a flooding tide within a 2 km stretch of each estuary, and were separated by at least 60 m. Fifteen platters in total were available, they were split into two groups and simultaneously soaked in the estuaries for 30 min ($n = 8$ platters per estuary) or 90 min ($n = 7$). The preliminary power investigations described in Chapter 4 indicated that a minimum of 7 platters were necessary to stabilise the variance around the mean proportion scavenged in a sampling event. Two weighed pilchards (*Sardinops sagax*: mean (SE), 55.6 (1.0) g) were used as carrion (see Chapter 4 for details).

At the same time and in each estuary, three BRUVs were deployed in a similar location to the platters. Scavenging activity was recorded for 90 min. These data provided information about the proportion of carrion scavenged by individual taxa (refer to Chapter 4 for details).

5.3.4 **Analysis**

To test the hypothesis that there would be a positive relationship between scavenging potential during 2007 and the published 2006 EHI scores, the mean proportion of carrion scavenged within each estuary was regressed against the 2006 EHI values. Although published EHI scores for any particular year are precise and without variability (what’s written is written), a reasonable argument can be made that because they are derived from samples they are not fixed, and therefore breach an assumption of ordinary least squares regressions (Model I regressions). The hypothesis test is, however, primarily interested in a prediction, whether or not $\beta$ is $> 0$, and not with the functional relationship between scavenging potential and EHI, therefore Model I regression analysis is acceptable (Sokal & Rohlf 1995, Quinn & Keough 2002). Because causality is implied between the EHI and scavenging potential, correlation analysis is inappropriate (Sokal & Rohlf 1995). Heterogeneity of variance
was checked by examining the size of standard errors across the nine estuaries and the distribution of data around the regression line (Quinn & Keough 2002).

These regressions were calculated for both soak times to test the hypothesis that the shorter soak time was better able to resolve differences across estuaries, which would be demonstrated by a significant and larger $R^2$ value for the shorter soak time.

To analyse the multivariate BRUV data (proportion scavenged by taxa), estuaries were placed into one of two levels of the factor Condition: ‘unhealthy’ (EHI $< 0.7$, $n = 3$) or ‘healthy’ (EHI $> 0.7$, $n = 4$) (Figure 5.1). This cutoff (0.7) was chosen after the experiment but before analysing the data to create two condition groups with an EHI range of 1.00 – 0.91 (‘healthy’: Noosa, Mooloolah, Coomera and Currumbin) and 0.64 – 0.54 (‘unhealthy’: Maroochy, North Pine and Tingalpa). Oxley Creek and Albert River were omitted because high turbidity prevented identification of any scavengers.

For each BRUV tape where scavenging occurred, the proportion of carrion scavenged by individual taxa relative to all scavenging on that tape (Proportion Scavenged $_{\text{Taxa}}$ / Proportion Scavenged $_{\text{Total}}$) was calculated. These data were used in all multivariate analyses within the PRIMER software (Clarke 1993). A Bray-Curtis dissimilarity matrix was calculated from the untransformed data (proportions) and analysed with a nested ANOSIM. Estuaries were nested within Condition. The SIMPER function determined which taxa contributed most to any differences between the groups using the index of dissimilarity (Diss/SD). Non-metric multidimensional scaling (nMDS) plots were used to visualise differences between the two condition groups.
5.4 Results

5.4.1 Scavenging potential - platters

There was a significant but negative relationship between the mean proportion of carrion scavenged from platters with a 30 min soak time and the EHI ($R^2 = 0.70$, $F_1 = 16.36$, $P < 0.005$; Figure 5.2). The standard error bars and spread of data around the regression line indicate that the assumption of homogeneity of variance was met. For platters soaked for 90 min, the relationship was not significant ($R^2 = 0.05$, $F_1 = 0.35$, $P = 0.571$). The shorter soak time resolved the relationship better.

![Figure 5.2: Mean proportion of carrion scavenged in 9 different estuaries spanning a range of Ecosystem Health Index scores from 0.2 (worse) to 1.0 (better), using a 30 min soak time. $R^2 = 0.70$, $P < 0.005$.](image)

5.4.2 Scavenging assemblage - BRUVs

Thirteen different taxa were observed scavenging carrion at the BRUVs. The mud crab (S. serrata) and the yellowfin bream (Acanthopagrus australis) were the most active scavengers (Table 5.1). Mud crabs scavenged in both types of estuaries
but dominated scavenging activity in unhealthy estuaries. Yellowfin bream dominated scavenging activity in healthy estuaries and were only observed scavenging in healthy estuaries. The nMDS plot revealed a slight separation of the scavenging assemblages from unhealthy and healthy estuaries (Figure 5.3), but this separation was not significant (ANOSIM: $P = 0.314$). The scavenging assemblages within the estuaries nested within Condition were different (ANOSIM: $P < 0.002$). The index of contribution to dissimilarity (Diss/SD) shows that mud crabs and yellowfin bream are the major contributors to dissimilarity among the healthy and unhealthy estuaries (Table 5.1). Mud crabs were the dominant scavengers in unhealthy estuaries and yellowfin bream dominated within the healthy estuaries.

| Table 5.1: Index of contribution to dissimilarity (Diss/SD) and proportional contribution (mean, SE) to scavenging activity for species within unhealthy ($n = 3$) and healthy ($n = 4$) estuaries in southeast Queensland. Only species where the proportional contribution was $> 0.05$ are shown. |
|-----------------|-------|----------------|----------------|
| Taxa            | Diss/SD | Unhealthy estuaries | Healthy estuaries |
| Mud crab (*Scylla serrata*) | 1.50   | 0.50 (0.25) | 0.21 (0.20) |
| Yellowfin bream (*Acanthopagrus australis*) | 1.35 | 0.06 (0.06) | 0.47 (0.23) |
| Common eel (*Muraenesox bagio*) | 0.35   | no activity | 0.11 (0.11) |
| Whiting (*Sillago sp.*) | 0.33   | 0.11 (0.11) | no activity |
| Banded toadfish (*Marilyna pleurosticta*) | 0.43 | 0.07 (0.06) | no activity |
| Blue swimmer crab (*Portunus pelagicus*) | na | no activity | 0.05 (0.05) |
Figure 5.3: Two dimensional nMDS plot of scavenging assemblages in healthy and unhealthy estuaries.
5.5 Discussion

The hypothesis predicting that scavenging potential would be greater in estuaries which had better EHI's was rejected. In fact, scavenging potential was lower in estuaries with better EHI's. This interesting result suggesting that in estuaries with better EHI's, competition for food is less intense, the animals there are less likely to scavenge, there are fewer animals, or any combination of these things. This result appears paradoxical, because healthier estuaries by definition should have more diverse assemblages, and more vigorous processes (Rapport et al. 1998).

The BRUV tapes revealed that, although not significant, the scavenging assemblages from unhealthy and healthier estuaries were different. Mud crabs (S. serrata) were the dominant scavengers within the unhealthy estuaries, but yellowfin bream (A. australis) dominated within the healthier estuaries. The healthier estuaries tended to have less turbid water, which may have aided yellowfin bream in locating food. Many fish use a combination of vision and chemoreception to locate food, whereas the mud crab primarily uses chemoreception (Hill 1979). As turbidity decreases, the effectiveness of vision in locating food will increase. This combination of senses and the faster movement of yellowfin bream over the mud crab increase this fish’s chances of arriving at carrion first in clear water. Mud crabs are likely, however, to be more effective scavengers in more turbid waters where vision is impaired (Hill 1979, Heasman 1980).

As with many experiments, this experiment assumes that the sampling units, platters and BRUVs, are representative independent replicates. To enhance the independence of platters they were separated from each other by at least 60 m and soaked for short periods of either 30 min or 90 min. In past work, a separation distance of 40 m was sufficient to ensure independence in traps designed to capture the moses perch (Lutjanus russelli) and the yellowfin bream over a period of 2 days (Sheaves 1992); both species are able to move faster than mud crabs. Experiments which capture mud crabs often use a pot spacing of 100 m, however the pots soak overnight or for longer (Williams & Hill 1982). The longest soak time used here was 90 min and the shortest was 30 min. These relatively short soak times reduce the probability of animals locating and scavenging on two or more platters, thereby increasing the likelihood that these platters are independent replicates. Further evidence supporting
their independence comes from the BRUV tapes. Individually identifiable mud crabs observed scavenging at BRUVs were never seen at other BRUVs. The BRUV tapes showed that individual yellowfin bream appeared satiated after consuming 50% of the carrion on a platter (J. Webley pers. obs., Chapter 4). Therefore, I consider that the platters and BRUVs were effectively independent replicates.

This experiment rejected the hypothesis that scavenging activity increases as the EHI increases. The EHI is used as proxy for estuarine health, but its accuracy at measuring estuarine health is not known. Therefore rejection can be interpreted in two ways: (1) scavenging potential decreases as estuarine health increases or (2) that the EHI is not a good measure of the health of these estuaries. I chose to use the EHI as a proxy for estuarine health because it is the current published measure used by managers (EHMP 2007). Whilst all care has been taken by managers in developing and adopting the EHI, the possibility that it is not representative of ecosystem health in these estuaries should be considered.

The EHI is essentially a measure of water quality, and whilst good water quality is a prerequisite for a healthy estuary, it is just that, only a prerequisite. The health of the estuary is a function of its living organisms and processes, which the EHI does not directly measure. Disturbances which negatively affect the assemblage of organisms or the ecosystem processes without altering water quality will reduce estuarine health without reducing the EHI. An example of such a disturbance is overfishing. Selectively harvesting certain taxa alters the estuarine assemblage and likely depresses the vigour of the processes they participated in. Fishing with carrion baits, however, is unlikely to affect water quality or the EHI. Other examples which may reduce ecosystem resilience and vigour include pollutants such as heavy metals, PCBs and herbicides (Scarlett et al. 1999). None of these are incorporated into the EHI.

Events beyond the spatial scale of the estuary may affect the apparent health of the ecosystem. For example in San Francisco Bay, against a trend of increasing water quality, exceptional plankton blooms occurred. Variation in the Californian oceanic current system increased the recruitment of bivalve predators into the estuary, starting a trophic cascade that released algae from grazing pressure, generating 'unhealthy' blooms (Cloern et al. 2007). For these reasons, composite indicators incorporating both physical and biotic components are recommended when monitoring the integrity

If the EHI is not a good measure of ecosystem health and my model is correct (that scavenging potential is greater in healthier estuaries), then some factor(s) may be depressing the health of the estuaries with good water quality (healthy EHI scores), to a greater degree than those with poor water quality (unhealthy EHI scores). These factors, whatever they may be, could explain the negative relationship between scavenging potential and the EHI obtained here.

5.5.1 **Recreational use of estuaries**

People in southeast Queensland have many choices of places in which to pursue aquatic recreational activities such as fishing and boating. Factors affecting this choice are likely to be the ease of access to waterways and the aesthetic beauty of the waterway (Stewart 1993). In choosing among estuaries, people tend to use estuaries with clean, clear water over turbid, polluted and pungent ones. This model drives local government agencies to invest in enhancing or maintaining the aesthetic beauty and accessibility of their estuaries. These government actions are perceived to enhance the lifestyle of residents and attract visitors who stimulate the local economy (Stewart 1993). The EHI ranks clean and clear water as healthier than turbid or green water. Based on water quality, therefore, estuaries with higher EHI scores will tend to be more attractive for aquatic recreational activities (boating and fishing) than estuaries with lower EHI scores. This model was supported by my observations in the field; there were more people using the ‘healthy’ than the ‘unhealthy’ estuaries.

5.5.2 **Impacts of fishing**

Overfishing has had profound effects on ecosystem health (Jackson 2001, Jackson et al. 2001b, Hughes et al. 2007). The Queensland Department of Primary Industries and Fisheries (QDPI&F) monitors the Queensland commercial fisheries and has recently commenced monitoring the coastal and estuarine recreational fisheries in Queensland (E. Jebreen, QDPI&F, pers. comm.). Fishing within the estuaries is regulated by the QDPI&F by regulating the size, sex and quantity limits for specific target species caught by fishermen. Recreational fishing within these estuaries tends to use carrion baits to capture a range of crustaceans and fish. This fishing method
selectively targets opportunistic scavengers and, at high and persistent pressure, alters the estuarine assemblage, either by reducing total numbers or by removing the larger animals. This was demonstrated in the Northern Territory, for example, where Walters et al. (1997) estimated that almost all of the legal-sized mud crabs were captured each season. Intense fishing pressure using carrion baits may reduce scavenging potential and the vigour of related ecosystem processes because it selectively removes animals with a propensity to scavenge from the ecosystem.

In Queensland, recreational fishing is a growing and popular activity. Recreational fishers spent $320 million and 25.4 million fishing hours pursuing this activity during 1999-2000, with 76% of this effort focused on estuaries and coasts (Henry & Lyle 2003). Without effective management this recreational fishing pressure is likely to increase and affect the assemblage of organisms utilising coastal and estuarine ecosystems.

5.5.3 Effects of current fishing pressure?

It is not yet possible to compare scavenging potential to fishing pressure across estuaries because fishing data at these fine spatial scales is not yet available. It is likely that fishing pressure will vary at multiple temporal and spatial scales (Kingsford et al. 1991, Bucher 2006). An appropriately designed long term monitoring program spanning the estuaries at appropriate temporal scales will provide the data from which effective management strategies can be developed and audited.

Moreton Bay Marine Park encompasses a substantial portion of southeast Queensland’s coastal waterways. There are several ‘green’ zones within the park where fishing is prohibited (No-Take zones). I can determine whether the current fishing pressure in southeast Queensland alters the scavenging potential and assemblage by comparing scavenging activity inside and outside these protected zones. This model was tested and is presented in the following chapter.
Chapter 6: Does current fishing pressure affect estuarine ecosystem health?

6.1 Abstract

People have been fishing for thousands of years for subsistence, profit and recreation. Fishing with carrion baited traps and hooks, selectively removes those animals with a propensity to scavenge, possibly depressing scavenging potential in heavily fished places. Recreational anglers are motivated to fish by a range of factors in addition to the desire to catch fish, for example to relax and enjoy the outdoors. The visual appeal of a fishing site ranks highly among factors affecting anglers’ choice of site. In populated places, where many anglers have easy access to waterways, fishing pressure in places of good water quality is likely to be greater. This concept was used in Chapter 5 to explain the surprising negative relationship between scavenging potential and good water quality. This chapter tested the model that current fishing pressure in southeast Queensland is sufficient to depress scavenging potential and alter the assemblage of scavengers. Scavenging potential was measured inside and outside visually appealing No-Take zones within the Moreton Bay Marine Park of southeast Queensland. Carrion platters and BRUVs were used to collect these data. Scavenging potential was greater inside the No-Take zones and the assemblages scavenging inside were different to those scavenging outside. Therefore fishing pressure is likely to have depressed scavenging activity. Because scavenging potential is embedded within two of the key components of ecosystem health, it is likely that where scavenging potential is altered, ecosystem health is also altered. Although measures of water quality are integral to the monitoring of ecosystem health, they are not sufficient in places subject to fishing pressure at levels occurring in southeast Queensland.
6.2 Introduction

Fishing has been a part of human culture for thousands of years. Today, fishing is an industrial, recreational and subsistence pursuit throughout the world. Unlike agriculture, fishing often harvests a commonly owned stock. Commonly owned fisheries can be rapidly depleted where fishing is competitive and on an industrial scale (Myers et al. 1997, Pauly et al. 1998, Jackson et al. 2001b). This ‘tragedy of the commons’ has occurred in estuaries and coasts where property rights are absent, resulting in substantial losses of biodiversity and, in some cases, leading to a phase shift in the state of some ecosystems (Jackson 2001, Hughes et al. 2005, Worm et al. 2006). Ecosystem phase shifts are not readily reversible; simply reducing fishing pressure may not restore the ecosystem (de Roos et al. 2006). Our understanding of the mechanisms generating and reversing ecosystem phase shifts is in its infancy (Folke et al. 2004, Bellwood et al. 2006). Effective management of fishing is therefore desirable and necessary, because economically competitive fisheries exploiting a common stock tend to overharvest the resource, which can have large and practically irreversible impacts on the ecosystem.

In Australia and elsewhere, the management of fisheries is moving towards an ecosystem-based methodology and away from single species management (Anon 2007, Francis et al. 2007, Marasco et al. 2007). Managing the ecosystem, as opposed to the fishery, requires the manager to maintain the characteristics and functions of the ecosystem within a predetermined ‘healthy’ or acceptable range (Fairweather 1993, Rapport et al. 1998). To gauge the effectiveness of their actions, managers need a measure of the organisation, vigour and resilience of the ecosystem. In southeast Queensland estuaries, synergies should be available between the current Ecosystem Health Monitoring Program (EHMP) and the fisheries manager, the Queensland Department of Primary Industries and Fisheries (DPI&F).

Fishers using carrion attract their quarry to a trap or a hook. Compared to methods such as bottom trawling, which can scour the substratum and increase turbidity (Dellapenna et al. 2006), fishers using carrion baits are able to remove animals from the ecosystem with relatively little disturbance to the physical environment. Water quality parameters such as turbidity and dissolved oxygen are rarely affected by this form of fishing. Commercial and recreational fishers use this
method in many Queensland estuaries, catching a variety of species including mud crabs (*Scylla serrata*), blue swimmer crabs (*Portunus pelagicus*), yellowfin bream (*Acanthopagrus australis*) and whiting (*Sillago spp.*). Recreational fishing can, however, impact the environment if pressure is localised and intense. For example, fishing pressure reduced the number of male mud crabs caught outside two marine reserves in southeast Queensland (Pillans et al. 2005). Disturbances from activities such as boat traffic, trampled vegetation on coastal paths, and bait collection, can also have detrimental impacts (Lewin et al. 2006). Lost fishing gear such as fishing line, lead sinkers and hooks can harm water birds and turtles, and litter can leave the environment unsightly (Ballance et al. 2000, Tonge & Moore 2007). Fishing with baits thus potentially disturbs the environment even though it may not affect water quality.

### 6.2.1 Fishing with carrion baits: effects and motives

Fishing with carrion baits is selective in that it tends to catch those species with a greater propensity to scavenge. Anecdotal evidence for this selectivity is provided by experienced fishers who will use lures and live baits to capture species which they rarely catch on carrion (J. Webley, pers. obs.). Because fishing with carrion baits is selective and tends not to disturb the physical environment, it has the potential to reduce the abundance of harvested species and alter the species assemblage within estuaries, without directly reducing water quality. Baited traps can also affect the assemblage of non-target species, for example small sub-populations of Australian sea lion (*Neophoca cinerea*) may be at risk of local extinction through entanglement in lobster pots while preying on the trapped lobsters (Goldsworthy & Page 2007). Altering the assemblage of organisms alters the organisation of the ecosystem and potentially alters the vigour of some processes and the ecosystem’s resilience.

Unlike commercial fishers, recreational fishers are not in the business of fishing. Rather than the primary motive being to catch fish profitably, catching fish is just one of many motives of recreational fishers, and it is rarely the primary one. International research asking ‘Why people go fishing?’ reveals that the top five reasons for going fishing are: (1) relaxation, (2) to be outdoors, (3) to get away from the regular routine, (4) to experience the catch, and (5) to experience unpolluted natural surrounds (Schramm & Gerard 2004). These motives influence the selection of the places that people go to fish (Schramm et al. 2003). People seeking to relax, be outdoors and
experience unpolluted natural surrounds tend to select places that are aesthetically pleasing, free of litter and, in the case of aquatic activities, have clean water (Chhetri 2006, Johnstone & Markandya 2006, Tudor & Williams 2006). Other factors such as the ease of access, safety and accommodation also affect site selection for recreational activities.

In southeast Queensland, conversations with recreational fishers suggests that motives for going fishing are similar to those described by Schramm and Gerard (2004), and include: to relax, to get outdoors, to catch fish and to ‘get away’ (J. Webley, pers. obs.). Within southeast Queensland estuaries, recreational fishing activity appeared to be greater in estuaries which have cleaner water, less litter and shores lined with natural vegetation (Webley, J. pers. obs.). Fishing activity appeared to be lower in places which have turbid water, and large amounts of litter or shores lined with concrete walls.

The previous experiment (Chapter 5) showed that scavenging potential was lower in places with better Ecosystem Health Index (EHI) scores. The ‘healthy’ estuaries such as Noosa, Currumbin and Coomera had clean water with little rubbish visible on the shores. Less ‘healthy’ estuaries such as Tingalpa, Oxley and North Pine had turbid water with a noticeable amount of rubbish caught in mangroves (J. Webley, pers. obs.). Although fishing activities appeared to be greater in the healthier estuaries, which is consistent with those more attractive places being selected as fishing sites, it is unlikely that the fishing activities had a significant effect on water quality.

In summary, recreational and commercial fishing with carrion baits can alter the faunal assemblage by selectively removing animals with a propensity to scavenge. Recreational fishers, because of their motivations, tend to prefer sites that have cleaner water and are aesthetically pleasing. These sites are represented by the estuaries with better EHI scores because the EHI rates clean water highly. Therefore, I propose the model that within southeast Queensland, fishing pressure is positively related with the estuaries EHI scores and that, in the aesthetically pleasing estuaries, those with a higher EHI score, fishing pressure is sufficient to depress scavenging potential. If this is supported, then it follows that current fishing pressure is depressing scavenging potential within ‘healthy’ estuaries to a greater extent than in ‘unhealthy’ estuaries, but not altering water quality.
6.2.2 **Testing the effect of current fishing pressure**

The proposed model has two parts. The first states that in southeast Queensland estuaries, fishing pressure is correlated with the EHI. The second states that current fishing pressure within aesthetically pleasing southeast Queensland estuaries, is sufficient to depress scavenging potential. Testing the first part requires data on total fishing effort among the estuaries of southeast Queensland for which the EHI is calculated. Testing the second part requires data on scavenging potential from aesthetically pleasing estuaries fished at current intensities and from similar places where fishing intensity is lower.

Data on the current total fishing effort in individual estuaries is not available. The DPI&F monitors the commercial but not recreational catch and effort. The DPI&F is currently planning to complete a series of creel surveys at southeast Queensland boat ramps to estimate recreational fishing effort (L. Olyott, DPI&F, pers. comm.). These surveys are expensive and encompass large temporal and spatial scales due to the effect that seasons, weather and holidays have on fishing activity (Kingsford et al. 1991, McGlenon & Kinloch 1997, Bucher 2006). It would be futile to determine the relationship between fishing pressure and the EHI across the estuaries of southeast Queensland if current fishing pressure is insufficient to depress scavenging potential. The more prudent path is, therefore, to test the tractable component of my model first. This requires resolving whether current fishing pressure in aesthetically pleasing estuaries in southeast Queensland is sufficient to depress scavenging potential.

Whether or not current fishing pressure is sufficient to depress scavenging potential can be tested by comparing scavenging potential inside and outside areas where fishing is prohibited. Within Moreton Bay Marine Park there are five protected zones where fishing is prohibited, namely Tripcony Bight, Willes Island, Swan Bay, McCoy’s Creek and Coombabah Lake. All of these sites are estuarine, aesthetically pleasing, and have relatively low turbidity compared to other estuaries within the region. I tested the model that current levels of fishing pressure in southeast Queensland are sufficient to generate a significant reduction in the scavenging potential and alter the scavenging assemblage by sampling scavenging potential inside and outside these protected zones.
6.3 Methods

6.3.1 Sites

Sampling was done inside (No-Take zone) and outside (Take zone) the protected zone at five sites in Moreton Bay Marine Park being: Tripcony Bight; Willes Island; Swan Bay; McCoy’s Creek and Coombabah Lake (Figure 6.1). All of these sites are estuarine, however, due to its proximity to the Pacific Ocean, Swan Bay is more strongly influenced by oceanic tidal flow and has the clearest water. Sampling in the No-Take zone was done from 60 m to 2 km inside the boundary. Sampling in the Take zone was done at least 60 m outside the boundary and extending up to 2 km away. Sample sites were adjacent to mangrove-lined shores both inside and outside the No-Take zones so that results would not be confounded by habitat differences and would also be comparable with previous chapters.

6.3.2 Experimental design

The scavenging potential and the scavenging assemblage were sampled using the same platters and BRUVs described in Chapter 4. Sampling was done once at each of the five sites (Factor: Sites, 5 levels, fixed) over a short period (3 – 11 May 2007). It was not possible to sample all sites on the same day because of the large spatial scale, however the results from Chapter 4 show that scavenging potential is not significantly different over 12 days. At each site, thirteen platters were deployed in both the No-Take zone and the Take zone (Factor: Zone, 2 levels, fixed). Prior experiments detected differences in scavenging potential using fewer than thirteen platters, but I used thirteen platters here because the cost of soaking additional platters is low, and the time taken to set thirteen platters left a small time window before retrieval was required. Platters were soaked for 30 min during the flooding tide and separated by at least 60 m. Only a single soak time of 30 min was used here because Chapter 4 showed that this time was better able to resolve potential differences than 90 min. Two pilchards (Sardinops sagax: mean (SE), 55.6 (1.0) g) were secured to platters using zip-ties and the proportion of carrion consumed per platter was calculated (as in Chapters 4 and 5).
At the same time, at each site, 3 BRUVs baited with 2 pilchards were deployed for 60 min. BRUVs were separated from each other and the platters by at least 60 m. On retrieval the BRUVs were moved across the zone boundary, baited and deployed again to record scavenging activity for another 60 min. This procedure was repeated twice to provide 6 replicate BRUV tapes both inside and outside the protected zone during the flooding tide. Video tapes were viewed in the laboratory and the proportion of carrion consumed by individual taxa estimated following the method described in Chapter 4.

6.3.3 **Analysis**

Analysis of variance was used to test the hypothesis that there was a difference in the proportion of carrion scavenged from platters among the two zones and the five sites. Data were arc-sine transformed and Cochran’s test was used to assess
heterogeneity of variance. Student-Newman-Keuls test (SNK) was used to determine differences among the five sites.

The BRUVs provided multivariate data which were analysed using the PRIMER software. A Bray-Curtis dissimilarity matrix was made from these untransformed proportions and used to create an nMDS plot, which graphically presents differences in the scavenging assemblage in the Take and No-Take zones. A 2-factor ANOSIM was used to test for a significant difference in the proportion of carrion scavenged by different species between the levels within Zone and Site. The SIMPER function determined which taxa contributed most to any differences between the two zones using the index of dissimilarity (Diss/SD).
6.4 Results

6.4.1 Scavenging potential - platters

Scavenging potential was significantly greater inside the No-Take zones (mean 0.49, SE 0.05) than in Take zone (0.36, 0.05; Table 6.1, Figure 6.2). Scavenging potential at Swan Bay was significantly greater than at the other sites, which were similar to each other (SNK: \( P < 0.05 \), Table 6.1, Figure 6.3). There was no significant interaction between Site and Zone.

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
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<td>7666</td>
<td>12.78</td>
<td><strong>0.001</strong></td>
</tr>
<tr>
<td>Zone</td>
<td>1</td>
<td>4462</td>
<td>7.44</td>
<td><strong>0.007</strong></td>
</tr>
<tr>
<td>Site ( \times ) Zone</td>
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<td>818</td>
<td>1.36</td>
<td>0.251</td>
</tr>
<tr>
<td>Residual</td>
<td>120</td>
<td>600</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 6.1: ANOVA testing for an effect of Site and Zone on the proportion of carrion scavenged. Cochran’s test = ns.

Figure 6.2: Mean (SE) proportion of carrion scavenged in No-Take zones and adjacent Take zones.
6.4.2 Scavenging assemblage - BRUVs

There was a significant difference in the proportion of carrion scavenged by different taxa inside and outside the protected zones (ANOSIM: Global $R = 0.235$, $P < 0.004$, Figure 6.4). SIMPER analysis showed that the average dissimilarity between No-Take and Take zones was 76.48%. The relative contribution to dissimilarity (Diss/SD) was greatest for mud crabs ($S. serrata$), followed by blue swimmer crabs ($P. pelagicus$), striped trumpeter ($Pelates sexlineatus$), a stingray and yellowfin bream ($A. australis$) (Table 6.2). The mud crab was the dominant scavenger in No-Take zones (mean proportion scavenged 0.49; SE 0.09), but was less important in Take zones (0.18; 0.07). The other portunid crab, the blue swimmer crab, showed the opposite pattern, with greater scavenging in Take zones (mean 0.18; SE 0.05) than No-Take zones (0.03; 0.02, Figure 6.5). Scavenging also differed among sites (ANOSIM: Global $R = 0.314$, $P < 0.001$).
Figure 6.4: nMDS plot of the proportion of carrion scavenged by different taxa in the No-Take (unfilled) and Take zones (filled) of each site: △ Lake Coombabah, ▽ McCoys Creek, □ Swan Bay, ◇ Tripcony Bight, ○ Willes Island.

Table 6.2: Index of contribution to dissimilarity (Diss/SD) to scavenging activity for species among Take and No-Take zones ($n = 5$) in southeast Queensland. Scavenging proportions are shown on Figure 6.5.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Diss/SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mud crab (<em>Scylla serrata</em>)</td>
<td>1.23</td>
</tr>
<tr>
<td>Blue swimmer crab (<em>Portunus pelagicus</em>)</td>
<td>0.95</td>
</tr>
<tr>
<td>Striped trumpeter (<em>Pelates sexlineatus</em>)</td>
<td>0.52</td>
</tr>
<tr>
<td>Stingray (Dasyatidae)</td>
<td>0.36</td>
</tr>
<tr>
<td>Yellowfin bream (<em>Acanthopagrus australis</em>)</td>
<td>0.33</td>
</tr>
</tbody>
</table>
Figure 6.5: The mean proportion (SE) of carrion scavenged in No-Take and Take zones by the five most common scavengers: blue swimmer crab, mud crab, stingray, striped trumpeter and the yellowfin bream.
6.5 Discussion

6.5.1 Scavenging potential is depressed by current fishing pressure

The results from the platters showed that scavenging potential was significantly greater inside the protected zones than outside them. There was no interaction between the sites and zones, showing that this is a general pattern across the sites. This experiment has supported the model that the current level of fishing pressure, across a range of aesthetically pleasing sites in southeast Queensland, is sufficient to depress scavenging potential generally.

Not all of the sites had similar scavenging potential. The greater scavenging potential at Swan Bay relative to the other four sites might have arisen from site specific factors, such as proximity to the ocean, salinity, sediment type, and disturbance history. Swan Bay was closer to the Pacific Ocean than the other sites and likely to be more strongly influenced by oceanic tidal flows. The factors or combination thereof which might cause this spatial variability are interesting, however, this experiment was not designed to investigate them. Spatial variation is an inherent part of field ecology and is expected to increase as the spatial scale of the experiment increases.

6.5.2 Scavenging assemblage is affected by current fishing pressure

The BRUVs revealed a significant difference in the assemblage of scavengers inside the protected zones compared to outside. This supports the model that current fishing pressure has altered the scavenging assemblage by the selective removal of animals with a greater propensity to scavenge, or those that are more readily caught by fishing methods using carrion.

The mud crab was the dominant scavenger inside the protected zones. Outside the protected zones its scavenging activity was depressed to a level similar to that of the blue swimmer crab. The blue swimmer crab showed the opposite pattern. This interaction in scavenging potential between mud crabs and blue swimmer crabs and the presence of fishing may be the result of blue swimmer crabs being released from competition pressure by the preferential removal of mud crabs by fishers.
Adult mud crabs tend to be larger than adult blue swimmer crabs and will kill a blue swimmer crab if they catch one. From observations of the BRUV tapes, blue swimmer crabs rapidly surrender carrion when similar-sized mud crabs approach. Because mud crabs tend to win agonistic interactions with blue swimmer crabs, then in places where mud crabs are abundant, they may reduce the catchability of blue swimmer crabs by discouraging them from entering baited crab pots when mud crabs are present, or, alternatively, there may be fewer blue swimmer crabs in places where mud crabs are abundant. In the absence of mud crabs, or in places where their numbers are depressed (e.g. outside protected zones, Pillans et al. 2005), blue swimmer crabs may be released from the competitive pressures exerted by the mud crabs. This can explain the increase in the proportion of carrion scavenged by blue swimmer crabs outside the protected area.

Whilst it is most likely that these differences are due to the prohibition of fishing inside the protected zones, other explanations should be considered. The sites declared as protected zones are often chosen because they are unique or possess some unusual or special characteristic (Pillans et al. 2005). This may be a confounding factor when sampling inside and outside protected zones and may be impossible to overcome. However, to endeavor to reduce this spatial confounding, sampling outside the protected zone was done in places with similar habitat to that found inside the protected zone. For example, if the substratum was muddy with mangrove-lined shores inside the protection zone, then a similar environment was selected outside the protected zone. Other factors such as the age of these no-take zones or, possibly, the time at which fishing ceased may mean that results from these No-Take zones may not be applied to new No-Take zones which may be exposed to different temporal patterns of recruitment.

BRUV data reveal a change in the extent of the role played by a species within this ecosystem after anthropogenic disturbance. Within the less impacted places (No-Take zones), mud crabs are the dominant scavenger, but blue swimmer crabs may have a latent scavenging function that is expressed in the absence or reduction in abundance of mud crabs. Video is a non-destructive, cost-effective tool for obtaining observational data, which can lead to insights into animal behaviour not available from extractive sampling methods, for example trawling (Bailey et al. 2007). On the Great
Barrier Reef, video has allowed surprising insights into latent functions. Bellwood et al. (2006) used video data to show that the batfish (*Platax pinnatus*), previously considered to mainly feed on invertebrates, switched its diet to macroalgae, thus commencing the reversal of an ecosystem phase shift by eating macroalgae smothering a coral reef. These latent or hidden functions may enhance the resilience of ecosystems, improving their health. Conserving these functions is problematic because they are hidden and unknown to science. Maintaining biodiversity may, by chance, conserve species which have important but hidden functions, however, these hidden functions can easily be lost if they are performed by only a few scarce species. Scarce species have relatively low weighting in biodiversity indices are therefore unlikely to have specific management plans when managers are focussed on gross biodiversity. This highlights the importance of matching management metrics to management goals, and will be beneficial in measuring and conserving estuarine ecosystem health.

6.5.3 **Conclusion**

I proposed the model that within southeast Queensland, fishing pressure in estuaries with better EHI scores is greater than in estuaries with worse scores, and that the greater fishing pressure has depressed scavenging potential in the ‘healthier’ estuaries. The current experiment attempted to test the second part of this model. If fishing pressure outside No-Take zones and the assemblages of animals there are representative of fishing activity and the assemblage in aesthetically pleasing estuaries, then it is likely that fishing depresses scavenging potential and alters the assemblage in those estuaries. Properly testing the first part of the model requires an extensive experiment covering a large spatial and temporal scale (McGlennon & Kinloch 1997). When faced with complex models, it is prudent to answer the more tractable, fundamental questions first (Fairweather 1999a). The first part of the model may be tested with data to be collected by the DPI&F recreational fishing survey planned for the future (L. Olyott, DPI&F, pers. comm.).

If fishing pressure in southeast Queensland does increase as EHI increases, it is unlikely that this relationship will be generally applicable across the entire state. Southeast Queensland is a large conurbation stretching almost continuously along 150 km of coastline. High densities of people are found throughout the region and a substantial network of roads and highways ensure that most estuaries can easily be
accessed by many thousands of people. In more remote places, including far north Queensland, estuaries may be isolated and accessible to far fewer people. In these remote places, fishing pressure may not be great enough to alter the assemblage sufficiently.
Chapter 7: General discussion

World human population now exceeds 6.5 billion people, an increase of more than 3.5 billion since 1950 (United Nations 2005). This explosive growth has subjected almost every ecosystem in the world to unprecedented anthropogenic disturbance such as over-harvesting, habitat modification, pollution and climate change (Foley et al. 2005). Within Australia, as elsewhere (Small & Nicholls 2003), urbanised coastal regions are experiencing tremendous population growth (Stimson & Minnery 1998, Australian Bureau of Statistics 2004). This growth stresses estuaries and coasts by changing hydrological and sedimentation regimes, altering nutrient and pollutant loadings, removing or fragmenting habitats, harvesting resources and increasing disturbance through recreational and industrial activities (Lee et al. 2006).

The aesthetic natural beauty and ecosystem services are two major attractions drawing people to the coast (Salt 2003). Boating and fishing in attractive and productive estuaries are examples of this. If the natural benefits of coastal living are to be conserved for current and future generations, then in places where population growth is fast, environmental management needs to be effective. Effective management requires that the management methodology be scientifically sound, and that its implementation or enforcement ensures that the method is applied.

Managers of ecosystems are better placed to develop scientifically sound policies and methods if they have sufficient knowledge of ecosystem function and the biology of the species within the estuaries. This knowledge extends from the biology of individual species to the rates and resilience of ecosystem processes. A biological example is recruitment mechanisms of mud crabs, and rate examples are scavenging and primary production.

Urbanised estuaries are often altered by activities such as the construction of marinas, canals, rock groynes, weirs and by dredging. Among other things, these structures and activities can fragment or destroy habitats, alter estuarine flows, and disturb the gradient and constituents of estuarine plumes (Bowen & Valiela 2001, Lee et al. 2006, Tu et al. 2007). Animals which use or interact with these habitats, flows or plumes during their recruitment process, are likely to face a novel set of conditions, potentially affecting the success of recruitment (Kingsford et al. 2002, Seitz et al.)
2006). For managers to assess the impact of such novel physical modifications, they need to understand the recruitment mechanisms of the species likely to be affected. Without the mechanistic knowledge, management is relying on observations from other places and hoping the effects will be similar. They are ‘best guessing’ when developing management methodology.

7.1 Part I: Mud crabs: recruitment and nursery grounds

7.1.1 The general model of colonising estuaries

Mud crab (*Scylla serrata*) larvae are pelagic, developing through 5 zoeal stages in offshore coastal waters before molting into postlarvae or megalopae (Hill 1994). In many crabs the megalopa is the transitional life stage between this pelagic existence and the more benthic life style of the true crab (Moser & Macintosh 2001, Bryars & Havenhand 2004, Lee et al. 2004). In several portunid species, the megalopae colonise shallow coastal habitats such as estuaries, before settling and moulting into crablets.

Whilst being relatively good swimmers for their size, megalopae are unable to swim against the currents commonly flowing out of estuaries (Chia et al. 1984). To colonise estuaries, many megalopae use selective tidal-stream transport to ride the flooding tidal currents and move from the coast into estuaries (Forward & Tankersley 2001). This general model has been developed by extensive studies of the blue crab (*Callinectes sapidus*) in the USA. It predicts that offshore, megalopae swim near the surface during the day and utilise currents generated by the daytime prevailing onshore winds, to prevent them from being swept away from the coast (Forward et al. 1997). This behaviour changes within estuaries. In estuaries, megalopae descend during the day and during ebb tides. The ebb tide current is reduced near the bottom due to drag forces. The complexity of the bottom also provides refuge from visual predators active in the estuary during daytime. During night time flooding tides, the megalopae rise into the water column to ride the flooding current further into the estuary and avoid visual predators. This rhythm works like a ratchet sweeping the megalopae upstream during the flooding tides and preventing them from being swept out of the estuary during the ebbing tides.

This model predicts that there are distinct changes in the vertical migration behaviour of megalopae in estuarine and offshore water in response to light.
Megalopae using selective tidal-stream transport should swim high in the water column during daytime in offshore water, however, in estuarine water, the model predicts that they will descend during daytime as a strategy to avoid visual predators.

7.1.2 Mud crab megalopae do not fit the selective tidal streaming model

The results from Chapter 2 show that mud crab megalopae do not conform to the general model of selective tidal-stream transport developed for the blue crab. The vertical migration behaviour of mud crab megalopae was similar in both offshore and estuarine water. My laboratory experiments showed that mud crab megalopae swam towards the surface when illuminated and descended when in darkness, irrespective of whether it was day or night, in both offshore and estuarine water.

Swimming near the surface in offshore water during the day will enable the megalopae to utilise the prevailing wind-driven onshore currents and remain near the coast and estuary entrances. This is consistent with the general blue crab model. Within estuarine water, however, mud crab megalopae still swam up into the water column when illuminated; their behaviour was no different. Swimming up in the estuarine water column when illuminated is inconsistent with the general model and likely exposes them to greater predation pressure than if they descended (Forward et al. 1997). This inconsistency might be understood if mud crab megalopae rarely enter estuaries. This may be the case as they are rarely caught in plankton nets or ‘hogs hair’ megalopae collectors, within estuaries at any depth or time of day (Moser & Macintosh 2001, J. Webley pers. obs.), however, other reasons such as spatial/temporal variability cannot be discounted before a rigorous recruitment monitoring program has been completed (van Montfrans et al. 1995). If they tend not to enter estuaries then they would not have been exposed to the selective pressures found within estuaries, for example a greater predation pressure. Consequently, they may not have evolved a beneficial response, and therefore maintain their offshore swimming behaviour in estuarine water. The experiment shows that the behaviour of mud crab megalopae is inconsistent with the general model developed for the blue crab.

Alternative explanations should be considered. It is possible that in estuaries, mud crab megalopae do swim near the surface during flooding tides and during the day, irrespective of the predation risk, but descend during ebb tides and at night.
Theoretically, this behaviour would allow mud crab megalopae to colonise estuaries using selective tidal-stream transport, but would expose them to visual predators within the estuaries. Superficially, this seems unlikely, but megalopae are themselves also predators. They have large eyes, powerful chelae, are cannibalistic and can catch live prey. They may swim up during the day and inhabit the illuminated surface waters where they can more easily see their prey. Although this is possible, it is unlikely to be the case, because mud crab megalopae are rarely caught within estuaries. The more parsimonious explanation is that they tend not to colonise estuaries but settle near the shore on the coastal shelf instead.

7.1.3 Megalopae do not exhibit selectivity among estuarine habitats whereas crablets do

Blue crab megalopae tend to select seagrass among other estuarine habitats and both the blue crab megalopae and crablets are associated with seagrass in the field (van Montfrans et al. 2003). Many other organisms settling from the plankton make choices among the habitats they could settle to (Leis et al. 2002, Stevens 2003, Lecchini et al. 2007). These choices are likely driven by evolutionary selective pressures. Often, settling organisms select habitats which are considered to provide refuge and food during this vulnerable life stage (Moksnes et al. 1998, Stevens & Swiney 2005). It is unlikely that all habitats commonly occurring within estuaries offer the same degree of refuge and food; to a particular species, some habitats are more beneficial than others. Habitats with a complex three dimensional structure, for example seagrass beds, offer greater refuge than more simple uniform habitats such as sand. If mud crab megalopae do regularly colonise estuaries before settling from the plankton, I expect that they would have evolved and exhibit a preference for one or more types of estuarine habitat. It is also reasonable to predict that the habitat preference of the megalopae and early stage crablets would be similar.

The experiments assessing habitat selectivity of mud crab megalopae and crablets (Chapter 3) rejected this model and showed that megalopae are not strongly selective among the commonly occurring estuarine habitats, seagrass, mud and sand, whereas crablets (CW < 30 mm) strongly selected seagrass. There are several plausible explanations for why megalopae have not evolved selectivity, but I consider the most likely to be that megalopae do not normally encounter these habitats and
therefore no selectivity has evolved. This explanation builds on the findings of the vertical migration experiment of Chapter 2, which supported the model that the megalopae do not colonise estuaries. The fact that crablets show a strong selection for structured habitat, in this case seagrass, is consistent with the behaviour of blue crab crablets. It suggests that for mud crabs it is the crablets which colonise estuaries, not megalopae.

Alternative explanations for the difference in preferences should also be considered. It is possible that megalopae prefer an estuarine habitat which was not presented in the experiment. The megalopae chose among seagrass, mud and sand, the commonly occurring subtidal habitat types found near entrances to estuaries in southeast Queensland. These habitats would be the initial habitats that megalopae and crablets encounter if they colonise estuaries from the coast. In southeast Queensland estuaries, habitats such as oyster beds and muddy mangroves tend to occur farther upstream. Mud crab megalopae are rarely caught in estuaries and if they do colonise them it is likely they settle near the mouth, so offering a choice of habitats which occur farther upstream seemed inappropriate. Further, if these upstream habitats were selected by the megalopae, then I would be unsure whether this was an artefact of the experiment, or whether megalopae do settle to these habitats but the previous fruitless searches for megalopae, by many researchers in many estuaries, were simply unfortunate anomalies.

Often, refuge is a major reason given for small animals to recruit to three-dimensional habitats (Moksnes et al. 2003, Stevens & Swiney 2005). Alternatively, small juvenile predators such as megalopae and crablets may recruit to three dimensional habitats because of the greater abundance of prey seeking refuge there, rather than for their own protection (Perkins-Visser et al. 1996). Likewise, there are significantly more predatory fish, many of them juveniles, which are associated with seagrass beds than with unvegetated habitats (Bloomfield & Gillanders 2005). It is unlikely that any single factor explains the reason for recruiting to structurally complex habitats; the reason is more likely a combination of the risks of predation and the benefits of the catchability of food. With the natural variability of ecosystems, at certain times the disadvantages of being eaten may outweigh the benefits of eating. However, for mud crab crablets to have a preference for a particular habitat, it is likely
the preferred habitat enhanced the fitness of their ancestors more than the non-preferred habitats did.

7.1.4 **Evolution of preferences and ecological traps**

Underlying the interpretation of this experiment is the concept that if a species prefers a particular habitat, then that habitat should enhance their survival because the behavioural preference has been selected for through the evolutionary process. This experiment does not test whether the preference is adaptive but assumes that it is, and my interpretation is open to theoretical criticism in this regard (Gould & Lewontin 1979). This is an important consideration for ecosystem managers of rapidly changing environments. Animals can exhibit maladaptive preferences and be caught in ecological traps (Schlaepfer et al. 2002, Robertson & Hutto 2006). There is a greater likelihood of ecological traps existing in places subject to rapid and enduring disturbance, for example estuaries and their catchments undergoing rapid human population growth. Examples of ecological traps created by anthropogenic disturbances include dragonflies mistaking polished black marble tombstones as the surfaces of ponds and spending time there trying to oviposit (Horvath et al. 2007). Another example is the American robin (*Turdus migratorius*), that nests in exotic shrubs with a branch structure similar to native shrubs, but the exotic shrubs lack thorns and nest sites are lower to the ground, increasing nest predation rates (Schmidt & Whelan 1999).

Similar traps could exist within estuaries. For example, crablets within estuaries which recruit to three-dimensional, complex habitats such as seagrass may be responding to the structure, but benefit from the abundant food found within it. If an invasive plant has similar three-dimensional structure (e.g. Caulerpa, Montefalcone et al. 2007, Wright et al. 2007), but the prey species of crablets are not associated with it, then there is a potential for a maladaptive preference. In this example of maladaptive preference, the cause, i.e. an invasive species, is likely to be noticed by managers. However, more subtle changes, for example alterations to the assemblages of predators, prey or competitors of recruiting crabs, could also alter the beneficial qualities of habitats and environments (e.g. Holker et al. 2007).
The potential for an ecological trap exists in places where changes occur faster than animals can evolve. A mismatch can develop between the behavioural preferences and fitness. Therefore, knowledge about the interactions of new recruits with their habitats and the organisms which live there is needed to effectively manage estuaries, especially those which are likely to have been recently altered or are under chronic pressure.

7.1.5 The coastal settlement model

Both the vertical migration experiment (Chapter 2) and the habitat selection experiment (Chapter 3) support what I call the coastal settlement model; for mud crabs, the megalopae settle near the shore on the coastal shelf and the crablets (CW < 30 mm) colonise the estuaries. After entering the estuaries the crablets recruit to seagrass or other habitats with a complex, three-dimensional structure. This coastal settlement model has similarities with the mechanism of estuarine colonisation described by Rothlisberg et al. (1995) for the penaeid, Penaeus plebejus. This prawn has a pelagic larval stage within the waters of the coastal shelf and exhibits a diel vertical migration behaviour. The post-larvae, however, switch to a tidal vertical migration behaviour in shallow water, remaining buried during the ebb tide and rising up into the water column during flooding tides regardless of the time of day. This behaviour causes them to accumulate near the coast where they ride the along-shore current near the surf zone and then, by chance, are swept into estuaries as they are washed across the mouth during a flooding tide. In this scenario, there is no necessity to sense an estuarine plume gradient or other chemical cues to locate estuary mouths (Rothlisberg et al. 1995).

I propose that for mud crabs, the megalopae tend to settle near the shore on the coast and metamorphose into crablets. The crablets, whilst staying close to the substratum into which they can bury when threatened, colonise estuaries sporadically by scurrying along the substratum, using along-shore currents and flooding tides to penetrate estuary mouths. Inside estuaries, they seek seagrass habitats where they reside for a short period of a few weeks to grow. They tend to leave the seagrass beds and journey farther upstream to muddy mangrove habitats, where they occur as juvenile crabs (CW > 30 mm) (Heasman 1980, J. Webley pers. obs.).
The validity of this basic model should be tested and, undoubtedly, will be refined. The estuarine colonisation part of the model can be tested by setting traps on the substratum in several estuary mouths across southeast Queensland. These traps should be able to capture crablets scurrying along the substratum and prevent them from being consumed by predators attracted to the traps. The sporadic sightings of mud crab crablets in the field suggests that their successful recruitment into estuaries is also likely to be sporadic. Therefore, these recruitment traps should be checked frequently, preferably daily, to generate the continuous data set to increase the probability of detecting sporadic and cryptic recruitment events (Metcalf et al. 1995, Forward et al. 2004). Simultaneously, a rigorous plankton survey should be completed within the mouths of estuaries to test the alternate model that megalopae do recruit to estuaries. If the abundance of mud crab megalopae is spatially and temporally variable, the survey must be extensive to provide enough data to justify a conclusion of absence. To develop a general model, this procedure would need to be maintained for several years to provide replicate seasons, perhaps as part of a long-term monitoring program.

### 7.2 Part II: The role of mud crabs in the ecosystem: neither engineer nor keystone

#### 7.2.1 Mud crabs: one of many scavengers in the estuary

My research has shown that mud crabs are the dominant but not the sole opportunistic scavenger within the estuaries of southeast Queensland. The video data of Chapters 5 and 6, together with the fact that fishers using carrion baits catch a broad range of species, shows that many other animals within these estuaries are opportunistic scavengers. The scavenging process effectively recycles and retains nutrients within food webs at higher trophic levels. If carrion was not scavenged, then the nutrients and energy bound up in it would decompose and fall to the bottom of food webs (Putman 1983). The opportunistic scavengers can, in turn, become food for other predators. For these reasons, carrion and the scavenging process can maintain larger populations of predators and omnivores than would otherwise exist (Wassenberg & Hill 1987, 1990, Rose & Polis 1998, DeVault et al. 2003).
7.2.2 *Scavenging potential and measuring ecosystem health*

The key components of ecosystem health or integrity are essentially its organisation, the vigour of its processes and its resilience to perturbation (Rapport 1998, Fairweather 1999a, Vugteveen et al. 2006, Thrush et al. 2008). Because of its implied subjectivity, scientists may never settle on an objective definition of ecosystem health, and in any case, the health of anything is assessed using a number of directly measured characters or processes. For example, human health is often assessed using many direct measures of physiological characters and processes such as blood pressure, liver function tests, and core temperature. In ecosystems we can measure ecosystem characters and processes, for example the assemblage of organisms and primary productivity. As our understanding of how ecosystems function develops, it is likely that these data will be used to judge whether an ecosystem is functioning within the bounds of what society considers ‘healthy’, i.e. a socially acceptable but variable state space (Walker et al. 2004).

Scavenging potential may be a useful measure of both the assemblage of potential scavengers and an ecosystem process. It is affected by two factors: (1) the assemblage of species, because some may have a greater propensity to scavenge than others, and (2) the degree of hunger or competition for food within this assemblage. Therefore, scavenging potential is affected by the organisation of the ecosystem and the vigour of trophic transfer processes within the ecosystem. Importantly, scavenging potential does not measure the natural occurrence of scavenging within an ecosystem. The natural rate is likely to be small and ecologically insignificant because carrion is rarely available (Britton & Morton 1994). Scavenging potential measures the propensity of animals to consume fresh carrion when available, which is determined in part by the vigour of competition for food, an ecosystem process. The research presented in Chapter 4 shows that measuring scavenging potential using carrion platters is technically and logistically practicable. Determining which species are scavenging is, to a large extent, dictated by the turbidity of the water and the quality of the images obtained from the BRUV cameras. The theoretical development of scavenging potential presented here, combined with my experimental evidence (Chapters 4, 5 and 6) and the practical simplicity of the method, suggest that
scavenging potential is a useful metric for incorporation into assessments of ecosystem health. Its efficacy should be examined further.

7.2.2.1 The need for reference regions

Determining the efficacy of scavenging potential as part of a comprehensive measure of ecosystem health monitoring requires ecologists to understand how the scavenging rate changes as the health of an ecosystem changes. This knowledge can be obtained by comparing scavenging rates in impacted systems with those of healthy or reference systems. What is considered to be a healthy system is a subjective decision and, depending on that definition, may or may not be congruent with a pristine system. In practice however, it is likely that managers will use the most natural or least disturbed places available as reference systems. The methodology for these comparisons will be similar to concepts developed for assessing restoration projects and environmental impacts (Underwood 1992, Stewart-Oaten & Bence 2001, Osenberg et al. 2006). The rates of ecosystem processes likely change through time (Stewart-Oaten & Bence 2001, Osenberg et al. 2006). Therefore, scavenging rates within impacted systems should be compared continually through time, to the scavenging rates within the representative benchmark or healthy systems. This presents potential logistical problems, the most overwhelming of which is that representative healthy systems may not be available.

Estuaries are often separated by tens of kilometres and the closest healthy systems may be a significant distance from the monitored systems. Therefore, comparisons may be spatially confounded and the healthy systems may not be representative of the monitored or impacted systems. Fortunately, in southeast Queensland waterways, several estuaries and bays are declared protected zones under the Marine Parks (Moreton Bay) Zoning Plan 1997. Protected zones are supposed to reduce anthropogenic disturbance by prohibiting extractive or damaging activities. This foresight in planning enables researchers to assess the impacts of the presence or absence of many anthropocentric activities. Comparisons can be made inside and outside these protected areas (e.g. Pillans et al. 2005 and the research presented here). Within an urbanised region, these protected places are potentially the best sites to determine the rates of processes within ‘healthy’ or less disturbed systems.
Some anthropocentric activities encompass large spatial scales, for example climate change or reduced estuarine flows under freshwater extraction. These wide ranging activities are likely to impact both protected and non-protected places within the region. Where representative, healthy systems are unavailable, managers have to ask: what is the appropriate rate that can be expected in such a place if it were healthy (Fairweather 1999a)? This is a difficult question to answer today, because our understanding of ecosystem processes and rates is limited. Without this ecological knowledge, or the representative ‘healthy’ reference systems, managers may have to choose to set a target using their ‘best guess’ (Pitcher 2001). This provides a rationale for establishing a network of places which are representative of the surrounding region and where anthropogenic impacts are limited, so that management and restoration methods can be assessed (Osenberg et al. 2006).

7.2.2.2 Combining abiotic and biotic characteristics of ecosystem health

Water quality is no doubt a component of estuarine ecosystem health and is measured in many ecosystem health monitoring programs (EHMP 2007, Haynes et al. 2007). Aspects of water quality such as clarity and cleanliness are important factors affecting people’s choices among waterways used for recreation (Ballance et al. 2000, Schramm et al. 2003). Because of the potential economic benefit recreational use of waterways provides local communities, water quality should be monitored and maintained (Ballance et al. 2000, Johnstone & Markandya 2006). Using only measures of water quality to gauge the health of an estuary, however, is analogous to measuring air quality to assess the health of a forest. Many other factors can also affect the health of an estuary.

For example, in San Francisco Bay, water quality and biological communities have been monitored for over twenty years (Cloern et al. 2007). The bay receives high loads of nutrient from wastewater treatment and agriculture, sufficient to maintain nutrient concentrations ten times greater than that required to limit algal growth. Phytoplankton blooms are minor, however, because of the physical (tidal and wind) characteristics of the bay, its turbidity, and a large abundance of filter feeding bivalves. In 1999, the biological communities began to change rapidly. The important changes were: an increase in the abundance of bivalve predators; a large reduction in the abundance of bivalves; an increase in the abundance of phytoplankton and new
seasonal blooms. Paradoxically, though, water quality continued to improve as wastewater treatment made further reductions in nutrient input into the bay. Cloern et al. (2007) propose that the shift was consistent with a trophic cascade, generated from exceptional recruitment of bivalve predators driven by a state change in the California Current System. This example demonstrates how the composition and function of coastal ecosystems can change in complex ways without corresponding changes to water quality. Similarly, invasive species may also alter ecosystems without affecting water quality by changing food webs or biodiversity, and in some cases inducing ecosystem phase shifts (Vander Zanden et al. 1999, Montefalcone et al. 2007).

In southeast Queensland estuaries, fishing may well be affecting ecosystem processes. Fishing with carrion baits does not directly affect water quality, but it does selectively remove organisms with a propensity to scavenge (Pitcher 2001). The research presented in Chapter 5 shows that across nine southeast Queensland estuaries, scavenging potential decreased as water quality increased. Chapter 6 showed that current fishing pressure is sufficient to reduce scavenging potential. Because recreational fishers prefer to fish in accessible, aesthetically pleasing places (Schramm et al. 2003), fishing pressure may be greater in those estuaries where water quality and naturalness is perceived to be better. Therefore, the selective removal of predators with a tendency to scavenge is likely greater in those estuaries with better water quality, leading to changes to the community, and potential changes to estuarine ecosystem health.

The scavenging model tested in Chapter 5 predicted that scavenging potential would be greater in places which are healthier. In places where fishing pressure is much less than throughout the conurbation of southeast Queensland, water quality may be a good indicator of estuarine health. In these places, for example in remote far north Queensland, scavenging potential may be positively correlated with water quality. This could be tested in several remote estuaries with different water quality.

Indices of water quality, such as the Ecosystem Health Index (EHI) used in southeast Queensland, are useful because they provide a quantitative metric which can be used to set management targets, such as the reduction of nutrient inputs or turbidity. Water quality relates to ecosystem health but will rarely be sufficient to predict ecosystem-wide changes. It can be enhanced, however, by incorporating additional
biotic measures of ecosystem organisation, vigour and resilience. Biotic measurements, such as benthic respiration and the assemblage of organisms, are recommended to be included in ecosystem health metrics for other environments, for example freshwater streams (Bunn & Davies 2000, Fellows et al. 2006). Biotic indices are beginning to be used in estuaries, too (e.g. Harrison & Whitfield 2004), and their utility in estuarine ecosystem health monitoring programs is worthy of further investigation.

7.2.2.3 A representative suite of ecosystem process rates

In cases where several independent factors affect an outcome, using just one factor to make predictions is inappropriate (Underwood 1997). Many processes occur within ecosystems, for example: pollination, predation, reproduction, primary production, respiration and scavenging (Bertness et al. 2001, Krebs 2001). Ecosystem vigour is a measure of the total function, productivity and throughput of the ecosystem (Costanza et al. 1998). All ecosystem processes consume or fix energy and therefore contribute to the net energy throughput of the ecosystem. The vigour of the ecosystem is a combination of them all. Many of these processes, however, are to some extent independent of each other, or can become decoupled over time. For example, in the earlier example of San Francisco Bay (Cloern et al. 2007), the phytoplankton growth rate was mostly in balance with its filtration rate by bivalves, but during 1999 these rates were decoupled. Measuring only one rate (e.g. the scavenging rate or the rate of primary production) may not provide a representative estimate of the vigour of the whole ecosystem. Just as the EHI in southeast Queensland is generated from a suite of water quality variables, measuring a suite of processes is preferable to measuring just one.

Scavenging potential incorporates several fundamental processes and characters of ecosystems. It is affected by the composition of the assemblage of all animals which scavenge, because some animals have a greater propensity to scavenge than others. It is also affected by the abundance of food and the abundance of organisms seeking to consume that food; i.e. it is driven by competition for food. Scavenging potential is therefore likely to be a useful ecosystem process to incorporate into an indicator of ecosystem health because it already encompasses two key characteristics of ecosystems, being the organisation and the vigour of ecosystems. Incorporating
scavenging potential with measures of other ecosystem processes, for example larval recruitment rates, would help to develop an index of ecosystem vigour. The combination of this index of vigour with current abiotic indices is an exciting prospect for estuarine ecosystem management and monitoring.

Choices about which metrics to monitor should be based on an understanding of how the ecosystem functions. Ideally, these choices should be supported by rigorously tested models of ecosystem function. Our current predictive ability is limited, but there is a need to manage society’s environmental impact. This is best done in an adaptive management framework where management changes are seen as experimental tests of hypotheses (Walters 1997, Gunderson 2000, Ewel et al. 2001).

7.3 Summary

The thesis has resulted in a new model of coastal settlement being proposed to explain how mud crabs colonise and recruit to estuaries. The coastal recruitment model has implications for conserving complex, three-dimensional habitats near estuarine mouths. The research completed here on the role of mud crabs within estuarine ecosystems has led to the development of a method to measure scavenging potential, and a recommendation that it be incorporated into an index of ecosystem vigour. It has also raised an important question about the efficacy of using water quality metrics as measures of ecosystem health in regions where fishing pressure significantly affects the assemblage of organisms.

These outcomes raise interesting future research topics in themselves. The mud crab coastal recruitment model should be further investigated, tested and refined. Investigating the relationship between scavenging potential and ecosystem health, both in aquatic and terrestrial environments, is exciting because scavenging potential is influenced by both the organisation of the assemblage and the degree of competition for food. When applied to estuaries, scavenging potential may reveal many aspects about their health and assist in managing them effectively.
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