RESPIRATORY, OSMOREGULATORY AND BEHAVIOURAL DETERMINANTS OF DISTRIBUTION OF TWO TROPICAL MARINE HERMIT CRABS

by

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ABSTRACT

The hermit crabs *Clibanarius taeniatus* (H. Milne Edwards, 1848) and *Clibanarius virescens* (Krauss, 1843) are common tropical species on the rocky intertidal shores of Queensland, Australia. This area is frequently hot and dry with temperatures in excess of 38°C. Sudden, heavy rains in river catchment and local coastal areas often result in flood events that dilute coastal waters, exposing hermit crabs to prolonged periods when salinity is as low as 14% seawater (SW), while extreme evaporation may result in tidepool concentrations of up to 125% SW. Such conditions in the intertidal area result in the combined stresses of fluctuating temperature, salinity and oxygen availability resulting in the need for physiological tolerances and/or behavioural changes.

In an attempt to determine if differences in the distribution of *C. virescens* and *C. taeniatus* on the shore could be related to differences in metabolic costs of physiological responses to changes in environmental conditions, oxygen consumption was measured in adults of both species exposed to one of 12 factorial temperature-salinity combinations for a period of six hours. Results only demonstrated a significant difference in metabolic responses between species at the acclimation salinity. At 100% SW *C. virescens* showed metabolic sensitivity to temperature, while *C. taeniatus* did not. This may indicate a greater tolerance of higher temperatures by *C. taeniatus*. The osmoregulatory ability of both hermit crab species was also investigated. Crabs were exposed to one of eight salinities at one of three temperatures over a period of seven hours. Haemolymph was sampled from each crab and its osmolarity compared with that of the medium to produce a profile of osmoregulation in seawater of various salinities. Results showed both species
to be hyperosmoregulators over the entire range of salinities tested (11 – 140% SW). However, there was no statistical difference between species in their ability to osmoregulate. Nor was any overall difference between species in haemolymph concentrations of sodium, potassium, calcium and magnesium found after prolonged exposure to a range of salinities.

Laboratory investigations into the survival of *C. virescens* and *C. taeniatus* when exposed to very low salinities (22% SW) over 27 – 72 hours at each of three temperatures (15, 25 and 35°C) demonstrated significant differences between the two species, with *C. taeniatus* surviving better at low salinities than *C. virescens*, particularly at 35°C. Experiments in the field also indicated that *C. taeniatus* has better tolerance to low salinity than *C. virescens*. Species caged for up to 48 hours in an estuarine environment survived equally well at 75 – 95% SW, but at 20 – 35% SW *C. taeniatus* survived significantly better than *C. virescens*. Taken together, these results indicate that *C. taeniatus* is able to tolerate lower salinities and perhaps higher temperatures, better than *C. virescens*. The greater survival of *C. taeniatus* in low salinities appears to be based, at least in part, on a greater tolerance of diluted body fluids rather than osmoregulatory ability.

It was hypothesised that differences in the tolerance of *C. virescens* and *C. taeniatus* to changes in environmental salinity and/or temperature may influence the geographical distribution of these species. As predicted, surveys of a large area of the Queensland rocky coast have demonstrated that there is a tendency for *C. taeniatus* to be found near areas of freshwater runoff (eg. estuaries), while *C. virescens* is more abundant on open coasts and islands. While interspecific competition does not appear to be a main
factor in the greater abundance of *C. virescens* on open coasts and islands, reasons why *C. taeniatus* is not more abundant at these sites remain unclear.

The ability of *C. taeniatus* and *C. virescens* to compete with each other for limited shells was investigated to determine if *C. virescens* was able to out-compete *C. taeniatus* and potentially exclude *C. taeniatus* from inhabiting open coast and island shores. In this preliminary experiment, it was shown that *C. virescens* was unable to acquire significantly more shells than *C. taeniatus* when species were compared weight for weight. It is therefore suggested that competition for shell resources is not likely to be a major factor in the low abundance of *C. taeniatus* on exposed intertidal sites.

Since there is good evidence that the distribution and abundance of *C. taeniatus* and *C. virescens* is influenced by freshwater, it is proposed that these species may be used as indicators of freshwater runoff and may be a cost efficient tool for monitoring the effects of changed environmental flows on coastal ecosystems.
1.0 **CHAPTER 1: GENERAL INTRODUCTION**

1.1 **Scope of Thesis**

This thesis is an investigation into the influence of differences in physiological tolerances to environmental conditions and competitive interactions, on the local and geographical distribution of two closely related species of tropical marine hermit crabs.

1.1.0 **General Hermit Crab Biogeography**

Among the decapod crustaceans in the class Malacostraca, is the infraorder Anomura (Jones and Morgan, 1994). As described by McLaughlin (1983) and McLaughlin and Holthuis (1985), the anomurans include the Paguroidea (hermit crabs) as one of four major taxa. According to Jones and Morgan (1994), Forest *et al.* (2000) and McLaughlin and Lemaitre (2001), the superfamilies Coenobitoidea and Paguroidea contain the families Coenobitidae, Pylochelidae, Diogenidae, Paguridae, Parapaguridae, Lithodidae and Pylojacquesidae.

Hermit crabs are unique among decapods. Since their abdomens are permanently soft they require an external form of body protection which is acquired by inhabiting various shelter, including empty gastropod shells. The Robber Crab, *Birgus latro* is one exception. Adults of this species have hardened abdomens which are tucked under the carapace and do not require the protection of gastropod shells (Jones and Morgan, 1994; Debelius, 1999). The diogenid *Cancellus* and the pagurids *Paguritta* and *Xylopagurus* also have abdomens that are well calcified.
Hermit crabs are found inhabiting coastal areas and coral reefs of temperate, sub-tropical and tropical regions as well as mangrove forests, sand beaches and mudflats worldwide. While a few species are semi-terrestrial (Birgus and Coenobita spp.), the majority are marine, existing primarily in intertidal and/or subtidal environments, although the genus Parapagurus are found at depths down to 5000 metres (R. Lemaitre, personal communication).

1.1.1 Feeding Habits of Hermit Crabs

Most species of hermit crabs are omnivorous, but there are differences in feeding processes among some species (Greenwood, 1972; Gerlach et al., 1976; Kunze and Anderson, 1979; Schembri, 1982a,b; Manjulatha and Babu, 1991). The majority are detritus feeders that scavenge opportunistically (Kunze and Anderson, 1979; Barnes, 1997a,b). Barnes (1997b) found that the semi-terrestrial hermit crab, Coenobita cavipes, used mangrove propagules and algae as principal food sources. When human excreta were present, however, more individuals of this species fed on it rather than on their usual sources of food. Other species are predators. On Christmas Island Birgus latro feeds on the gecarcinid crabs, Gecarcinidae natalis and Cardiosoma hirtipes which it stalks or digs up from shallow burrows (Greenaway, personal communication). On the island of Aldabra, however, B. latro is even known to prey on hatchling tortoises (Swingland, in Alexander, 1979).

Filtering material from the water is also an important mechanism of acquiring food for many species of hermit crabs (Greenwood, 1972; Gerlach et al., 1976; Kunze and Anderson, 1979; Schembri, 1982a,b; Manjulatha and Babu, 1991). In some species, the antennae are modified with two rows of plumose setae,
producing “feathered antennae” to allow a “cast-net” type of filter feeding that has being described by Boltt (1961), Greenwood (1972), Schuhmacher (1977) and Kunze and Anderson, (1979) as important in paguroids such as *Diogenes brevirostris*, *Paguritta harmsi* and *Pagurus setosus*. Schembri (1982a) has also described several species of hermit crabs from different habitats in New Zealand that supplement deposit feeding, predation and scavenging by filter feeding with their plumose antennae.

Hermit crabs can detect food odours, but are more attracted by odours of foods they have not recently eaten, which may ensure that they avoid nutritional deficiencies that might occur if they were reliant on a single food source (Thacker, 1996, 1998).

### 1.1.2 Longevity of Hermit Crabs

There are few published records on the life span of hermit crabs, but Lyla *et al.* (1998) reported the life span of *Clibanarius longitarsus* as being 4 years and Chace (1971) reports a male specimen of *Coenobita clypeatus* living 11 years.

### 1.2 The Rocky Intertidal Habitat

Rocky intertidal habitats have long been recognised as uniquely dynamic environments in which there are rapid and sometimes very large fluctuations in temperature, salinity and oxygen saturation. Tidepools in this habitat are often shallow and thus experience extremes in these physical factors making them difficult places in which to live (Meadows and Campbell, 1972; Moore, 1972;
Morton and Harper, 1995; Raffaelli and Hawkins, 1996), although some authors have proposed that tidepools themselves constitute a more stable environment than the areas of emersion around them (Metaxas and Scheibling, 1993). Underwood (1981) has even suggested that tidepools are not representative of an intertidal habitat since pool organisms do not experience emersion during low tide. Whether the fluxes in physico-chemical factors are greater on temperate or tropical shores is unclear since many studies have focused on only a few pools at a particular location (Klug, 1924; Truchot and Duhamel-Jouve, 1980; Morris and Taylor, 1983; Agnew and Taylor, 1986; Huggett and Griffiths, 1986; Chan, 2000), and the dynamics of tidepools themselves have received little attention in temperate areas and even less in the tropics (Huggett and Griffiths, 1986; see reviews by Brosnan, 1992; Metaxas and Scheibling, 1993 and Raffaelli and Hawkins, 1996).

Another consideration is that intertidal pools have been classified in a variety of ways by different authors (Ganning, 1971). For example, Levander (1900 in Ganning, 1971) classified pools in terms of their salinity, vegetation and distance from the sea. Gislén (1930 in Ganning, 1971) classified pools by position and defined the terms ‘supralittoral, littoral and sublittoral’. Forsman (1951 in Ganning, 1971) grouped pools according to their salinity and this grouping was modified by Ganning (1971) in his study of Swedish rockpools. Therefore, differences in the interpretations of intertidal community structure among studies are, in some cases, confounded by the different criteria used to define pool types and height on the shore (Underwood, 1992; Metaxas and Scheibling, 1993).

Despite the difficulty of comparing temperate and tropical intertidal regions, Moore (1972) has suggested that stress in the tropics is greater than in mid-latitudes
since temperatures are higher and salinities lower with a greater seasonal range in the tropics than in temperate regions. Moore also reported that in mid-latitudes, where the difference in the range between neap and spring tides is small, conditions in the intertidal remain relatively constant. In the tropics, however, the range between neap and spring tides is often high and intertidal conditions are much less stable. Moore (1972) concluded that tropical shores are more stressful than temperate or polar shores.

1.2.1 Temperature

On rocky shores, temperature stress is well recognised as a critical factor in the structuring of communities (Morris and Taylor, 1983; see also reviews by Little and Kitching, 1996 and Raffaelli and Hawkins, 1996; Bertness et al., 1999). Most work concerning rocky shore communities has been on temperate shores (see reviews by Hawkins et al., 1992 and Vadas and Elner, 1992).

In New Brunswick, Canada, Klugh (1924) measured temperature in six intertidal pools and found that it rose from 15 to 28.5°C in the uppermost one within 7.5 hours of exposure on a clear day. He concluded that temperature was the most limiting factor for epibenthic species inhabiting high shore pools.

A detailed study of both diurnal and seasonal variation in tidepool conditions was carried out by Morris and Taylor (1983) on the West coast of Scotland. They found that water temperature varied between 14.5 and 23°C over a 24 hour period and daily temperature ranges were much greater in summer than in winter. Over a year, temperatures in upper pools ranged between 0.5 and 25°C, more than twice the range recorded for near-shore seawater. In one of the few
attempts to establish the extent of within-pool variation of some physico-chemical factors, Morris and Taylor (1983) reported that warmer water almost always occurred at the bottom of the pool, most likely resulting from both surface cooling by wind and warming by surrounding rocks heated by the sun.

On a boulder beach in Scotland, Agnew and Taylor (1986) found little difference in temperatures between the upper and lower shore, although the latter had a generally lower temperature. On a 24 hour timescale they found that there was a relatively small range of temperature change (approximately 15 – 21°C) during low tide exposure during the day and that changes in temperature associated with the returning tide were also small. These authors, however, measured only one wet site at high shore and one at low shore.

In the sub-tropical conditions of Cape Peninsula, South Africa, Huggett and Griffiths (1986) measured temperature in four rock pools at different heights on the shore and found that high tide pools increased in temperature more rapidly than pools in successively lower regions of the shore. They also found that the temperature drop in all pools was very sudden when they were flooded by the returning tide. This was especially dramatic during spring tide periods when the temperature in high shore pools dropped from 28°C to 16°C within a few minutes.

On tropical shores of Hong Kong, Morton and Harper (1995) reported that both direct sun and conductive heat from rock surfaces increased temperatures in tidepools to more than 40°C. However, temperatures rapidly dropped to 15°C when pools received seaspray.

In India, Rao and Sundaram (1974) reported intertidal water temperatures in the Gulf of Mannar between 26 and 31°C and between 24.8 and 35.8°C in Palk
Bay. Rao and Sundaram suggested that the greater range in water temperatures at Palk Bay was due to the fact that the intertidal region there was more shallow than the Gulf of Mannar.

1.2.2 Salinity

When Klugh (1924) measured salinity in a high shore pool in New Brunswick, he found that immediately after the tide had retreated from the pool salinity was 28.13‰. After 7.5 hours of daylight exposure, however, salinity had only increased to 29.02‰, well within the regular range of seawater in that area. Unfortunately, Klugh made only two individual determinations from a single pool on a single day, so the generality of his conclusions are questionable.

In Scotland, Morris and Taylor (1983) found that tidepool salinity rarely fluctuated significantly during a 24 hour period, except during, or immediately after heavy rain at which time the salinity of near shore water was also reduced due to large volumes of freshwater runoff. They found no distinct seasonal variation, except that the annual minimum occurred in winter or early spring, corresponding to periods of maximal rainfall. Furthermore, these authors reported that tidepool dilution due to rain or freshwater runoff happened during approximately 50% of their 24 hour recording periods. From detailed transects carried out in the uppermost pool, Morris and Taylor (1983) reported vertical stratification, with a layer of low salinity water overlying a layer of higher salinity. Usually the low salinity layer was only 2-10mm deep, but increased after heavy rain. Drainage from other pools as well as mixing by the wind produced a pool of thoroughly mixed brackish water.
Salinity of a boulder shore on Millport Island, Scotland was reported by Agnew and Taylor (1986) to vary most during autumn and spring daily recordings when tidepools were diluted by fresh water run-off. Although both upper and lower sites had similar maximum and minimum salinities (approximately 10 – 38‰), the lower shore showed more seasonal variation.

Morritt and Williams (2000a) recorded salinities between 0.9 and 49.1‰ for tidepools of the high intertidal in Hong Kong and Morton and Harper (1995) reported measurements of 0 – 60‰ in pools of the same region.

Coates (1992) reported that salinity of the inshore waters of Keppel Bay, Australia ranged from 8.0 – 41.0‰ between April, 1989 and January, 1992. During this period, intertidal areas of the region were inundated by freshwater from local, seasonal flooding as well as irregular catchment scale flooding of the nearby Fitzroy River.

In the Gulf of Mannar, Rao and Sundaram (1974) reported salinities between 29.9 and 35‰ between October and January, but at Palk Bay the range of salinities was between 22.3 and 35.8‰ over the same time period. Although there were wide ranges of salinity recorded throughout the intertidal, Rao and Sundaram did not observe any well-defined differences in salinity between low and high tides.

1.2.3 Oxygen

The work of Truchot and Duhamel-Jouve (1980) in five tidepools on a north-western shore of France demonstrated a range of partial pressure of oxygen ($P_{O_2}$) from 577mmHg during daytime emersion to almost 0mmHg during the night.
On the West coast of Scotland, Morris and Taylor (1983) reported that when emersion occurred during the day, the partial pressure of oxygen in tidepools ranged from a minimum of approximately 40mmHg just before sunrise to a maximum of about 435mmHg by late afternoon. When tides returned to pools during the day, the authors recorded a rapid decline in P_{O_2} from 362mmHg to 150mmHg in 10 minutes. However, if immersion occurred near sunrise, there was a large and rapid increase in oxygen tension. Morris and Taylor (1983) also found that the daily ranges of oxygen tension were larger in the summer than in the winter. When samples were taken at different depths within a single pool during the day, measurements of P_{O_2} ranged from 68mmHg near the surface to more than 500mmHg at the bottom, or near the alga *Cladophora albida* during photosynthesis (Morris and Taylor, 1983).

Huggett and Griffiths (1986) reported that percent saturation of oxygen in pools at different shore heights varied, but a similar pattern occurred for all pools. Percent oxygen saturation was high (over 260) when low tide exposure occurred in the day, but during night time low tides, oxygen saturation was less than 20%. In Hong Kong, Chan (2000) also found that the oxygen levels in intertidal pools reached a maximum during daylight low tides and a minimum during night low tides.

Several authors have recognised that the processes determining these differences in tidepool oxygen are biological. By day, photosynthetic activity overrides respiration and high levels of oxygen accumulate, while at night, respiration depletes available oxygen (Truchot and Duhamel Jouve, 1980; Morris and Taylor, 1983; Metaxas and Scheibling, 1993; Raffaelli and Hawkins, 1996, Chan, 2000).
1.3 Physiological Responses of Hermit Crabs

Rapid fluxes in physico-chemical parameters on tropical intertidal shores may require adaptations to wide ranges of ambient conditions, especially temperature and salinity, in order to reduce the physiological costs of successfully inhabiting such a dynamic and stressful environment. Variations in physico-chemical factors are especially large in the intertidal zone. Organisms in this habitat must necessarily be more tolerant of some stresses, or at least be able to respond to them more rapidly than would be required subtidally (Davenport, 1972a; Meadows and Campbell, 1972).

It is generally believed that tropical marine organisms live at environmental temperatures much closer to their upper thermal limits than do temperate organisms and that respiratory rates of the former are generally higher than those of the latter when measured within the normal range of environmental temperatures experienced by the organisms in question (Moore, 1972; Johannes and Betzer, 1975). Consequently, Moore (1972) argued that not only are the tropic regions of higher stress than temperate ones, tropical marine species are generally less able to tolerate temperature changes than temperate species. Since the rates of most metabolic processes are correlated with each other, Johannes and Betzer (1975) assumed that metabolic processes, in general, are higher for tropical marine organisms than for comparable cold water ones. However, these authors are also quick to add that the paucity of data for tropical species has allowed little testing of this assumption.

The physiological responses of hermit crabs to changes in salinity (Davenport, 1972b; Shumway, 1978; Young, 1979b; Davenport et al., 1980; Sabourin and Stickle, 1980; Castillo et al., 1988), temperature (Burggren and
McMahon, 1981) and combinations of these factors (Young and Hazlett, 1978; Sherman and Eichrodt, 1982; Moreira and Nelson, 1990) have not received extensive study. This is especially true of the effects of acute changes in these parameters on physiological responses. In addition, some of these studies on combined effects have been undertaken on hermit crabs removed from their shells (Biggs and McDermott, 1973; Young, 1979a, 1980, 1991), possibly leading to erroneous indications of physiological capabilities (Sherman and Eichrodt, 1982). Since the majority of studies have been done in temperate regions, there are few investigations on the physiology and ecology of tropical hermit crabs.

1.4 Geographical Distribution

While factors affecting intertidal community organisation have received much attention, most research has tended to focus on sessile species such as algae, mussels and barnacles as important constituents of community structure (Endean et al., 1956; Underwood, 1981; Bertness and Callaway, 1994; Little and Kitching, 1996; Bertness and Leonard, 1997; Bertness et al., 1999; see also reviews by Connell, 1975; Hawkins et al., 1992; Vadas and Elner, 1992; Metaxas and Scheibling, 1993). However helpful this work is in constructing a framework for the interpretation of intertidal community organisation, it ignores major differences between sessile and highly motile organisms (Underwood, 1979). Underwood (1979) emphasised that the distribution of motile species may not, like sessile species, be set simply by the physiological limits to physical factors, since they may well respond to environmental factors by temporarily moving away from an area.
Connell (1975), Underwood (1979), Field and Griffiths (1991), Raffaelli and Hawkins (1996) and Barnes and Hughes (1999) have reviewed some of the factors affecting geographical patterns of distribution and abundance in intertidal organisms, including modes of reproduction, the influence of predators, competition and resources, and the consequences of morphology. While competitive interactions and the mode of reproduction may have an influence on distribution and an effect on abundance (Young and Hazlett, 1978; Underwood, 1979; Ajmal Khan and Natarajan, 1981b; Minchinton and Scheibling, 1991), the presence of predators and the natural selection of specific morphs potentially influence the actual presence or absence of a species in an area, and thus, the geographical distribution. In order to understand the processes influencing distribution and abundance, Underwood (1981) suggested that there is a need for well-documented observations from which hypotheses can be formulated and tested. He stated, however, that this background is lacking in the literature, especially for the shores of eastern Australia.

Many abiotic factors also influence the intertidal zone and its associated inshore waters. As well as affecting the vertical distribution of organisms on the shore (Connell, 1975; Underwood, 1979; Bertness, 1981a; Huggett and Griffiths, 1986; Russell, 1991; Little and Kitching, 1996), physico-chemical parameters may also have an important influence on the geographical distribution of rocky intertidal organisms (Endean et al., 1956; Meadows and Campbell, 1972), especially by influencing the dispersal, survival and settlement of invertebrate larvae (Crisp, 1976; Young and Hazlett, 1978; Ajmal Khan and Natarajan, 1981b).

While there has been much work on habitat selection by aquatic invertebrates in relation to both physico-chemical and biological factors, Meadows
and Campbell (1972) emphasise that very few studies give a complete picture of habitat preference of a species. Furthermore, few investigations integrate results of laboratory experiments with distribution in the field or with experiments carried out under field conditions. In addition, Meadows and Campbell state that little is known about any changes in physiology that are associated with intertidal invertebrates living in favourable, compared with less favourable habitats.

Despite numerous reports on the distribution of hermit crab species over local and large geographical areas (Grant and McCulloch, 1906; Ball and Haig, 1974; Haig and Ball, 1988; Morgan, 1987, 1989, 1990; Mather and Bennett, 1994; Richmond, 1997; Forest et al., 2000) the relationship between physiological responses of hermit crabs to environmental conditions and distribution has received very little attention, especially in reference to tropical species on a geographical scale.

1.5 The Behaviour of Hermit Crabs in Relation to Shells

Many investigations into hermit crab ecology have focused on aspects of behaviour relating to the acquisition and utilisation of shells.

Studies of hermit crabs in relation to shells have illustrated the complexity of behaviours during shell investigation (Reese, 1962, 1963; Vance, 1972a; Conover, 1978; Mesce, 1982, 1993a,b; Scully, 1986; Elwood, 1995; Barnes, 1997a; Elwood et al., 1998), shell exchange/fighting (Hazlett, 1970, 1996; Vance, 1972b; Absher et al., 2001) and in resource partitioning (Mitchell, 1975; Reddy and Bisewar, 1993; Rittschof et al., 1995; Gherardi and Nardone, 1997; Leite et al.,
1998; Turra et al., 1999; Bertini and Fransozo, 2000). The influence of shells on both intra- and interspecific population dynamics have also been a major focus of hermit crab studies (Grant, 1963; Fotheringham, 1976a; Kellogg, 1976; Spight, 1977; Bertness, 1980, 1981a,b; LaBarbera and Merz, 1992; Barnes, 1999; Turra and Leite, 1999; Barnes and De Grave, 2000; Mantelatto and Garcia, 2000). Many authors have proposed that when shells are in short supply they constitute a major limiting resource to populations of these crabs (Vance, 1972a; Fotheringham, 1976b; Kellogg, 1976; Bertness, 1980, 1981b). However, shell shortages may not necessarily occur. Abundant shells were found above high tide by Haas (1950, in Kellogg, 1976) in Bermuda and Hazlett (1970) in Hawaii, although these would only have been available to terrestrial hermit crabs. Nevertheless, Markham (1968), MacGinitie (1955, in Kellogg, 1976), Emmerson and Alexander (1986) Martinelli and Mantelatto (1999) and Leite et al. (1998) did record abundant shells below high tide mark in Denmark, Alaska, S. Africa and Brazil, respectively. Kellogg (1976) has argued that temporary shell surpluses due to gastropod and perhaps hermit crab mortality were to be expected in seasonal environments, but that the lack of shells, even during brief periods, may act to regulate the population of crabs.

1.6 Environmental Management

Extensive coastal development that has been characteristic of temperate regions, is now increasing in tropical regions around the globe, resulting in the convergence of population pressures, tourism and industrialisation in coastal areas (Johannes and Betzer, 1975; Vernberg, 1981b; Ward, 2000). An awareness of
environmental degradation has called for the integrated action of scientists, policy makers and the general public in many temperate regions. However, in the tropics, there has been far less research on the effects of coastal development on inshore ecosystems and the responses of intertidal communities to such large-scale and long-lasting changes.

Ward (2000) has suggested that biological indicators that track changes in environmental conditions are needed for large-scale reporting, and that the most important attribute of these indicators is that they be simple, direct and easy to interpret.

A variety of intertidal invertebrates have been extensively investigated as indicators of the presence and intensity of marine pollution (Reish, 1972). An increase in the abundance of the polychaete *Capitella capitata* has been shown to indicate pollution from domestic outfalls (Filice, 1954: Reish, 1959; Kitamori and Funae, 1959, 1960; Kitamori, 1963; Bellan, 1967). Imposex in marine gastropods is an indicator of the antifouling agent Tributyltin (Bright & Ellis, 1989; Stickle *et al.*, 1990; Nias, 1991; Nias *et al.*, 1993) and filter feeding oysters and mussels are often used as indicators of lipid soluble pollutants in the marine environment (Riedel *et al.*, 1995; Chen *et al.*, 1996; Al-Madfa *et al.*, 1998).

Intertidal hermit crabs are relatively easy to identify and sample in the field, and are common in coastal areas around the world. These factors make them useful organisms for use in monitoring changes occurring in intertidal conditions and community structures. As such, they constitute a valuable tool for managers responsible for the health of coastal environments.
It is therefore rather surprising, that scientific investigations into the use of hermit crabs as indicators of ecological health are limited to studies by Ismail et al. (1991) who used *Clibanarius* sp. as indicators of Pb, Cu, Cd and Zn in Malaysia and Lyla and Ajmal Khan (1996) who used the estuarine hermit crab, *Clibanarius longitarsus* as an indicator of changes in heavy metals (iron and manganese) in the Vellar estuary, India, over a period of one year. Lyla et al. (1998) are the only authors, to my knowledge, that propose the use of hermit crabs as test organisms for studying the effects of environmental consequences on estuarine inhabitants. To date however, no such studies have been done.

### 1.7 Thesis Aims

The general aim of this thesis is to determine if physiological tolerances to ecological stresses in tropical intertidal areas and behavioural differences between species act as factors in determining the distribution patterns of the marine hermit crabs, *Clibanarius taeniatus* (H. Milne Edwards, 1848) and *Clibanarius virescens* (Krauss, 1843) on both local and geographical spatial scales. The specific aims of this thesis are:

1) *to compare the physiological responses of both species to combinations of temperature and salinity representative of conditions in which they are found.*

This is done by determining and comparing the oxygen consumption of both species in various combinations of temperature and salinity. The osmoregulatory
abilities of these species are also determined and compared over a wide range of environmental salinities and temperatures.

2) to study and compare the survival of these hermit crabs in both normal and prolonged low salinity conditions.

Both species were exposed to low salinity in the laboratory to compare their ability to survive extended periods. The ability to regulate common ions was also investigated for differences between species. Translocation experiments were done to see if these species differed in their ability to survive both normal and low salinity in the field.

3) to investigate whether the distribution of these hermit crabs could be predicted on the basis of their physiology, salinity tolerance and the influence of freshwater onto coastal ecosystems.

A survey of the coast of Queensland, Australia was undertaken to determine the relative abundances of these species in relation to the influence of freshwater runoff on coastal ecosystems. Repeated sampling was carried out at two sites to compare relative abundances and to potentially track changes in the relative abundances of these crabs.

4) to investigate the use of these species as indicators of freshwater inundation on tropical shores.

The relative abundances of *C. taeniatus* and *C. virescens* in areas influenced by freshwater runoff are compared with the relative abundances of these species in
areas uninfluenced by freshwater to see if changes in intertidal communities due to freshwater inundation could be tracked by the use of these species of marine hermit crabs.

5) to determine if there were differences between species in their ability to secure limited shell resources.

Crabs were supplied with a limited number of shells to determine if one species could out-compete the other.

1.8 Respiratory, osmoregulatory and behavioural determinants of distribution of tropical marine hermit crabs.

This thesis discusses the role of tolerance of some environmental factors in the distribution of the tropical marine hermit crabs *Clibanarius taeniatus* and *Clibanarius virescens* on both local and geographical scales. Hypotheses about the influence of environmental conditions on physiology, survival, behaviour and distribution are proposed and tested.
2.0 **CHAPTER 2: LOCAL DISTRIBUTION**

2.1 **INTRODUCTION**

The tropical, intertidal hermit crabs, *Clibanarius taeniatus* (H. Milne Edwards, 1848) and *Clibanarius virescens* (Krauss, 1843) were identified on the basis of their morphology and colouration from taxonomic keys in Jones and Morgan (1994) and Tudge (1995). *C. taeniatus* has been recorded from Shark Bay in the north of Western Australia to Port Hacking, New South Wales (Morgan, 1990). *C. virescens* has been recorded from East Africa to Indonesia, Japan, east to Fiji Islands and from Geraldton, Western Australia to Port Jackson, New South Wales (Haig and Ball, 1988; Morgan, 1990; Richmond, 1997). *C. taeniatus* can be distinguished from *C. virescens* by its colour and a number of morphological differences. The most obvious are the colour and patterns of markings on the chelipeds and pereopods which are clearly visible when these crabs emerge from their shells. Full descriptions of the colouration of both *C. taeniatus* and *C. virescens* are given in Morgan (1987).

Initial qualitative observations were made at S. Cooee Bay and Emu Point in the Keppel Bay region of Queensland where both *C. taeniatus* and *C. virescens* were abundant on the rocky intertidal. When observations were made on days during neap tide when low water levels did not drop below approximately 1.3 metres above datum (Anonymous, 1998a – 2001), *C. virescens* was more difficult to find. This initial observation suggested that a difference existed in the vertical distribution of the two species. Therefore, I decided to quantify their distribution in relation to
shore height at three rocky intertidal sites within Keppel Bay; S. Cooee Bay, Emu Point and Fisherman’s Beach (see Figure 2.1).

2.2 MATERIALS AND METHODS

2.2.1 Local Environmental Conditions

For each site, a brief, overall description was recorded, together with a description of the substratum at each shore height.

2.2.2 Local (Small Scale) Distribution

Rocky intertidal sites were inspected for the distributions of *C. taeniatus* and *C. virescens* between November, 1997 and June, 1999. While I have devised my own scheme of shore height divisions, not unlike others discussed in Section 1.2 (page 4), I have also carefully defined each one. Each site was divided into three transects (Low Shore (LS); Mid Shore (MS); High Shore (HS)) that were approximately equal in vertical width and parallel to the water’s edge. These shore heights were defined in the following manner: LS = Mean Low Water Springs up to Mean Low Water Neaps; MS = Mean Low Water Neaps up to Mean Sea Level; HS = Mean Sea Level up to Mean High Water Springs.

Ten tidepools were randomly selected along each transect and a total of 15 animals counted from within or around (i.e. within roughly one metre) each pool and recorded. Data from surveys on three separate occasions were combined. From these counts, relative abundances were calculated to give a profile of the distribution of
Figure 2.1  Three sites along the Keppel Bay coast at which surveys for the local distribution of *C. taeniatu*us and *C. virescens* on the shore were done. A = S. Cooee Bay; B = Emu Point; C = Fisherman’s Beach. Inset shows geographical location of Keppel Bay area.
both species at each site. Only hermit crabs that were readily visible were counted, so I cannot present estimations of the presence or absence of individuals that may have been beneath rocks or in crevices.

2.2.3 Physico-Chemical Characteristics

Measurements of physico-chemical parameters of tidepool waters were taken throughout the intertidal zone at all three sites during daytime low tides. Temperature and salinity were measured with a TPS WP84 salinity/temperature meter, but were not recorded throughout the study period, so data presented for each site were collected within only a single month. Temperature and salinity were analysed separately for each site by one way ANOVA’s for “Shore Height” followed by post-hoc Tukey pairwise comparisons.

Salinity and temperature data from the three sites were combined and analysed by a Pearson correlation to determine if the salinity of tidepool water varied together with tidepool temperature.

The percent oxygen saturation of randomly chosen tidepools at S. Cooee Bay was measured with a TPS 90D DO₂ dissolved oxygen meter during both day and night low tides. Paired measurements of night and day percent saturations for each pool were analysed by a two way ANOVA without replication. Differences between LS and HS measurements were analysed by one way ANOVA.

The significance level for all statistical analyses was set at 0.05.
2.2.4 Observations on Activity

The activities of *C. taeniatus* and *C. virescens* in and around tidepools at the three survey sites were observed and irregularly recorded. Some interesting behaviours, although recorded only qualitatively, are presented in this chapter. Some aspects of the activity of “Posing” (described in Section 2.3.4) were quantified and measurements of this behaviour were statistically analysed by Chi-square 2×2 contingency table in relation to parasitic infestation. In addition, individuals were collected from random tidepools along unmarked transects at the three shore heights (LS, MS, HS) on one occasion in September, 1999 at S. Cooee Bay and one occasion during the same month at Emu Point. The species of shell occupied by individuals found in tidepools (“In”), out of tidepools (but within an area of approximately 0.5m) (“Out”), and those posing (“Posing”) were identified, counted and totalled for each site.

Shell species were identified on the basis of morphological features from keys in Hinton (1978), Short and Potter (1987) and Davey (1998).

2.3 RESULTS

2.3.1 Local Environmental Conditions

The topography and substrate composition of the intertidal zones differed among sites. As a result, the physical dimensions of tidepools were extremely variable, not only among, but within sites (see Table 2.1). Most tidepools at HS had solid rock as the main substrate. At MS and LS, however, tidepool substratum varied
<table>
<thead>
<tr>
<th>Site Name</th>
<th>Latitude, Longitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>S. Cooee Bay</td>
<td>S23°08.5', E150°45.7'</td>
</tr>
<tr>
<td>Emu Point</td>
<td>S23°15.5', E150°50.0'</td>
</tr>
<tr>
<td>Fisherman’s Bch</td>
<td>S23°06.4', E150°45.3'</td>
</tr>
</tbody>
</table>

**Low Shore**
- Medium to small, unstable stones on solid and sand substrates. Many small, shallow pools. Rocks provide many refugia and cover from exposure to sun. Many algae present.

**Mid Shore**
- Large boulders on solid rock give way to medium to small boulders. Pools are deeper with rocks producing many refugia and cover from exposure to sun. Some algae present.

**High Shore**
- Low-lying solid rock platform gives way to large boulders. Shallow, medium to large pools. Pools are highly exposed to sun. Little algae.

**LOCAL DISTRIBUTION**

Table 2.1: Brief descriptions of substrate and pool type for three shore heights at sites in Keppel Bay where *C. taeniatus* and *C. virescens* were found.
between solid rock, sand-covered rock, and soft sand depressions surrounded by small to medium sized boulders near the water’s edge. Often the cleft in a single boulder formed a small tidepool in which crabs could be found.

### 2.3.2 Local (Small Scale) Distribution

Surveys of the three sites in Keppel Bay revealed local, small-scale differences in distribution patterns for the hermit crabs *C. taeniatus* and *C. virescens*. In Figure 2.2A, combined results from three surveys are presented as relative abundances for both species at each height on the shore at S. Cooee Bay. It can be seen that *C. taeniatus* was very abundant at LS, MS and HS. *C. virescens* was present at all shore heights, but only three individuals were counted at HS giving a relative abundance of less than 4% there. The results of these surveys suggested that *C. virescens* were very uncommon on the HS region of S. Cooee Bay.

Results of surveys carried out at Emu Point (Figure 2.2B) showed that *C. taeniatus* was abundant at all three shore heights. While many *C. virescens* were found at LS, very few were found at MS and only four individuals were seen throughout HS transects, representing less than 2% of hermit crabs at that height. At Emu Point, *C. virescens* was extremely rare at HS.

At Fisherman’s Beach (Figure 2.2C) *C. taeniatus* was very abundant at LS, MS and HS. The abundance of *C. virescens* at LS was moderate, but only six individuals were counted at MS and none were found at HS. These surveys provided evidence that *C. virescens* was not a common inhabitant of HS at Fisherman’s Beach.
Figure 2.2 Relative abundances (%) of *C. taeniatus* (■) and *C. virescens* (□) along transects at three shore heights (low shore, mid shore and high shore) at A: S. Cooee Bay, B: Emu Point and C: Fisherman’s Beach.
Results of surveys at the three sites demonstrated that *C. taeniatus* was highly abundant at all shore heights, while *C. virescens* was found mainly at MS and LS.

Throughout the intertidal zones at the three sites, both species were found in tidepools that varied in depth and substratum. *C. taeniatus* occupied available microhabitats, as previously defined, and was even found in exposed tide pools at the extreme upper reaches of HS transects. Even where physical features of the shore were very inconsistent from LS to HS, *C. taeniatus* was common at all levels irrespective of whether tidepools were shaded, sheltered from the wind by surrounding rocks, or fully exposed to sun and wind. Although *C. virescens* was mainly found at or below MS, individuals also occupied a variety of microhabitats in terms of substrate and topography.

### 2.3.3 Physico-Chemical Characteristics

Figure 2.3A shows the mean tidepool temperature at each shore height at S. Cooee Bay during March, 2001. No difference in temperature was found between shore heights (one way ANOVA, F$_{2,57}$=0.568, P>0.05). Tidepool temperatures were the most variable at LS, measuring between 28.9 and 32.8°C.

In Figure 2.3B, the means of 20 independent measurements of salinity at each height on the shore at S. Cooee Bay are shown. Salinity was significantly different among tidepools at different heights on the shore (one way ANOVA, F$_{2,57}$=17.592, P<0.001). Analyses by post-hoc, Tukey pairwise comparisons between shore heights showed LS tidepool salinity to be no different than MS, but these were both significantly lower than tidepool salinity at HS (P<0.01).
Figure 2.3  A: Temperature (°C) and B: salinity (ppK) of tidepools in relation to shore height at S. Cooee Bay. For each shore height, n=20. Means ± 1 standard error are shown. Data were collected during March, 2001.
In Figure 2.4A, the mean temperature during April for each shore height at Emu Point is graphically presented. Tidepool temperatures differed significantly among shore heights (one way ANOVA, $F_{2,102}=7.468$, $P<0.05$). Post-hoc, Tukey analyses showed that temperatures were not different between MS and LS pools, nor between MS and HS pools, but LS pools were significantly cooler than those at HS.

At Emu Point, significant salinity differences occurred among shore heights (one way ANOVA, $F_{2,102}=38.141$, $P<0.001$) (Figure 2.4B) and Tukey comparisons showed significant differences between all three shore heights.

When data from Fisherman’s Beach for April were analysed, significant differences in water temperature were found at different shore heights (one way ANOVA, $F_{2,87}=12.141$, $P<0.001$). Tukey comparisons showed no difference between LS and MS tidepools, but a significant difference in water temperature between these heights and HS tidepools ($P<0.001$). These differences can be seen in Figure 2.5A.

Figure 2.5B shows that a significant difference in salinity also occurred at different heights at Fisherman’s Beach (one way ANOVA, $F_{2,87}=31.492$, $P<0.001$). Pairwise comparisons showed no difference between tidepools at LS and MS, but significant differences between salinity at these heights and HS ($P<0.001$).

A scatterplot of combined data for salinity against temperature is shown in Figure 2.6. A significantly positive correlation existed between tidepool salinity and water temperature (Pearson = 0.452, $P<0.001$).

Percent oxygen saturation measurements of tidepool water were compared between day and night. These findings are divided into data for low shore and high shore pools in Figure 2.7. The percent oxygen saturation of tidepool water during
Figure 2.4  A: Temperature (°C) and B: salinity (ppK) of tidepools in relation to shore height at Emu Point. For each shore height, n=35. Means ± 1 standard error are shown. Data were collected during April, 2001.
Figure 2.5  **A**: Temperature (°C) and **B**: salinity (ppK) of tidepools in relation to shore height at Fisherman’s Beach. For each shore height, n=30. Means ± 1 standard error are shown. Data were collected during April, 2001.
Figure 26 Scatterplot of tidepool salinity (ppk) and water temperature (°C). Data from S. Coce Bay, Emu Point and Fisherman’s Beach were combined.
daytime low tide ranged between 30.6 and 296.9%, but only ranged from 3.4 to 70.5% at night. It can be seen in Figure 2.7 that, in general, those tidepools with the highest percent oxygen saturation readings during the day had the lowest relative readings at night. These data suggested that differences between day and night oxygen saturations were related to the amount of algae in the pools. Differences between day and night percent oxygen saturation in pools were found to be highly significant (two way ANOVA without replication, $F_{1,11} = 22.602, P<0.01$).

Despite differences in abiotic and biotic factors, there was no significant difference in percent oxygen saturation of tidepools between LS and HS (one way ANOVA, $F_{1,10}=1.756, P>0.05$).

2.3.4 Observations on Activity

Many hermit crabs were found in tidepools within which there was either macro or micro algae. Both species of crabs were active throughout several hours of observation, despite full exposure to sunlight and air temperatures in excess of 34°C. During low tide, these crabs were seen grazing algae off rock and sand substrates in tidepools. Some inter- and intraspecific shell fighting was also observed, although this did not occur frequently.

Individuals of both species were seen leaving tidepools and walking as far as four metres on sandy substrate. Upon encountering nearby tidepools, some crabs entered these, while others bypassed pools and came to rest on open sand areas. These individuals would then withdraw into their shells and remain exposed to direct sun for several hours.
Figure 2.7: Comparison of percent oxygen saturation within a random selection of tidepools at low shore (LS) and high shore (HS) at S. Cooee Bay during the day (o) and night (■). Each set of paired histograms represents one tidepool.
Another activity observed and recorded on many occasions was that crabs climbed out of tidepools and onto rocks that were fully exposed to sun and breeze (Figure 2.8A). While individuals were right side up, they pushed their shells posteriorly so that the apertures were facing upward (Figure 2.8B). Once balanced, these crabs would slowly retreat into their shells, leaving them in what I call a “posing” position (Figure 2.8C). Posing was observed in both scattered individuals and within aggregations during the day and at night.

In Figures 2.9A and B the number of hermit crabs found in tidepools (“In”), out of tidepools, but not posing (“Out”) and “Posing” are shown according to shell type during a single collection event at both S. Cooee Bay (Figure 2.9A) and Emu Point (Figure 2.9B). It can be seen that at S. Cooee Bay the highest number of crabs posing were in shells of Clypeomorus petrosa and Planaxis sulcatus followed by Cronia sp., Lunella cinerea and Austrocochlea spp. Very few crabs in Monodonta labio shells were found posing during this collection. The proportion of shell types used by posers and non-posers at S. Cooee Bay was significantly different ($\chi^2 = 17.274, \text{df} = 5, P<0.01$). Of the three shell types in which most posers were found, the proportion of posers to non-posers was less in Planaxis sulcatus and greater in both Clypeomorus petrosa and Cronia sp. Although there was a smaller proportion of posers in Austrocochlea spp., there was a larger proportion in shells of Lunella cinerea and Monodonta labio.

At Emu Point, the largest numbers of crabs were also found posing in the same three shell species as at S. Cooee Bay although the order was slightly different: Clypeomorus petrosa, Cronia sp. and Planaxis sulcatus. The number of individuals posing in shells of Austrocochlea spp. was less than that in
Figure 2.8. "Posing" behaviour observed in both C. taeniatus and C. virescens. A: Hermit crabs climb out of tidepools and onto exposed rock. B: By pushing backwards with the pereopods, the aperture of the shell is rotated back and upward. C: When the shell has been balanced with the aperture up, the crab withdraws into the shell (sometimes, the crab does not withdraw completely and the pereopods remain visible).
Figure 2.9  The number of hermit crabs found in tidepools (“In”) ( ■ ), out of tidepools, but not posing (“Out”) ( □ ) and “Posing” (■) in shells types commonly inhabited by hermit crabs at A: S. Cooee Bay and B: Emu Point. Shells are identified as Aust: Austrocochlea; Mono: Monodonta; Plan: Planaxis; Clype: Clypeomorus; Cron: Cronia; Lune: Lunella; Neri: Nerita; Thai: Thais; Bemb: Bembicium.
Planaxis sulcatus shells followed by Monodonta labio, Thais spp., Lunella cinerea and Bembicium spp. No crabs were found posing in Nerita spp. shells. Posers and non-posers at Emu Point also used a significantly different proportion of shells ($\chi^2 = 101.257, \text{df} = 8, P<0.001$). The proportion of posers in the three main shell types was, again, smaller for Planaxis sulcatus and greater for Clypeomorus petrosa and Cronia sp. There was a smaller proportion of posers to non-posers in each of the remaining six shell types in which hermit crabs were found at this site.

The abdominal ectoparasitic bopyrid isopod, Pseudostegias setoensis was found on both C. taeniatus and C. virescens (Dunbar and Coates, 2000) and it was thought that posing may be related to parasite infestation. However, when the occurrence of parasites on posing crabs was compared to crabs not posing, no significant difference was found ($\chi^2 = 0.963, P > 0.05$)

2.4 DISCUSSION

2.4.1 Local Environmental Conditions

The abiotic conditions at the sites surveyed are a result of several environmental factors. The presence of several reefs and islands very close to shore protect intertidal areas along Keppel Bay from severe wave action, so the surf in this region is not consistently heavy (Endean et al., 1956). The relatively wide, shallow-sloping shores, especially at S. Cooee Bay and Fisherman’s Beach, result in HS exposure times that can exceed 10 hours.
The proximity to the Fitzroy River and prevailing near-shore currents combine to result in the deposition of sediments into Keppel Bay. Consequently, the water near the shore is very often turbid (although this was not measured during my study).

Quantitative measurements of the amounts of algae present in tidepools at the survey sites were not taken, and I did not identify algal species. However, it was observed that some micro algae were present in HS tidepools, but very little macro algae could be found at this height. More macro algae were apparent at MS and LS (see Table 2.1). It is interesting to note, and consistent with proximity to supra intertidal vegetation, that decaying plant matter was also seen in some tidepools at HS.

2.4.2 Local (Small Scale) Distribution

The zonation of many intertidal invertebrates has been investigated in relation to their abilities to tolerate increased emersion and higher temperatures with increasing height on the shore (Southward, 1958; Newell, 1969; Russell, 1991; Stillman & Somero, 1996). In tropical, rocky intertidal environments, the ability of shore dwelling invertebrates to withstand long exposure to high temperature may be especially important. Indeed, I recorded water temperatures as high as 42°C in some high shore pools.

Results of surveys in the Keppel Bay region showed a difference in the local distribution of these two species of hermit crabs on the shore. *C. taeniatus* was consistently found throughout transects at all shore heights at the three sites. At the
same sites, *C. virescens* was rarely found along HS transects, but consistently found in MS and LS transects.

### 2.4.3 Physico-Chemical Characteristics

During the summer months, extreme air temperatures may be in excess of 42°C (Endean *et al*., 1956), causing the rapid evaporation of tidepool water and an increase in tidepool salinity. In my study, it was demonstrated that tidepools at HS had a significantly higher salinity than MS and LS tidepools, even at times of the year when water temperature did not necessarily differ in relation to height on the shore. Another factor causing increased salinity is surface evaporation due to wind. Since HS pools are exposed to winds for longer periods than pools at LS, surface evaporation may cause a greater increase in salinity at HS than at LS.

Low salinity is also an important factor in tidepools, particularly at HS and may occur due to either local ground run off, or direct dilution by rainwater. I recorded salinities between 1.4 – 16.0‰ in the high intertidal during a rainstorm and Morritt and Williams (2000a) found that the salinity of upper shore rock pools in Hong Kong was less than 2‰ after a rainfall.

Hyperoxia in tidepools has previously been reported (Truchot and Duhamel-Jouve, 1980; Agnew and Taylor, 1986; Huggett and Griffiths, 1986; Metaxas and Scheibling, 1993) and occurs as a result of the production of oxygen from algae undergoing photosynthesis during daylight hours. Results from measurements of percent oxygen saturation of tidepools at S. Cooee Bay demonstrated extremely hyperoxic conditions during the day, while the same tidepools demonstrated severely hypoxic conditions at night. Hugget and Griffiths (1986) also reported
depressed values of oxygen in tidepools at night, as did Truchot and Jouve-Duhamel (1980), the latter especially at night in warm weather. Very low levels of percent oxygen saturation in tidepools at night most likely result from decreased photosynthetic activity and increased respiratory activity by tidepool algae (Truchot and Duhamel-Jouve, 1980). This may affect the inhabitation of tidepools by hermit crabs at night (although this remains to be studied). Decaying terrestrial vegetation may be a factor that results in hypoxia in tidepools during the day. Nevertheless, hyperoxic and hypoxic conditions may not, necessarily, act as stress factors. During periods of high temperature when oxygen demand is greatest, uptake is made less severe by the fact that in tidepools, high temperatures coincide with periods of hyperoxia (Morris and Taylor, 1983). In contrast, hypoxia is associated with the lowest temperatures of the day and, consequently, with reduced oxygen demand (Morris, 1991). I found no relationship between percent oxygen saturation and position of tidepool on the shore. Therefore, oxygen saturation is not likely to be a factor determining the distribution of *C. taeniatus* and *C. virescens* on the shore.

### 2.4.4 Observations on Activity

During low tides hermit crabs have been seen clustering (Snyder-Conn, 1981; Gherardi, 1990; Gherardi and Vannini, 1993; Leite *et al.*, 1998), migrating and digging (Vannini, 1975, 1976; Barnes, 1997a), feeding (Barnes, 1997a), engaged in shell investigation and exchange (Snyder-Conn, 1981; Barnes, 1997a) and what I have called “posing”, also observed by Reese (1969); Ball and Haig (1974); Snyder-Conn (1981); Gherardi and Nardone (1997); Leite *et al.* (1998); Bertini and Fransozo (2000) and Turra and Leite (2000).
Both *C. taeniatus* and *C. virescens* were active throughout the low tide period of the day and activities ranged from feeding and fighting for shells to migrating and posing individually and in aggregations.

Reese (1969) observed *Calcinus laevimanus* and *Clibanarius corallinus* posing (he called it the “aperture-up position”) on tidal reef flats in the Marshall Islands and proposed that it allowed the crabs to control evaporation and desiccation. Reese suggested that by completely withdrawing into the shell during the day and partially withdrawing during night time low tides, crabs could control their temperature and the rate of desiccation. However, Reese did not quantitatively investigate the phenomenon. Snyder-Conn (1981) observed *Clibanarius digueti* posing in the Gulf of California throughout the entire low tide duration, adding that this behaviour was hard to explain by the desiccation hypothesis by Reese (1969) unless evaporative cooling was involved. Snyder-Conn tested the ability of isolated hermit crabs and those within clusters to survive desiccation in open petri dishes embedded in a sand plot for up to 21 hours at an exposure temperature of 26.0 ± 4°C and relative humidity of 50%. She found that up to 15 hours, there was a significantly better survival of clustered individuals versus isolated individuals. Snyder-Conn did not, however, indicate whether any individuals (clustered or isolated) were posing during her investigation. Gherardi and Vannini (1993) found that some scattered individual *Clibanarius laevimanus* would pose (“sunbathe”) when exposed to the sun. However, they also found this behaviour difficult to explain in the context of the dehydration reduction hypothesis proposed by Reese (1969). Unfortunately, Gherardi and Vannini (1993) also did not explicitly state whether they observed clustered individuals posing. Turra and Leite (2000)
observed *C. antillensis* posing on cobble/boulder shores at São Sabastião, Brazil and assumed that this position resulted in a “higher retention of water inside the shell as suggested by Reese (1969)”, but neither they, nor Reese (1969) present any data for water retention in shells. So, while the “aperture-up” position has raised many questions, work initiated in this thesis is the first to quantitatively investigate the behaviour.

Single surveys at S. Cooee Bay and Emu Point demonstrated that of all the shell species utilised by crabs in these locations the greatest proportion of individuals posed in *Clypeomorus petrosa*, followed by *Cronia* sp., then *Planaxis sulcatus* shells.

There was no evidence that posing was related to tidepool conditions since some crabs from the same pool posed, while others continued normal activity within the pool. There was also no evidence that parasitism by *Pseudostegias setoensis* caused hermit crabs of either species to pose.

Although Newell (1969) reported that during summer months, upper shore invertebrates showed a suppression of activity compared with lower shore individuals, my unquantified observations did not reveal a difference in activity in relation to shore height. Furthermore, activities did not appear to be restricted to any particular height on the shore (although “posing” generally occurred at MS or LS), so it is unlikely that these activities determine the difference in local distributions of *C. taeniatus* and *C. virescens*, although they may contribute to maintaining a difference. The subject of interspecific competition for shells will be discussed further in Chapter 6.
2.5 Discussion Summary

Initial observations and subsequent surveys at S. Cooee Bay, Emu Point and Fisherman’s Beach showed that the local distribution of *C. taeniatus* and *C. virescens* differed in relation to height on the shore. *C. taeniatus* was abundant at HS, MS and LS, while *C. virescens* was very rare at HS, but consistently found at MS and LS.

There are differences in topography both among and within sites. Therefore, there was no evidence to suggest that the difference in distribution between species was solely attributable to physical features of the shore.

No inter- or intraspecific differences in the amount or type of activities related to height on the shore were apparent. The only exception was the activity of posing which was never observed at HS. However, it must be emphasised that quantitative data were not collected on activities, other than some aspects of posing, so statistical analyses were not performed on most behaviours. Data from one survey at S. Cooee Bay and another at Emu Point suggested that the proportion of shell types used by posers and non-posers was significantly different. The largest proportion of individuals posed in *Clypeomorus petrosa* and *Cronia* sp. shells at both sites. Posing, therefore, does not simply reflect shell occupancy. In addition, posing was found to be unrelated to infestation by the ectoparasite *Pseudostegias setoensis*. The qualitative information gathered gave no evidence for a direct relationship between activity and differences in distribution between these species.

Other studies have shown that temperature and/or salinity are frequently correlated with height on the shore (see review by Metaxas and Scheibling, 1993). In addition, I found that temperature and salinity at S. Cooee Bay, Emu Point and
Fisherman’s Beach differed at different heights on the shore. Therefore, I proposed that *C. taeniatus* and *C. virescens* would have different respiratory and/or osmoregulatory responses to acute changes in temperature and salinity of the medium. Furthermore, I proposed that differences in physiological responses could be related to differences in local distribution of these species. Investigations into the physiological responses of both species to changes in combinations of temperature and salinity may provide clues to factors influencing their local distribution. These investigations are addressed in the following chapter.
3.0 **CHAPTER 3: PHYSIOLOGICAL RESPONSES**

3.1 **INTRODUCTION**

There have been numerous studies on the respiratory and osmoregulatory physiology of intertidal decapod crustaceans (Kinne, 1963, 1964; Newell, 1976; Vernberg, 1979, 1981a, 1983; McMahon, 1988; Somero, 1995). Nevertheless, the relationship between differences in tolerances to environmental stress and the distribution of intertidal animals remains unclear (Newell, 1976). Furthermore, investigations of anomuran physiology are few and limited to only a small number of coenobitid and pagurid species, most of which are semi-terrestrial (see citations in Zainal et al., 1992).

Intertidal organisms in tropical regions are frequently subjected to rapid changes in salinity and temperature (Newell, 1969; Shumway, 1978; Sabourin and Stickle, 1980; Brosnan, 1992). Tidepool temperatures can range from 14 to 42°C (Glynn in Newell, 1969; Morton and Harper, 1995; Chan, 2000; this study) and their inhabitants may also be exposed to sudden, heavy rainfall or extreme evaporation so that salinities may vary from 1.3 to 100‰ (Morton and Harper, 1995; Morritt and Williams, 2000a,b; this study). In addition, salinity and temperature stress may increase with height on the shore (Newell, 1969, 1978; Brosnan, 1992; Metaxas and Scheibling, 1993; Stillman and Somero, 1996; see Section 2.3.3, Figures 2.3 – 2.6, pages 28-32).

The relatively wide geographical distribution of most hermit crabs suggests that they are able to tolerate extremes of temperature and salinity. At the same time,
however, the positive relationship between metabolic rate and environmental temperature (Clarke, 1991; Johnston et al., 1991; Hawkins, 1995) as well as the inverse relation between the metabolic rate of many marine ectotherms and salinity (Todd and Dehnel, 1960; King, 1965; Dimock and Groves, 1975; Taylor, 1977; Findley et al., 1978; Einarson, 1993) have important implications for tropical intertidal animals, since temperature and salinity stresses are two of the most important environmental influences directly affecting the metabolism of ectotherms (Fry, 1947; Todd and Dehnel, 1960; Kinne, 1970, 1971; Newell and Bayne, 1973; Gilles and Pequeux, 1983; Pequeux and Gilles, 1984; Hawkins, 1995, Stillman and Somero, 1996).

The observed differences in the local distribution of C. taeniatus and C. virescens lead to the hypothesis that C. taeniatus is better able to tolerate high shore conditions because it has adaptations to reduce metabolic costs when it is exposed to the stresses of higher temperatures and lower salinity, which C. virescens does not have. A second hypothesis was that C. taeniatus is a better osmotic regulator than C. virescens and is thus better able to tolerate the lower and higher salinities that are characteristic of the upper shore.

In order to test these hypotheses, two investigations were carried out. The first aimed to compare the weight-specific oxygen consumption of C. taeniatus to that of C. virescens as an indirect measure of metabolic response during acute exposure to changes in environmental temperature and salinity. The second was to determine and compare the osmoregulatory abilities of C. taeniatus and C. virescens in a range of temperatures and salinities.
3.2 MATERIALS AND METHODS

3.2.1 Oxygen Consumption

Intermolt adult *C. taeniatus* and *C. virescens* were collected from two sites on the Capricorn Coast region of Queensland, Australia throughout June, 1998 - May, 1999.

Crabs were placed in a continuously aerated acclimation tank with a salinity* of 100 ± 2.8% SW at 25 ± 2°C under a 12L : 12D regime for at least 7 days before being used in treatments. Algae were supplied by regularly adding algae-covered rocks to the aquaria and crabs were also fed frozen fish at the same time once a week. Animals were not sexed, but work on *Hemigrapsus nudus* and *Hemigrapsus oregonensis* by Todd & Dehnel (1960), *Carcinus maenus* by Siebers *et al.* (1972), *Pagurus longicarpus* Say by Biggs & McDermott (1973) and *Callinectes sapidus* by Findley *et al.* (1978) have indicated no effect of gender on physiological response.

In order to avoid the confounding effects of reducing oxygen availability and increasing concentrations of waste products during the course of the experiment, I used a flow through recirculating water system to measure oxygen consumption. Many studies have measured oxygen consumption in intertidal organisms exposed to environmental stress in sealed, no-flow or closed-circuit

---

*The term “salinity” is recognised as referring to a measure of the dissolved salts in seawater in parts per thousand (‰) in the classical sense. However, throughout this thesis it is used to refer to the concentration of seawater reported here in units of percent seawater (% SW).*
respirometers (Dehnel, 1958, 1960; King, 1965; Lange et al., 1972; Quetin et al., 1978; Davenport et al., 1980; Wernick & Pentaedo, 1983; Reid & Aldrich, 1989; Einarson, 1993). Sealed, no-flow respirometry introduces reduced oxygen saturation, increased carbon dioxide and increased excretory products as factors affecting respiration and oxygen consumption rate (Bayne et al., 1985). In preliminary experiments lasting several hours, I found that the percent saturation of oxygen in a sealed vessel was frequently reduced to less than 50%. Therefore, in the following experiment I sought to avoid confounding factors related to sealed, no-flow respirometers.

The apparatus was made of three 250mL plastic chambers connected in series by inflow and outflow rubber tubing passing through rubber bungs. The two outer chambers were fitted with oxygen electrode probes connected to two TPS 90D DO₂ meters in order to measure differences in percent saturation of oxygen.† These chambers also contained magnetic stirring bars to facilitate water movement past the probe membranes. From an 18L header tank, supported 58cm above the test chambers, water was gravity fed into the incurrent chamber of the apparatus (Figure 3.1). The first oxygen probe measured percent saturation of oxygen in incoming water, which then flowed into the second chamber where oxygen was consumed by test crabs. Continuing to the excurrent chamber, the percent saturation of oxygen was measured by the second oxygen probe. Oxygen measurements were automatically data logged by dissolved oxygen meters in units of percent saturation.

† Oxygen electrodes were calibrated in air, so water in equilibrium with air would be 100% saturated.
every 300 seconds. From the excurrent chamber water was directed into a 22L floor tank from which the water was recycled into the header tank by a peristaltic pump. The header tank was kept at a constant pressure by an outlet that routed overflow water directly to the floor tank. Treatment temperatures were kept constant (± 1.0°C) by having the three chambers of the apparatus submersed in a constant temperature water bath. For the 25°C and 35°C treatments, two Thermoline, Mini Unistat heater-stirrers were used to maintain temperature. For 15°C treatments, temperature was maintained by two Thermoline, Mini Unistat heater-stirrers in combination with a Tecam unregulated coil dip cooler.

For each oxygen consumption run, four similarly sized hermit crabs (1-2.5g total weight, including shell) of the same species were used to increase the amount of oxygen consumed in the animal chamber. Although four crabs were exposed to a single treatment at the same time, these individuals were not considered replicates (see Hurlbert, 1984). Instead, all treatment and control experiments were replicated four times using four similar sized hermit crabs for each replicate. Each individual was gently shaken to remove trapped water from within the shell and then weighed. The total weight of all four animals was recorded before the group was placed in the central, 250mL clear perspex animal chamber of the oxygen consumption apparatus (Figure 3.1). Groups were acutely exposed to one of 12 factorial combinations of temperature and salinity (see Table 3.1) in a constant flow of recirculated water over a 6 hour period, comparable to mean tidal exposure time in the field as calculated from the Official Tide Tables and Boating Safety Guide (Anonymous, 1998a).
Figure 3.1 Diagram of the experimental flow-through, recirculating oxygen measurement system with open header tank for continual oxygen saturation. Temperature was controlled by a constant temperature water bath. Percent saturation of oxygen in the incurrent chamber was measured and data logged on a TPS 90D DO₂ meter. Water passed through the animal chamber where oxygen was consumed. In the excurrent chamber, percent saturation of oxygen was again measured and data logged by a separate TPS 90D DO₂ meter. Flow rate through the system was measured so that oxygen consumption per unit time could be calculated.
Table 3.1 Experimental design for comparing the oxygen consumption between species at 12 combinations of temperature and salinity. Groups of four *C. taeniatus* or *C. virescens* were acutely exposed to each treatment for six hours. Note that at the acclimation temperature of 25°C, treatments test for salinity effects. At the acclimation salinity of 100% SW (36‰), treatments test for temperature effects.

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Salinity (± 1.4% SW)</th>
<th>Salinity (± 1.4% SW)</th>
<th>Salinity (± 1.4% SW)</th>
<th>Salinity (± 1.4% SW)</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td>100</td>
<td>35</td>
<td>35</td>
<td>35</td>
</tr>
<tr>
<td>25</td>
<td>100</td>
<td>35</td>
<td>35</td>
<td>35</td>
</tr>
<tr>
<td>35</td>
<td>100</td>
<td>35</td>
<td>35</td>
<td>35</td>
</tr>
</tbody>
</table>
Seawater was collected from a tidal creek and diluted with distilled water or concentrated with “Kiln Dried Coarse Salt” (Pacific Salt, suppliers) to produce the required salinity.

Upon completion of treatments, crabs were again shaken and weighed in the shell to determine weight gain or loss. Each shell was cracked open in a small, metal vice and the occupants removed. Individuals were dabbed dry and weighed again in order to determine the wet tissue weight for calculations of weight-specific oxygen consumption.

3.2.1.1 Controls for Unfiltered Seawater

In order to attribute observed differences in percent saturation of oxygen between incurrent and excurrent chambers to oxygen consumption of live hermit crabs, controls for water borne microbes and algae were performed with seawater only. Subsequent to oxygen consumption tests on hermit crabs, unfiltered seawater was tested in the same manner, and over the same treatment time at the 12 factorial combinations of salinity and temperature.

3.2.1.2 Controls for Shell Epibionts

Subsequent to oxygen consumption tests on hermit crabs, empty shells were also tested over the same treatment time in all combinations of temperature and salinity.
3.2.1.3 Calculations of Oxygen Consumption

Weight-specific oxygen consumption was calculated from percent oxygen saturation readings using the formula:

\[ S_i - S_e (C'_ts) (F) \cdot W^{-1} \]  

where \( S_i \) and \( S_e \) are the measured percent saturation of oxygen in the incurrent and excurrent treatment water, respectively; \( C'_ts \) is the calculated value for oxygen solubility at a given temperature and salinity in mLO₂/L SW; \( F \) is the average flow rate per hour; \( W \) is the total wet weight of tissue for samples in the treatment.

Values of oxygen solubility in water up to 20‰ chlorinity given by Kennish (1989) were converted to salinity by multiplying by the conversion constant, 1.80655. After conversion, values were extrapolated out to 180% SW by linear regression for the temperatures used (15°, 20°, 25°, 30° and 35°C) (Figure 3.2).

The appropriate values of shell-only oxygen consumption were subtracted from oxygen consumption values of live, shelled hermit crabs to get a corrected value of oxygen consumption. Correction for microbial oxygen consumption was unnecessary because results of tests showed negligible oxygen consumption by seawater only. After correction, oxygen consumption was analysed by Model I, three way ANOVA for “Species”, “Salinity” and “Temperature” followed by post-hoc Tukey pairwise analyses.
Figure 3.2 Extrapolation of interpolated values of oxygen solubility (mL O₂/L SW) in increasing salinity (% SW) at temperatures of 15°C, 20°C, 25°C, 30°C, 35°C. The linear equation and R² value for each line is given in the same order in which the lines are presented. Adapted from Kennish (1989).
3.2.1.4 Calculations of Temperature Coefficients (Q₁₀’s)

Temperature coefficients (Q₁₀’s) were calculated using the formula:

\[
Q_{10} = \left( \frac{K_2}{K_1} \right)^{\frac{10}{t_2 - t_1}}
\]  

(2)

where \(K_1\) and \(K_2\) are the oxygen consumption rates at temperatures \(t_1\) and \(t_2\), respectively.

Temperature coefficients were calculated for both species for changes in temperature between 15 - 25°C, 25 – 35°C and 15 – 35°C for each of the salinities in which oxygen consumption was measured.

3.2.2 Preliminary Tests to Determine Osmoregulation

Four preliminary tests were conducted to: 1) determine if changes in the osmolarity of \(C.\ taeniatus\) and \(C.\ virescens\) haemolymph occurred when these crabs were exposed to different salinities, 2) determine if haemolymph osmolarity varied with the total weight (including shell) of the hermit crab, 3) determine the length of time over which any changes to haemolymph osmolarity did occur and, 4) determine an appropriate length of time for subsequent investigations into the ability of both species to osmoregulate.

Experimental design, sampling method and analysis procedures for hemolymph and water osmolarity for all preliminary tests were as outlined below, although sample sizes differed.

In the initial preliminary test, one \(C.\ taeniatus\) and one \(C.\ virescens\) were placed together in a 250mL perspex chamber in one of three salinities (22, 100, or
Crabs were exposed to treatment for 1, 3, 6, 9 or 27 hours and then the haemolymph was sampled. No effort was made to select crabs of a specific size, shell type, weight or sex. There were two replicates for each combination of salinity and exposure time. All treatment chambers were placed in a random block design within a continually stirred water bath at a temperature of 25 ± 1.0°C. Although samples were not taken at the initiation of the experiment, crabs from each treatment were sacrificed at designated times to withdraw at least 10μL of hemolymph by thoracic puncture with 29-gauge needle syringes. At the same time, water samples were taken directly from the same specimen chamber. Both media and hemolymph samples were immediately analysed by a Wescor VAPRO 5520 vapour pressure osmometer to see if changes in haemolymph osmolarity occurred in both species when exposed to different salinities.

In the second preliminary experiment, crabs of various size and shell type were weighed in the shell and placed in 50mL of either 22 or 42% SW in individual 250mL perspex chambers. Fourteen individuals of both species were used in each salinity treatment. All chambers were maintained in a water bath at 25 ± 1.0°C for 6 - 7 hours. After this time haemolymph was withdrawn from crabs, analysed as above, and osmolarity recorded in units of mmol/kg. The experiment was repeated once. Data sets for each species in each salinity were analysed by Pearson correlation to examine whether osmolarity and total weight varied together.

Two further preliminary tests were performed in order to determine the length of exposure for subsequent experimental treatments. For the first, of these, two individuals of each species were exposed to one of four salinities (22, 42, 100
or 125% SW) for 1, 3, 6, 9 or 12 hours at 25 ± 1.0°C. A total of 80 crabs (40 of each species) was used.

The final, replicated preliminary test consisted of exposing a total of 39 individuals of each species to one of three salinities (22, 42 or 100% SW) for 1, 3, 5, 7, 9, or 11 hours at 25 ± 1.0°C. The haemolymph and water sampled at these times were compared with the mean of pre-treatment samples of haemolymph taken from three individuals of each species as well as the mean of six samples of acclimation medium (100 ± 2.8% SW).

In order to establish an appropriate exposure time for osmolarity experiments, two factors were considered: 1) the duration of semidiurnal, low-tide exposures in the field, and 2) whether significant changes in haemolymph osmolarity occurred during exposure times greater than this duration. Field exposure time was calculated from The Official Tide Tables and Boating Safety Guide to be approximately 5-7 hours (Anonymous, 1999).

To investigate whether significant changes in haemolymph osmolarity occurred after seven hours of continuous exposure, data from the third preliminary test in 22 and 42% SW were analysed by one way ANOVA’s and post-hoc Tukey pairwise comparisons over “Time”.

Since low tide field exposure was calculated to be approximately seven hours and haemolymph osmolarity showed no change between seven and 11 hours in either species (see Results section), an exposure time of seven hours was established for subsequent experiments on the osmoregulatory abilities of C. taeniatus and C. virescens.
3.2.3 Differences in Osmoregulatory Ability Between Species Over 7 Hours of Exposure to Low Salinity

To examine whether there were differences in osmoregulatory ability between *C. taeniatus* and *C. virescens*, crabs were collected from Emu Point and placed in aquaria to acclimate at 25 ± 2.0°C in 100 ± 2.8% SW, with a 12L: 12D regime for at least seven days. Water was changed weekly and crabs were fed frozen fish and supplied with algae-covered rocks.

Thirty-six individuals of each species were randomly chosen from the acclimation tank. No effort was made to standardise size, since preliminary tests showed no difference in hemolymph osmolality due to size. In addition, no effort was made to sex animals or select individuals in a particular species of shell.

Each specimen was placed in a separate 250mL, perspex chamber containing 50mL of one of eight salinities (11, 22, 42, 69, 100, 111, 125, or 140% SW). Treatments were replicated four times and the experiment repeated on three separate occasions. Chambers were randomly placed in a large constant temperature circulating water bath. Consecutive replicates were initiated at least one hour after the previous replicate so that sampling times did not overlap. Hemolymph and an equivalent sample of the medium were taken at the same time and measured as previously described. Experiments were conducted at 15, 25 and 35 ± 1.0°C. Repetition 2 of the experiment at 25°C was discarded since the acclimation tank salinity for this repetition was much higher than for all other repetitions at 15, 25 and 35°C. All measurements of haemolymph osmolarity at the three temperatures (not including repetition 2 of 25°C) were analysed by Model III, three way ANOVA for “Species”, “Temperature” and “Repetition”.
3.2.4 The Effect of Temperature on Osmoregulation

Data from the above experiments were pooled and analysed by Model I, two way ANOVA’s for “Salinity” and “Temperature” for the effect of temperature on haemolymph osmolarity at each salinity tested.

3.2.5 Comparisons of Laboratory and Field Samples

Osmolarity measurements of laboratory sampled hemolymph and acclimation water were compared with field sampled hemolymph and tidepool water. From the field, six replicates of haemolymph from *C. taeniatus*, eight from *C. virescens* and 14 replicates of tidepool water were compared with 27 replicates of *C. taeniatus* haemolymph, 27 from *C. virescens* and 27 replicates of laboratory acclimation water. Crabs and water in the field were sampled in the same manner as in the laboratory. Haemolymph samples from both species in the field were compared with haemolymph samples taken from both species kept in acclimation tanks at $25^\circ \pm 2.0^\circ$C in $100 \pm 2.8\%$ SW, by a two way ANOVA for “Species” and “Place”. Since acclimation water was not considered a body fluid it was not analysed with haemolymph. Instead, haemolymph osmolarity of both species in the lab was compared with acclimation water osmolarity by two-tailed, T-tests, as were both species in the field with tidepool water.
3.3 RESULTS

3.3.1 Oxygen Consumption

3.3.1.1 Controls for Unfiltered Seawater

Control chambers containing unfiltered seawater only, demonstrated no detectable oxygen consumption in any of the temperature-salinity combinations tested and therefore, will not be further discussed.

3.3.1.2 Controls for Shell Epibionts

Shell-only control tests resulted in some oxygen consumption by shell epibionts. Consequently, mean weight-specific oxygen consumptions of both species were corrected by subtracting the mean oxygen consumption of shell-only controls in the corresponding temperature-salinity treatment.

3.3.2 Oxygen Consumption by Hermit Crabs

Mean weight-specific oxygen consumption rates for *C. virescens* and *C. taeniatus* at different temperatures and salinities are presented as µL O₂/hr/g in Table 3.2.

Table 3.3 gives the results of the Model I, three way ANOVA for data corrected for shell control oxygen consumption. There was no significant difference between species, but salinity and temperature both had a significant (P<0.001) effect on oxygen consumption. There were no interactions between species × salinity, salinity × temperature, or species × salinity × temperature. However, a significant interaction did occur between species × temperature (P=0.048). Because of this,
<table>
<thead>
<tr>
<th>Salinity (% SW)</th>
<th>C. taeniatus</th>
<th>C. virescens</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>15°C</td>
<td>25°C</td>
</tr>
<tr>
<td>22</td>
<td>47.2 ± 12</td>
<td>244.7 ± 26</td>
</tr>
<tr>
<td>100</td>
<td>120.2 ± 11</td>
<td>210.2 ± 28</td>
</tr>
<tr>
<td>225</td>
<td>169.9 ± 32</td>
<td>191.9 ± 39</td>
</tr>
</tbody>
</table>

Table 3.2 Comparison of mean oxygen consumption (µL/O2/hr/g) between C. taeniatus and C. virescens at experimental salinities (% SW) and temperatures (°C). Means are reported with ± 1 standard error.
Table 3.3: Results of Model I, three way ANOVA performed on oxygen consumption data corrected for shell – only control tests.

<table>
<thead>
<tr>
<th>Source</th>
<th>Sum of Squares</th>
<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>SPECIES</td>
<td>4.179E-03</td>
<td>73</td>
<td>3.05</td>
<td>4.48E-03</td>
<td>6</td>
</tr>
<tr>
<td>TEMP</td>
<td>1.47E-02</td>
<td>1</td>
<td>1.47E-02</td>
<td>2.034E-02</td>
<td>6</td>
</tr>
<tr>
<td>SALIN</td>
<td>6.102E-02</td>
<td>3</td>
<td>2.034E-02</td>
<td>4.868</td>
<td>9</td>
</tr>
<tr>
<td>SPECIES * TEMP</td>
<td>2.457</td>
<td>2</td>
<td>1.2285E-02</td>
<td>41.736 &lt;.001</td>
<td>9</td>
</tr>
<tr>
<td>SPECIES * SALIN</td>
<td>9.267</td>
<td>3</td>
<td>3.08E-02</td>
<td>44.87E-02</td>
<td>11</td>
</tr>
<tr>
<td>SPECIES * SALIN</td>
<td>9.548E-05</td>
<td>1</td>
<td>9.548E-05</td>
<td>.023</td>
<td>32</td>
</tr>
<tr>
<td>Error</td>
<td>3.05</td>
<td>73</td>
<td>4.179E-03</td>
<td>2.69E-02</td>
<td>9</td>
</tr>
</tbody>
</table>

63
pairwise Tukey comparison tests were conducted on all factorial combinations of “Salinity” and “Temperature” to further investigate main effects of the ANOVA (Zar, 1999). Results of pairwise comparisons are presented in Tables 3.4 and 3.5.

### 3.3.2.1 Respiratory Responses to Temperature and Salinity

Results of pairwise *a posteriori* comparisons showed that the oxygen consumption of *C. taeniatus* in 22% SW, at 15°C was significantly lower than in any of the other three salinities tested (Table 3.2 and Table 3.4). There was no significant difference in oxygen consumption between 56 and 100%, 100 and 125%, and 56 and 125% SW at 15°C (Table 3.4). At temperatures of 25 and 35°C *C. taeniatus* showed no significant difference in oxygen consumption at any of the salinities tested.

Table 3.2 reveals that at all three temperatures, oxygen consumption in *C. virescens* was lower in 22% SW compared with 56% SW and with the acclimation salinity (100% SW), although these differences were not significant (Table 3.4).

For *C. virescens* at 25°C, oxygen consumption in 56% SW was significantly higher than in 125% SW (Tables 3.2 and 3.4). No other pairwise comparisons of salinities at any of the three experimental temperatures showed a significant difference in oxygen consumption by *C. virescens*.

When the oxygen consumption of both species was compared in 56 and 22% SW at all three temperatures, there was a general trend for the oxygen consumption of *C. virescens* to be higher than that of *C. taeniatus*. The exception was in 22% SW
### Table 3.4

Results of Tukey pairwise comparisons of mean oxygen consumption (µLO₂/hr/g) in ecologically representative salinities (% SW) at three temperatures (°C). *: P ≤ 0.05, N.S.: P > 0.05.

<table>
<thead>
<tr>
<th>Salinity (% SW)</th>
<th>65</th>
<th>80</th>
<th>95</th>
<th>110</th>
<th>125</th>
</tr>
</thead>
<tbody>
<tr>
<td>C.t. 15°C</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
</tr>
<tr>
<td>C.t. 25°C</td>
<td>*</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
</tr>
<tr>
<td>C.t. 35°C</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
</tr>
<tr>
<td>C.v. 15°C</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
</tr>
<tr>
<td>C.v. 25°C</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
</tr>
<tr>
<td>C.v. 35°C</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
</tr>
</tbody>
</table>

OXYGEN CONSUMPTION, OSMOREGULATION
In Table 3.5 oxygen consumption is compared between temperatures at each experimental salinity. For *C. taeniatus*, there was a significant difference in oxygen consumption between 15 and 25°C in 22% SW as well as between 15 and 35°C in 22, and 125% SW, but there was no difference between 25 and 35°C at any of the experimental salinities. In Table 3.6 it can be seen that there was a noticeably large Q₁₀ value of 5.2 for *C. taeniatus* between 15 and 25°C in 22% SW. The large increase in oxygen consumption between 15 and 25°C also influenced the Q₁₀ value for this species when oxygen consumption rates in 22% SW were compared between 15 and 35°C. Between 25 and 35°C Q₁₀’s for *C. taeniatus* in all salinities were very close to unity. It is important to note that although there was a slight increase in oxygen consumption at the acclimation salinity of 100% SW, (Table 3.2) this was not significantly different from oxygen consumption over the entire range of temperatures at which *C. taeniatus* was tested.

In order to further investigate the similarity in oxygen consumption at 100% SW over the range of treatment temperatures, *C. taeniatus* was additionally tested in 100% SW at both 20 and 30°C. These temperatures were chosen as intermediates between 15 and 25°C and 25 and 35°C. The mean oxygen consumptions for *C. taeniatus* from these tests are presented in Table 3.7 compared to oxygen consumption at 15, 25 and 35°C in the same salinity. Again, no significant differences in oxygen consumption occurred at any temperature tested in 100% SW (one way ANOVA, F₄,₁₅= 0.383, P>0.05).
Table 3.5 Results of Tukey pairwise comparisons of mean oxygen consumption (µLO₂/hr/g) of *C. taeniatus* and *C. virescens* between treatment temperatures (°C) at four treatment salinities (% SW).

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>15-25</td>
<td>*</td>
<td>N.S.</td>
<td>125%</td>
<td>C.'a.</td>
</tr>
<tr>
<td>25-35</td>
<td></td>
<td>N.S.</td>
<td>100%</td>
<td>C.'a.</td>
</tr>
<tr>
<td>15-35</td>
<td></td>
<td>N.S.</td>
<td>56%</td>
<td>C.'a.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>N.S.</td>
<td>222%</td>
<td>C.'a.</td>
</tr>
</tbody>
</table>
A comparison of $Q^{10}$ values for oxygen consumption of *C. taeniatus* (*C.t.*), *C. virescens* (*C.v.*), and *C. cyanurus* (*C.c.*), between the three experimental temperatures in all test salinities.

<table>
<thead>
<tr>
<th>Salinity (%SW)</th>
<th>15 - 25°C</th>
<th>25 - 35°C</th>
<th>15 - 35°C</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.25</td>
<td>1.7</td>
<td>1.5</td>
<td>1.5</td>
</tr>
<tr>
<td>0.9</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>0.6</td>
<td>1.6</td>
<td>1.6</td>
<td>1.6</td>
</tr>
<tr>
<td>0.2</td>
<td>2.2</td>
<td>2.6</td>
<td>2.6</td>
</tr>
</tbody>
</table>

Table 3.6
Table 3.7 Results of Tukey comparisons of oxygen consumption ($\mu LO_2/hr/g$) of *C. taeniatus* in intermediate treatment temperatures (20 and 30°C) to confirm no difference in oxygen consumption between temperatures at the acclimation salinity of 100% SW. Oxygen consumption is presented as mean ± 1 standard error. For each temperature n = 4. N.S. : $p > 0.05$

<table>
<thead>
<tr>
<th>Temperature ± 1°C</th>
<th>Temperature ± 1°C</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>OXYGEN CONSUMPTION</td>
</tr>
<tr>
<td></td>
<td>(µLO₂/hr/g)</td>
</tr>
<tr>
<td></td>
<td>191.1 ± 32</td>
</tr>
<tr>
<td>20</td>
<td>155.3 ± 21</td>
</tr>
<tr>
<td>25</td>
<td>190.9 ± 39</td>
</tr>
<tr>
<td>30</td>
<td>188.9 ± 9.8</td>
</tr>
<tr>
<td>35</td>
<td>191.1 ± 16</td>
</tr>
</tbody>
</table>

OXYGEN CONSUMPTION

Temperature ± 1°C

Temperature ± 1°C

OXYGEN CONSUMPTION
For *C. virescens*, although Q10’s ranged from 1.5 to 2.6 (Table 3.6), there were no significant differences in oxygen consumption between 15 and 25°C, except in 100% SW (Table 3.5). The comparisons of oxygen consumption between 25 and 35°C showed no difference for *C. virescens* tested in 22, 56, or 100% SW. Only in 125% SW was there a difference, with oxygen consumption at 35°C significantly higher than oxygen consumption at 25°C (Table 3.2). Q10 values between 25 and 35°C for 22, 56 and 100% SW were relatively close to unity, while at 125% SW, the Q10 value was more than 2 (Table 3.6). When oxygen consumption was compared between 15 and 35°C, significant differences occurred in all salinities tested (Table 3.5). It is important to note that at the acclimation salinity (100% SW) oxygen consumption was significantly lower at 15°C than at 25 or 35°C (Tables 3.2 and 3.5).

### 3.3.2.2 Temperature Coefficients (Q10’s)

In Table 3.6, the temperature coefficients for both species are given for each temperature change in all salinities tested. This shows that there was a general trend for the Q10’s of *C. taeniatus* to be lower than for those of *C. virescens*.

It can be clearly seen that the Q10’s between 25 and 35°C in all salinities were very close to unity for *C. taeniatus*, while for *C. virescens* the values were higher and lay within a wider range. In addition, when temperature coefficients for the two species were compared across all temperatures at the acclimation salinity (100% SW), those for *C. taeniatus* remained at unity. However, the values for *C. virescens* at the acclimation salinity were almost twice those of *C. taeniatus*. 
3.3.3 Preliminary Tests to Determine Osmoregulation

An important finding from initial preliminary tests on *C. taeniatus* and *C. virescens* in 22, 100 and 125% SW (Figures 3.3A and B, respectively) was that both species were able to survive up to 27 hours of continual exposure to either lower (22%) or higher (125%) salinity than acclimation (100% SW) at 25 ± 1.0°C. Although sufficient samples for analysis were not obtained from some test animals, both *C. taeniatus* and *C. virescens* showed marked changes in haemolymph osmolarity in both increased and reduced salinities of the media.

In the case of *C. taeniatus* (Figure 3.3A) it appears that initial exposure to higher salinity water resulted in haemolymph osmolarity above ambient within the first hour. This was followed by a decline to a steady state just hyperosmotic to ambient throughout the remaining 24 hours of exposure. High haemolymph osmolarity also probably occurred when a *C. taeniatus* individual was initially introduced to the control salinity of 100% SW, although no haemolymph samples were available for analysis from hermit crabs at the 1 hour exposure point. Between 3 and 6 hours of exposure at this salinity, *C. taeniatus* haemolymph osmolarity dropped to, and remained just hyperosmotic to ambient osmolarity for the remainder of the experiment.

Haemolymph samples drawn from *C. virescens* (Figure 3.3B) exposed to 125% SW showed that haemolymph osmolarity reached a steady state above ambient water osmolarity by 3 hours. Haemolymph osmolarity of *C. virescens* in 100% SW also remained above ambient osmolarity and did not obviously differ throughout the experimental period.
Figure 3.3  Results of a preliminary comparison of **A**: *C. taeniatus* and **B**: *C. virescens* haemolymph osmolarity (solid markers) with ambient water osmolarity (open markers) in 22% (◊), 100% (□) and 125% (△) SW over 27 hours at 25 ± 1°C.
When exposed to reduced salinity (22% SW), the haemolymph osmolarity of both species decreased to a relatively stable state within 6 hours. After a total of 27 hours exposure, the haemolymph osmolarity of both *C. taeniatus* and *C. virescens* were not different (*C. taeniatus*: 378mmol/kg; *C. virescens*: 384mmol/kg). It can also be seen by inspection of Figures 3.3A and B that from 6 – 27 hours, haemolymph osmolarity did not vary greatly in either species in 22, 100 or 125% SW, although it declined slightly in 22% SW for *C. virescens*.

3.3.3.1 The Effect of Size on Haemolymph Osmolarity

When the haemolymph osmolarities of *C. taeniatus* from 1.357 – 5.943g total weight exposed to 42% SW at 25°C for 6 – 7 hours were compared, no significant correlation between haemolymph osmolarity and total weight (crab and shell) was found (*r* = 0.298, *P*>0.05) (Figure 3.4A). Similarly, the haemolymph osmolarity of *C. virescens* in the weight range from 1.413 – 9.933g in 42% SW for 6 – 7 hours did not correlate with the total weight of crabs (*r* = 0.248, *P*>0.05) (Figure 3.4B). Nor did the haemolymph osmolarity of *C. taeniatus* or *C. virescens* exposed to 22% SW at 25°C for approximately 7 hours vary in relation to the total weight of the animals (*C. taeniatus*: *r* = -0.065, *P*>0.05; *C. virescens*: *r* = 0.043, *P*>0.05) (Figures 3.5A and B). In this set of experiments, the weight ranges of *C. taeniatus* and *C. virescens* were 1.577 – 12.367g and 1.328 – 11.792g, respectively.

3.3.3.2 Determination of Appropriate Length of Exposure

By inspection of Figures 3.6A and B, results of the third set of preliminary osmolarity experiments demonstrated that in 100% SW at 25°C, both *C. taeniatus*
Figure 3.4 Scatterplots of A: *C. taeniatus* and B: *C. virescens* haemolymph osmolarity (mmol/kg) against total hermit crab weight (shell weight plus body weight) (g) after 6 – 7 hours of exposure to 42% SW at 25 ± 1°C.
Figure 3.5 Scatterplots of A: *C. taeniatus* and B: *C. virescens* haemolymph osmolarity (mmol/kg) against total hermit crab weight (shell weight plus body weight) (g) after 6 – 7 hours of exposure to 22% SW at 25 ± 1°C.
(Figure 3.6A) and C. virescens (Figure 3.6B) had little variation in haemolymph osmolarity over the 12 hour treatment. Unlike results from the first preliminary test, no change in osmolarity was recorded for C. taeniatus when put into 100% SW controls.

In higher salinity medium (125% SW), both species reached a new steady state haemolymph osmolarity hyperosmotic to the medium within the first hour of exposure. Haemolymph osmolarity changed little over the remaining 11 hours of exposure and was not different between species.

It can be seen from Figure 3.6A that the adjustment of C. taeniatus haemolymph osmolarity to salinities below the acclimation salinity began within the first hour of exposure to both 42 and 22% SW. In 42% SW haemolymph osmolarity did not change significantly between three and 12 hours of exposure. In 22% SW haemolymph osmolarity continued to drop slightly over the course of the experiment. However, at the end of the experiment, C. taeniatus haemolymph osmolarity remained above the osmolarity of the medium in both 42 and 22% SW.

C. virescens (Figure 3.6B) exposed to both 42% and 22% SW had measurements of haemolymph osmolarity that were virtually the same (42% SW: 790mmol/kg; 22% SW: 809mmol/kg) after one hour of exposure. Over the remainder of the treatment, haemolymph osmolarity dropped only slightly in 42% SW, but dropped from a mean of 809.5mmol/kg (n=2) at one hour to a mean of 452mmol/kg (n=2) at 6 hours of exposure to 22% SW. A steady state haemolymph osmolarity was established between 6 and 9 hours of exposure. Haemolymph remained hyperosmotic to the medium in both lower salinities.
In summary, for both species, initial adjustments of haemolymph osmolarity occurred within the first hour of acute exposure to either higher or lower salinity. Adjustments continued during further exposure, but a new steady state appears to have been reached within 1-2 hours of exposure to the higher salinity (125% SW) and within approximately 6 hours of exposure to the lower salinities (22 and 42% SW).

Comparisons between Figures 3.6A and B suggest that in adjusting to 125% SW, both species reached the same haemolymph osmolarity within the first hour of acute exposure (C. taeniatus, 1471.5mmol/kg (n=2); C. virescens, 1475mmol/kg (n=2)). When adjusting to 22% SW, the haemolymph of C. taeniatus reached a lower osmolarity than that of C. virescens within the first hour of acute exposure (C. taeniatus, 674mmol/kg (n=2); C. virescens, 809.5mmol/kg (n=2)). However, at the conclusion of the experiment, the haemolymph osmolarity of C. virescens in 22% SW had dropped below that of C. taeniatus in the same salinity (C. taeniatus, 454.5mmol/kg (n=2); C. virescens, 383.5mmol/kg (n=2)). Both species did, however, maintain haemolymph osmolarity above ambient osmolarity in all four salinities tested.

Results of the fourth preliminary test on changes in C. taeniatus and C. virescens haemolymph osmolarity are shown in Figure 3.7. One way ANOVA’s were done to compare initial haemolymph osmolarity to haemolymph osmolarity after one hour of exposure to 22 and 42% SW, and for C. virescens haemolymph osmolarity between one and seven hours in 42% SW. For both species, significant reductions in haemolymph osmolarity occurred within the first hour of acute exposure to both 22 and 42% SW (one way ANOVA’s, C. taeniatus, 22% SW:
Figure 3.6 Results of a preliminary comparison of A: *C. taeniatus* and B: *C. virescens* haemolymph osmolarity (solid markers) with ambient water osmolarity (open markers) in 22% (○), 42% (○), 100% (□) and 125% (△) SW over 12 hours at 25 ± 1°C. Some standard error bars are too small to appear from behind markers. Data points represent the mean of two samples.
OXYGEN CONSUMPTION, OSMOREGULATION

Figure 3.7 Results of a comparison between C. taeniatus haemolymph osmolarity (shaded markers) (n=36), C. virescens haemolymph osmolarity (solid markers) (n=36), and ambient water osmolarity (open markers) (n=6) in 22% (□) and 42% (○) SW at 25 ± 1°C. Pre-treatment haemolymph osmolarity (C. taeniatus, shaded marker; C. virescens, solid marker; C. lucidus, open marker) (n=3 for each species) and pre-acclimation water (100% SW) (n=6) are shown as initial points.
OXYGEN CONSUMPTION, OSMOREGULATION

\( F_{1,4}=83.246, \ P<0.01; \ C. \text{ taeniatus}, \ 42\% \ SW: \ F_{1,4}=130.544, \ P<0.001; \ C. \text{ virescens}, \ 22\% \ SW: \ F_{1,4}=1869.604, \ P<0.001; \ C. \text{ virescens}, \ 42\% \ SW: \ F_{1,4}=1162.957, \ P<0.001). \) As in the previous preliminary test, the osmolarity of \( C. \text{ taeniatus} \) haemolymph was reduced more than that of \( C. \text{ virescens} \) in the first hour of exposure, but the difference between species at this point was not significant (one way ANOVA, \( F_{1,4} = 2.206, \ P>0.05). \)

Haemolymph osmolarity of both species continued to fall for up to three hours, after which these crabs established steady state haemolymph osmolarity.

For \( C. \text{ taeniatus} \) in 42\% SW, a steady state haemolymph osmolarity was reached by the third hour. For \( C. \text{ virescens} \) in 42\% SW, haemolymph osmolarity continued to decrease until the seventh hour at which it was significantly lower than in the first hour (one way ANOVA, \( F_{1,5} = 34.272, \ P<0.001). \) From the seventh hour to the end of the experiment, haemolymph osmolarity remained stable.

As in the previous preliminary tests, the haemolymph osmolarity of \( C. \text{ taeniatus} \) in both 22 and 42\% SW was higher than the haemolymph osmolarity of \( C. \text{ virescens} \) at the end of the test.

A Model I, three way ANOVA of “Species”, “Salinity” and “Time” for haemolymph osmolarity showed no effect of species (\( F_{1,50} = 1.640, \ P>0.05). \) but significant effects of salinity (\( F_{1,50} = 110.615, \ P<0.001 \)) and time (\( F_{5,50} = 25.238, \ P<0.001). \) No significant interactions between independent factors occurred. Post-hoc Tukey test comparisons of these data showed that between 5 and 11 hours there was no significant effect of time on haemolymph osmolarity for samples taken from \( C. \text{ taeniatus} \) and \( C. \text{ virescens} \) exposed to 22\% SW and for \( C. \text{ taeniatus} \) exposed to 42\% SW (see Table 3.8). A significant difference in hemolymph osmolarity did
<table>
<thead>
<tr>
<th>Time (hrs)</th>
<th>C. taeniatus</th>
<th>C. virescens</th>
<th>C. taeniatus</th>
<th>C. virescens</th>
<th>C. taeniatus</th>
<th>C. virescens</th>
</tr>
</thead>
<tbody>
<tr>
<td>5-7</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
</tr>
<tr>
<td>7-9</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
</tr>
<tr>
<td>9-11</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
</tr>
</tbody>
</table>

Table 3.8: Results of Tukey pairwise comparisons of C. taeniatus and C. virescens haemolymph osmolarity at different times after exposure to 22% and 42% SW at 25°C. *: P ≤ 0.05, N.S.: P > 0.05.
occur between 5 and 7 hours and between 5 and 11 hours in *C. virescens* exposed to 42% SW, but the difference between 7 and 11 hours was not significant (Table 3.8). This can also be seen by inspection of Figure 3.7.

### 3.3.4 Test for Differences in Osmoregulatory Ability Over 7 Hours of Exposure to Low Salinity

In one instance during this experiment, evaporation caused the salinity of the acclimation tank to increase to a level much higher than usual. Crabs from this tank were used for the second repetition of the experiment at 25°C. Since acclimation history is important in the responses of hermit crabs to further changes in salinity, this repetition was excluded from statistical analyses.

A Model III, three way ANOVA for “Species” (fixed), “Temperature” (fixed) and “Repetition” (random) was performed on all remaining data (repetitions 1-3 for 15° and 35°C, and repetitions 1 and 3 for 25°C). This ANOVA showed no difference between species ($F_{1,495} = 10.040$, $P>0.05$) or repetitions ($F_{2,495} = 1.513$, $P>0.05$), but a significant effect of temperature ($F_{2,495} = 11.085$, $P<0.05$). There were no significant interactions among independent factors. Subsequent independent sample T-test analyses showed a significant difference was maintained between the treatment medium and crab haemolymph osmolarity over all salinities (df=15, $P<0.001$ in all cases).

In Figures 3.8, 3.9 and 3.10, the establishment and maintenance of haemolymph osmolarity hyperosmotic to the medium is demonstrated over the entire range of treatment salinities (11 – 140% SW) at 15°, 25° and 35°C, respectively. It can be seen that the polynomial trendlines increase in distance away.
Figure 3.8. Comparison of *C. taeniatus* haemolymph osmolarity (▲, light line) (n=12) and *C. virescens* haemolymph osmolarity (▼, dark line) (n=12) in salinities from 11 - 140% SW at 15°C. Hermit crab haemolymph osmolalities are presented in relation to an isosmotic line. Values for initial *C. taeniatus* (●) and *C. virescens* (●) haemolymph osmolarity are presented. R² values for each polynomial trendline are given.
<table>
<thead>
<tr>
<th>Species</th>
<th>Osmolarity (mmol/kg) at 15°C</th>
<th>Water Osmolarity (mmol/kg)</th>
<th>C. taeniatus Osmolarity (mmol/kg)</th>
<th>C. virescens Osmolarity (mmol/kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. taeniatus</td>
<td>1107.0 ± 11.0</td>
<td>118.9 ± 1.7</td>
<td>1430.6 ± 2.7</td>
<td>1639.2 ± 8.4</td>
</tr>
<tr>
<td>C. virescens</td>
<td>1319.4 ± 12.6</td>
<td>568.5 ± 14.9</td>
<td>1325.5 ± 24.4</td>
<td>1664.1 ± 7.7</td>
</tr>
</tbody>
</table>

Table 3.9 Variation resulting from analyses of C. taeniatus and C. virescens haemolymph osmolarity (mmol/kg) at various medium osmolarities (mmol/kg) at 15°C. Variations in water samples taken at the time of haemolymph sampling are shown in the column labelled „water“. Means ± 1 standard error are presented. n = 12
Figure 3.6. Comparison of C. taeniatus (•) and C. virescens (X) haemolymph osmolarity in relation to an isosmotic ( ▲ ) dark line (n=8) in salinities from 11–140% SW at 25°C. Hermit crab osmoralties are presented in relation to an isosmotic line. Values for initial C. taeniatus (○) and C. virescens (□) haemolymph osmolarity are presented. R² values for each polynomial trendline are given.

C. virescens R² = 0.994
C. taeniatus R² = 0.996
Table 3.10 Variation resulting from analyses of *C. taeniatus* and *C. virescens* haemolymph osmolarity (mmol/kg) at various medium osmolarities (mmol/kg) at 25°C. Variations in water samples taken at the time of haemolymph sampling are shown in the column labelled "water". Means ± 1 standard error are presented. n = 8.

<table>
<thead>
<tr>
<th>Species</th>
<th>Water</th>
<th><em>C. taeniatus</em></th>
<th><em>C. virescens</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>OS (mmol/kg)</td>
<td></td>
<td>OS (mmol/kg)</td>
<td>OS (mmol/kg)</td>
</tr>
<tr>
<td>1428.8 ± 1.4</td>
<td>1161.4 ± 5.3</td>
<td>1657.4 ± 9.1</td>
<td>1666.4 ± 9.8</td>
</tr>
<tr>
<td>1219.6 ± 1.2</td>
<td>1161.4 ± 5.3</td>
<td>1657.4 ± 9.1</td>
<td>1666.4 ± 9.8</td>
</tr>
<tr>
<td>1118.4 ± 1.7</td>
<td>1161.4 ± 5.3</td>
<td>1657.4 ± 9.1</td>
<td>1666.4 ± 9.8</td>
</tr>
<tr>
<td>760.8 ± 2.0</td>
<td>1161.4 ± 5.3</td>
<td>1657.4 ± 9.1</td>
<td>1666.4 ± 9.8</td>
</tr>
<tr>
<td>449.0 ± 1.8</td>
<td>1161.4 ± 5.3</td>
<td>1657.4 ± 9.1</td>
<td>1666.4 ± 9.8</td>
</tr>
<tr>
<td>229.8 ± 1.8</td>
<td>1161.4 ± 5.3</td>
<td>1657.4 ± 9.1</td>
<td>1666.4 ± 9.8</td>
</tr>
<tr>
<td>116.3 ± 3.3</td>
<td>1161.4 ± 5.3</td>
<td>1657.4 ± 9.1</td>
<td>1666.4 ± 9.8</td>
</tr>
<tr>
<td>1126.0 ± 1.0</td>
<td>1161.4 ± 5.3</td>
<td>1657.4 ± 9.1</td>
<td>1666.4 ± 9.8</td>
</tr>
</tbody>
</table>
Figure 3.10 Comparison of *C. taeniatus* haemolymph osmolarity (●, light line) (n=12) and *C. virescens* haemolymph osmolarity (▲, dark line) (n=12) in salinities from 11 – 140% SW at 35°C. Hermit crab haemolymph osmolarities are presented in relation to an isosmotic line. Values for initial *C. taeniatus* (●) and *C. virescens* (▲) haemolymph osmolarities are presented. R² values for each polynomial trendline are given.
<table>
<thead>
<tr>
<th>Species</th>
<th>C. taeniatus</th>
<th>C. virescens</th>
<th>C. lancanus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Osmolarity (mmol/kg)</td>
<td>1628.8 ± 3.7</td>
<td>1101.7 ± 2.4</td>
<td>1430.9 ± 7.2</td>
</tr>
<tr>
<td></td>
<td>1183.5 ± 9.2</td>
<td>1324.7 ± 8.8</td>
<td>1231.8 ± 1.0</td>
</tr>
<tr>
<td></td>
<td>1047.8 ± 8.3</td>
<td>1169.4 ± 1.1</td>
<td>1123.3 ± 2.7</td>
</tr>
<tr>
<td></td>
<td>765.8 ± 2.4</td>
<td>823.0 ± 1.3</td>
<td>751.9 ± 1.8</td>
</tr>
<tr>
<td></td>
<td>448.2 ± 3.9</td>
<td>620.7 ± 2.5</td>
<td>442.8 ± 1.8</td>
</tr>
<tr>
<td></td>
<td>225.7 ± 1.9</td>
<td>317.8 ± 1.8</td>
<td>231.8 ± 1.8</td>
</tr>
<tr>
<td></td>
<td>116.1 ± 1.7</td>
<td>413.0 ± 2.0</td>
<td>118.9 ± 1.7</td>
</tr>
<tr>
<td></td>
<td>1108.8 ± 1.5</td>
<td>1224.7 ± 1.3</td>
<td>1107.0 ± 1.0</td>
</tr>
</tbody>
</table>

Table 3.11: Variation resulting from analyses of C. taeniatus and C. virescens haemolymph osmolality at various medium osmolalities (mmol/kg) at 35°C. Variations in water samples taken at the time of haemolymph sampling are shown in the column labelled "water." Means ± 1 standard error are presented. n = 12.
from the isosmotic line as salinity decreases. Tables 3.9, 3.10 and 3.11 show the variation found in osmolarity measurements from treatment temperatures 15°, 25° and 35°C, respectively.

In all cases, given the removal of repetition 2 from the 25°C data set, Model III, two way ANOVA’s showed that there were no significant differences in osmoregulatory ability between *C. taeniatus* and *C. virescens*.

### 3.3.5 The Effect of Temperature on Osmoregulation Over 7 Hours of Exposure

Since no difference in haemolymph osmolarity existed between species, data for both were pooled and are shown in Table 3.12 for a comparison among temperatures at all salinities tested. In this table the osmolarity value of the medium is given for each salinity. Results show that there was a tendency for the mean haemolymph osmolarity to decrease with increasing temperature. Exceptions were in 1251.8mmol/kg (111% SW) and 1586.8mmol/kg (140% SW) from 15 to 25°C and in 1122.3mmol/kg (100% SW), 1430.6mmol/kg (125% SW) and 1585.8mmol/kg (140% SW) from 25 to 35°C. Results of a Model I, two way ANOVA for salinity and temperature demonstrated a significant effect of salinity and temperature on haemolymph osmolarity. A significant interaction between the two factors also occurred (Table 3.13) and results of post-hoc Tukey pairwise comparisons are shown in Table 3.14. These results, in combination with Table 3.12, show that the haemolymph osmolarity of both species decreased significantly as temperature increased from 15 to 25°C for all salinities tested (P<0.001), except in 111% SW, where haemolymph osmolarity increased insignificantly, and in 140%
For 25°C, n = 8.

Mean haemolymph osmolarity (mmol/kg) at three temperatures after 7 hours of exposure. Medium osmolarities (mmol/kg) are given for the salinities (in brackets in % SW) in which hermit crabs were tested. Means ± 1 standard error are presented. Each mean represents pooled data for *C. magnus* and *C. virgatus* haemolymph osmolarity. For 15 and 35°C, n = 12.

<table>
<thead>
<tr>
<th>Temp (°C)</th>
<th>Medium Osmolarity (mmol/kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td>118.9 (11) 231.8 (22) 442.8 (42)</td>
</tr>
<tr>
<td>25</td>
<td>231.8 (22) 470.13 ± 16.66</td>
</tr>
<tr>
<td>35</td>
<td>470.13 ± 16.66 581.87 ± 16.41</td>
</tr>
</tbody>
</table>

Mean haemolymph osmolarity (mmol/kg) at three temperatures after 7 hours of exposure. Medium osmolarities (mmol/kg) are given for the salinities (in brackets in % SW) in which hermit crabs were tested. Means ± 1 standard error are presented. Each mean represents pooled data for *C. magnus* and *C. virgatus* haemolymph osmolarity. For 15 and 35°C, n = 12.

<table>
<thead>
<tr>
<th>Temp (°C)</th>
<th>Medium Osmolarity (mmol/kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td>118.9 (11) 231.8 (22) 442.8 (42)</td>
</tr>
<tr>
<td>25</td>
<td>231.8 (22) 470.13 ± 16.66</td>
</tr>
<tr>
<td>35</td>
<td>470.13 ± 16.66 581.87 ± 16.41</td>
</tr>
</tbody>
</table>

Table 3.12 OXYGEN CONSUMPTION, OSMOREGULATION
Table 3.13. Results of a Model I, two way ANOVA for the effect of salinity and temperature on haemolymph osmolality measurements pooled for *C. lenticus* and *C. viriscens*.

<table>
<thead>
<tr>
<th>Source</th>
<th>Sum of Squares</th>
<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>Sig.</th>
<th>Type II Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td>SALINITY</td>
<td>8.59E+07</td>
<td>7</td>
<td>1.228E+07</td>
<td>3540.800</td>
<td>&lt; .001</td>
<td></td>
</tr>
<tr>
<td>TEMP</td>
<td>5.053E+05</td>
<td>2</td>
<td>2.527E+05</td>
<td>72.873</td>
<td>&lt; .001</td>
<td></td>
</tr>
<tr>
<td>SALINITY * TEMP</td>
<td>6.829E+05</td>
<td>14</td>
<td>4.878E+04</td>
<td>14.068</td>
<td>&lt; .001</td>
<td></td>
</tr>
<tr>
<td>Error</td>
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<td>487</td>
<td>3.467E+03</td>
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OXYGEN CONSUMPTION, OSMOREGULATION

Table 3.13

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<th>Source</th>
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<td>487</td>
<td>3.467E+03</td>
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OXYGEN CONSUMPTION, OSMOREGULATION

Table 3.14 Results of Tukey comparisons between temperatures (°C) for each salinity (% SW). Haemolymph osmolarities have been pooled together for each temperature and salinity. 15°C, n=192; 25°C, n=128; 35°C, n=191. NS: P>0.05; *: P≤0.05; **: P<0.001.

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<tr>
<td>*</td>
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<td>1586.8</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>15 - 35</td>
<td>25 - 35</td>
<td>15 - 25</td>
<td>(mmol/kg)</td>
<td>(°C)</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>25</td>
<td>15</td>
<td>35</td>
<td>C. taeniatus</td>
</tr>
<tr>
<td>123</td>
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<td>442</td>
<td>442</td>
<td>15</td>
</tr>
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</table>
OXYGEN CONSUMPTION, OSMOREGULATION

SW where there was a significant increase. When temperature increased from 25 to
35°C, an insignificant increase in haemolymph osmolarity occurred in 100% SW, while an insignificant decrease occurred in 111% SW. In the two highest salinities there was a significant rise in the osmolarity of the haemolymph (P<0.001) when temperature increased from 25 to 35°C. Between 15 and 35°C, haemolymph osmolarity decreased significantly in salinities from 11 – 100% SW and in 125%SW (P<0.001). However, in both 111 and 140% SW, haemolymph osmolarity was significantly increased (P<0.001).

It can be seen from Tables 3.12 and 3.14 that in medium osmolarities below that of seawater, a decrease in haemolymph osmolarity occurred in both species. Although regulation was occurring and crabs maintained the osmolarity of haemolymph above that of the medium, regulatory ability was reduced with increasing temperature. At osmolarities like that of seawater, or above, this trend was not seen.

3.3.6 Comparisons of Laboratory and Field Samples

Figure 3.11 shows the comparison of both laboratory and field sampled C. taeniatus and C. virescens haemolymph, as well as acclimation tank and tidepool water. This figure demonstrates that water in the laboratory, in which animals were acclimated before testing, was more concentrated than water in the field (one way ANOVA, field: 1014.57 ± 7.0; laboratory: 1111.85 ± 27.7, F1,39=165.269, P<0.001).

When haemolymph osmolarity was compared between field and laboratory sampled crabs, Model I, two way ANOVA for “Species” and “Place” showed a significant effect of where haemolymph was sampled (F1,64 = 34.170, P<0.001).
Figure 3.11 Results of comparisons between osmolarity of laboratory and field sampled seawater ( ), C. taeniatus ( ), and C. virescens ( ). Laboratory samples were at 25 ± 2°C. Temperature measurements were not taken for field samples. Error bars represent 1 standard error. For C. taeniatus: lab (n = 27), field (n = 6); for C. virescens: lab (n = 27), field (n = 8); for water: lab (n = 27), field (n = 14).
However, there was no difference in haemolymph osmolarity between species in either the field or the laboratory ($F_{1,64} = 0.00$, $P>0.05$), and no significant interaction of species and place occurred ($F_{1,64} = 0.269$, $P>0.05$).

Two-tailed, T-tests showed significant differences when haemolymph osmolarities from both species in the field were compared with tidepool water and when laboratory sampled haemolymph was compared with acclimation water (field: *C. taeniatus*: $t_5=8.885$, $P<0.001$, *C. virescens*: $t_7=4.246$, $P<0.01$; laboratory: *C. taeniatus*: $t_{26}=9.127$, $P<0.001$, *C. virescens*: $t_{26}=7.786$, $P<0.001$). Table 3.15 summarises comparisons analysed by one way ANOVA’s and two-tailed T-tests.

Consistent in both sampling situations and with the findings of osmoregulatory ability investigations reported in this chapter is that haemolymph osmolarity was significantly higher than medium osmolarity for both *C. taeniatus* and *C. virescens*, but no difference in haemolymph osmolarity was found between species.

### 3.4 DISCUSSION

#### 3.4.1 Oxygen Consumption

Results of the Model I, three way ANOVA (Table 3.3) suggested that the respiratory responses of both *C. taeniatus* and *C. virescens* were significantly affected by changes in both temperature and salinity as independent factors ($P<0.001$). Apart from a significant interaction between species × temperature, no
Table 3.15 Results of ANOVA and T-test analyses of haemolymph and water sampled from C. taeniatus (C.t.), C. virescens (C.v.), and the medium, respectively, in the field and in the lab. **: p < 0.001, *: p > 0.001, N.S.: p > 0.05, ----: comparison not possible.

<table>
<thead>
<tr>
<th>Species</th>
<th>Haemolymph</th>
<th>Field water</th>
<th>Field</th>
<th>Lab</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. t</td>
<td>**</td>
<td>N.S</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>C. v</td>
<td>*</td>
<td>N.S</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>C. t – C. v</td>
<td>*</td>
<td>N.S</td>
<td>**</td>
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OXYGEN CONSUMPTION, OSMOREGULATION
other significant interactions occurred. The species × temperature interaction is due to the lesser respiratory response to some temperatures by *C. taeniatus*.

### 3.4.1.1 Effects of Temperature

#### 3.4.1.1.1 *C. taeniatus*

In almost all salinities tested, oxygen consumption of *C. taeniatus* increased with increasing temperature (Table 3.2), although these changes were significant in only 25% of all treatment comparisons (Table 3.5). The exception was when temperature increased from 25 – 35°C in 22% SW oxygen consumption was slightly, but not significantly, lower. For *C. taeniatus* no effect of temperature occurred between 25 and 35°C at any of the salinities tested (Table 3.5). This was also reflected in temperature coefficients (Q₁₀’s) for *C. taeniatus* that were at or very near unity over the range of salinities tested between 25 and 35°C (Table 3.6).

Additionally, and importantly, temperatures from 15 – 35°C did not have a significant effect on the oxygen consumption of *C. taeniatus* at the acclimation salinity of 100% SW (Tables 3.5 and 3.7). Q₁₀ values at the acclimation salinity were at unity between 15 and 35°C, further demonstrating temperature insensitive respiration in *C. taeniatus* over the range of temperatures tested at the acclimation salinity (Table 3.6).

Newell (1970) showed that the standard rate of respiration in intertidal animals could include both temperature dependence and temperature insensitivity, depending on the range of temperatures regularly experienced. Newell and Northcroft (1967) have suggested that relative insensitivity of metabolism is necessary for ectotherms to survive environments subject to rapid changes in
temperature. Thus, temperature insensitivity, as demonstrated by *C. taeniatus* at all
temperatures in 100% SW (the acclimation salinity) may provide an advantage to
these organisms facing variable temperature conditions on highly exposed intertidal
areas. Newell (1979) believes that it is those organisms that typically occur on the
upper shore, and experience the widest variations in temperature, that demonstrate
temperature independency. This may be the case with *C. taeniatus*.

However, little is known of the mechanisms that facilitate temperature
insensitivity. Hawkins (1995) reported that in mussels acclimated to a constant
temperature, animals with higher rates of metabolism usually had greater metabolic
sensitivity to temperature change. This general pattern of responses has been
explained in terms of the concentration of substrate within the cell and the
permeability of the membrane (Newell and Bayne, 1973; Newell, 1979; Newell and
Branch, 1980). When levels of available substrate are in excess of the Michaelis
constant\(^\dagger\) (\(K_m\)) value for a particular enzyme, reaction rates will be temperature-
dependent since the fraction of molecules that can overcome activation energy
greatly increase with even a small increase in temperature (Hochachka and Somero,
1973; Somero and Hochachka, 1976). On the other hand, when substrate levels for
enzymatic reactions fall below the \(K_m\)-value for the particular enzyme, the reaction
rate of the enzyme is then controlled by the enzyme-substrate affinity. Therefore, a
reduced enzyme-substrate affinity may maintain the rate of reaction independent of
changes in temperature (Hochachka and Somero, 1973). Experiments beyond the
scope of this thesis are needed to investigate whether there is agreement between

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\(^\dagger\) The concentration of a substrate required for hyperbolic enzymes (or \(S_{0.5}\) for sigmoidal enzymes) to
act at half their maximum velocity. This value acts as a measure of the affinity of an enzyme for its
substrate (Somero and Hochachka, 1976).
the influence of temperature on substrate affinities of the main enzymes that regulate rates and directions of metabolic flow and observed effects of temperature on oxygen consumption (Somero and Hochachka, 1976). However, Newell and Pye (1971) observed that oxygen uptake by isolated mitochondria from the intertidal mollusc, *Littorina littorea* was basically temperature-independent at low concentrations of substrate (pyruvate), but when supplied with high concentrations, oxygen consumption became significantly temperature-dependent. Similar temperature effects on metabolism have also been observed for lipid oxidation in isolated trout tissue (Dean, 1969) and a variety of metabolites in low concentrations in fish liver homogenates (Hochachka, 1968).

There is little doubt that mechanisms controlling respiratory responses may be highly influenced by genetic controls (Hazel and Prosser, 1974; Hochachka and Somero, 1984; Hawkins *et al.*, 1986; Hawkins *et al.*, 1987; Koehn and Bayne, 1989; Hawkins, 1995). The study of multi-locus heterozygosity has advanced understanding of how genotype may affect the physiological function of some intertidal invertebrates (Hawkins *et al.*, 1986; Hawkins 1995). An important point here is that if metabolic insensitivity to temperature is genetically controlled, and multi-locus heterozygosity increases with increasing height on the shore, as has been shown by Koehn *et al.* (1973, in Hawkins, 1995) and Lavie and Nevo (1986), this physiological response to temperature will be subject to natural selection and therefore, adaptation.
3.4.1.1.2 *C. virescens*

A slight temperature effect occurred in the oxygen consumption of *C. virescens* in all treatment salinities (Table 3.2), although this was only significant in half of the temperature-salinity comparisons (Table 3.5). In every instance, oxygen consumption of *C. virescens* increased as temperature increased (Table 3.2).

It is of interest to note that results reported here for *C. virescens* demonstrated a significant influence of temperature when oxygen consumption was compared between 15 and 25°C as well as between 15 and 35°C at the acclimation salinity of 100% SW (Table 3.5). Q$_{10}$ values for *C. virescens* showed a much wider, and generally higher range, nearing double that shown for *C. taeniatus* (Table 3.6).

Hawkins *et al.* (1986) concluded that large metabolic responses to changes in temperature were associated with greater maintenance metabolism in more homozygous individuals. As well, a high energy expenditure for maintenance means that net production is sustained across a narrower environmental range, resulting in tissue wasting under conditions that differ even a little from those in which maximal production occur (Koehn and Bayne, 1989; Hawkins, 1995).

Thus it appears that when metabolic sensitivity to environmental temperature increases, there is a resultant reduction in the ability to survive extreme temperature stress due to higher, long-term energy cost (Hawkins, 1995).

3.4.1.1.3 Temperature Coefficients (Q$_{10}$’s)

The values of Q$_{10}$ for oxygen consumption in the experimental salinities at temperatures between 15 and 35°C confirm that *C. virescens* is metabolically stressed when exposed to acute changes in temperature at the acclimation salinity
Q_{10} for *C. virescens* is lowest at the 25 – 35°C comparison, but remains above unity. In contrast, the values for *C. taeniatus* remain very near to unity throughout the temperature range experienced in the acclimation salinity.

While there have been many studies on the metabolic responses of intertidal organisms to temperature (see reviews by Newell, 1969, 1976, 1978), only a few have investigated such responses in hermit crabs, especially respiratory responses in relation to acute changes in temperature (Burggren and McMahon, 1981; Vernberg *et al.*, 1981; Moreira and Nelson, 1990). However, the tropical and temperate crab species previously studied all demonstrated relatively high Q_{10}'s, and thus metabolic sensitivity, over the range of temperatures reported. Nevertheless, in the investigation by Burggren and McMahon (1981) intertidal crabs did show a somewhat lower Q_{10} for oxygen consumption than either the subtidal or supratidal species examined.

In her study on the respiratory responses of the intertidal hermit crab *C. vittatus*, Wernick (1982) found that after acclimation to 20°C and 35‰, crabs tested within the temperature range from 10 – 35°C (at 5°C intervals) showed little sensitivity of oxygen consumption rates to changes in temperature. Q_{10} values for *C. vittatus* were close to unity in temperatures between 20 – 30°C, but increased significantly at 35°C. In the range of 15 – 20°C, Q_{10} doubled, but between 10 – 15°C, oxygen consumption was depressed with a correspondingly reduced Q_{10} value. Wernick explains the increased Q_{10} at the highest temperature as a result of higher activity observed at what was probably near lethal temperature for *C. vittatus*. In the range of 15 – 20°C, higher Q_{10} values for oxygen consumption are explained as occurring due to temperatures below the normal range of the habitat.
This has also been reported for a number of other tropical crustaceans by Vernberg and Vernberg (1972, in Wernick, 1982) and Vernberg and Costlow (1966, in Wernick, 1982).

3.4.1.2 Effects of Salinity

3.4.1.2.1 C. taeniatus

Across the range of salinities tested in this investigation, C. taeniatus showed no change in oxygen consumption at the acclimation temperature of 25°C (Tables 3.2 and 3.4). McLusky (1969) has suggested that no change in oxygen uptake in the euryhaline amphipod, Corophium volutator, subjected to lower than normal salinities may be the result of a metabolic shift of energy from growth processes into osmoregulation. Thus, even though energy requirements for osmoregulation would increase, no net change in oxygen consumption would be observed.

Qualitative observations on the activity of C. taeniatus exposed to salinities from 11 – 140% SW at 25°C for 7 hours suggested that at both low (<69%) and high (>125%) salinities visible activity was reduced or ceased. In extreme salinities, walking as well as antennal and antennule movement occurred much less frequently than in moderate salinities. Since oxygen consumption in this species was highest in the lower salinities at 25°C (see Table 3.2) it is unlikely that external activity was a major contributor to the high metabolic rates observed in low salinities at the acclimation temperature.
3.4.1.2.2 *C. virescens*

For *C. virescens* oxygen consumption at all three temperatures was lowest at the upper and lower salinities (Table 3.2). These results do not agree with those of Shumway (1978) working with *P. bernhardus* or Sabourin & Stickle (1980) who studied *C. vittatus*; both found oxygen consumption highest in hermit crabs when salinities were lowest. Furthermore, Dehnel (1960), Todd and Dehnel (1960) and McFarland & Pickens (1965) reported increased oxygen consumption when the intertidal crabs, *Hemigrapsus oregonensis* and *H. nudus*, and the grass shrimp *Palaemonetes vulgaris*, respectively, were exposed to decreasing salinities.

McFarland & Pickens (1965) proposed that increased oxygen uptake at lowered salinities is due to an increase in osmoregulatory work and an increase in locomotory activity. Dehnel (1960) and Todd and Dehnel (1960), however, proposed that increased oxygen consumption resulted from increased osmotic activity and not increased muscular activity. Since both of these authors used animals capable of osmoregulation, it is most likely that increased oxygen consumption was mainly due to increased osmoregulatory activity (Shumway, 1978). King (1965) also reported increased respiration by *Carcinus mediterraneus* and *Callinectes sapidus* in dilute seawater. Both of these species are osmoregulators and are often found in brackish water. However, results obtained for *C. virescens* in the present study demonstrated the decrease of oxygen consumption in sub- or supranormal salinities described as typically associated with stenohaline organisms (Kinne, 1967, 1971).

These results agree with King (1965) who also reported a 50% reduction in respiration rate in *Maja verrucosa* and a 30% reduction in respiration rate in *Libinia*
emarginata in 50% SW (17‰). It was noted that for Maja in low salinity water there was an obvious decrease in neuromuscular activity as well as the rate of ventilation, while Libinia showed increased muscular activity in the same medium (King, 1965). King (1965) suggested that neither osmotic work nor increased cellular hydration were adequate to explain the extent of salinity effects on oxygen consumption by intact animals.

Elevated oxygen consumption for C. virescens in 56 compared to 100% SW at all temperatures (Table 3.2) are most likely to be the result of osmoregulatory processes as reported by Dehnel (1960), Todd and Dehnel (1960) and Dimock & Groves (1975). It may be that osmoregulation in lower salinities is a more energy expensive process for C. virescens than for C. taeniatus as reflected in the trend for the former species to have a higher rate of oxygen consumption at both 56 and 22% SW than the latter. Qualitative observations of C. virescens exposed to low (<69%) and high (>125%) salinity at 25°C for 7 hours suggested that walking activity, as well as antennal and antennule activity slowed or stopped completely. Unlike C. taeniatus, the trend toward lower activity in extreme salinities is consistent with lower metabolic rates for C. virescens in low and high salinities (see Table 3.2). Still, it is also possible that reduced oxygen consumption by C. virescens at all temperatures in 22 and 125% SW compared to 100% SW (Table 3.2) may result from a mechanism to reduce influx and efflux of ions and water. In low salinities hermit crabs may experience ionic efflux and osmotic influx, while in high salinities they may experience ionic influx and osmotic efflux. In order to reduce both the efflux and influx of ions and water, the permeability of their gill membranes may be reduced by either physiological or mechanical means. It is possible that
OXYGEN CONSUMPTION, OSMOREGULATION

Scaphognathite activity may be responsive to changes in the ionic composition of the medium (Taylor, 1977). Taylor (1977) showed that, in Carcinus maenas exposed to low salinity, gill ventilation was associated with scaphognathite movement. In C. taeniatus and C. virescens, scaphognathite and ventilation activity may be involved in the mechanical regulation of water and ionic influx and efflux at the gills, if indeed osmoregulatory processes do occur at this site. Since this is the surface through which respiration takes place, a change in permeability could also change respiratory rate (see review by Gilles and Delpire, 1997).

3.4.2 Osmoregulation

Results from experiments on the ability of C. taeniatus and C. virescens to osmoregulate in a range of salinities and temperatures over 7 hours found no significant difference in osmoregulatory ability between the two species. Both were equally capable of maintaining haemolymph osmolarity above medium osmolarity (hyperosmoregulation) in every combination of temperature and salinity tested.

Young (1979a) suggested that a basic difference in physiological responses exists between the hermit crab superfamilies Coenobitoidea and Paguroidea. He found that studies on osmoregulation demonstrated the ability of Coenobitoidea to hyperosmoregulate in dilute media, while the Paguroidea studied did not. The results of studies on shell-less Clibanarius erythropus (a member of the Coenobitoidea) by Castillo et al. (1988) did not agree. They found that in media from 64 – 217% SW (23 – 78‰), haemolymph osmolarity of C. erythropus was slightly lower than the medium. However, it has been argued that experiments with shell-less hermit crabs are unrealistic and that the osmoregulatory abilities of
coenobitoid or paguroid hermit crabs will be reduced when shells are absent (Shumway, 1978). Additionally, Castillo et al. (1988) found that in dilute media from 62 – 31% SW (22 – 11‰ salinity), *C. erythropus* haemolymph osmolarity was only slightly hyperosmotic. *C. erythropus* does not, therefore, follow the hypothesised pattern of hyperosmoregulating for coenobitoids.

The findings of this chapter are consistent with the hypothesis that hermit crabs in the superfamily Coenobitoidea are hyperosmoregulators. Both *C. taeniatus* and *C. virescens* maintained haemolymph osmolarity well above the osmolarity of the medium in 11 – 140% SW, and especially below 69% SW (see Figure 3.8, Figure 3.9 and Figure 3.10).

The difference between results reported by Castillo et al. (1988) for *C. erythropus* exposed to salinities between 14 and 222% SW, and results for *C. taeniatus* and *C. virescens* may demonstrate that species belonging to the same superfamily may undergo adaptations specific to their environmental conditions, despite their common phylogeny (Castillo et al., 1988).

### 3.4.3 The Interaction of Salinity and Temperature on Osmoregulation

The significant interaction of salinity and temperature (Table 3.13) indicates that changes in haemolymph osmolarity due to salinity did not occur uniformly over the changes in temperature.

Comparisons of pooled *C. taeniatus* and *C. virescens* haemolymph osmolarity data showed that in 100% SW there was a slight, but insignificant increase in haemolymph osmolarity when temperature rose from 25 to 35°C, but in 125% SW blood osmolarity increased significantly over the same temperature.
change. In 140% SW osmolarity climbed with increases in temperature from 15 to 25°C and from 25 to 35°C (Table 3.12). However, there was an inverse effect of temperature on haemolymph osmolarity in salinities between 11 and 111% SW. This means that in dilute seawater it becomes increasingly difficult for both species to maintain haemolymph hyperosmotic to the medium as temperature increases reducing their ability to osmoregulate. Therefore, although low salinities and high temperatures are stressful as independent factors, the combination of the two is especially stressful and results in greater dilution of body fluids. Combined conditions of low salinity and high temperature are most likely to occur in the upper shore of the intertidal zone where C. taeniatus is very abundant, suggesting that this species is better able to tolerate these stresses.

### 3.4.4 Comparisons of Laboratory and Field Samples

Comparisons between laboratory and field sampled water demonstrated that laboratory acclimation water of 100% SW had a significantly higher osmolarity than the osmolarity of less concentrated “normal” field water. Correspondingly, haemolymph osmolarity of laboratory acclimated hermit crabs was significantly higher than that of field hermit crabs. However, no difference in haemolymph osmolarity existed between species in either laboratory or field situations. The haemolymph osmolarity of both laboratory and field crabs was significantly higher than laboratory acclimation water, or tidepool water osmolarity, respectively (Figure 3.11, Table 3.15). These results also demonstrated that the hyperosmotic state of haemolymph from laboratory acclimated hermit crabs in 100% SW (36‰ salinity) was not a laboratory induced artefact.
3.5 Discussion Summary

Results from investigations into the respiratory responses of *C. taeniatus* and *C. virescens* to short term, acute changes in combinations of temperature and salinity, showed a significant difference between species in respiration, as measured by oxygen consumption rate, in 100% SW (Table 3.5). This suggested that for adult *C. taeniatus* in the total weight range of 1 - 2.5g, acutely exposed to temperatures from 15 – 35°C, respiration was temperature insensitive. This was not the case for *C. virescens*.

The results from oxygen consumption experiments demonstrated a more sensitive metabolic response to changes in intertidal stressors (especially temperature) by the low shore species *C. virescens*, while the high shore species, *C. taeniatus*, showed much less sensitivity in metabolic response to changes in environmental stressors. Thus, the results of respiratory experiments done in this study and the distribution of *C. taeniatus* and *C. virescens* on the shore may be consistent with the possibility that heat resistance increases with increasing intertidal exposure (Koehn *et al.* (1973 in Hawkins, 1995); Lavie and Nevo, 1986; Hawkins, 1995) and greater multi-locus heterozygosity (Hawkins *et al.*, 1986; Hawkins, 1995). It is important to note, therefore, that if temperature insensitivity is genetically controlled, it is subject to natural selection and may lead to physiological adaptation.

In this chapter the original hypotheses that differences in respiratory responses may relate to differences in distribution were supported by results of oxygen consumption experiments. There was, however, no significant difference in the abilities of the two species to adjust the concentration of the extracellular fluid
in response to changes in salinity. Both species were equally able to maintain haemolymph osmolarity above the osmolarity of the medium (hyperosmoregulate) in a range of salinities from 11 – 140% SW and in temperatures ranging from 15 – 35°C. For both species increased temperature significantly reduced the osmolarity at which haemolymph was maintained in dilute seawater resulting in greater dilution of body fluids. This indicates that the combined factors of low salinity and high temperature are stressful to both species. These conditions, however, are more likely to occur at high shore where *C. taeniatus* is more abundant and suggests that this species is better able to tolerate this combined stress, possibly by combined adaptations that reduce metabolic sensitivity to high temperature and physiological sensitivity to body fluid dilution.

The hyperosmolarity of field sampled crab haemolymph to tidepool water was consistent with the hyperosmolarity of lab-sampled haemolymph to acclimation water. Although laboratory water had a significantly higher osmolarity than field water, crab haemolymph osmolarity was not different between species in either the field or laboratory.

In the next chapter, I examine the hypothesis that *C. virescens* is not as tolerant of high shore habitats in local environments as *C. taeniatus* is and that survival on the upper shore will be relatively greater for the latter species than for the former. I also address the hypothesis that physiological mechanisms in *C. virescens* for survival during extended exposure to unique environmental conditions may be less adequate than those in *C. taeniatus*. 
4.0 **CHAPTER 4: SURVIVAL**

4.1 **INTRODUCTION**

In Chapter 3, I concluded that there was a difference in respiratory responses between *C. taeniatus* and *C. virescens* exposed to short term changes in temperature, especially when tested at the acclimation salinity of 100% SW. The respiratory rate of *C. virescens* was sensitive to rapid changes in temperature, while that of *C. taeniatus* was not.

It has been suggested that respiratory responses to temperature are genetically determined (Koehn and Bayne, 1989; Hawkins, 1995) and that organisms with less sensitive metabolic responses to temperature have greater multi-locus heterozygosity (Hawkins *et al.*, 1986; Koehn and Bayne, 1989; Hawkins, 1995). As well, both multi-locus heterozygosity and temperature insensitivity are known to increase with increasing height on the shore (see Hawkins, 1995). In this context, Newell (1969) suggested that temperature insensitivity over a wide range of temperatures is part of the process of acclimation to high and rapidly changing temperatures experienced in the upper intertidal zone.

In addition to temperature stress, hermit crabs are also vulnerable to osmotic stress since tidepool salinities fluctuate widely over short periods of exposure in the intertidal zone (Davenport, 1972a; Young, 1980, 1991). The ability to maintain an osmotic gradient between extracellular fluid and the external medium may allow these crabs to cope with large and rapid changes in salinity. From my experiments on respiratory responses and osmoregulatory ability (see Chapter 3), I concluded
that there were no differences between species in ability to maintain haemolymph osmolarity above that of the medium in the entire range of salinities tested over “normal” periods of intertidal exposure (about 7 hours). Evidence from these experiments suggested that both species osmoregulated less in salinities from 140 - 69% SW and more in salinities from 69 - 11% SW, although the ability to osmoregulate in dilute seawater decreased with increasing temperature in both species.

These laboratory experiments provided evidence that there was a difference between species in their metabolic responses to temperature, but that there was no difference between species in their ability to maintain haemolymph osmolarity over a wide range of salinities. Yet, exposure to low salinity may also occur over longer periods than low tide exposure. The surface waters of intertidal areas in close proximity to river outfalls are frequently diluted due to seasonal and irregular flood events.

In order to investigate differences in susceptibility to prolonged low salinity, experiments into the survival of *C. taeniatus* and *C. virescens* under conditions of long term exposure to dilute media were carried out under controlled conditions in the laboratory. Nevertheless, Underwood (1979) strongly argued that conclusions drawn from laboratory experiments alone may not necessarily be applicable to situations in the field, since laboratory conditions may not occur in nature. He also emphasised that experimental manipulations in the field are often the best methods for determining factors which influence distribution and abundance (Underwood, 1979).
Although the importance of field manipulations has been emphasised in a number of studies (see review by Underwood, 1979; Metaxas and Scheibling, 1993), to my knowledge, no experiments other than that of Bertness (1981a) report the translocation of rocky intertidal hermit crabs from one height on the shore to another. Additionally, I found no reports in the literature on the translocation of marine intertidal hermit crabs into brackish water.

I designed a series of experiments to investigate if there were differences in the ability of both species to survive translocations in the field. One set of experiments was carried out to determine if *C. virescens* was able to survive the physical conditions of high shore and potentially inhabit this area of the intertidal zone. The other set of translocations was undertaken to determine if there was a difference in survival between species under conditions of long term, low salinity that may occur on intertidal shores in the vicinity of river estuaries during regular river flows and irregular flood events.

Further, in an attempt to determine if differences in ionic regulation occurred between species, haemolymph samples from both species under conditions of long term, low salinity in the laboratory were analysed for sodium, potassium, calcium and magnesium. These analyses were considered to be important in investigating whether changes in the concentration of cations in the haemolymph of crabs exposed to low salinity could also help to explain differences in survival between the two species and be related to their distribution on the shore.
4.2 MATERIALS AND METHODS

4.2.1 Survival in the Laboratory

Crabs were collected from Emu Point between December, 1999 and February, 2001. They were taken to the laboratory and placed in aquaria in 100% SW under the same acclimation conditions as animals used for oxygen consumption experiments described in the previous chapter.

A preliminary survival trial was carried out with 15 _C. taeniatus_ and 15 _C. virescens_. Crabs were taken from the acclimation tank 15 minutes prior to the start of the experiment. Each one was individually and randomly placed in one of 30, 250mL clear perspex chambers containing 50mL of 22% SW in a constant temperature room at 25 ± 2°C. Chambers were numbered for ease of recording repeated information on individuals. Crabs were irregularly checked for survival over a period of 78 hours. This experiment was repeated a second time and all data pooled.

Further survival tests were carried out on individuals at 25 and 35°C using the procedure described above. One experiment, with 30 replicates was carried out at each temperature for each species. Controls consisted of 15 crabs of each species placed individually in 50mL of 100% SW in 250mL perspex chambers. Exposure to 15°C was for 83 hours, to 25°C for 73 hours and to 35°C for 29 hours. In all treatments and controls, individuals were counted as “Dead” if there was no antennal, antennule or maxilliped movement even after they were prodded for one or two minutes.
For each temperature, all data from experimental repetitions were pooled and analysed by Chi-squared 2×2 contingency table.

4.2.2 Intertidal Translocation

An intertidal, translocation experiment was conducted between July, 2000 and February 2001 at Tanby Point (S23°14.13’, E150°49.657’), Keppel Bay, Australia.

Translocation chambers were made from 1mm thick, 90mm diameter PVC pipe, cut to lengths of 160mm. Several holes were drilled along the length of the chambers to allow water exchange and the flushing of waste materials. A covering of nylon mesh was permanently fixed to one end of the chamber and held in place by a plastic zip tie. A removable solid PVC cap was placed on the opposite end to provide an easy method for adding and removing hermit crabs in the field.

All *C. taeniatus* and *C. virescens* were collected one and a half hours before low tide from the lower intertidal zone immediately prior to the start of the experiment. Hermit crabs were collected without determination of size, sex or shell species, so that animals placed in experimental chambers varied in size, sex and shell type. A group of 12 crabs was placed together in each chamber. Groups consisted of six of each species, or 12 of one species. Chambers were pre-numbered and randomly selected to be in either the treatment or control group so that some crabs were moved up the shore, while controls were returned to the shore height they were collected from.

Control group chambers were secured to heavy rocks by nylon string at randomly selected points along the water’s edge during low tide. Treatment group
chambers were secured in the same way, but placed so that they would receive some tidal wash during high tide. The latitude and longitude for each chamber were recorded.

All chambers were exposed to prevailing conditions in the field for 48 – 72 hours (although one chamber at high shore could not be relocated and remained in the field for 28 days until it was found, with all crabs alive).

At the end of the exposure period, all hermit crabs were removed from the chambers and placed in a container of seawater collected from a nearby tidepool. Crabs were counted as “Alive” if they emerged from the shell, or moved their pereopods, antennae, antennules or maxillipeds. In instances where crabs did not emerge, shells were gently broken at the apex and the crab “tickled” in an attempt to evoke a movement response. The experiment was repeated eight times. Although the total number of chambers differed among experimental repetitions, the number of control group chambers versus the number of treatment group chambers set out during a repetition was the same. However, total numbers of control and treatment chambers were different in the end, due to losses of both types.

The number of each species “Alive” and “Dead” for “Control” and “Treatment” chambers was tallied over all 32 control replicates and 40 treatment replicates and analysed by a 3-dimensional Chi-squared $2 \times 2 \times 2$ contingency table test for mutual independence, followed by $2 \times 2$ contingency table tests for partial independence (Zar, 1999).
4.2.3 Translocation into an Estuarine Environment

This experiment compared the survival of *C. taeniatus* and *C. virescens* translocated to a long term, low salinity environment.

*Clibanarius taeniatus* and *C. virescens* were collected from Tanby Point in January, 2001 without measuring their size, sex or shell species. All individuals were used in experiments within two weeks of collection.

Crabs were transported to the experimental sites in the Fitzroy River, Rockhampton in a 50cm long × 35cm wide × 14cm deep, open plastic container in approximately 2L of 100% SW (36‰). Treatment sites were chosen that provided prolonged exposure to, predominantly 20 – 35% SW, while control sites farther downstream were chosen to provide predominant exposure to salinity in the range of 75 – 95% SW, despite semi-diurnal ebb flows of fresh water from upstream at both sites (see Table 4.2). Although Table 4.2 gives the impression that repetition 2 was continuously exposed to very low salinities, this is because at each site salinity was recorded at the start and end of the experiment. In reality, repetition 2 would have been exposed to higher salinities during flood tide.

Pre-numbered chambers made of PVC pipe (as described previously) were randomly assigned to seven concrete blocks. Each chamber contained either six of each species, or 12 of one species of variable size, sex and shell species. Chambers were kept just below the surface of the water by securing them to the top one metre of a length of rope tied to a concrete block on one end, and a Styrofoam buoy on the other (see Figure 4.1). This arrangement prevented the chambers from drifting and allowed them to be easily located for retrieval.
Figure 4.1 Diagram of the block, buoy and chambers arrangement used for estuarine translocation experiments. Note that experimental chambers sit within one metre of the surface.
Hermit crabs were exposed to experimental conditions for 48 hours (repetition 1) and 28 hours (repetition 2). The time of exposure for repetition 2 was reduced in an effort to increase the number of surviving animals in the experimental treatment.

Upon retrieval of the chambers, each group of crabs was placed in 100% SW and given approximately 3 minutes to revive. Each individual was inspected for signs of life. If hermit crabs did not respond to abdominal prodding by moving their antennae, antennules, pereopods or maxillipeds, they were considered dead. The remainder were counted as “Alive”, placed in a separate bath of normal seawater and returned to the laboratory. Each hermit crab was used only once.

The total number of “Alive” versus “Dead” of both species for all 35 replicates was analysed by a Chi-squared 2×2 contingency table.

4.2.4 Ionic Regulation

During survival experiments in 22% SW at 15 and 35°C, haemolymph samples of more than 50µL were withdrawn from both dying hermit crabs and individuals that survived until the end of the experiment by thoracic puncture with 29-gauge syringe needles. Dying crabs were identified as those that demonstrated very little resistance to being removed from the shell and had a delayed physical response to abdominal prodding. Samples were taken at 4 hour intervals in both 15 and 35°C experiments. However, in some intervals in the 15°C experiment the number of dying crabs was low, so intervals were pooled into 24 hour groups. In the 35°C experiment, the number of dying crabs was sufficient to allow the use of 4 hour groups. Fifty microlitres of haemolymph from each specimen were pipetted
into 10mL vials and diluted to 5.0mL by the addition of 4950µL of 2% nitric acid. As a control, 50µL haemolymph samples were taken from each species in the acclimation aquaria and analysed in the same way. These are presented as “Initial” measurements. Five, 5.0mL control blanks of 2% nitric acid, 22% SW and 100% SW were also prepared. All samples were kept refrigerated at 4.0°C until analysed.

Samples were analysed by a Perkin Elmer Optima 3000DV Inductively Coupled Plasma Emission Spectroscope (ICPES) for the concentrations of sodium ions (Na⁺), potassium ions (K⁺), calcium ions (Ca++) and magnesium ions (Mg++). Previously prepared standards were used to calibrate readings for each of these ions. Standards were prepared in concentrations of 0.0mg/L, 0.100mg/L, 1.00mg/L and 10.00mg/L for each ion. An additional 50.00mg/L standard was prepared for Na⁺ since expected concentrations of this ion were approximately 4 – 5 times greater than for the others. Standards were used to generate calibration curves which are provided in Appendix I.

Three of the prepared 5.0mL control blanks were analysed first, followed by all diluted haemolymph samples and finally the remaining two control blanks.

Fifteen replicates each of C. taeniatus and C. virescens were used for each experiment. The experiment was performed once at 15°C and three times at 35°C, but unfortunately, the acclimation salinity for the third experimental repetition at 35°C was lower than the other two, so it was excluded from the pooled data presented below. Haemolymph concentrations of each ion were compared with the concentrations of the medium by one way ANOVA’s.
4.3 RESULTS

4.3.1 Survival in the Laboratory

In this experiment, both species were exposed to low salinity seawater at 15, 25 and 35°C to compare survival.

Figure 4.2A shows the comparison of the percent survival between *C. taeniatus* and *C. virescens* when exposed to 22% SW at a temperature of 15°C. Within 24 hours the number of live individuals of both species had decreased to less than 80%. After 48 hours, 63% of *C. taeniatus* and only 26% of *C. virescens* remained alive. By 65.5 hours of exposure, 43% of *C. taeniatus* still remained alive, but 97% of *C. virescens* had died.

Chi-square analysis of the data at 65.5 hours showed that *C. taeniatus* survived these conditions significantly better than *C. virescens* ($\chi^2 = 1.69$, P<0.01). In control experiments where both species were held at 15°C in 100% SW, all *C. taeniatus* (n=15) and *C. virescens* (n=15) survived exposure until the end of the experiment after 83 hours.

In Figure 4.2B, the percent survival of the two species exposed to 22% SW at 25°C is shown over an exposure time of 76.5 hours. At 46 hours, 79% of *C. taeniatus* remained alive compared with only 42% of *C. virescens*. While 76% of *C. taeniatus* were still alive at the end of 76.5 hours, only 35% of *C. virescens* survived the same exposure.

At 25°C, a Chi-square analysis of the data at 76.5 hours also showed a significant difference in survivorship in favour of *C. taeniatus* ($\chi^2 = 8.31$, P<0.01).
Figure 4.2  Comparison of survival between *C. taeniatus* (■) (n=30) and *C. virescens* (□) (n=30) exposed to 22% SW (8‰) medium A: at 15°C over 68.5 hours and, B: at 25°C over 76.5 hours.
Figure 4.3  A: Comparison of survival between *C. taeniatus* (■) (n=30) and *C. virescens* (■) (n=30) exposed to 22% SW medium at 35°C over 28.5 hours. B: Controls. *C. taeniatus* (■) (n=15) and *C. virescens* (■) (n=15) exposed to 100% SW at 35°C over 29 hours (control).
In contrast, all *C. taeniatus* (n=15) and all *C. virescens* (n=15) survived at 25°C in 100% SW for the 73 hour control experiment.

The survival of the two species was also different when exposed to 22% SW at 35°C (Figure 4.3A). After only 5.25 hours *C. virescens* survivorship was reduced to 52%, while 93% of *C. taeniatus* remained alive. After 10 hours, only 7% of *C. virescens* were living compared with 80% of *C. taeniatus*. Within 13 hours, 97% of *C. virescens* had died, while 70% of *C. taeniatus* were still alive. A comparison of the data after 13 hours demonstrated a highly significant difference in survival between species, again in favour of *C. taeniatus* ($\chi^2 = 25.16, P<0.001$).

The control at 35°C (Figure 4.3B) showed that *C. virescens* was less tolerant of the higher treatment temperature than *C. taeniatus*, even in 100% SW. The number of live individuals of both species decreased slightly in the first six hours, but there was no statistical difference in survival between species for up to 29 hours of exposure ($\chi^2 = 1.88, P>0.05$).

The results in Figures 4.2A and B and 4.3A showed a significant difference in survival, both within and between species in conditions of low salinity at 15, 25 and 35°C when compared with normal salinity controls at the same temperatures.

### 4.3.2 Intertidal Translocation

In this field experiment, both species were collected from the water’s edge. Some crabs of each species were put at high shore, while controls were returned to the low shore.

The data presented in Table 4.1 were analysed for mutual independence of species, location and survival (alive or dead). A significant difference in the overall
<table>
<thead>
<tr>
<th></th>
<th>C. taenius</th>
<th>C. virescens</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Alive</td>
<td>Dead</td>
</tr>
<tr>
<td>Control (Low Shore)</td>
<td>111</td>
<td>0</td>
</tr>
<tr>
<td>Treatment (High Shore)</td>
<td>94</td>
<td>1</td>
</tr>
</tbody>
</table>

Table 4.1 A comparison of the proportions of *C. taenius* and *C. virescens* dead and alive over all control and treatment repetitions for the intertidal translocation experiment at Tanby Point.
3-dimensional Chi-squared was found ($\chi^2 = 11.86$, $P<0.05$). Location and species were not independent due to the experimental design in which the number of each species at each location was different, but survival was shown to be independent of species and location ($\chi^2 = 1.79$, $P>0.05$). Thus, there was no difference in survival between low shore and high shore for both species.

### 4.3.3 Translocation into an Estuarine Environment

*Clibanarius taeniatus* and *C. virescens* were taken from the intertidal zone and translocated to a low salinity environment in the Fitzroy River estuary for at least 24 hours in order to compare survival between species.

Survival of both species changed with distance up the tidally dominated Fitzroy River estuary. In control sites where salinity was between 75 – 95% SW during high tides (Table 4.2), 100% of both species survived over 48 hours of exposure (Table 4.3A). At experimental sites, where salinity during high tide was between 20 - 35% SW (Table 4.2), 32.4% of *C. taeniatus* survived, while no *C. virescens* survived exposure for up to 48 hours (Table 4.3B). After an exposure time of 24 hours at the same sites, the survival of *C. taeniatus* was virtually unchanged at 30% and that of *C. virescens* remained low at 1.4% (Table 4.3C). These differences were highly significant ($\chi^2 = 36.04$, $P<0.001$).

### 4.3.4 Ionic Regulation

Analyses of haemolymph samples from dying and surviving crabs by ICPES revealed that in both test temperatures, the concentrations of Na$^+$, K$^+$, Ca$^{++}$ and Mg$^{++}$ followed similar trends in both species over time. Although the chloride ion
Salinity readings (% SW) at the start and end of estuarine translocation experiments. Latitude and longitude are also given.

Table 4.2

<table>
<thead>
<tr>
<th>Site</th>
<th>Start Salinity</th>
<th>End Salinity</th>
<th>Start Lat/Long</th>
<th>End Lat/Long</th>
<th>Start Long/Long</th>
<th>End Long/Long</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>30.3%</td>
<td>0.9%</td>
<td>S23°28.24'</td>
<td>S23°28.24'</td>
<td>150°37.73'</td>
<td>150°37.73'</td>
</tr>
<tr>
<td>2</td>
<td>30.0%</td>
<td>0.9%</td>
<td>S23°28.26'</td>
<td>S23°28.26'</td>
<td>150°37.73'</td>
<td>150°37.73'</td>
</tr>
<tr>
<td>3</td>
<td>31.4%</td>
<td>0.9%</td>
<td>S23°28.27'</td>
<td>S23°28.27'</td>
<td>150°37.74'</td>
<td>150°37.74'</td>
</tr>
<tr>
<td>4</td>
<td>31.1%</td>
<td>0.8%</td>
<td>S23°28.24'</td>
<td>S23°28.24'</td>
<td>150°37.47'</td>
<td>150°37.47'</td>
</tr>
<tr>
<td>5</td>
<td>30.3%</td>
<td>0.8%</td>
<td>S23°28.22'</td>
<td>S23°28.22'</td>
<td>150°37.47'</td>
<td>150°37.47'</td>
</tr>
<tr>
<td>6</td>
<td>31.1%</td>
<td>0.7%</td>
<td>S23°28.20'</td>
<td>S23°28.20'</td>
<td>150°37.47'</td>
<td>150°37.47'</td>
</tr>
<tr>
<td>7</td>
<td>31.9%</td>
<td>0.9%</td>
<td>S23°28.18'</td>
<td>S23°28.18'</td>
<td>150°37.47'</td>
<td>150°37.47'</td>
</tr>
</tbody>
</table>

For each site, Note that Repetition 2 started and ended on ebb tide so measurements of salinity were lower at these times than during flood tide.
### Table 4.3

Results from **A**: 11 control replicates (48 hours exposure), **B**: 18 treatment replicates (48 hours exposure) and, **C**: 17 treatment replicates (24 hours exposure) of the estuarine environment translocation comparing the proportion surviving between *C. taenius* and *C. virescens*.

<table>
<thead>
<tr>
<th></th>
<th>Alive</th>
<th>Dead</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>C. taenius</em></td>
<td>24</td>
<td>0</td>
<td>24</td>
</tr>
<tr>
<td><em>C. virescens</em></td>
<td>72</td>
<td>0</td>
<td>72</td>
</tr>
<tr>
<td><strong>B</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>C. taenius</em></td>
<td>11</td>
<td>23</td>
<td>34</td>
</tr>
<tr>
<td><em>C. virescens</em></td>
<td>0</td>
<td>156</td>
<td>156</td>
</tr>
<tr>
<td><strong>C</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>C. taenius</em></td>
<td>18</td>
<td>42</td>
<td>60</td>
</tr>
<tr>
<td><em>C. virescens</em></td>
<td>2</td>
<td>142</td>
<td>144</td>
</tr>
</tbody>
</table>
(Cl) concentration was not measured, it was assumed that Na\(^+\) and Cl usually vary together, especially when changes in concentration are large (see Burton, 1986).

Haemolymph ion concentrations from crabs that were not exposed to low salinity are reported as “Initial” concentrations. For figures in which \textit{C. taeniatus} haemolymph ion concentration is graphed, the final data point represents the ionic concentration in haemolymph from surviving crabs. In Figure 4.4A and B, the concentration of Na\(^+\) in the haemolymph is compared between \textit{C. taeniatus} and \textit{C. virescens}, respectively, over three days at 15°C. Exposure to 22% SW resulted in a sharp reduction in haemolymph Na\(^+\) concentration in both species. In \textit{C. taeniatus} (Figure 4.4A), haemolymph Na\(^+\) was reduced to the same concentration as that in the medium within the first day of exposure. Over the next two days, haemolymph Na\(^+\) concentration in hermit crabs near death (as evidenced by individuals showing little response to stimuli) remained the same as ambient. The concentration of this ion in haemolymph from \textit{C. taeniatus} that were still alive at the end of the experiment was significantly lower than ambient Na\(^+\) concentration (one way ANOVA, \(F_{1,4}=16.915, P<0.05\)).

The drop in \textit{C. virescens} (Figure 4.4B) haemolymph Na\(^+\) below ambient concentration also occurred within the first day of exposure. The result of this drop was that \textit{C. virescens} haemolymph Na\(^+\) concentration was no different from the ambient Na\(^+\) concentration (one way ANOVA, \(F_{1,5}=2.136, P>0.05\)). By the end of the second day, all \textit{C. virescens} in the experiment were dead. Measurements showed that haemolymph Na\(^+\) concentration in these individuals remained below that of the water, although not significantly so (one way ANOVA, \(F_{1,7}=2.594, P>0.05\)).
Figure 4.4 Results of analyses for haemolymph sodium concentration in A: *C. taeniatus* (○) and B: *C. virescens* (■) exposed to 22% SW (▲) at 15°C for up to three days. The concentration of sodium in 100% SW (●) is given for comparison. Bars represent 1 standard error. Each point represents the mean of two or more replicates. Initial points represent live hermit crabs, as does the final point for *C. taeniatus*. 

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Figure 4.5A and B show the changes in K\(^+\) concentration for *C. taeniatus* and *C. virescens*, respectively, over three days when subjected to 22% SW at 15°C. Analyses of haemolymph samples showed that for *C. taeniatus* (Figure 4.5A), initial K\(^+\) concentration was above the concentration present in 100% SW, but dropped to less than half the initial concentration within hours of exposure to 22% SW. Before the end of the first day of exposure, K\(^+\) levels increased, equivalent to that in 100% SW, and remained there in crabs dying at the end of 48 hours exposure. *C. taeniatus* that remained alive for up to three days had haemolymph K\(^+\) that, due to small sample size and large standard error, was not significantly different from individuals that died during the first day of exposure, although the concentration of K\(^+\) in crabs alive at three days was lower than for those that died (three days = 2.54mg/L; two days = 5.00mg/L). The K\(^+\) concentration in haemolymph from *C. taeniatus* was never reduced to the same concentration as the medium.

In *C. virescens* (Figure 4.5B) the initial haemolymph concentration of K\(^+\) was significantly higher than that of 100% SW (one way ANOVA, F\(_{1,7}\)=112.152, P<0.001). Following introduction into 22% SW, however, the K\(^+\) concentration of haemolymph decreased, but not significantly so (one way ANOVA, F\(_{1,6}\)=5.837, P>0.05) and was maintained at that level throughout the remainder of the experiment.

Figure 4.6A and B show the concentration of Ca\(^{++}\) in the haemolymph of *C. taeniatus* and *C. virescens* in 22% SW at 15°C. The initial Ca\(^{++}\) concentration in the haemolymph of *C. taeniatus* (Figure 4.6A) was the same as in the acclimation medium (100% SW). During the first day of exposure to 22% SW, this was
Figure 4.5 Results of analyses for haemolymph potassium concentration in A: *C. taeniatus* (○) and B: *C. virescens* (■) exposed to 22% SW (▲) at 15°C for up to three days. The concentration of potassium in 100% SW (●) is given for comparison. Bars represent 1 standard error. Each point represents the mean of two or more replicates. Initial points represent live hermit crabs, as does the final point for *C. taeniatus*. 
Figure 4.6 Results of analyses for haemolymph calcium concentration in A: *C. taeniatus* (○) and B: *C. virescens* (■) exposed to 22% SW (▲) at 15°C for up to three days. The concentration of calcium in 100% SW (●) is given for comparison. Bars represent 1 standard error. Each point represents the mean of two or more replicates. Initial points represent live hermit crabs, as does the final point for *C. taeniatus*. 
reduced, but did not drop to the level of the experimental medium (22% SW). Following the initial fall, haemolymph concentration of Ca$^{++}$ did not change for all *C. taeniatus* that died throughout the experiment, or for those still alive at the end.

Initial haemolymph Ca$^{++}$ concentration in *C. virescens* (Figure 4.6B) was significantly higher (one way ANOVA, $F_{1,6}=71.648$, $P<0.001$) than Ca$^{++}$ in 100% SW. When *C. virescens* was exposed to 22% SW, the Ca$^{++}$ concentration in haemolymph was significantly reduced below that in 100% SW (one way ANOVA, $F_{1,6}=7.689$, $P<0.05$). Ca$^{++}$ in the haemolymph continued to fall throughout the first day of exposure to 22% SW, but did not fall to the same concentration as that in the medium. Within the second day of exposure, Ca$^{++}$ concentration in the haemolymph rose slightly, but was basically unchanged from the previous day.

When the haemolymph concentration of Mg$^{++}$ was compared between species (Figure 4.7A and B) it was seen that the concentration in the haemolymph of both species was initially the same and equivalent to the concentration of Mg$^{++}$ in the acclimation medium (100% SW). Upon exposure to 22% SW, the haemolymph Mg$^{++}$ concentration of *C. taeniatus* (Figure 4.7A) was rapidly reduced and was not significantly different from the medium (one way ANOVA, $F_{1,4}=7.376$, $P>0.05$) remaining there over the next day of exposure. Crabs that remained alive after three days in 22% SW had the same concentration in the haemolymph as the medium.

Upon exposure to 22% SW, the concentration of Mg$^{++}$ in the haemolymph of *C. virescens* (Figure 4.7B) also decreased. Although it decreased to the equivalent of the medium, it did not drop as rapidly as for *C. taeniatus*. Throughout the second day of exposure, haemolymph levels of Mg$^{++}$ remained the same as in
Figure 4.7 Results of analyses for haemolymph magnesium concentration in A: *C. taeniatus* (♦) and B: *C. virescens* (■) exposed to 22% SW (▲) at 15°C for up to three days. The concentration of magnesium in 100% SW (●) is given for comparison. Bars represent 1 standard error. Each point represents the mean of two or more replicates. Initial points represent live hermit crabs, as does the final point for *C. taeniatus*. 
the medium.

When *C. taeniatus* and *C. virescens* were exposed to 22% SW at a treatment temperature of 35°C, the trends for haemolymph ionic concentrations in both species were similar to those at 15°C (see Figures 4.8 – 4.11). However, at 35°C, both species died more quickly than at 15°C.

Three notable exceptions to the common trends in haemolymph ion concentration occurred at 35°C. In both *C. taeniatus* and *C. virescens*, the initial concentrations of Na\(^+\) and Mg\(^{++}\) were much lower at 35°C than at 15°C, although throughout the remainder of the exposure at 35°C the concentrations of these ions followed the same trend as at 15°C.

A second exception was that in *C. virescens*, the haemolymph concentration of K\(^+\) (Figure 4.9B) steadily increased from initial measurements equivalent to that in the acclimation medium, to a significantly higher concentration (one way ANOVA, \(F_{1,14}=14.131, P<0.01\)) after 8 hours. The final two measurements were not analysed by ANOVA and must be viewed with some scepticism since they represent only one replicate at each time.

Finally, measurements showed that initial concentration of Ca\(^{++}\) in acclimated *C. virescens* was equivalent to the medium (Figure 4.10B). In 22% SW, haemolymph Ca\(^{++}\) decreased significantly (one way ANOVA, \(F_{1,14}=12.901, P<0.05\)), but after 16 hours of exposure to 22% SW at 35°C, haemolymph Ca\(^{++}\) returned to a concentration equal to the concentration in the acclimation water. However, the accuracy of the final measurement of increased Ca\(^{++}\) concentration is questionable since it results from only one replicate.
Figure 4.8 Results of analyses for haemolymph sodium concentration in A: *C. taeniatus* (○) and B: *C. virescens* (■) exposed to 22% SW (▲) at 35°C for over 28 hours. The concentration of sodium in 100% SW (●) is given for comparison. Bars represent 1 standard error. Each point represents the mean of two or more replicates. Initial points represent live hermit crabs, as does the final point for *C. taeniatus*. 
Figure 4.9 Results of analyses for haemolymph potassium concentration in A: *C. taeniatus* (■) and B: *C. virescens* (▲) exposed to 22% SW (▲) at 35°C for over 28 hours. The concentration of potassium in 100% SW (●) is given for comparison. Bars represent 1 standard error. Each point represents the mean of two or more replicates. Initial points represent live hermit crabs, as does the final point for *C. taeniatus*.
Figure 4.10 Results of analyses for haemolymph calcium concentration in A: *C. taeniatus* (♦) and B: *C. virescens* (■) exposed to 22% SW (▲) at 35°C for over 28 hours. The concentration of calcium in 100% SW (●) is given for comparison. Bars represent 1 standard error. Each point represents the mean of two or more replicates. Initial points represent live hermit crabs, as does the final point for *C. taeniatus*. 
Figure 4.11 Results of analyses for haemolymph magnesium concentration in A: *C. taeniatus* (○) and B: *C. virescens* (■) exposed to 22% SW (▲) at 35°C for over 28 hours. The concentration of magnesium in 100% SW (●) is given for comparison. Bars represent 1 standard error. Each point represents the mean of two or more replicates. Initial points represent live hermit crabs, as does the final point for *C. taeniatus*. 
4.4 DISCUSSION

4.4.1 Survival in the Laboratory

Results of laboratory experiments on the survival of both species in a constant medium of 22% SW at three different temperatures demonstrated a significant difference in survival between species. These results suggested that *C. taeniatus* is able to tolerate long term exposure to low salinity water significantly better than *C. virescens*.

Furthermore, survival of both species was reduced at high and low temperatures, but these extremes appeared to influence the survival of *C. virescens* more than *C. taeniatus*. The combination of high temperature and low salinity was especially detrimental to *C. virescens*, which is consistent with the relatively high Q₁₀ values for oxygen consumption of this species reported in Section 3.3.2.2, page 70. Differences between the metabolic responses of *C. taeniatus* and *C. virescens* may reflect differences in the ability to supply energy to processes of protein turnover during the period of adjustment to acute changes in temperature. Energy is also likely to be needed for osmoregulation. During periods of combined temperature and osmotic stress, *C. virescens* in particular, may not be able to partition enough energy to all processes dealing with the effects of the combined stress.

The lethal temperature and salinity limits in two northern hemisphere populations of *P. longicarpus* from different latitudes were shown by Young (1991) to be nearly identical when individuals from the two populations were acclimated identically. Thus, they were suggested to have the same physiological limits,
although variation would be possible. However, the salinity ranges at which survival was predicted to be at least 10% were wider for the northern population (13 – 40‰), than for the southern (21 – 30‰). Young (1991) suggested that since the interaction of temperature and salinity significantly affected survival of *P. longicarpus*, the population from the higher latitude was more tolerant to salinity because it experienced less thermal stress than the population from the lower latitude. Results reported by Young (1991) were similar to those by Biggs and McDermott (1973) in their study on the survival of two populations of *P. longicarpus* from the same latitude in southern New Jersey, exposed to various combinations of temperature and salinity. They also suggested that, for *P. longicarpus*, extreme temperatures reduce the salinity range in which greatest survival occurs.

In tolerance experiments with cold and warm acclimated *C. vittatus*, *Pagurus longicarpus* and *P. pollicaris*, Young (1980) found that the intertidal species, *C. vittatus*, was much more tolerant of environmental changes than the subtidal species, *P. longicarpus* and *P. pollicaris*. He found that temperature, salinity (and the interaction of these factors) had approximately equal importance on the mortality of *P. longicarpus* and *P. pollicaris*, but that mortality in *C. vittatus* was affected more by temperature than either salinity or the interaction of these factors. However, the effect of temperature only seemed important because there was almost no effect of salinity on *C. vittatus*. 

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4.4.2 Intertidal Translocation

There is evidence that physiological tolerance to extreme environmental conditions is greater in organisms from the high intertidal than from low on the shore (Southward, 1958; Reese, 1969; Young, 1978; Bertness, 1981a; Agnew and Taylor, 1986; Gherardi, 1990; Stillman and Somero, 1996). While my results from oxygen consumption experiments also showed a difference between high shore and low shore species in metabolic responses to acute changes in temperature and salinity (Section 3.3.2.1, page 64), results from intertidal translocation experiments did not demonstrate differences in survival between *C. taeniatus* and *C. virescens*. On the contrary, these results showed that *C. virescens* was able to survive “normal” physico-chemical conditions at low and high shore equally well.

During the time in which intertidal translocation experiments were conducted, hermit crabs of both species were exposed to a wide range of environmental conditions (see Figure 4.12 for temperature and rainfall during this period). Experimental chambers were exposed to relatively cool, dry days (July), sudden downpours (November) and sudden downpours during warm temperatures (February). Both *C. virescens* and *C. taeniatus* survived the physical conditions of the upper intertidal shore within chambers during semidiurnal emersion equally well. Returning tides may keep exposure to low salinity relatively brief, so such exposure may not result in a demonstrable difference in survival. However, it must be re-emphasised that coastal areas within the vicinity of river outflows can undergo large seasonal reductions in sea surface salinities over extended periods (Endean et al., 1956; Rao and Sundaram, 1974; Coates, 1992; O’Neill et al., 1992; Brosnan, 1992) resulting in high mortalities of intertidal organisms (Endean et al., 1956;
Figure 4.12 The mean monthly temperature (°C) ( ■ ) and mean daily rainfall (mm) ( ● ) in the area along Keppel Bay where translocation experiments were done between July, 2000 and February, 2001. Adapted from the Commonwealth of Australia, Bureau of Meteorology, 2001a,b.
Hodgkiss, 1984; Coates, 1992). During such events, hermit crabs may not be able to escape prolonged exposure to low salinity.

### 4.4.3 Translocation into an Estuarine Environment

Results from a translocation experiment of both species to an estuarine environment provided evidence that a significant difference in survival did exist in favour of *C. taeniatus* when both species were exposed to conditions of prolonged low salinity. These results were consistent with those from laboratory experiments into the survival of these species in 22% SW at 15, 25 and 35°C.

These experiments suggested that in “normal” intertidal conditions where semidiurnal high tides reduce extended exposure to extremes in desiccation, temperature and/or salinity both species survived equally well. However, when both species are submersed in persistent low salinity *C. taeniatus* survived significantly better than *C. virescens*.

Endean *et al.* (1956) has indicated that salinity in parts of Keppel Bay can be considerably reduced as a result of the volume of freshwater carried into the bay by the Fitzroy River. Coates (1992) and O’Neill *et al.* (1992) showed that after large flood events, the salinity of surface waters in some areas of Keppel Bay were reduced to between 12 – 58% SW for up to 24 days resulting in heavy mortality of several intertidal species. Therefore, I decided to survey rocky intertidal areas along the Queensland coast that were under the long term, regular and/or irregular influence of river outfalls, as well as those beyond the influence of river outfalls, for the distribution of *C. taeniatus* and *C. virescens* on the shore. Comparisons among
sites may indicate whether the influence of freshwater was affecting local distribution. This is described in Chapter 5.

It is appreciated that the survival experiments undertaken in the laboratory and in the estuarine environment lack some realism in that they were not designed to allow hermit crabs to escape stressful conditions by climbing out of the water, as may occur in the field. Nevertheless, these experiments have shown that the two species differ in their abilities to survive prolonged exposure to low salinity. Such conditions may, indeed occur in the field when inshore waters remain diluted for long periods, as shown by Coates (1992) and O’Neill et al (1992).

4.4.4 Ionic Regulation

Results from analyses of haemolymph concentrations of $Na^+$, $K^+$, $Ca^{++}$ and $Mg^{++}$ from *C. taeniatus* and *C. virescens* subjected to 22% SW at 15 and 35°C after initial acclimation in 100% SW at 25°C, revealed similar patterns for each species. Although the mechanisms for ionic regulation in *C. taeniatus* and *C. virescens* have not been elucidated in this study, it is clear that the movement of the main osmotic effector, $Na^+$ ion (and by assumed association, $Cl^-$, although see below) into the extracellular fluid may somehow be inhibited. In decapod crustaceans, $Na^+/H^+$ (or $NH_4^+$) antiporters, $Na^+/K^+/2Cl^-$ cotransporters and simple $Na^+$ channels on the apical membrane have each been proposed as the mechanism by which $Na^+$ and $Cl^-$ are moved from the medium, through the apical membrane of the posterior gill and into the cell (Leray, 1984; Towle, 1984; Willmer et al., 2000), although these details remain controversial (Willmer et al. 2000). In exchange for these ions, $K^+$, bicarbonate ($HCO_3^-$) and potentially ammonium ($NH_4^+$), are moved through the
apical membrane to the medium. At the basal membrane Na$^+$ is exchanged into the extracellular fluid for K$^+$ or NH$_4^+$ (Greenaway, 1991; O’Donnell, 1997; Willmer et al. 2000), while Cl$^-$ may move into the haemolymph by Cl$^-$ channels (O’Donnell, 1997) or a separate Cl$^-/HCO_3^-$ exchange system (Willmer et al. 2000). It is also possible that during prolonged exposure to dilute media intertidal hermit crabs may rely on cellular adaptations to adjust intracellular osmotic potential to match blood osmotic potential and to continue cellular metabolism at reduced osmolarity (Greenaway, personal communication).

In the case of both C. taeniatus and C. virescens subjected to a prolonged, dilute medium, the greatly reduced concentration of Na$^+$ and the high concentration of K$^+$ in the haemolymph suggested that the active movement of both ions had been inhibited or slowed. If a failure of Na$^+$ regulation occurs at the outer surface of the gill, Na$^+$ would be lost to the medium resulting in a reduction in the concentration of this ion in the blood to ambient levels. Since the concentration of Na$^+$ in the blood would be reduced, intracellular levels of Na$^+$ would continue to be depleted. The requirement of Na$^+$ for Na$^+/K^+$ ATPase operation means that reduced intracellular Na$^+$ would lead to a reduced activity of this membrane enzyme and thus, to reduced uptake of K$^+$ from the blood into the cells. Since K$^+$ would continue to move from the cells into the blood by passive means, the cellular concentration of K$^+$ would continue to decline, while that of the blood remains above ambient concentration. Therefore, the reduced activity of Na$^+/K^+$ ATPase at the basal membrane, as a result of the initial loss of Na$^+$ is a plausible reason for the low concentrations of Na$^+$, and high concentrations of K$^+$ observed in the haemolymph. The high concentration of K$^+$ in the haemolymph may also indicate that cells are
unable to maintain a sufficiently high resting potential within the cells, becoming more and more negative on the inner surface relative to the outer. Florkin and Schoffeniels (1965, in Boone & Claybrook, 1977) proposed that the decrease in cellular cation content occurring during low salinity adaptation could potentially modulate an enzyme or group of enzymes with direct involvement in amino acid metabolism.

Castillo et al. (1988) suggested that the euryhalinity of *Clibanarius erythropus* was likely to depend mainly on intracellular mechanisms in which amino acids and the ions Na\(^+\) and K\(^+\) play an important role.

In *Clibanarius vittatus*, Sabourin and Stickle (1980) also reported that the haemolymph concentration of Na\(^+\) was essentially isoionic to medium of 30‰ (approximately 83% SW), while K\(^+\) was regulated well above its concentration in the medium. In contrast to the results of my study, these authors found that when *C. vittatus* was acclimated in 20 and 10‰ (approximately 56 and 28% SW, respectively) Na\(^+\), Mg\(^{++}\) and K\(^+\) were all hyper-regulated. Nevertheless, they concluded that high concentrations of K\(^+\) in all treatments indicated that the concentration of this ion was maintained independent of ambient seawater concentration in low salinities.

In the Atlantic ribbed mussel, *Modiolus demissus*, Shumway and Youngson (1979) found no evidence for the regulation of Na\(^+\), K\(^+\), Ca\(^{++}\) and Mg\(^{++}\) when specimens were subjected to both gradual (sinusoidal) and abrupt (square wave) reductions in salinity down to 30% SW. They reported that K\(^+\) concentrations showed only small fluctuations compared with those in the external medium. Gilles (1972) found that although the bivalves, *Mytilus edulis* and *Glycmeris glycmeris*
could not osmoregulate when exposed to low salinities, they could regulate haemolymph K$^+$ ions to the same levels they had in normal seawater. When *Crassostrea virginica* was exposed to 10, 15 and 20% SW, Hand and Stickle (1977, in Shumway and Youngson, 1979) found that haemolymph K$^+$ was hyper-ionic to ambient concentrations.

While it is clear that regulation occurs in many marine and estuarine crustaceans, the exact mechanisms of osmotic and ionic regulation remain unclear (Pequeux and Gilles, 1984; Towle, 1984; Gilles and Delpire, 1997), especially in anomurans. There is, however, evidence that in crustaceans amino acids are used as intracellular osmotic effectors, and that the regulation of intracellular amino acid concentration is, in part, due to modifications of the cellular membrane permeability to amino acids (Gilles, 1972). Nevertheless, the role of K$^+$ regulation in the process of osmoregulation remains unclear (Gilles, 1972).

Changes in the haemolymph concentrations of Ca$^{++}$ and Mg$^{++}$ are difficult to explain and the mechanisms of their movements can only be speculated about here. The concentration of Ca$^{++}$ also remained high in *C. taeniatus* and *C. virescens* haemolymph relative to ambient concentration. When Greenaway (1976) acclimated the shore crab, *Carcinus maenas* to dilute seawater during their intermoult, he found that this species maintained haemolymph calcium concentration significantly higher than that of the external medium, the difference being inversely related to salinity. In media of less than 50% SW, Greenaway found that there was a marked electrochemical gradient leading to calcium loss from the haemolymph, strongly suggesting a mechanism other than passive regulation for high Ca$^{++}$ concentrations maintained in the haemolymph. While Greenaway did not
show direct evidence for increased calcium uptake from the medium, he did suggest that a mechanism of active transport would be the only way to regulate haemolymph calcium concentration against an electrochemical gradient. In agreement with the findings of Greenaway (1976), Neufeld and Cameron (1992) found that the haemolymph calcium concentration of *Callinectes sapidus* in 2‰ was also regulated at significantly higher concentrations than the surrounding medium. They also found that electrochemical gradients favoured the loss of calcium from the haemolymph to the medium through gill epithelia. Despite this transepithelial gradient, there was a net uptake of calcium implicating an active transport of calcium from water to blood. There is evidence that the transport of calcium across the gill epithelium of crustaceans in dilute water involves: (i) a Na\(^+\)/Ca\(^{++}\) antiporter kept active by the Na\(^+\) gradient maintained by Na\(^+\)/K\(^+\) ATPase and (ii) active uptake by Ca\(^{++}\) ATPase (for details, see review by Wheatly, 1997). In *Carcinus* spp. Ca\(^{++}\) ATPase has been reported to have a high affinity and capacity in 50% SW. The Na\(^+\)/Ca\(^{++}\) antiporter has also been shown to have a higher affinity in dilute seawater and is most likely the main mechanism for basolateral movement of Ca\(^{++}\) into the haemolymph (Wheatly, 1997). However, if there is indeed a passive loss of Na\(^+\) from the extracellular fluid of *C. taeniatus* and *C. virescens*, as proposed above, it would be difficult to explain the regulated maintenance of relatively high levels of calcium in the haemolymph by any active mechanism involving Na\(^+\).

The regulation of haemolymph Mg\(^{++}\) in crustaceans is an area of active speculation (Cornell, 1979 in Mantel and Farmer, 1983). It has been proposed by Robertson (1960, in Mantel and Farmer, 1983) that while animals maintaining concentrations of Mg\(^{++}\) about 80% of that in seawater tend to be relatively
‘unresponsive’ to stimulation, those that have concentrations of less than 50% are more ‘active’. Since magnesium is thought to have an anaesthetic effect on neuromuscular junctions, high concentrations of this ion in the haemolymph might result in reduced ability to maintain activity (Mantel and Farmer, 1983). It is clear that further studies are needed to understand the relationship between haemolymph concentrations of Mg\(^{++}\), physical activity and osmoregulation in different concentrations of seawater.

Reasons for the low initial concentrations of Na\(^{+}\) and Mg\(^{++}\) in 35°C are unclear. Despite slight variations in ionic concentrations, no evidence was found to show significant differences in ionic regulatory ability that could be directly related to the difference between species in survival in lowered salinity.

### 4.5 Discussion Summary

Taken together, the experimental results presented in this chapter indicated that *C. taeniatus* survived significantly better than *C. virescens* in low salinity at 15, 25 and 35°C and that in very extreme conditions, such as those likely to occur at high shore during prolonged flooding, *C. taeniatus* would have better survival than *C. virescens*. However, in the relatively stable conditions that occurred throughout the period in which intertidal translocations were conducted, *C. virescens* was able to survive the conditions at high shore as well as did *C. taeniatus*. This included heat, desiccation, increasing salinity due to evaporation and rapid dilution of tidepool water due to rain. Yet, despite the fact that crabs were submersed without escape from treatment conditions in both laboratory survival experiments and

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estuarine translocations, these investigations have allowed the testing of physiological models and have shown that *C. virescens* has a reduced ability to endure prolonged dilution of the medium, especially in combination with high temperature. According to Vernberg (1981a), tolerance to one environmental factor may be reduced when there is a combined effect of unfavourable conditions of another factor (see also Moore, 1972).

Investigations into the regulation of ions in both species demonstrated no significant differences in various ion concentrations, but no differences in general trends of ionic concentrations between species, although statistical analyses were not done to compare species. However, low extracellular concentrations of the major osmotic effector, Na⁺ (and probably to a lesser degree, Cl⁻) and high haemolymph concentrations of K⁺ may suggest the passive loss of intracellular Na⁺ resulting in a deterioration of the ability of membrane ATPases to pump K⁺ from the blood into the cells. This may effectively limit the ability of the cell to maintain the necessary potential gradient between the inner and outer surfaces of the cells. The increased concentration of Ca²⁺ in the haemolymph relative to the medium may suggest that Ca²⁺ is being actively taken up from the water into the haemolymph, since an electrochemical gradient favouring the loss of Ca²⁺ has been reported (Greenaway, 1976; Neufeld and Cameron, 1992; Wheatly, 1997). Since ionic regulation did not appear to differ between species, it is suggested that the overall dilution of body fluids may have a more detrimental effect on *C. virescens* than on *C. taeniatus*.

I conclude that in conditions of prolonged low salinity, the ability of *C. taeniatus* to survive significantly better than *C. virescens* is evidence of adaptation.
allowing *C. taeniatus* to better tolerate the dilution of body fluids and the reduction of Na\(^+\) (and Cl\(^-\)) in extracellular fluid (whatever the mechanisms may be).

It was apparent from results of translocation experiments presented in this chapter, that *C. virescens* was able to inhabit HS in some locations. Yet, data on survival in low salinity suggested that this species was significantly less tolerant of extended exposure to fresh water than is *C. taeniatus*, especially when low salinity occurred in combination with high temperature. On the basis of evidence presented in the previous chapters, I proposed that differences in the large scale geographical distribution of these species would be influenced by freshwater flows.

In order to test this proposal, it was necessary to survey several rocky shores that were either influenced or uninfluenced by freshwater, for the presence and distribution of *C. taeniatus* and *C. virescens* on the shore. The next chapter presents the description and results of that survey.
CHAPTER 5: GEOGRAPHICAL DISTRIBUTION

5.1 INTRODUCTION

Several factors have been implicated in the local distribution of intertidal and/or, estuarine decapods. The combination of differences in salinity tolerance and substrate type (Meadows and Campbell, 1972; Jones, 1976), interspecific competition (Chapman, 1973, Connell, 1975), tolerances to dehydration (Russell, 1991), a large range of habitat variety, a high abundance and diversity of shell resources, and low levels of habitat damage or loss in the low tide zone (Barnes, 1997a; Turra et al., 1999), behavioural responses to physico-chemical parameters, thermal tolerance, predation pressure (Paine, 1966; Bertness, 1981a), disturbance (Connell, 1978; Jørgensen and Padisák, 1996; Dial and Roughgarden, 1998; Zacharias and Roff, 2001) have all been suggested to have significant impacts on the distribution of intertidal animals on the shore (also see reviews by Kinne, 1963, 1964; Meadows and Campbell, 1972; Newell, 1976; Field and Griffiths, 1991; Russell, 1991; Vadas and Elner, 1992; Raffaelli and Hawkins, 1996; Barnes and Hughes, 1999; Menge, 2000).

While studies on the influence of physiological adaptations on the local distribution of intertidal organisms are numerous, systematic research on the relationship between physiological capabilities and geographical distribution (Meadows and Campbell, 1972), especially of tropical intertidal organisms, is almost completely lacking (Southward, 1958; Vernberg, 1981b; Brosnan, 1992).
Despite considerable literature on intertidal invertebrates and particularly reports on the collection of intertidal decapods of the Queensland coast, few ecological studies have investigated the relationship between physiological and behavioural adaptations and the distribution and abundance of decapod species over a broad scale area such as the Queensland coast.

The results of physiological investigations (Chapter 3) and of survival experiments (Chapter 4) suggested that *C. taeniatus* and *C. virescens* differ in both their physiological responses to rapid and extreme changes in temperature and in their ability to withstand extended exposure to reduced salinity. Differences in survival were especially apparent when low salinity occurred in combination with high temperatures. It would, therefore, be consistent with these results that when two rocky intertidal areas, one influenced by frequent freshwater flows and the other having no freshwater influence, are repeatedly monitored, the relative abundance of *C. taeniatus* should be found to be high in the former habitat.

Another testable prediction was that over a large geographical scale *C. virescens* should have a low relative abundance compared to *C. taeniatus* in areas where freshwater reaches the rocky coast, since the former species is more sensitive to low salinity, particularly at higher temperatures. As well, *C. virescens* should have a higher relative abundance than *C. taeniatus* on islands or open coasts. Furthermore, the more temperature insensitive and low salinity tolerant species, *C. taeniatus*, should have a higher relative abundance on rocky shores that are influenced by the long-term presence of freshwater.
5.2 MATERIALS AND METHODS

5.2.1 Repeated Sampling

Methods for the collection of data for this section can also be found in Kay and Coates (2000).

Two rocky sites in the Bundaberg area were selected for extensive, repeated sampling to determine if the relative abundances of the two species were maintained over time. One of the sites has no substantial freshwater influence, while the other experiences continuous low freshwater flows and occasional heavy flows.

Hoffman’s Rocks (S24°50.4’, E152°28.7’) are located on the open coast and no storm water drains or natural creeks empty onto this site. It was divided into six sectors (see Figure 5.1). All sectors were sampled on February 20 and May 20, 2000, and March 23, 2001. At each sampling time, hermit crabs were randomly collected from tidepools within each section. Species were identified and counted and all crabs were then returned to the pools from which they were taken as was done by Kay and Coates (2000).

At Bauer Street (S24°48.9’, E152°28.0’), storm water drains channel freshwater runoff from a natural creek into the rocky intertidal area. Runoff is continuous, but of low volume except during times of heavy rainfall. A series of tidepools extends from the top of the shore at the outlet of the storm drain to the bottom of the intertidal area. This site was divided into 9 sectors (see Figure 5.2) and at each sampling time tidepools in each were surveyed in the same way as Hoffman’s Rocks. Sampling was done on February 20, May 20, July 8, October 24, 2000 and March 23, 2001.
For each sampling time, relative abundances of *C. taeniatus* and *C. virescens* were determined for each sector at both sites. In addition, the overall percentages of these species was calculated for each site as a whole based on the total number of each species counted divided by the total number of both species counted.

Although tidepool salinity was not measured on a regular basis over the 13 month sampling period, salinities at this site were recorded during one episode of runoff following heavy local rainfall (S. Sargent, personal communication, Bureau of Meteorology, 2001a,b) (see Table 5.3).

### 5.2.2 The Movement of Freshwater

There is little recent information available for direction of currents and no regularly recorded salinity data for the Queensland coast as a whole. However, data on nearshore currents within the Capricornia Coast and Hervey Bay regions were taken from Beach Protection Authority Reports of those areas for 1979 and 1989, respectively (Anonymous, 1979; Anonymous, 1989), as background information for this study.

Intertidal salinity and air temperature data for Keppel Bay were collected daily between April, 1989 and January, 1992 (Coates, unpublished data) and salinity measurements at the surface, mid stratum and within 1m of the bottom were collected by O’Neill *et al.* (1992) for Keppel Bay during and immediately after a catchment scale flood of the Fitzroy River.
5.2.3 Geographical (Large Scale) Distribution

5.2.3.1 Coastal Survey

A survey of 86 rocky intertidal shores was carried out along the coast of Queensland, Australia from Redcliffe (S27°15.78’, E153°06.28’) to Cape Kimberley (S16°16.72’, E145°29.14’) between March, 2000 – February, 2001 (see Figure 5.3). Each site was surveyed for the relative abundances of *C. taeniatus*, *C. virescens*, other hermit crab species§ and empty shells. It is important to note that measurements of relative abundance can be misleading without a minimum sample size.

At each site transects were laid at three different heights on the shore (low shore, mid shore and high shore) at increasing distance from and parallel to the water line. In each of these transects, 10 tide pools were randomly selected and a total of 15 hermit crabs and/or empty gastropod shells was randomly collected from each pool. This resulted in approximately 450 hermit crabs and/or empty gastropod shells recorded at each site. Numbers of hermit crabs and empty gastropod shells were tabulated and converted to relative abundances for *C. taeniatus*, *C. virescens*, other species and empty gastropod shells for each site. At sites where *C. taeniatus* and *C. virescens* were not found together, the relative abundances of other species, empty shells and either *C. taeniatus* or *C. virescens* were compared.

§ Throughout this chapter “other species” refers to hermit crab species not directly under investigation in this thesis.
A brief description and the latitude and longitude for each site were recorded and are presented in Appendix II.

Where possible salinity readings were also recorded and are presented in Table 5.6.

5.2.4 Indicator System

All sites at which *C. taeniatus* and/or *C. virescens* were found were combined into two categories; “Influenced by Freshwater” and “Not Influenced by Freshwater”. These categories were decided on the basis of proximity to creeks and/or rivers according to map locations, data on general directions of wind-wave currents and personal observations. Those sites that were near outfalls and likely to receive a regular or irregular input of freshwater were grouped together in the first category. Island and open coast sites that were distant from creeks or rivers and unlikely to receive freshwater inputs were grouped in the second.

5.3 RESULTS

5.3.1 Repeated Sampling

From Figure 5.1, it appears as though the sectors selected at Hoffman’s Rocks were at low shore, but they occur on a raised rock platform and are considered to be at mid shore.

Table 5.1A shows the relative abundances of *C. taeniatus* and *C. virescens* in each sector at Hoffman’s Rocks on the three dates they were sampled. The total
Figure 5.1 Aerial photograph of the Hoffman’s Rocks site showing the arrangement of sectors 1 – 6.
### A

<table>
<thead>
<tr>
<th>Sectors</th>
<th>1</th>
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<th>3</th>
<th>4</th>
<th>5</th>
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<th>2</th>
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### B

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<td>C.v.</td>
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<td>99.6</td>
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<td>96.5</td>
</tr>
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<td>1092</td>
<td>782</td>
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<td>877</td>
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Table 5.1 Relative abundances (%) of *C. taeniatus* and *C. virescens* at Hoffman’s Rocks A: for each sector over the three sampling dates and B: overall, resulting from repeated sampling. Total sample numbers are shown. Dates are represented as numbers 1 – 5. 1: 20 Feb.’00, 2: 20 May’00, 3: 8 Jul.’00, 4: 24 Oct.’00, 5: 23 Mar.’01. Sectors 1 – 6 were at mid shore.
percentage of each species over all sectors at Hoffman’s Rocks is shown in Table 5.1B for the combined three dates on which this site was sampled. Table 5.1A shows that a very high percentage of *C. virescens* was maintained in each sector at this site over time. In contrast, the percentage of *C. taeniatus* remained extremely low.

Figure 5.2 is a site map of Bauer Street showing the locations of sectors 1 to 10 and their proximity to the storm water drain and to the water’s edge.

Table 5.2A shows the relative abundances of both species arranged by sector and sampling date. In general, as sectors progressed down the shore, the percentage of *C. taeniatus* decreased, while *C. virescens* increased. In Table 5.2B the overall percentages of both species at Bauer Street are presented according to five dates on which this site was sampled.

It can be seen from Tables 5.1B and 5.2B that although the relative abundances of these species vary from sampling time to sampling time at Bauer Street, the percentage of *C. taeniatus* always remains higher there than at Hoffman’s Rocks.

In Table 5.3, sectors 1 to 5 and 7 (the remaining sectors were already submerged) are arranged according to their relative position on the shore and the corresponding salinity of tidepools in each area and in seawater are presented in parts per thousand (‰). This table shows that those sectors in closest proximity to the storm water drain have the lowest tidepool salinities. Tidepool salinities tend to increase with decreasing height on the shore.
Figure 5.2 Aerial photograph of the Bauer Street site showing the arrangements of sectors 1 – 9. Arrow indicates storm water drain.
### A

<table>
<thead>
<tr>
<th>Sectors</th>
<th>1</th>
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<th>4</th>
<th>5</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
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<td>91.4</td>
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<td>2.1</td>
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<td>x</td>
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<td>27.3</td>
<td>80.2</td>
<td>x</td>
<td>37.6</td>
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<td>x</td>
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<td>61.9</td>
<td>49.6</td>
<td>2.9</td>
<td>x</td>
<td>41.8</td>
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<td>x</td>
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<tr>
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<td>42.4</td>
<td>x</td>
<td>48.5</td>
<td>47.5</td>
<td>40.6</td>
<td>57.6</td>
<td>x</td>
<td>51.5</td>
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<td>59.5</td>
<td>93.4</td>
<td>20.6</td>
<td>40.6</td>
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<td>29.2</td>
<td>52.1</td>
<td>72.4</td>
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<td>70.8</td>
<td>47.9</td>
<td>27.6</td>
<td>85.4</td>
<td>76.4</td>
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### B

<table>
<thead>
<tr>
<th></th>
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<th>2</th>
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</tr>
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<tbody>
<tr>
<td>C. t.</td>
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<td>38.3</td>
<td>80.6</td>
<td>66.7</td>
<td>61.4</td>
</tr>
<tr>
<td>C. v.</td>
<td>52.6</td>
<td>61.7</td>
<td>19.4</td>
<td>33.3</td>
<td>38.6</td>
</tr>
<tr>
<td>n</td>
<td>1119</td>
<td>911</td>
<td>743</td>
<td>2597</td>
<td>1400</td>
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</tbody>
</table>

Table 5.2 Relative abundances (%) of *C. taeniatus* and *C. virescens* at Bauer Street

**A**: for each sector over the five sampling dates and **B**: overall, resulting from repeated sampling. Total sample sizes (n) are given for each sampling date. Dates are represented as numbers 1-5. 1: 20 Feb.'00, 2: 20 May’00, 3: 8 Jul.’00, 4: 24 Oct.’00, 5: 23 Mar.’01. x: data unavailable. Sectors 1 – 4 were at high shore, sectors 5 – 8 were at mid shore and sector 9 was at low shore.
Table 5.3  Salinity measurements for sectors 3 to 9 and position on the shore at Bauer Street on March 20, 2001. †: indicates sectors in close proximity to the storm water drain at this site (Kay and Coates, unpublished data).
5.3.2 Geographical (Large Scale) Distribution

5.3.2.1 Coastal Survey

In Figure 5.3, the area covered by the coastal survey is shown.

Table 5.4 presents the site number and name, latitude and longitude and the relative abundances of *C. taeniatus*, *C. virescens*, other species and empty gastropod shells for all survey sites along the coast of Queensland. At some sites, searches did not reveal the presence of any hermit crabs. Populations of other species were prevalent along the Queensland coast and in many localities were sympatric with *C. taeniatus*, *C. virescens*, or both.

Figure 5.4A shows that at seven of the 12 sites where *C. taeniatus* occurred together with other species, the other species accounted for 20% or more of the total hermit crab population. At 10 of the 12 sites where *C. taeniatus* was found with other species, empty shells accounted for 10% or more of the total relative abundance.

At sites where *C. virescens* was found with other species (Figure 5.4B), only two of 12 sites had a relative abundance of other hermit crabs of 20% or more. Empty shells had a relative abundance of 10% or more at only one of 12 sites where *C. virescens* were found with other hermit crab species.

In Table 5.5, three main patterns of distribution can be detected: 1) where *C. taeniatus* was found in the absence of *C. virescens*, or with other species (refer to footnote, Section 5.2.3.1, page 157), it tended to be present over the entire intertidal; 2) where *C. virescens* was found in the absence of *C. taeniatus* or with other species, it also tended to be present over the entire intertidal, and 3) where
Figure 5.3 The rocky shore area of Queensland covered by the coastal survey. Inset shows the geographical location of this coastal region.
<table>
<thead>
<tr>
<th>Site Number</th>
<th>Site Name</th>
<th>Latitude, Longitude</th>
<th>C. taeniatus (%)</th>
<th>C. virescens (%)</th>
<th>Other Species (%)</th>
<th>Empty Shells (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>32</td>
<td>Woody Point (Redcliffe)</td>
<td>S27°15.8', E153°06.3'</td>
<td>17.6</td>
<td>0</td>
<td>56.2</td>
<td>26.1</td>
</tr>
<tr>
<td>28</td>
<td>S. Scott Point (Redcliffe)</td>
<td>S27°15.3', E153°06.6'</td>
<td>49.1</td>
<td>0</td>
<td>48.0</td>
<td>2.9</td>
</tr>
<tr>
<td>74</td>
<td>Osbourne Point</td>
<td>S27°14.9', E153°08.9'</td>
<td>97.3</td>
<td>0</td>
<td>2.7</td>
<td>0</td>
</tr>
<tr>
<td>33</td>
<td>Moonta Head</td>
<td>S27°14.2', E153°09.2'</td>
<td>97.0</td>
<td>0</td>
<td>3.0</td>
<td>0</td>
</tr>
<tr>
<td>31</td>
<td>S. Scott Point (Redcliffe)</td>
<td>S27°15.3', E153°06.6'</td>
<td>49.1</td>
<td>0</td>
<td>48.0</td>
<td>2.9</td>
</tr>
<tr>
<td>32</td>
<td>Woody Point (Redcliffe)</td>
<td>S27°15.3', E153°06.3'</td>
<td>17.6</td>
<td>0</td>
<td>56.2</td>
<td>26.1</td>
</tr>
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</table>

Table 5.4: Coastal survey sites organised from the southernmost site (Woody Point) to the northernmost site (Cape Kimberley).
<table>
<thead>
<tr>
<th>Site Number</th>
<th>Site Name</th>
<th>Latitude, Longitude</th>
<th>Relative Abundance (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>46</td>
<td>N. Indian Head (Fraser Is.)</td>
<td>S24°09.1', E153°21.1'</td>
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</tr>
<tr>
<td>45</td>
<td>S. Middle Rocks (Fraser Is.)</td>
<td>S24°09.1', E153°21.1'</td>
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</tr>
<tr>
<td>44</td>
<td>Champagne Pools (Fraser Is.)</td>
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<tr>
<td>43</td>
<td>S. Middle Rock (DNP)</td>
<td>S24°09.1', E153°21.1'</td>
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</tr>
<tr>
<td>42</td>
<td>N. Bargara Beach (2nd Storm Drn)</td>
<td>S24°48.9', E152°28.0'</td>
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<tr>
<td>41</td>
<td>Burnett Heads</td>
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<tr>
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<td>Elliott Heads</td>
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</tr>
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<td>S. Bargara Beach</td>
<td>S24°48.9', E152°28.0'</td>
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</tr>
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<td>37</td>
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<td>36</td>
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<td>34</td>
<td>The Gables Park (Fraser Is.)</td>
<td>S24°09.1', E153°21.1'</td>
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<tr>
<td>33</td>
<td>Sandy White Memorial Park</td>
<td>S24°16.3', E153°25.0'</td>
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</tr>
<tr>
<td>32</td>
<td>Dairin Point (Big Woody Is.)</td>
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</tr>
<tr>
<td>31</td>
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</tr>
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<td>Bargara Beach</td>
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</tr>
<tr>
<td>27</td>
<td>S. Bargara Beach</td>
<td>S24°48.9', E152°28.0'</td>
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<td>0</td>
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<td>25</td>
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<td>24</td>
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<tr>
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Other Species
Empty Shells
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<tr>
<th>Site Number</th>
<th>Site Name</th>
<th>Latitude, Longitude</th>
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<th>C. virescens</th>
<th>Other Species</th>
<th>Empty Shells</th>
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<tr>
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Figure 5.4  Relative abundances of other species (■), empty gastropod shells (■) and A: C. taeniatus (■), B: C. virescens (■) at sites where the species under study occurred allopatrically or sympatrically with other species (see text for definition of other species).
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GEOGRAPHICAL DISTRIBUTION, INDICATOR SYSTEM, MANAGEMENT IMPLICATIONS

Presence/Absence
*C. taeniatus* and *C. virescens* occurred sympatrically, the former was found over the entire intertidal, but the latter was usually found at or below mid shore.

When occurring in the absence of *C. virescens*, *C. taeniatus* was found in exposed tide pools even at the extreme upper reaches of HS transects. The crabs were also withdrawn into their shells on exposed or shaded sand and “posing” on rocks in full sun at LS at most sites. Where substrate features of the site were very inconsistent from HS to LS (i.e. Site 31, S. Scott Point), *C. taeniatus* inhabited all levels of the shore irrespective of the shelter type or exposure at each.

When *C. virescens* occurred in the absence of *C. taeniatus*, it was also found to inhabit all levels of the shore. In several cases (i.e. Site 71, Cape Capricorn; Site 54, W. Shellving Beach; Site 30, Point Cartwright), this species was also found at the upper reaches of HS transects occupying highly exposed tide pools. Many sites at which only *C. virescens* were found had habitat features that changed greatly with tidal height. This species inhabited each tidal height irrespective of differences in topography and substratum.

Where *C. taeniatus* and *C. virescens* were sympatric, *C. taeniatus* most often inhabited the entire intertidal zone irrespective of inconsistencies in habitat features, while *C. virescens* was usually found at or below MS despite the homogeneity (i.e. Site 17, Burnett Heads) or heterogeneity (i.e. Site 74, Emu Point; Site 40, S. Hay Point) of the habitat. Consistent with this is that at only four sites out of 53 were *C. taeniatus* and *C. virescens* found together throughout the entire intertidal area and in two of these only three or four individuals of *C. virescens* were seen at HS (refer to Chapter 2). Thus, in areas where *C. virescens* was not found, *C. taeniatus* occupied all levels of the shore. In contrast, where *C. taeniatus* was not found, *C. virescens*
occupied all levels. However, when both species were found together *C. taeniatus* was found at all shore heights, while *C. virescens* was restricted to lower levels.

### 5.3.3 Indicator System

In Table 5.6, all sites in which *C. taeniatus* and/or *C. virescens* were present are reported in two categories. In each category, sites were arranged according to latitude and longitude from south to north. Salinity data are reported for sites at which it was measured. It is clear from this table that there was a distinct pattern of abundance in the distribution of *C. taeniatus* and *C. virescens* on a geographical scale in relation to the influence of freshwater. In coastal areas influenced by the presence of freshwater, there was a tendency for the relative abundance of *C. virescens* to be very low, while that of *C. taeniatus* was high.

Although the two Bargara sites had relatively high abundances of *C. virescens* at the time of my surveys, it is important to note that *C. taeniatus* was also very abundant. Later surveys by Kay and Coates (unpublished data) showed a change in the abundances of these species (see Tables 5.2A and B) potentially caused by periods of moderate rains in that area.

In coastal areas devoid of freshwater outfall, on open coastlines and on island sites, *C. virescens* was very abundant while few *C. taeniatus* were found.
Table 5.6 The percentages of *C. taeniatus* and *C. virescens* present at sites along the eastern coast of Queensland, Australia. Sites have been divided into A: those influenced by freshwater and B: those with no freshwater influence and arranged from south to north.
<table>
<thead>
<tr>
<th>Site Name</th>
<th>Latitude, Longitude</th>
<th>Sal(‰)</th>
<th>Relative Abundance (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wickham Point</td>
<td>S26°48.2', E153°08.8'</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Moffat Head</td>
<td>S26°47.5', E153°08.9'</td>
<td>0.6</td>
<td>99.4</td>
</tr>
<tr>
<td>Point Cartwright</td>
<td>S26°40.7', E153°08.3'</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Alexandra Headlands</td>
<td>S26°40.3', E153°06.6'</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Double Island Point</td>
<td>S25°56.2', E153°11.3'</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Woongarra Marine Prk.</td>
<td>S24°50.4', E152°28.7'</td>
<td>7.0</td>
<td>93.0</td>
</tr>
<tr>
<td>N. Middle Rock</td>
<td>S24°17.0', E151°57.1'</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Rocky Point</td>
<td>S24°14.0', E151°56.2'</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Yellow Patch</td>
<td>S24°30.4', E151°13.3'</td>
<td>38.2</td>
<td>44.4 55.5</td>
</tr>
<tr>
<td>Cape Capricorn (Curtis Is.)</td>
<td>S23°29.1', E151°13.9'</td>
<td>38.2</td>
<td>0 100</td>
</tr>
<tr>
<td>Long Beach (Great Keppel Is.)</td>
<td>S23°11.6', E150°50.8'</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>W.Shellving Bch (Grt Keppel Is.)</td>
<td>S23°11.3', E150°50.6'</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>E.Shellving Bch (Grt Keppel Is.)</td>
<td>S23°11.2', E150°50.6'</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Conical Island</td>
<td>S23°03.3', E150°52.7'</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Five Rocks</td>
<td>S22°48.1', E150°48.5'</td>
<td>0.1</td>
<td>99.9</td>
</tr>
<tr>
<td>Lambert’s Beach</td>
<td>S21°03.8', E149°13.5'</td>
<td>19.4</td>
<td>80.6</td>
</tr>
<tr>
<td>Pandanas Bay (Long Is.)</td>
<td>S20°20.4', E148°51.0'</td>
<td>3.3</td>
<td>96.7</td>
</tr>
<tr>
<td>Back Beach (Long Is.)</td>
<td>S20°20.2', E148°51.3'</td>
<td>3.6</td>
<td>96.4</td>
</tr>
<tr>
<td>Bauer Bay (S. Molle Is.)</td>
<td>S20°15.6', E148°50.1'</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Horseshoe Bay</td>
<td>S19°58.7', E148°15.7'</td>
<td>2.2</td>
<td>97.8</td>
</tr>
<tr>
<td>Bingil Bay</td>
<td>S17°50.1', E146°06.0'</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Nudey Beach (Fitzroy Is.)</td>
<td>S16°56.2', E145°59.0'</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>N.Welcome Bay (Fitzroy Is.)</td>
<td>S16°55.9', E145°59.3'</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>N. Ellis Beach</td>
<td>S16°42.9', E145°39.1'</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Port Douglas</td>
<td>S16°29.1', E145°28.2'</td>
<td>29.9</td>
<td>1.0 99.0</td>
</tr>
<tr>
<td>Dayman Point</td>
<td>S16°22.9', E145°24.9'</td>
<td>0</td>
<td>100</td>
</tr>
</tbody>
</table>
5.4 DISCUSSION

5.4.1 Repeated Sampling

Repeated sampling at two sites in Bundaberg provided evidence that in an area where there was no input of freshwater (Hoffman’s Rocks) a very high relative abundance of *C. virescens* was maintained over time. In contrast, the relative abundances of *C. taeniatus* and *C. virescens* were seen to fluctuate over time in an area that was frequently inundated with freshwater (Bauer Street), although the abundance of *C. taeniatus* remained high. In addition, a reversal in abundance took place between two sampling periods at this site, so that *C. taeniatus* became significantly more abundant than *C. virescens* and generally remained so throughout subsequent sampling events. Reasons for this reversal are not clearly evident from the data obtained. However, there is evidence that low to moderate rainfall events can drastically depress tidepool salinities for the duration of low tide exposure (Table 5.3). It would therefore be reasonable to conclude that heavy rainfalls or events lasting several days would severely reduce tidepool and inshore salinities for prolonged periods.

Prolonged reduction in salinity may have two main effects on freshwater intolerant hermit crab species. It may so severely depress tidepool salinities that these species move further down on the shore, or migrate into the subtidal region where they are less likely to experience prolonged exposure to the most dilute seawater. The second effect is that adult crabs may not be able to find refuge from diluted seawater and thus, succumb to low salinity exposure, especially if this occurs in combination with high water temperatures (i.e. during summer months). If
this does occur, mortality of some hermit crabs may result in an abundance of shells available to surviving crabs.

Depending in part on patterns of dispersal, the larvae of different species may also have very different tolerances to environmental conditions. Young and Hazlett (1978) found that the larvae of the temperate hermit crab, *Clibanarius vittatus*, reared in the laboratory only metamorphosed to juvenile crabs in the very narrow range of salinities between 25 and 30‰ in combination with temperatures of 25 and 30°C. However, Ajmal Khan and Natarajan (1981b) reported that in their studies of laboratory reared *Clibanarius longitarsus* from the Vellar estuary, India, complete development of the larvae occurred in the wider range of salinities between 20 and 35‰. Therefore, it may be speculatively suggested that differences in larval survival between species may be related to changes in the relative abundances of the *C. taeniatus* and *C. virescens* at Bauer Street. Future work is needed to determine if, indeed, there is a difference in the survival of the larvae of these species under various environmental conditions.

As yet, not enough data have been collected within the Bauer Street site to detect any consistent relationship between changes in tidepool salinity and changes in the abundances of the two species at this site. Since data have been collected for only one year, seasonal changes in relative abundances may not yet be evident. However, there was evidence from repeated sampling at Bundaberg between sites, that *C. virescens* had a consistently high relative abundance on open coasts compared with *C. taeniatus*, while the percentage of *C. taeniatus* was consistently higher on a shore influenced by freshwater.
An important aspect of future work may be to investigate the association of rainfall events, changes in tidepool salinity, duration of tidepool dilutions and changes in the relative abundances of these species.

5.4.2 The Movement of Freshwater

Endean et al (1956) recognised that there were many rocky sites along the Queensland coast that could be affected by freshwater from nearby river outfalls. Data they obtained indicated that large enough volumes of freshwater were carried by the Burdekin and Fitzroy Rivers, in particular, into their respective bays as to considerably reduce the salinity of nearby coastal waters. They further emphasised that (of the sites they visited) the areas most likely to be affected by river outfall would be Point Vernon, near the Mary River and Yeppoon and Cape Capricorn (Curtis Island), near the Fitzroy River. Their analysis also showed that the majority of rainfall occurs over the summer months, during which time long periods of calm weather in lagoonal areas lead to relatively little mixing and surface salinities that are frequently low.

Currents caused by both wind and wave conditions along coastal shores can drive low salinity, surface waters long distances from the outfall source. The Hervey Bay and Capricorn Coast regions are typical of the general patterns and directions of water movements along the Queensland coast.

In the Hervey Bay region (Figure 5.5), the East Australian Current has little influence on the movement of nearshore sediments (Anonymous, 1989), and would assumedly have correspondingly little effect on surface freshwater. However, nearshore currents in this region are tidal and between ebb and flood tides there is
Figure 5.5  Hervey Bay region showing the usual direction of freshwater movement (→) on ebb tides from the Mary River, through Great Sandy Strait, around Urangan and north-westward toward Point Vernon.
an almost 180 degree reversal in direction (Anonymous, 1989). Flooding of the Mary and Burnett Rivers, in particular, are likely to carry large volumes of freshwater and flush sediments from the estuaries out onto coastal shores. On ebb tides, freshwater generally moves northward from the Mary River through the shallow Great Sandy Strait, around Dayman Point at Urangan and north-eastward to Point Vernon (Anonymous, 1989).

In the Burnett River area, currents are mostly wind driven with the net current running north-west in the morning and afternoon (Anonymous, 1989).

There is also little effect of the East Australian Current along the area of the Capricorn Coast within the Great Barrier Reef (Maxwell, 1968), but nearshore tidal currents and especially wind drift currents can be an important mechanism of surface freshwater distribution. Along this coastal region, there are frequent periods when south-easterly winds persist and wind drift currents to the north predominate (Anonymous, 1979). At the southern end of the Capricorn Coast, tidal direction is mainly controlled by the southerly flood and northerly ebb flows of the Fitzroy River, while further north at Lammermoor Beach, a net northward flow is consistent with winds and waves mostly coming from a south-easterly direction (Anonymous, 1979). There is also evidence that the freshwater outflow from Ross Creek onto the coast, just north of Fisherman’s Beach and S. Cooee Bay (see Figure 2.1, Section 2.2.2, page 21), is predominantly forced in a southward direction around Wreck Point due to localised eddy conditions at this site (Anonymous, 1979).

During a catchment scale flood event, O’Neill et al. (1992) recorded sea surface salinities below 10‰ for over two days throughout much of Keppel Bay from the Mouth of the Fitzroy to north of Yeppoon and to the east of Great Keppel
Island. Daily records collected by Coates (unpublished data) showed that shoreline salinity in Keppel Bay was reduced by both local, seasonal flooding (see Figure 5.6, arrow A) as well as large, irregular catchment scale flooding (see Figure 5.6, arrow B). During the latter event, Coates (1992) found that salinities less than 15‰ persisted on rocky shores in that area for up to 13 days. In addition, it can be seen by inspection of Figure 5.6, that low salinities can coincide with peak summer temperatures, resulting in the combined stress of low salinity and high temperature. This combination was found to be especially detrimental to \textit{C. virescens}. In 22% SW and 35°C, more than 50% of \textit{C. virescens} died after only six hours under laboratory conditions while over 90% of \textit{C. taeniatu}s survived (refer to Section 4.3.1, page 123).

5.4.3 Geographical (Large Scale) Distribution

5.4.3.1 Coastal Survey

This set of field studies was carried out in order to investigate large scale, geographical distribution patterns for the hermit crabs \textit{C. taeniatu}s and \textit{C. virescens} on tropical, rocky intertidal shores along the coast of Queensland, Australia.

Results of physiological investigations (Chapter 3), survival experiments (Chapter 4) and repeated sampling at two sites (this chapter) lead to the prediction that these species should show a specific pattern of distribution related to the influence of freshwater on a broad scale. The prediction was that in areas of freshwater influence, such as inshore areas near the mouths of rivers or regularly flowing creeks, the freshwater tolerant species, \textit{C. taeniatu}s, should be highly abundant, while the freshwater sensitive species, \textit{C. virescens}, should be less...
Figure 5.6 Daily shoreline salinity (---) and temperature (---) readings between April, 1989 and January, 1992 along Keppel Bay.

Arrow A indicates a regular, seasonal flood event on a local scale; arrow B indicates an irregular, flood event on a larger scale. From Coates, unpublished data.

GEOGRAPHICAL DISTRIBUTION, INDICATOR SYSTEM, MANAGEMENT IMPLICATIONS
abundant. Furthermore, in areas devoid of freshwater runoff, such as island or open coast sites, I predicted that *C. virescens* should occur in higher abundance than *C. taeniatus*.

Results of the geographical survey were very consistent with the predicted distributions of these species. At several sites, *C. taeniatus* was found in the absence of *C. virescens* or sympatrically with other species (refer to footnote, Section 5.2.3.1, page 157). In the latter case, the other species taken together were often as abundant as *C. taeniatus*. In addition, shells appeared to be plentiful in almost every situation where *C. virescens* was not present. This could indicate that: 1) shells are not being utilised for a variety of reasons. Leite *et al.* (1998), in a study of habitat and shell use by nine species of hermit crabs in São Sebastião, Brazil, found that shell use did not follow shell availability. They reported that various species of shells were unused by hermit crabs, most likely due to their architecture and the fact that some shell designs may reduce attachment of crabs to rocks, enhancing potential displacement by wave action. Emmerson and Alexander (1986) also reported abundant *Nerita albicilla* and *Conus* spp. shells that were unused by *Diogenes breviostris*, likely due to the architecture of these shell types. Some authors have demonstrated that shell use follows crab shell preference, unless preferred shell types are absent or scarce (Bertness, 1980; Reddy and Bisewar, 1993; Leite *et al.*, 1998). In two sites in Brazil, Leite *et al.* (1998) found that *Paguristes tortugae* did not use the shells of the most abundant gastropod, *Morula nodulosa* because the dimensions of these shells did not match crab size. In Denmark, Markham (1968) found small *Pagurus bernhardus* mostly occupying shells of *Littorina littorea*, but when larger, they were almost exclusively found in
shells of *Buccinum undatum* and *Neptunea antiqua*. He also found that both these species of shells were abundant in the area where *P. bernhardus* was found. 2) the population of available shells is greater than the carrying capacity of the habitat in relation to other resources, or 3) survival of hermit crabs is reduced by habitat conditions.

In contrast, where *C. virescens* was found in the absence of *C. taeniatus*, there was usually a low percentage of the other species and very few available shells. This could indicate that: 1) shells are a more limiting resource on open coast and island habitats due to loss of shells as a result of wave action and currents. 2) there may be heavy predation on shell bearing animals by shell-damaging predators. In Guam, Vermeij (1976) found various reef-flat crabs that were readily able to feed on gastropods and hermit crabs by crushing the shells in their large master claw. Bertness (1981a) found that predation on shell inhabitants was an important selective pressure in the Bay of Panama. He demonstrated that predation intensity increased with decreasing height on the shore, since significantly larger shells were broken in the lower intertidal than in the upper. Both shell-crushing crab predators, such as *Eriphia squamata* and *Ozius verreauxii*, and shell-crushing teleost fish predators, like *Diodon hystrix* and *D. holocanthus*, have been suggested to increase in importance and predatory ability in the tropics (Bertness, 1981a). 3) there is greater survival of *C. virescens* larvae and/or adults due to increased food availability and carrying capacity on exposed shores, thus shells become limiting.

It is, however, difficult to interpret this apparent pattern since these sites were visited only once. Repeated sampling at several sites may provide data necessary to draw any conclusions. In addition, data on the population density of
both hermit crabs and empty shells, as well as experiments on shell preferences versus shell availability would provide an idea of the extent to which empty shells are limiting.

Surveys demonstrated that where *C. virescens* was absent, *C. taeniatlus* was found throughout the intertidal. Conversely, where *C. taeniatlus* was absent, *C. virescens* was present at all levels of the shore. Where both species were present, *C. taeniatlus* occupied all shore heights, while *C. virescens* was restricted to the lower levels. These differences in distribution on the shore may reflect the fact that in inshore areas, *C. virescens* is less able to tolerate conditions of the combined stress of high temperature and low salinity most likely to occur at high shore and is thus restricted to low shore by physiological constraints. It is also possible that in habitats where freshwater stress occurs, the more tolerant *C. taeniatlus* may outcompete *C. virescens* for shells and limit the distribution of the latter species to the lower shore.

While the link between differences in physiological responses, tolerances and geographical distribution appears to be a valid one, other factors such as differences in feeding behaviours and the availability of food sources may also play very important roles in influencing the large scale distribution of *C. taeniatlus* and *C. virescens*. Kunze and Anderson (1979) found that these species had slight differences in their feeding mechanisms. They reported that *C. taeniatlus* is predominantly a soft food detritivore, while *C. virescens* is both detritivorous and macrophagous and uses the chelae and crista dentata for trituration. *C. taeniatlus* does not appear to use the chelipeds to tear *Zostera* sp. seagrasses apart, unless the tissue is decayed and already breaking down. Instead, this species uses the chelipeds
to scrape epiphytic algae from the laminae of *Zostera* sp. (Kunze and Anderson, 1979).

Other species of epiphytic algae may also be used by *C. taeniatus* as food sources since they may occur in areas where *C. taeniatus* is abundant, but are not likely to be present in areas where this species of crab is not found. It is possible, therefore, that differences in potential food sources available in the intertidal zone may have an influence on the geographical distribution of these species.

Large scale distribution may also be affected by the ability of larval recruits to detect, avoid or survive low salinity waters. Since the early work of Wilson (1932, 1937 in Crisp, 1976) on the larvae of several polychaetes and Jägersten (1940 in Crisp, 1976) on the polychaete, *Protodrilus rubropharyngeus*, it has become increasingly clear that the larvae of a great many marine invertebrates are not only able to discriminate between favourable and unfavourable habitats, but are also able to delay metamorphosis under unfavourable conditions. While there are numerous reports on the recruitment and settlement behaviours of many marine invertebrates (see review by Crisp, 1976), reports on the larval distribution of hermit crabs are few, including those by Sadler (1984, in Gherardi, 1995), Asakura (1991), Gherardi (1995) and Worcester and Gaines (1997) and there are almost no reports on larval recruitment processes in hermit crabs. In addition, I could find no literature on the recruitment and settlement processes of anomurans under various conditions of salinity. Instead, the focus of larval investigations in hermit crabs has been on development and morphology under various conditions in the laboratory (Coffin, 1958, 1960; Young and Hazlett, 1978; Ajmal Khan and Natarajan, 1981a,b; Gherardi and McLaughlin, 1995; Lyla *et al*., 1998).
Young and Hazlett (1978) examined the effects of temperature and salinity combinations on the larval development of *Clibanarius vittatus* in an attempt to help explain the geographical distribution of this hermit crab species, which occurs from Virginia, U.S.A., to Rio de Janeiro, Brazil. They found that increased temperature resulted in more rapid development, but that salinity had little or no effect. Complete development to juvenile crabs occurred only at combinations of 25 and 30‰ at 25 and 30°C. While the temperature tolerance limits of adult *C. vittatus* ranged from 5 to 35°C (in salinities from 20-32‰), those of both *Pagurus longicarpus* (12-20°C in 25-30‰) and *P. pollicaris* (10-23°C in 24-27‰) were much narrower. Yet, the geographical ranges of *P. longicarpus* and *P. pollicaris* along the western coast of the Atlantic extend north to Nova Scotia and Massachusetts, respectively, while *C. vittatus* is not found north of Virginia. Young and Hazlett (1978) concluded that the tolerance of adult *C. vittatus* to temperature was not the limiting factor for the geographical distribution of adults, but that the inability of the larvae to develop at low temperatures could be responsible.

5.4.4 Indicator System

When sites were arranged into the categories “Influenced by Freshwater” and “Not Influenced by Freshwater” one anomaly resulted. In the first category, *C. virescens* had relative abundances that were higher than *C. taeniatus* at the two sites at Bargara, Bundaberg. These percentages are similar to measurements of relative abundances for these species taken by Kay and Coates (unpublished data) in the same vicinity at Bauer Street at approximately the same time (May 20, 2000) (see Table 5.2B). One reason for the higher relative abundance of *C. virescens* at Bauer
Street may simply be that the influence of freshwater is not as great here as at other sites sampled. However, data subsequently collected by Kay and Coates (unpublished) in the same region showed that an increase in the relative abundance of *C. taeniatus* occurred sometime previous to the next sampling period on July 8, 2000. Although reasons for this change are not clear, further re-sampling at this site may demonstrate the sensitivity of these populations to freshwater inundation and alterations in salinity.

Despite the lack of quantitative data for the influence of some factors, there is still good evidence that the geographical distribution of *C. taeniatus* and *C. virescens* is highly influenced by the dilution of coastal waters. Evidence presented in this chapter also indicates that these species can be used as a simple and convenient indicator system for freshwater inundation of intertidal shores, provided that a minimum sample size is used for measurements of relative abundance.

Ward (2000) defines environmental indicators as “measurable variables that track changes in important elements, functions or issues in the environment, uses of natural resources, or management of the environment” (Ward, 2000. pp. 436). Indicators should be simple, direct and easy to interpret if they are to be used in large scale reporting (Ward 2000). Further, an indicator needs to be specific to the type of pollution concerned. There is a long history of the use of marine invertebrates as indicators of the presence and intensity of pollution (Reish 1972). For example, an increase in the abundance of the polychaete *Capitella capitata* has been shown to indicate pollution (probably increased nitrates and phosphates) from domestic out falls (Filice 1954; Kitamori and Funae 1959, 1960; Reish 1959; Kitamori 1963; Bellan 1967). Imposex in marine gastropods is an indicator of the
antifouling agent Tributyltin (Bright and Ellis, 1989; Stickle et al., 1990; Nias, 1991; Nias et al., 1993). Filter feeding oysters and mussels are often used as indicators of lipid soluble pollutants in the marine environment (Riedel et al., 1995; Chen et al., 1996; Al-Madfa et al., 1998).

*C. taeniatus* and *C. virescens* are common, tropical intertidal species that, unlike the original gastropod owner of the shell, are unable to completely seal off the aperture in times of environmental stress, such as dilution of seawater by freshwater. Taken together with results on differences in survival in low salinity, these factors may make *C. taeniatus* and *C. virescens* better indicators of changes occurring in intertidal conditions and community structures than snails, clams and oysters which can effectively seal out unfavourable changes in surrounding conditions for a time (Gilles, 1972; Vermeij, 1993; Willmer et al., 2000 and see review by Underwood, 1979).

### 5.4.5 Management Implications

Intense coastal development, that has been typical of temperate regions, is now increasing in the tropical regions of the globe (Johannes and Betzer, 1975; Vernberg, 1981b). Coastal development can result in a range of pollutants being discharged into coastal habitats. Examples include untreated, or partially treated sewage, chemical effluent from a variety of industrial sources and stormwater runoff from residential areas. This last source of pollution is of increasing importance in tropical areas experiencing extensive residential development in the coastal zone. The majority of land based pollutants are carried to the marine and estuarine environments of Australia by freshwater sources such as rivers, pipes and
stormwater drains (Batley, 1995; Anonymous, 1998b; Hutchings and Haynes, 2000; Haynes and Johnson, 2000). While these are often the vehicles for the transport of pollutants, freshwater itself, can have a large impact on the marine environment, particularly the intertidal region and thus act as a “pollutant”. The greatest impact may occur when, due to coastal development, new freshwater sources such as stormwater drains are introduced onto intertidal shores that have not previously been under the influence of freshwater inputs.

No studies exist on the effects of sudden and prolonged inundation of intertidal habitats. Therefore, there is a real need for investigations into this phenomenon to gain greater understanding of the basic responses of intertidal communities to freshwater disturbances. An awareness that biological changes can occur to coastal habitats and invertebrate communities is important for coastal managers and developers. Equally important is a relatively easy, cost efficient mechanism by which these changes can be predicted and monitored over time and over a large scale reporting area (Ward, 2000).

An indicator system of this type may be provided by the use of *C. taeniatus* and *C. virescens* with the prediction that in areas where a new freshwater source is introduced, the relative abundance of *C. virescens* should decline fairly rapidly, while that of *C. taeniatus* should increase with time.

5.5 Discussion Summary

Repeated sampling at one site uninfluenced by freshwater showed that *C. virescens* maintained a very high relative abundance, while *C. taeniatus* was
consistently low. At a site where a freshwater creek was directed onto the intertidal area by a storm water drain, the relative abundance of *C. virescens* was not significantly different from *C. taeniatus* in the first sampling period, but was lower in other samples. It is important to see that while the relative abundance of *C. virescens* was consistently much higher than that of *C. taeniatus* at Hoffman’s Rocks, at Bauer Street, there was a consistently high relative abundance of *C. taeniatus*.

Reduced sea surface salinities may occur as a result of seasonal, small scale flooding or irregular catchment scale flooding. In either case, freshwater may be moved along coastal shores by the general northward direction of ebb tide currents. The geographical distribution of the low salinity sensitive *C. virescens* and low salinity tolerant *C. taeniatus* was predicted to be influenced by the presence of freshwater onto intertidal shores, with the percentage of the former being high on open coasts and islands and that of the latter being high on inshore areas near freshwater outfalls. The distribution of these species over a large area of the Queensland coast was consistent with predictions. It is therefore suggested that these species may constitute a simple, cost effective mechanism to track changes in intertidal communities subjected to freshwater inundation. In areas where neither *C. taeniatus* nor *C. virescens* are found, other indicator systems would be required. These systems might use other species of hermit crabs or a combination of other invertebrates, although their applicability would require investigation.

While the presence of freshwater appears to have an important influence on the geographical distribution of *C. taeniatus* and *C. virescens*, differences in feeding
behaviours, availability of food and the successful dispersal and recruitment of larvae are other possible influences on distributional differences.

Repeated sampling took place at one site already under the influence of freshwater (Bauer Street). It would be most valuable to undertake a regular monitoring program at the site of a proposed coastal development initially uninfluenced by freshwater and where *C. virescens* is found in the absence of *C. taeniatus*. Monitoring both before and after development and the introduction of freshwater onto the intertidal zone by stormwater drains could track changes in the relative abundances of *C. taeniatus* and *C. virescens* over time. It would also be important to monitor rainfall events and changes in tidepool salinity.

In addition, there is evidence that other pairs of hermit crab species, which differ from each other in a manner similar to *C. taeniatus* and *C. virescens*, occur on other tropical coasts (Ball and Haig, 1974; Bertness, 1981a; Gherardi, 1990; Barnes, 1997a; Gherardi and Nardone, 1997; Turra *et al.*, 1999). Therefore, it is suggested that there may be value in investigating this possibility with the intention of identifying indicator systems of freshwater intrusion on tropical shores in other areas of the world.

In areas where *C. virescens* dominates the intertidal zone, it is unclear why *C. taeniatus* is not also abundant since environmental conditions on open coasts appear to be less stressful, as far as combined low salinity and high temperature are concerned. It is possible however, that shells may be limiting on wave exposed open coasts. Hermit crabs rely on empty gastropod shells in order to protect their soft, vulnerable abdomens. Since these crabs are not able to structurally alter their shells, they must acquire larger shells as they grow. This necessitates a range of
shell sizes that are regularly available. However, it has often been observed that shells are a limiting resource for some hermit crab populations (Hazlett, 1970; Vance, 1972a; Fotheringham, 1976a; Kellogg, 1976; Bertness, 1980; Leite et al., 1998; Turra et al., 1999).

In the following chapter I present the results of a preliminary experiment that investigated the relative abilities of *C. taeniatus* and *C. virescens* to compete for a limited number of shells.
6.0 **CHAPTER 6: INTERSPECIFIC COMPETITION**

6.1 INTRODUCTION

In Chapters 3 and 4 evidence was presented demonstrating that the respiratory response of *C. virescens* was more sensitive than *C. taeniatus* to acute changes in temperature. Furthermore, *C. virescens* showed a lower tolerance of extended exposure to reduced salinity, resulting in survival well below that of *C. taeniatus*. Conditions of acute temperature change and exposure to low salinity are more likely to occur high in the intertidal due to rain and the flow of groundwater onto intertidal flats. The results of my experiments reported in Chapters 3 and 4 suggest that the local, small scale distribution of these species can be explained to some extent by physiological differences between them.

However, there are regions of the coast in which *C. virescens* is very common throughout the intertidal area and is abundant at high shore, while *C. taeniatus* may be few or absent (see Chapter 5, Section 5.3.1, page 161). Environmental conditions in these regions appear no more or less extreme than in regions where *C. taeniatus* is dominant, except in degree of wave exposure on some shores (see Endean *et al.*, 1956) and degree of exposure to freshwater. Yet, no evidence was found to support a reason for the low abundance or absence of *C. taeniatus* on open coasts or islands in the physiological data presented in Chapter 3, or the data on tolerance presented in Chapter 4.

In addition to physiological adaptations, behavioural interactions between organisms have been recognised as powerful influences on local and geographical

Paine (1966) proposed that in the absence of predation, competition in ecological communities has the effect of reducing community diversity by eliminating species that are competitively inferior. Understanding the action of competition in structuring natural communities must involve determining how many competing species can be supported by available resources (Vance, 1972a), although this is well beyond the scope of this thesis.

One possible resource that may be competed for both within and among hermit crab species is the supply of available shells. Abrams (1980) has reviewed evidence that the supply of empty gastropod shells limits hermit crab population size. When combined with observations that there is often considerable overlap in the use of habitat and shells between different species (Abrams, 1981b), this evidence suggests that interspecific competition for shell resources may occur (Abrams, 1981a).

Open coast and island intertidal areas of Queensland are continually exposed to winds, currents and wave action (Endean et al., 1956) that may reduce the number of empty gastropod shells. Although A. Kuris (personal communication) found that shell loss during storms on the California coast was minimal, Vance (1972a) reported that when 120 empty *Littorina sitkana* shells were placed at four intertidal locations with differing exposure to currents, only four were recovered after six days. He concluded that shell loss due to currents in the San Juan Islands area was considerable and that shells available to larger hermit crabs were especially limited. In the Bay of Panama, Bertness (1981b) also found that some of
the empty gastropod shells he added were removed from the experimental field site and suggested this occurred by wave action.

In a study by Hahn (1998) on the shell selection of the hermit crab, *Calcinus seurati*, it was found that this species selects heavier or larger shells when exposed to a high flow environment. This may have two advantages; reducing the likelihood of dislodgment by the current and also protecting the crab if it is dislodged (Hahn, 1998). Hahn (1998) suggested that extra energy costs involved in carrying heavier shells may be offset by the benefit of inhabiting an environment in which currents readily replenish food supplies.

Even though wave exposed shores are usually food-rich environments (Vermeij, 1993), hermit crabs on open coastal areas (especially at low shore) may be faced with a shortage of available shells (Vermeij, 1993; Barnes, 1999). Thus, for crabs inhabiting exposed shores, there may be a selective advantage to having behaviours that limit or exclude potential competitors for shell resources.

I therefore proposed that the reduced numbers or absence of *C. taeniatus* from regions in which *C. virescens* occurred in high numbers could be the result of competitive interactions for shells between these species. Although I rarely found naked hermit crabs in the field, it is clear that such individuals are extremely vulnerable to environmental conditions, predators, and cannibalism, and therefore securing a shell even in situations where they are very limited, is important for survival.

Initially, I tested the hypothesis that naked *C. virescens* could secure a greater number of shells when in competition with naked *C. taeniatus* for a limited shell supply. To test this, an interspecific competition experiment was carried out.
Since the lower intertidal has been shown to be an area of greater hydrodynamic activity (Short, 1991; Masselink and Short, 1993; Denny, 1988 in Vermeij, 1993) where shell loss due to breakage, bioerosion and removal, potentially occurs more rapidly than at high shore (Vermeij, 1993; Vermeij, personal communication; Barnes, 1999), it was further hypothesised that the shell weight of *C. virescens* would be greater than that of *C. taeniatus* of the same body weight when both species were collected from low shore in the field.

### 6.2 MATERIALS AND METHODS

#### 6.2.1 Interspecific Competition

Hermit crabs of both species inhabiting shells of *Monodonta labio*, *Austrocochlea concamerata* and *Austrocochlea porcata* were collected from low shore at Emu Point (S23°15.5’, E150°50.0’) or Tanby Point (S23°14.1’, E150°49.6’), Central Queensland, Australia between May, 2000 and February, 2001. Crabs were taken to Central Queensland University and acclimated in aquaria at 25 ± 2.0°C in 100% SW for at least three days before use in experiments.

Thirty hermit crabs of each species were individually selected and standardised for size. All were in a total weight** range from 1.21 – 5.47g. No attempt was made to sex individuals, as Abrams (in Barnes, 1999) and Bertness (in Barnes, 1999) found no alteration in shell selection behaviour due to gender. Each

**Throughout this chapter, “total weight” is defined as the combined weight of the shell and the crab within it.
crab was shaken to remove water and weighed in its shell, after which it was removed from the shell by gently breaking it in a small vice. The crab was then dabbed dry and weighed. Shell weight was calculated by subtracting body weight (crab only) from total weight.

For each repetition of the experiment, measurements of total weight, shell weight and crab body weight were individually analysed by one way ANOVA to examine if there were differences between species for these measurements. Although variations in total weight and shell weight did occur, body weight was considered the more important factor in acquiring a shell during naked interspecific competition.

From a collection of empty *Monodonta labio* shells, 15 were chosen so that the weight and size of each shell was within the range of those removed from the test crabs. All 60 naked crabs were randomly placed in a single 60cm × 30cm × 30cm aquarium prepared beforehand with a layer of unwashed beach sand to a depth of 1cm and covered by approximately 10L of 100% SW aerated and kept at 25 ± 1.0°C by a submersible water heater. The crabs were left in the aquarium for approximately one hour before the experiment began. At the start of the experiment, 15 empty shells were randomly placed on the sand at the bottom of the loosely covered aquarium and left undisturbed for 24 hours (although some observations did occur at irregular intervals during this time). At the end of the experiment, all crabs were assigned to one of four categories: Dead, Alive with shells, Alive without shells and Missing. Since no observations were made on how hermit crab deaths occurred over the experimental period, crabs counted as “Dead” or
“Missing” were not included in the analyses of shell acquisition for individual experimental repetitions or pooled data.

The experiment was repeated 10 times. In some repetitions, however, mean body weights for the two species were significantly different. The mean total weight, mean shell weight and mean body weight of repetition # 6, for example, were all significantly different from several other repetitions, and were thus excluded as outliers (see Table 6.1). After all exclusions, a Model III, two way ANOVA on body weights for “Species” (fixed factor) and “Repetition” (random factor) was performed on the three remaining repetitions (3, 4 and 8) (see Table 6.3).

Results for each, individual repetition were analysed by Chi-square 2×2 contingency tables for live crabs of both species with shells and without shells. Individual Chi-square 2×2 contingency table analyses were tested for heterogeneity (Zar, 1999) and found to be homogeneous. Therefore, repetitions were pooled and used for the overall Chi-square 2×2 contingency table analysis of shell acquisition. The final probability was calculated by a one-tailed Fisher Exact test.

### 6.2.2 Shell Weight versus Body Weight

To determine if one species occupied a heavier shell than the other, data for 600 shell and body weights of *C. taeniatus* and *C. virescens* inhabiting *Monodonta labio* shells in the field were calculated as described above. The data were plotted and analysed by ANCOVA for differences between species in shell weight as a function of body weight. In addition, the shell weights and body weights of the 180
crabs from retained experimental repetitions were also compared, plotted and analysed as above.

6.3 RESULTS

6.3.1 Interspecific Competition

In Figure 6.1 it can be seen that the mean body weights of both species had a large degree of variation over the 10 experimental repetitions. Results of a one way ANOVA for body weight showed that *C. virescens* weighed significantly more than *C. taeniatus* when “Species” were compared over all repetitions (ANOVA, $F_{1,598}=24.283$, $P<0.001$).

In Table 6.1 the mean total weights, mean shell weights and mean body weights are given for all 10 repetitions of the interspecific shell competition experiment. This table shows that although the total weights of both species were very similar, the shell weights of *C. taeniatus* were greater (in most cases) than those of *C. virescens*. However, the body weights of *C. virescens* were always greater than *C. taeniatus*, although not always significantly so.

Table 6.2 shows a comparison between species for the ability to acquire limited shells over all experimental repetitions (i.e. before exclusion of repetitions where body weights were significantly different between species). These totals show that there was no difference between species in obtaining shells ($\chi^2_{1}=0.01$, $P>0.05$). Included in Table 6.1 are those repetitions in which mean body weights for *C. taeniatus* and *C. virescens* were significantly different (see Figure 6.1). Greater
Figure 6.1 Comparison of the mean body weights of *C. taeniatus* ( ) and *C. virescens* ( ) over 10 experimental repetitions for interspecific shell competition. Repetitions in which mean body weight was statistically different between *C. taeniatus* and *C. virescens* were not included in shell acquisition analyses. Bars represent 1 standard error.
Table 6.1  Mean total weight, shell weight and body weight ± 1 standard error (S.E.) are given for both *C. taeniatus* and *C. virescens* over all experimental repetitions. Repetitions excluded from the Chi-squared analyses for shell acquisition are indicated by (†).

<table>
<thead>
<tr>
<th>Repetition</th>
<th>Total ± S.E.</th>
<th>Shell ± S.E.</th>
<th>Body ± S.E.</th>
<th>Total ± S.E.</th>
<th>Shell ± S.E.</th>
<th>Body ± S.E.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1†</td>
<td>3.10 ± 0.15</td>
<td>2.76 ± 0.14</td>
<td>0.34 ± 0.02</td>
<td>2.77 ± 0.13</td>
<td>2.39 ± 0.12</td>
<td>0.38 ± 0.02</td>
</tr>
<tr>
<td>2†</td>
<td>2.72 ± 0.12</td>
<td>2.39 ± 0.11</td>
<td>0.33 ± 0.02</td>
<td>2.77 ± 0.14</td>
<td>2.40 ± 0.12</td>
<td>0.37 ± 0.02</td>
</tr>
<tr>
<td>3</td>
<td>2.68 ± 0.15</td>
<td>2.34 ± 0.13</td>
<td>0.34 ± 0.02</td>
<td>2.58 ± 0.13</td>
<td>2.23 ± 0.11</td>
<td>0.35 ± 0.02</td>
</tr>
<tr>
<td>4</td>
<td>2.56 ± 0.13</td>
<td>2.23 ± 0.11</td>
<td>0.34 ± 0.02</td>
<td>2.47 ± 0.21</td>
<td>2.11 ± 0.18</td>
<td>0.37 ± 0.03</td>
</tr>
<tr>
<td>5†</td>
<td>2.71 ± 0.11</td>
<td>2.36 ± 0.10</td>
<td>0.35 ± 0.02</td>
<td>2.90 ± 0.12</td>
<td>2.44 ± 0.10</td>
<td>0.45 ± 0.02</td>
</tr>
<tr>
<td>6†</td>
<td>3.15 ± 0.16</td>
<td>2.74 ± 0.15</td>
<td>0.40 ± 0.02</td>
<td>3.04 ± 0.12</td>
<td>2.52 ± 0.10</td>
<td>0.52 ± 0.03</td>
</tr>
<tr>
<td>7†</td>
<td>2.50 ± 0.13</td>
<td>2.16 ± 0.11</td>
<td>0.35 ± 0.02</td>
<td>2.75 ± 0.15</td>
<td>2.32 ± 0.12</td>
<td>0.42 ± 0.03</td>
</tr>
<tr>
<td>8</td>
<td>2.83 ± 0.12</td>
<td>2.48 ± 0.11</td>
<td>0.35 ± 0.02</td>
<td>2.71 ± 0.12</td>
<td>2.34 ± 0.10</td>
<td>0.37 ± 0.03</td>
</tr>
<tr>
<td>9†</td>
<td>2.76 ± 0.12</td>
<td>2.38 ± 0.10</td>
<td>0.38 ± 0.02</td>
<td>2.70 ± 0.11</td>
<td>2.29 ± 0.09</td>
<td>0.42 ± 0.02</td>
</tr>
<tr>
<td>10†</td>
<td>2.78 ± 0.12</td>
<td>2.43 ± 0.11</td>
<td>0.35 ± 0.02</td>
<td>2.37 ± 0.13</td>
<td>1.99 ± 0.11</td>
<td>0.37 ± 0.03</td>
</tr>
</tbody>
</table>
Table 6.2 The pooled number of *C. taeniatus* and *C. virescens* that had acquired shells that died during the experiment are also compared between species. Those that did not acquire shells but remained alive at the end of the experiment as well as those that died during the experimental repetitions. Those that did not acquire shells, but remained alive at the end of the experiment as well as those that died during the experiment are also compared between species. The total number of each species used is also given.

<table>
<thead>
<tr>
<th>Species</th>
<th>Shells acquired</th>
<th>No shells acquired (alive)</th>
<th>Dead</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. taeniatus</em></td>
<td>73</td>
<td>154</td>
<td>300</td>
<td>300</td>
</tr>
<tr>
<td><em>C. virescens</em></td>
<td>77</td>
<td>168</td>
<td>55</td>
<td>300</td>
</tr>
</tbody>
</table>

Total 300
body weight was considered an advantage in securing shells and would therefore confound the comparison between species in acquiring shells. For this reason, repetitions 1, 2, 5, 6, 7, 9 & 10 were subsequently excluded from statistical analyses for shell acquisition.

The results of a Model III, two way ANOVA on body weight for “Species” and “Repetition” are provided in Table 6.3 for the three repetitions analysed. There were no significant differences between “Species” or among “Repetitions” and there was no significant interaction between these variables. In all experimental repetitions used for pooling, the mean total weights of *C. taeniatus* was more than the mean total weights of *C. virescens* (Figure 6.2), but this difference was not significant.

In Figure 6.3, it can be seen that the mean shell weights for *C. taeniatus* were slightly higher than the mean shell weights for *C. virescens*. The mean weight of supplied empty shells was intermediate between the mean weights of empty shells from both species (Figure 6.3) except in the case of repetition # 3 where the mean weight of empty shells was slightly, but not significantly, higher than the mean weight of shells from either species.

When mean body weights were plotted, they demonstrated that *C. taeniatus* had a lower body weight than *C. virescens* in all pooled repetitions, although this difference was not significant (Figure 6.4).

The number of *C. taeniatus* and *C. virescens* that acquired shells during the 24 hour experimental period, and those that did not acquire shells but remained alive at the end of the experimental period are given in Table 6.4 for the three repetitions retained. Also included in this table are the total number of each species
### Table 6.3

Results of a Model III, two way ANOVA on body weights for "Species" and "Repetitions" for the three repetitions pooled for shell acquisition analysis.

<table>
<thead>
<tr>
<th>Source</th>
<th>Sum of Squares</th>
<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Error</td>
<td>2.313E-02</td>
<td>174</td>
<td></td>
<td>1.313</td>
<td></td>
</tr>
<tr>
<td>SPECIES</td>
<td>1.422E-02</td>
<td>1</td>
<td>1.422E-02</td>
<td>7.348</td>
<td>.113</td>
</tr>
<tr>
<td>REPETITION</td>
<td>8.724E-03</td>
<td>2</td>
<td>4.362E-03</td>
<td>.328</td>
<td>.810</td>
</tr>
<tr>
<td>SPECIES * REPETITION</td>
<td>3.871E-03</td>
<td>2</td>
<td>1.936E-03</td>
<td>.146</td>
<td>.865</td>
</tr>
</tbody>
</table>

210
Figure 6.2 Mean total weights (shell and crab) of *C. taeniatus* (n = 30) and *C. virgatus* (n = 30) for each experimental repetition used in the analyses of shell acquisition. Bars represent 1 standard error.
Figure 6.3. Mean shell weight of *C. taeniatus* ( ■ ) (n = 30), *C. virescens* ( ▼ ) (n = 30), and supplied empty shells ( ◆ ) (n = 15) for each experimental repetition used for shell acquisition analyses. Bars represent 1 standard error.
For shell acquisition analyses, bars represent 1 standard error.

Figure 6.4: Mean body weight of C. lineatus (n = 30) and C. virescens (n = 30) for each experimental repetition used.
<table>
<thead>
<tr>
<th>Species</th>
<th>Shells acquired</th>
<th>No shells acquired (alive)</th>
<th>Dead</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. taeniatus</td>
<td>28</td>
<td></td>
<td>41</td>
<td>90</td>
</tr>
<tr>
<td>C. virescens</td>
<td>17</td>
<td></td>
<td>53</td>
<td>90</td>
</tr>
</tbody>
</table>

Table 6.4 Comparison of the pooled number of C. taeniatus and C. virescens that acquired shells by the end of the 24 hour experimental period over the three replications in which body weights did not differ between species. Those that did not acquire shells, but remained alive at the end of the experiment are also compared between species. The total number of each species used is also provided.
that died and the overall number of individual hermit crabs used in these three repetitions. Unexpectedly, the results showed that the proportion of *C. virescens* that acquired shells was not greater than *C. taeniatus* ($\chi^2 = 4.214$, Fisher exact $P<0.05$) and therefore, did not agree with the directional hypothesis. However, it must be pointed out that in hindsight, given a two-tailed hypothesis, this result would suggest that *C. taeniatus* was significantly better at acquiring shells under these test conditions.

### 6.3.2 Shell Weight versus Body Weight

In Figure 6.5 the significant relationship between shell weight and body weight of *C. taeniatus* ($t=11.956$, $P<0.001$, $R^2 = 0.324$) and *C. virescens* ($t=17.235$, $P<0.001$, $R^2 = 0.499$) from all experimental repetitions is shown. Lines were parallel (ANCOVA, $F_{1,596} = 0.260$, $P>0.05$) and indicated that, for a given body weight, shells inhabited by *C. taeniatus* were heavier ($P<0.001$) than those inhabited by *C. virescens*. The full results of this ANCOVA analysis are given in Table 6.5.

When shell weight was plotted against body weight for crabs used in the final acquisition analyses (three repetitions), a significant relationship still existed for both species (*C. taeniatus*, $t=7.164$, $P<0.001$, $R^2 = 0.3684$; *C. virescens*, $t=13.230$, $P<0.001$, $R^2 = 0.6658$) and is shown in Figure 6.6. Regression lines for both species were insignificantly different from being parallel (ANCOVA, $F_{1,176} = 1.850$, $P>0.05$) and indicated that, in general, the shells of *C. taeniatus* were heavier than those of *C. virescens* (ANCOVA, $F_{1,177} = 7.538$, $P<0.01$). Table 6.6 shows the
C. taeniatus: \( R^2 = 0.3243 \)

C. virescens: \( R^2 = 0.4992 \)

Figure 6.5. Regression lines for shell weight (g) as a function of body weight (g) for all C. taeniatus (n=300) and C. virescens (n=300) measurements used in all 10 replications of the shell competition experiment. \( R^2 \) values are given for lines shown.
Table 6.5 ANCOVA for shell weight as a function of body weight comparing *C. taeniatus* (*n* = 300) with *C. virescens* (*n* = 300).

Data are for all crabs from all 10 repetitions of the shell competition experiment.

<table>
<thead>
<tr>
<th>Source</th>
<th>Species</th>
<th>Body Weight</th>
<th>Error</th>
<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sum of Squares</td>
<td>Species</td>
<td>1.249E-01</td>
<td>1.564E-02</td>
<td>1</td>
<td>1.249E-01</td>
<td>47.656</td>
<td>&lt; .001</td>
</tr>
<tr>
<td>df</td>
<td>Body Weight</td>
<td>1.092E-02</td>
<td></td>
<td>1</td>
<td>1.092E-02</td>
<td>416.679</td>
<td>&lt; .001</td>
</tr>
<tr>
<td>Mean Square</td>
<td>Error</td>
<td>597</td>
<td>262</td>
<td></td>
<td>416.679</td>
<td>&lt; .001</td>
<td></td>
</tr>
</tbody>
</table>

BEHAVIOUR, SHELL COMPETITION, BENEFITS OF SURVIVAL DIFFERENCES
Figure 6.6 Regression lines for shell weight ($W_s$) as a function of body weight ($W_b$) for $C. taeniatus$ (--- ($n$=90)) and $C. virescens$ (----- ($n$=90)) measurements used in shell acquisition analyses. $R^2$ values are given for lines shown.
Table 6. ANCOVA for shell weight as a function of body weight comparing C. taeniatus (n=90) with C. virescens (n=90).

<table>
<thead>
<tr>
<th>Source</th>
<th>Squares</th>
<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>SPECIES</td>
<td>1.055</td>
<td>1</td>
<td>1.055</td>
<td>4.533</td>
<td>.035</td>
</tr>
<tr>
<td>BODY WEIGHT</td>
<td>42.733</td>
<td>1</td>
<td>42.733</td>
<td>183.523</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>SPECIES*BODYWT</td>
<td>1.850</td>
<td>1</td>
<td>1.850</td>
<td>.176</td>
<td></td>
</tr>
<tr>
<td>Error</td>
<td>40.982</td>
<td>176</td>
<td>0.233</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Data are from the three experimental replications used for shell acquisition analyses.
full results of the ANCOVA performed on the shell weight versus body weight data from the three pooled replicates used to analyse the ability to acquire limited shells.

6.4 DISCUSSION

The behavioural responses of individuals as well as interactions between intertidal species are sensitive to variations in such physical factors as desiccation, temperature and height on the shore (Bertness and Callaway, 1994; Raffaelli and Hawkins, 1996; Bertness et al., 1999). Most work relating species interactions to physical factors has focused on how physical stresses influence the intensity of competition. However, Bertness and Callaway (1994) and Bertness et al. (1999) have argued that responses to physical factors may alter more than just the intensity of competition, affecting the very nature of species interactions. There is evidence from the work of Gherardi (1990) that differences between hermit crab species in physiological resistance to physical stress may lead to differences in the ability to exploit shell resources. While Barnes (1999) did not find that habitat, shell abundance or availability had a major influence on shell utilisation by hermit crabs at Quirimba Island, he did find that the number of damaged shells used decreased and shell fit increased with increasing height on the shore.

In many locations, empty gastropod shells have been reported as limiting hermit crab populations (Childress, 1972; Kellogg, 1976; Abrams, 1980, Bertness, 1981b). Where habitat use overlaps, competition for shell resources may occur, especially between species of similar size.
6.4.1 Interspecific Competition

Abrams (1981a) has suggested that hermit crabs may use either mutual exploitation of a shell source, or shell fighting to compete for shells. In order for exploitative competition to occur there must be an overlap in shell and possibly habitat use, as well as a shortage of available shells.

Results reported in this chapter provided indirect evidence that body weight had an influence on the ability to acquire shells in experimental conditions. Measurements showed that the mean body weight of *C. virescens* was greater than *C. taeniatus* in all experimental repetitions. When all 10 repetitions were analysed for shell acquisition, there was no difference between species in the ability to acquire shells. However, when the repetitions where the body weights for *C. virescens* were significantly greater than for *C. taeniatus* were excluded, the latter species was able to acquire more shells than the former over 24 hours. No data were collected on whether *C. taeniatus* was able to exploit the supplied shells more rapidly than *C. virescens*, or whether *C. taeniatus* was able to evict the other species from inhabited shells. Although I observed some naked crabs evicting other crabs from shells by ‘shell-less rapping’ (see shell rapping in Hazlett, 1970, 1996; Elwood *et al.*, 1998), no quantitative data were recorded of this activity.

Gherardi (1990) found that in shell competition and habitat selection experiments with the hermit crabs, *Calcinus ornatus* and *Clibanarius erythropus* from the Bay of Naples, the two species selected different microhabitats that were consistent with differences in physiological tolerances to physical stress. *C. erythropus* exhibited greater resistance to desiccation as measured by the survival of individuals in shells exposed to air for 7 or 16 hours, either alone or in groups at 30
± 4°C and relative humidity of ≈60%. Gherardi also found that both species were less mobile when out of the water. When subjected to water of low temperature (14°C) and low salinity (0 or 20‰) C. ornatus showed less motility than C. erythropus. The ability to remain active under extreme environmental conditions (although crabs were not tested at temperatures above 22°C) meant that the more mobile C. erythropus could obtain shells more rapidly than C. ornatus.

McGaw et al. (1999) found that the crabs Callinectes sapidus, Carcinus maenas, Cancer magister, and Libinia emarginata also exhibited specific behaviours in response to changes in environmental conditions and that these behaviours were closely related to the physiological ability of individuals.

Thus, interspecific differences in physiological tolerances to intertidal conditions may lead to differences in behavioural responses both intra- and interspecifically.

In the case of C. taeniatus the ability to survive significantly longer than C. virescens in conditions of freshwater inundation may result in a competitive advantage allowing the former species to secure empty shells and habitat space before the latter. Why C. taeniatus should be able to acquire more shells in 100% SW at 25°C (the acclimation salinity and temperature) however, remains unclear. Whether C. virescens would do better under conditions of lower temperature and/or higher salinity remains unknown. Mesce (1993a) found that the closely related hermit crabs Pagurus samuelis and P. hirsutiusculus were affected differently by visual and chemical shell stimuli. P. samuelis relied on visual cues to locate shells and track objects resembling shells, while P. hirsutiusculus showed no evidence of tracking and did not investigate shells if a chemical stimulus was absent. Whether
C. taeniatus and C. virescens also differ in their abilities to detect shells under various conditions is a potentially important area of study that may contribute to understanding tactile mechanisms that underlie the detection, investigation and preference of shells.

### 6.4.2 Shell Weight versus Body Weight

The regression of shell weight with body weight for 600 individuals collected from the field showed that for both species shell weight was positively related to body weight. In addition, it also showed that C. taeniatus inhabited shells that were significantly heavier than those inhabited by C. virescens of the same weight.

The regression of shell weight with standardised body weight of crabs used in the final acquisition analyses also showed that C. taeniatus acquired significantly heavier shells than did C. virescens. It is, however, uncertain whether acquisition of heavier shells by C. taeniatus occurred in the field or in acclimation tanks in which both species were held together.

In a study of hermit crabs at Quirimba Island, Barnes (1999) found that the upper shore species, Clibanarius longitarsus carried significantly heavier shells at equivalent body sizes than did Coenobita cavipes and Coenobita rugosus, the semi-terrestrial, supralittoral species studied. Barnes explained the ability to carry heavier shells by C. longitarsus as energetically feasible because this species is mainly active when submerged and much of the mass of the heavier shell is supported by water. Barnes also observed a high diversity and abundance of portunid and xanthid crabs, reported to be some of the main predators of intertidal shell occupants.
Nevertheless, the strength of shells used by hermit crabs did not seem to be related to the presence of predators, but followed a pattern based more on individual species characteristics and behaviour. Instead, all species that were at some time covered by water achieved protection from predation by occupying shells large enough to completely withdraw in. Vance (1972a) and Bertness and Cunningham (1981) found that the occupation of large shells provided an advantage in avoiding predation.

In addition to predation, Conover (1978) suggested that availability of food and shells exert a strong selective pressure on hermit crabs, so that in the situation in which food is abundant and predation is high, selective pressure should lead to the use of heavier shells. He goes on to state that the type of predation should also affect the selection of shells with respect to weight or volume. If predation is mainly by shell breakers, there should be a selective advantage for hermit crabs that occupy heavier shells with thick walls (Conover, 1978). Along the Queensland rocky coast, *Thalmita* spp. are common shell-crushing crabs (Jones and Morgan, 1994) that may prey on hermit crabs. Nevertheless, no conclusions may be reached regarding the selective, ecological or distributional advantage differences in preferred shell weight may be to *C. taeniatus* or *C. virescens* from the data collected during this study.

### 6.4.3 Preliminary Suggestions on Some Behaviours of *C. taeniatus* and *C. virescens*

Although it is difficult to conclude any definite relationship between behaviours presented in this chapter and differences in the local or geographical
distribution of *C. taeniatus* and *C. virescens*, some important preliminary suggestions can be stated and areas for further study described.

Firstly, results presented in this chapter did not provide evidence in support of the directional hypothesis that *C. virescens* was a better interspecific competitor for shell resources and thus acts to exclude *C. taeniatus* from areas where the former is more abundant than the latter. In retrospect, however, given a two tailed hypothesis these results suggested that weight for weight *C. taeniatus* was a better competitor for limited shells than was *C. virescens* under these experimental conditions.

An additional suggestion is that in the field and/or in the laboratory, *C. taeniatus* inhabits heavier shells than does *C. virescens*. Whether *C. taeniatus* prefers heavier shells than *C. virescens*, or whether physical conditions, bioeroders or other causes result in a more rapid deterioration of shells at low shore than at high shore, causing a difference in weight, were not investigated. What is clear from this work and that of others is that shell use by hermit crabs is based on a complex interaction of at least some of the following factors: hermit crab size, hermit crab position on the shore, shell strength, weight, architecture, size and availability. In addition, predation pressures and environmental conditions may also influence shell utilisation and may also affect intra- and interspecific competition for shell resources. Although beyond the scope of this study, the sampling of a broader size-weight range of individuals, together with shell weight selection experiments, may provide data from which further conclusions could be drawn. Interspecific shell competition experiments using *C. virescens* from shores on which they dominate and in different temperature-salinity regimes may also provide interesting results. In
addition, I found no literature on differential shell deterioration between low and high shore. Investigations into this aspect of hermit crab ecology may also contribute to understanding intra- and interspecific interactions in relation to available gastropod shells.

There is also a need to study competitive interactions for habitat and food, as the utilisation of these resources by *C. taeniatus* and *C. virescens* may also influence their distribution.

From evidence presented in the previous three chapters and results presented in this chapter, I suggest that the absence of *C. taeniatus* from some intertidal shores is not likely to be a result of either physiological intolerance to environmental conditions or a disadvantage in competitive interactions with *C. virescens* for shell resources.

### 6.5 Discussion Summary

Reese (1969) has discussed several benefits that shells provide to intertidal hermit crabs including reducing desiccation and predation.

It was expected that since *C. virescens* is dominant on some shores (see Chapter 5), this species might demonstrate an advantage in competing for shell resources in order to exclude *C. taeniatus* and reduce competitive interactions. Furthermore, it was thought that the ability to secure shells and inhabit more exposed shores might be enhanced if weight for weight, *C. virescens* inhabited heavier shells than *C. taeniatus*. Additionally, if *C. virescens* had a greater body
weight than *C. taeniatus* on average, this might also lead to an advantage in competing for and securing limited shell resources.

Interestingly, results from interspecific shell competition experiments did not provide support for either of the first two hypotheses. However, body weight appeared to have an influence on securing empty shells in a highly competitive situation. When all experimental repetitions were analysed together (including repetitions in which *C. virescens* were significantly heavier than *C. taeniatus*) there was no difference between species in the number of shells acquired. Nevertheless, when crabs within a total weight range of 1.25 – 5.47g were compared weight for weight, *C. virescens* was not shown to be significantly better at securing limited shell resources. Since the data suggest that *C. taeniatus* has an advantage in competing for empty gastropod shells, other factors must be responsible for the low density of *C. taeniatus* and high density of *C. virescens* observed on open coast and island shores. Results also indicated that *C. taeniatus* in the field and/or in the laboratory inhabited heavier shells than *C. virescens*. Whether crabs selectively choose a weightier shell, or whether environmental conditions affect shells in the upper intertidal differently than shells lower down (a factor remaining unaddressed in the literature; G. Vermeij, personal communication), is unknown.

Although the influence of interspecific competition for shells on differences in distribution remains unclear, this preliminary experiment suggested that competition with *C. virescens* for shell resources is an insufficient factor, on its own, to limit the abundance of *C. taeniatus* on open coasts and islands. There is need for further investigation into reasons why *C. taeniatus* is not prevalent on open coasts and islands.
7.0  **CHAPTER 7: GENERAL DISCUSSION**

7.1  **GENERAL DISCUSSION**

This thesis has described the influence of some aspects of physiology, survival and behaviour on the distribution of natural populations of the hermit crabs, *Clibanarius taeniatus* and *Clibanarius virescens* along the Queensland coast of Australia. In surveys of three initial sites along Keppel Bay, these crabs were found to differ in their local distribution on the shore, with *C. taeniatus* inhabiting all levels (high, mid and low shore), while *C. virescens* was usually only found at or below mid shore. Results from experiments on metabolic responses to acute changes in combinations of temperature and salinity, as measured by oxygen consumption, suggested that both species were significantly affected by changes in temperature and salinity. However, at the acclimation salinity (100% SW), *C. taeniatus* was virtually insensitive to changes in temperature between 15 and 35°C, while *C. virescens* showed significant changes in oxygen consumption over the same range of temperatures.

Experiments were carried out to determine if there were differences in the abilities of *C. taeniatus* and *C. virescens* to osmoregulate in the range of salinities between 11 and 140% SW at 15, 25 or 35°C. While both species were hyperosmoregulators over the entire range of salinities tested, no significant difference was found between them in this ability. However, both species showed a reduction in the ability to osmoregulate when exposed to dilute seawater at higher
temperature, indicating an increase in physiological stress when low salinity and high temperature are combined.

In the laboratory, *C. taeniatus* was shown to survive significantly better than *C. virescens* when both species were exposed to dilute medium (22% SW). Although the combination of low salinity and high temperature was stressful on both species, the decline in survival was especially dramatic in *C. virescens*.

In the field, there was no difference in survival when *C. taeniatus* and *C. virescens* were translocated from low shore to high shore. Nevertheless, a significant difference in survival occurred in favour of *C. taeniatus* when both species were translocated into an environment of prolonged low salinity. These field studies were consistent with laboratory studies that indicated a greater tolerance of body fluid dilutions in *C. taeniatus* over prolonged exposure to dilute medium.

Repeated sampling at two locations demonstrated that at the first, where there was no freshwater influence on the intertidal zone, the relative abundance of *C. virescens* was very high, while that of *C. taeniatus* was extremely low. At the second location where there was a steady influence of freshwater, there was a consistently high relative abundance of *C. taeniatus*. When a survey of rocky shores was undertaken along the coast of Queensland, results were consistent with the hypothesis that *C. virescens* is more sensitive to freshwater, and that this factor influences their distribution. In contrast, *C. taeniatus* is more tolerant of freshwater, and the distribution of this species may also be influenced by the salinity of inshore waters.

Preliminary investigations suggested that, weight for weight, when both species are without shells, *C. virescens* was not a better competitor for limited shell
resources when tested in acclimation conditions. Analyses showed that body weight was an indirect, yet significant factor in acquiring shell resources. Results suggested that given a two-tailed hypothesis, *C. taeniatus* would acquire significantly more shells than *C. virescens*. In addition, *C. taeniatus* was shown to carry heavier shells in the field and/or in the laboratory. The following discussion, therefore, is based on the conclusion that the distribution of *C. taeniatus* and *C. virescens* is determined, in part, by their relative tolerances to variations in physico-chemical conditions.

*Clibanarius taeniatus* and *C. virescens* on tropical intertidal zones experience wide and, for the most part, unpredictable variations in temperature, salinity and desiccation and rather regular variations in tidepool oxygen availability. While all of these are important physico-chemical factors throughout the intertidal zone, the general conclusion of most investigations on intertidal stress is that, with the exception of oxygen saturation, both the magnitude and duration of these factors increase with increasing height on the shore (see reviews by Meadows and Campbell, 1972; Newell, 1976; Raffaelli and Hawkins, 1996). This means that organisms living in the upper shore may have adaptations that enable them to survive unfavourable conditions for prolonged periods, while those that inhabit low shore may only be able to resist exposure to such conditions for short periods (Newell, 1976). The influence of temperature on the respiration of intertidal animals has been extensively investigated because it is a physical factor, above most others, that obviously varies with season, latitude, height on the shore and, correspondingly, length of emersion. Even though temperatures are high in tropical regions, the range in seasonal temperatures is narrower than in higher latitudes (Moore, 1972). In any case, seasonal changes in temperature have not been
addressed in this thesis. However, the range of temperatures associated with shore height may be directly related to rapid changes in semi-diurnal conditions. There is evidence from a variety of intertidal organisms that the effects of temperature on the respiration of quiescent animals can be quite different from those on active respiration (Newell and Northcroft, 1967; Newell and Bayne, 1973; Newell and Branch, 1980). Respiration in some quiescent animals has been shown to have low $Q_{10}$ values over at least some of the range of temperatures to which the organism is routinely exposed. Temperature insensitive respiration has been demonstrated in a variety of upper shore intertidal animals (see reviews by Newell, 1969, 1970, 1976, 1978; Vernberg, 1981a) and appears to represent an adaptation to temperature fluctuations that allow organisms high on the shore to conserve energy despite increased temperatures during low tide exposure (Newell, 1978). Among hermit crabs, the work of Burggren and McMahon (1981) on the effect of temperature on oxygen consumption showed that $Q_{10}$ values for acutely determined oxygen consumption of different hermit crab species were significantly different from 1.0 in all species tested. They did, however, find that over a temperature increase of 15°C, the mean oxygen consumption of the intertidal species changed least when compared with the subtidal and supratidal species. Besides results presented in this thesis, only the work of Wernick (1982) (to my knowledge) has shown temperature insensitivity in hermit crabs. Temperature insensitivity in *C. taeniatus* is reported for the first time in this thesis and may be evidence that this species is able to spend less metabolic energy in compensating for the effects of increased temperature than the low shore species, *C. virescens*. There is good evidence from the work of Hawkins *et al.* (1986), Hawkins *et al.* (1987), Koehn (1991) and Hawkins (1995)
that reduced metabolic sensitivity to changes in temperature is related to lower relative rates of protein turnover associated with multi-locus heterozygosity. Lower energy costs in responding to temperature fluctuations lead to greater viability in the face of extreme temperatures. In addition, multi-locus heterozygosity has been shown to increase with increasing intertidal exposure (Lavie and Nevo, 1986). The possibility that populations of hermit crabs may vary in the degree of heterozygosity at multiple loci may be an important consideration in understanding the ecogeographical distributions of different species and an area of future work.

The effect of salinity may also have important implications for intertidal organisms. Reduced salinity may occur in intertidal pools due to sudden downpours or freshwater runoff from supratidal areas. However, this is usually limited to relatively short periods of dilution. Some authors have questioned whether the upper limits to distribution on the shore could be set by low salinity induced mortality in gastropods, since many intertidal species can survive dilution for periods longer than would occur under normal conditions (see review by Underwood, 1979). However, the effects of dilution may be greater for intertidal hermit crabs, since they lack an operculum and cannot effectively seal out the external medium as do snails. Nevertheless, both *C. taeniatus* and *C. virescens* were able to effectively hyperosmoregulate over a relatively short duration (7 hrs) of exposure to a wide range of salinities in temperatures between 15 and 35°C. These results suggested that, under the usual range of conditions that occur on rocky intertidal shores in the Keppel Bay region, both species are able to withstand both tidepool and haemolymph dilution, even in extreme temperatures, for the duration of low tide exposure. This was consistent with intertidal translocation experiments.
where there was no difference in survival between species when both were subjected to conditions at high shore for durations of between 48 and 72 hours. In one interesting circumstance, a single treatment chamber containing only *C. virescens* was lost at high shore and was not located for 28 days. When it was finally recovered at high shore, all hermit crabs were found alive. It was clearly evident that *C. virescens* was able to withstand ‘normal’ conditions at high shore. However, intertidal areas in close proximity to river outfalls may experience prolonged periods of freshwater inundation due to seasonal and irregular flooding. Endean et al. (1956) have suggested that the freshwater flows from the Fitzroy, Burdekin and Mary Rivers in particular, were sufficient to severely depress the salinity of inshore waters in their respective areas, especially affecting the Yeppoon and Point Vernon areas. Prolonged flooding has been shown to have detrimental impacts on marine habitats, particularly the intertidal (Goodbody, 1961; Fotheringham, 1975; Coates, 1992; Van Woesik et al., 1995). This has important implications for tropical rocky intertidal hermit crabs in areas influenced by freshwater flows.

When *C. taeniatus* and *C. virescens* were subjected to continued low salinity (22% SW) in the laboratory at 15, 25 and 35°C, the latter species showed a significantly lower survival in the diluted medium than the former, especially at the highest temperature. These findings were consistent with results from experiments exposing these crabs to a consistently low salinity environment in the field. While some studies have been carried out on the survival of hermit crabs in low salinity in the laboratory (Davenport, 1972a,b; Biggs and McDermott, 1973; Young, 1979a, 1980, 1991; Sherman and Eichrodt, 1982; Castillo et al., 1988), there have been no
reported attempts to test the tolerances of hermit crabs in conditions of chronic low salinity in the field. This thesis is the first report of results for the translocation of hermit crabs into conditions that may simulate prolonged freshwater inundation in the field. Results from this experiment were consistent with survival experiments in the laboratory and showed that *C. taeniatus* was able to survive low salinity significantly better than *C. virescens*.

The haemolymph concentrations of Na⁺, K⁺, Mg²⁺ and Ca²⁺ were investigated in surviving and dying crabs of both species after extended exposure to 22% SW at 15 and 35°C. I found that these ions followed similar trends in the haemolymph of all crabs at both temperatures, although *C. virescens* generally took longer to reach a steady state haemolymph concentration. In addition, death in both species occurred more rapidly at the higher temperature.

The concentration of haemolymph Na⁺ was reduced to that of the medium within a short time of exposure to low salinity and remained low throughout the remainder of the experiment. Although the concentration of Mg²⁺ in the haemolymph also dropped, this reduction occurred more slowly than that of Na⁺. Both dying crabs and those that remained alive until the end of the experiment had similar concentrations of Na⁺ in the haemolymph. This was also the case for the haemolymph concentration of Mg²⁺. In contrast, the concentration of K⁺ initially dropped, but then fluctuated near the ambient level of K⁺ in 100% SW. However, in crabs remaining alive at the end of the experiment, haemolymph K⁺ concentrations were lower than in crabs that died during exposure. The haemolymph concentration of Ca²⁺ also remained well above ambient levels in 22% SW despite an initial drop from the haemolymph concentration of Ca²⁺ in 100% SW. These changes in
haemolymph ion concentrations may be due to an inability to stem the loss of intracellular Na\(^+\) from gill epithelial cells into the blood, then to the medium. K\(^+\) would continue to move out of the cell into the blood by passive means. Due to the loss of intracellular Na\(^+\), Na\(^+\)/K\(^+\) ATPases at the basal membrane of gill epithelia would be unable to function, resulting in a decrease of Na\(^+\) to ambient levels and an increase in the concentration of haemolymph K\(^+\). The lower K\(^+\) haemolymph concentration in _C. taeniatus_ remaining alive at the end of experiments may reflect an increased ability in this species to pump K\(^+\) from the blood into the cytoplasm and thus, maintain cell membrane potential. Changes in haemolymph Ca\(^{++}\) and Mg\(^{++}\) are more difficult to explain and have only been speculated on in this thesis. However, some preliminary suggestions have resulted from combined investigations on survival and ionic regulation. Firstly, it does not appear likely that slight differences in the ability to regulate common ions are directly responsible for the differences in survival observed under conditions of prolonged exposure to low salinity. However, the link between ionic regulation and survival in prolonged low salinity conditions may be a subtle one and I have proposed that the ability of _C. taeniatus_ to survive prolonged dilution of the medium better than _C. virescens_ is the result of adaptation for the tolerance of body fluid dilution. Clearly there is a need for specific studies into the links between ionic regulation and survival in hermit crabs under various conditions of temperature and salinity.

There are numerous accounts of investigations into the effects of environmental conditions on the distribution of intertidal organisms on the shore. However, investigations on the influence of environmental conditions on geographical distribution have mainly been carried out on species of algae,
gastropods and bivalves from temperate regions and have focused on the effects of temperature on reproductive success (Ajmal Khan and Natarajan, 1981b and see reviews by Kinne, 1963, 1970; Moore, 1972; Underwood, 1979). There have been few studies of this kind in tropical regions, and investigations along the coast of Queensland are limited to Endean et al. (1956). In this thesis, repeated sampling at two locations and a survey of the rocky intertidal coast of Queensland have provided evidence to suggest that the geographical distributions of *C. taeniatus* and *C. virescens* are influenced by the presence of freshwater in inshore areas. In addition, the work of Pillay and Nair (1971), Ajmal Khan and Natarajan (1981a,b) and Lyla et al. (1998) have shown that regular and irregular reductions in salinity from river outfalls can also impact the survival of intertidal invertebrate larvae.

There is wide acceptance of the principle that where there is a deviation from the optimal value for one environmental factor the tolerance range for other factors will also be reduced (see Moore, 1972). A key conclusion of this thesis is that where salinity is less than optimal for *C. virescens*, sensitivity to temperature will be increased. In contrast, where salinity is rarely reduced from the optimal for *C. virescens*, this species is more able to withstand exposure to extreme temperatures. This conclusion is consistent with surveys demonstrating the high shore distribution of *C. virescens* on rocky intertidal zones uninfluenced by freshwater outfall.

On the basis of results reported for the differential distributions of *C. taeniatus* and *C. virescens* in relation to the influence of freshwater, I have argued that these species constitute a convenient indicator system of freshwater inundation on coastal ecosystems. Such a system may be particularly useful in areas where
coastal development and storm water drains introduce freshwater into marine habitats where freshwater was previously absent. For managers and developers, this simple tool may provide the ability to track and interpret changes to intertidal communities. This thesis represents the first proposal for the use of *C. taeniatus* and *C. virescens* as potential indicators of environmental change.

In species from the same location, distribution on the shore is often related to the ability to tolerate various physical conditions. According to Underwood (1979), tolerances of intertidal species are often greater than the usual conditions encountered in the field and may reflect physiological adaptations each species has to conditions occurring in the habitat. Therefore, Underwood (1979) argues that the limitations of a species vertical distribution on the shore must be determined by factors other than physiological tolerances. Wolcott (1973, in Underwood, 1979) has suggested that snails at lower levels of the shore are limited in their vertical distribution by snails at higher levels of the shore that are competitively superior because of their ability to withstand more extreme conditions.

In a preliminary investigation of competition for limited shells, both species were collected from an intertidal area where *C. taeniatus* dominates high shore and *C. virescens* is usually found only below mid shore. Possible future investigations in which these species compete for shells in extreme conditions may be consistent with the idea that competitive superiority may be related to greater ability to tolerate extreme conditions. They may also agree with more extensive studies by Gherardi (1990) in which she found the hermit crab, *Clibanarius erythropus* to be more tolerant of physical stress and more mobile under extreme conditions than *Calcinus ornatus*. Furthermore, Gherardi suggested that since the former species is able to
remain more active even in conditions at high shore, it would be able to secure shells that were scattered throughout the habitat faster and more efficiently than *C. ornatus*. While competition may maintain the low shore distribution of *C. virescens* at sites where *C. taeniatus* is more abundant, at sites where *C. virescens* is highly dominant competition for limited shell resources does not appear to be the reason for low relative abundances of *C. taeniatus*. Since my study has examined only one aspect of this occurrence, more research is required to elucidate why there are such low abundances of *C. taeniatus* on open coasts and islands.

In conclusion, the geographical distributions of *C. taeniatus* and *C. virescens* appear to be greatly influenced by the presence of freshwater in inshore areas. The sensitivity of *C. virescens* to prolonged exposure to low salinity is likely to restrict them from inhabiting areas that are strongly influenced by freshwater. In areas under the irregular influence of freshwater from large flood events, *C. virescens* may be restricted to low shore by the competitive superiority of *C. taeniatus*, although the intolerance of *C. virescens* to seawater dilution is likely to be the most important and restricting factor. In addition, where there is little threat of freshwater inundation, such as on open coasts and islands, the distribution of *C. virescens* often extends to the top of the shore. This may be further evidence for the principle that where a species exists within its optimal range for one environmental factor (such as salinity), there is a wider range of tolerance for other potentially unfavourable conditions (such as extreme temperatures). Species differences in survival in low salinity conditions are also consistent with the distributions and relative abundances of these species on a geographical scale. It is concluded that *C. taeniatus* is able to survive the combined stresses of low salinity and high temperature as a result of
adaptations that allow it to tolerate body fluid dilution and expend less energy in extreme temperatures than *C. virescens*. Furthermore, a flow-on effect of physiological adaptations in *C. taeniatus* may be the advantage of being able to remain active under a wider range of conditions and potentially secure limited shell resources better than *C. virescens* in the field. The distribution of both species is thus strongly influenced by the ability to survive and remain active in conditions of prolonged low salinity and high temperature, even though this combination may occur irregularly.

The findings of this thesis represent a unique investigation into relationships among respiratory and osmoregulatory tolerances, behavioural differences, environmental conditions and the relative abundances and distributions of *C. taeniatus* and *C. virescens* on rocky intertidal shores of Queensland, Australia.

### 7.2 FUTURE WORK

It is clear that there is a need for much future work if we are to understand the links between respiratory responses, osmoregulation, ionic regulation, survival, competition and distribution in hermit crabs under various ecological conditions. The following specific studies are particularly recommended:

#### 7.2.1 Oxygen Consumption

(i) It has been shown in this thesis that the distribution of *C. virescens* is different depending on whether a site is influenced, or uninfluenced by the presence of freshwater. The respiratory responses of this species from an area influenced by
freshwater have been investigated in this thesis, but future studies could be undertaken that compare the oxygen consumption of *C. virescens* from sites under the influence of freshwater, and those from open coast or island sites. Intraspecific differences in metabolic responses that reflect differences in habitat may provide insights into habitat specific adaptations.

### 7.2.2 Interspecific Shell Competition

(i) Since shells may afford some protection from abdominal swelling in dilute seawater (Shumway, 1978, but see Sabourin and Stickle, 1980), acquiring a shell under short term extreme conditions may be more important for susceptible species. Shell competition experiments between *C. taeniatus* and *C. virescens* carried out under different conditions of temperature and salinity may provide information on the influence of external conditions on interspecific shell competition.

(ii) Shell competition experiments between inshore *C. taeniatus* and offshore *C. virescens* in normal seawater conditions may demonstrate that less stressed populations of *C. virescens* are better interspecific competitors.

(iii) Investigations into the abilities of both species to detect shells under various conditions of temperature and salinity could be carried out to determine if interspecific differences occur. This has implications for sympatric species in areas where shells are limiting and competition for shells may be high. No studies under such conditions have been reported.
(iv) Shell species, size and weight preferences could be determined for these species providing further information about how competition for shell resources may be reduced in the field.

(v) Manipulative investigations into the deterioration rates of shells at different heights on the shore have never been done (G. Vermeij, personal communication) and may provide insights into shell preferences and competition by hermit crabs at different shore heights.

(vi) In an area where *C. taeniatus* and *C. virescens* occur sympatrically, a field study could be done where the former is removed from a section of high shore to see if the latter species would expand its vertical distribution up the shore. The role of competition could be investigated in such a study. Removal studies have not been done with hermit crabs, likely due to the logistics of dealing with such a mobile organism.

7.2.3 Geographical Survey

*Clibanarius taeniatus* and *C. virescens* may be reducing or avoiding competition by resource partitioning, using different foods and different feeding mechanisms, therefore:

(i) An investigation into differences in algal species between sites influenced and uninfluenced by freshwater may lead to some understanding of the low relative abundance or absence of *C. taeniatus* from sites uninfluenced by freshwater.

(ii) Feeding studies could be carried out at different sites to determine if growth, reproduction and competition are influenced by food type.
7.2.4 Larval Behaviour and Survival

(i) While there have been some studies on the development of hermit crab larvae in the laboratory, there is a need for studies on larval behaviour, recruitment and settlement under different conditions of temperature and salinity.

7.2.5 Indicator System

(i) A long term field study should be undertaken at the site of a proposed coastal development where *C. virescens* is present. It would be most interesting to monitor the relative abundances of the two species both before and after the introduction of freshwater onto intertidal areas by storm water drains, with the prediction that the relative abundance of *C. virescens* should be reduced fairly rapidly, and that of *C. taeniatus* should increase over time.

(ii) There would be value in investigating similarly distributed pairs of hermit crab species as indicators of freshwater inundation on intertidal shores in other areas of the world.

7.2.6 Multi-locus Heterozygosity

(i) Investigations of differences in individual, multi-locus heterozygosity between *C. taeniatus* and *C. virescens* may help to explain physiological changes that may lead to the ability to resist changes in environmental conditions.
7.2.7 Posing

(i) A thorough investigation could be conducted to determine if hermit crabs pose more in particular shell species. This determination would address the proposal by Reese (1969) that posing is an activity associated with the regulation of temperature and evaporation.

(ii) Field observations and measurements of water retention within the shells of posing crabs would suggest whether water reserves help crabs resist desiccation, and whether desiccation avoidance is a primary reason for posing. No quantitative studies on posing have been reported in the literature.
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APPENDIX IA

Calibrations for A: calcium at a wavelength of 315.887nm and B: magnesium at a wavelength of 280.270nm at 15°C in concentrations of 0, 0.1, 1.0 and 10mg/L.
Calibrations for C: sodium at a wavelength of 589.529nm in concentrations of 0, 0.1, 1.0, 10.0 and 50.0mg/L and D: potassium at a wavelength of 766.491nm in concentrations of 0, 0.1, 1.0 and 10mg/L at 15°C.
APPENDIX IB

Calibrations for A: calcium at a wavelength of 315.887nm and B: magnesium at a wavelength of 280.270nm at 35°C in concentrations of 0, 0.1, 1.0 and 10mg/L.
Calibrations for C: sodium at a wavelength of 589.529nm in concentrations of 0, 0.1, 1.0, 10.0 and 50.0mg/L and D: potassium at a wavelength of 766.491nm in concentrations of 0, 0.1, 1.0 and 10mg/L at 35°C.
APPENDIX II

The following are brief descriptions of each coastal survey site including site number, site name and latitude and longitude. High shore = HS, Mid shore = MS, Low shore = LS.

(32) Woody Point (Redcliffe) - S27°15.8’, E153°06.3’ Shallow sloping, small stone beach. Many pools have sand and clay base, surrounded by small stones, with stone and shell grit scattered on the bottom. Wave action is only slight at high tide; area protected by Moreton Is. One small clump of 3 mangrove trees at MS. See Plate 1A.

(31) S. Scott Point (Redcliffe) - S27°15.3’, E153°06.6’ A semi-protected beach with a flat, high intertidal area that has a shallow boulder zone becoming a more elevated solid rock platform at MS prior to dropping off at the outer edge of the platform. Only slight wave action present at outer rocks; area protected by Moreton Is. MS and HS have abundant green-foliose algae and a covering of fine branched red, brown algae.

(74) Osbourne Point - S27°14.9’, E153°06.9’ A large boulderzone, consisting of flat, small to medium sized boulders. Little wave action along outer edges of rock flats. Numerous pools scattered throughout.
(34) **Wickham Point** - S26°48.2’, E153°08.8’  Beach is flat. Platform sandstone from HS to MS, where it ends in an abrupt slope; a short boulder zone consisting of small, unstable boulders, continues to LS and subtidally. A very exposed site.

(33) **Moffat Head** - S26°47.5’, E153°08.9’  A flat platform of smooth sandstone from HS extends to LS, where it breaks up. Many basin pools are present, which are large towards LS and have boulders strewn in them. A very exposed site. Pools from HS to LS are all covered with algal turf; at HS this is a green mat, but from MS to LS it becomes a thick crustose turf mat. Sand found in HS pools; all pools, except those that are contiguous with the sea, have much shell grit. No empty shells found.

(30) **Point Cartwright** - S26°40.7’, E153°08.3’  The NE side of the point has a rock shelf from HS to LS, which is highly exposed. The N side of the point has flat sandstone with many pools in HS, that drops off to a short boulder field, then a lower solid flat stone platform that is protected from continual wave action by an outer rock wall resulting from the platform dropping off. Micro- and mat algae abounds at this site. See Plate 1B.

(29) **Alexandra Headlands (Middle)** - S26°40.3’, E153°06.6’ A solid rock platform at sea level from HS to LS. Relatively narrow littoral zone. Much green, foliose algae present on rocks in the pools. Constant, but not severe wave action at this highly exposed site. See Plate 2A.
(28) *N. Alexandra Headlands* - S26°40.1’, E153°06.5’ A flat, smooth, black sandstone platform that is level from the rock wall at highest tide to low tide. The platform drops off approximately 1.5 m, with many pools and bowls filled with shell grit and sand situated here. Empty shells found in the pools at LS. Outer area receives continual medium wave action.

(27) *Point Arkwright* - S26°32.9’, E153°06.1’ Short HS boulder area, mostly made of sandstone. Outer rocks form wave-cut platform with a few large pools and several small pools. Most pools at HS and MS are protected by outer rock. Micro- and macroalgae grows in most HS and MS pools.

(25) *S. Paradise Caves* - S26°23.7’, E153°07.0’ A slightly steep, small boulder field that is partially protected by outer solid rock that has continual wave action. No pools at this site.

(24) *Tea Tree Bay* - S26°22.8’, E153°06.2’ Wave cut, solid rock substrate platform. Several basins washed out of rock to form pools; micro- and macroalgae present in high and mid shore pools. LS very exposed with heavy wave action.

(22) *S. Little Cove* - S26°23.0’, E153°05.7’ A fairly exposed site with continuous wave action at LS. All solid rock with pools with little micro and macroalgae.

(23) *N. Little Cove* - S26°22.9’, E153°05.8’ HS made of unstable boulders and LS of solid rock. Outer rocks fairly exposed. No algae present in pools.
(49) **Double Island Point** - S25°56.2’, E153°11.3’ Short boulder zone of approximately 30m. Solid rocks form small and medium pools with sand, small, loose stones, shell grit and empty shells present. Constant, heavy wave action along outer edge of LS. Some microalgae in pools.

(48) **Rainbow Beach** - S25°54.1’, E153°05.6’ A collection of scattered, solid, black sandstone surrounded by sand. Constant, moderate wave action present, but rocks at very LS reduce this action at upper LS and MS. Some green algae found on MS rocks.

(47) **Round Island** - S25°17.3’, E152°55.9’ A very wide, flat clay and sandstone beach with many pools on this island in Great Sandy Strait. Almost no wave action, since this island is protected by Fraser Island.

(46) **N. North Bluff (Big Woody Is.)** - S25°16.4’, E152°56.8’ Very rocky beach with solid striated rock running almost parallel to water. Beach is approximately 60m wide with no wave action; is protected by Fraser Island.

(45) **Datum Point (Big Woody Is.)** - S25°16.3’, E152°56.6’ A very wide (>150m) solid rock and small boulder field which extends from HS - LS. At HS and MS rock is of iron base, which is mixed with or surrounded by clay substrate. Many pools covered in mangrove mud and a few mangrove trees are present to the south at MS. Little microalgae present at HS and MS, but most pools at LS are lined with microalgae. Virtually no wave action as site is very close to Fraser Island.
(50) Sandy White Memorial Park - S25°16.3’, E152°50.0’ Very wide (>175 m) solid rock beach with small, loose rocks and stones strewn on top. Pools appear from HS - LS. At LS rock gives way to mangrove mud flats, with few mangrove trees present on the beach. At HS and MS solid angle rock dominates, while at LS loose rocks form the main substrate in pools. Some green algae is present in pools at MS - LS.

(51) The Gables Park (Pt. Vernon) - S25°14.8’, E152°49.6’ A medium width, solid rock field with small boulders strewn on top. Solid rock appears as upturned, angular sheets with sand and mud collected in lower rock beds. Microalgae covers much of the pools in the rock beds, while pools at HS and MS in the angled rock are mostly bare or sand covered; pools in the angle rock at LS have many foliose algae and live coral in them. Very little wave action present at outer LS rock.

(52) Burrum Heads - S25°11.0’, E152°36.9’ Very short coffee rock pitted platform at the lowest part of a very wide sand beach. Much shell debris found in the hardened sand substrate. Site is at the mouth of the Burrum river.

(42) N. Indian Head (Fraser Is.) - S25°00.4’, E153°21.4’ Protected side of the headland with medium wave action from the SE. A short, raised solid rock platform of sandstone at the base of a cliff face. Rock substrate and sand found in pools.
(43) **S. Middle Rocks (Fraser Is)** - S24°59.5’, E153°21.1’ Site is at the bottom of a cliff face and is made of a short, solid raised platform of basaltic rock. Heavy, constant wave action present. Pools are mostly made of solid rock substrate with sand. Some are lined with macroalgae.

(44) **Champagne Pools (Fraser Is.)** - S24°59.3’, E153°21.1’ Several clumps of solid rock form large pools with sand substrate. Many pools are also solid rock substrate. Some pools have rock substrate and macroalgae. Wave action is heavy and constant.

(20) **Elliott Heads** - S24°55.2’, E152°29.6’ A large boulder wall to the north of this site juts into the water at low tide, while to the south is a sand beach. The northern area is a large, wide boulder field that has largest boulders through mid to low MS. At both HS and LS boulders are much smaller. The slope of the beach is shallow. An enclosed cement pipe runs vertically down the entire beach into the water. It produces a protected area to its immediate south, so that pools next to it are well protected from the persistent wind. Empty shells increased from low to high shore. See Plate 2B.

(21) **Woongarra Marine Park** - S24°50.4’, E152°28.7’ This is an extremely exposed site with waves continually crashing on the outer rocks with great force. There are two large boulder fields. The one at HS is much smaller with mostly solid rock substrate. Almost all rock is basaltic with many pockets in the rock producing small pools. The field to the S receives continual spray at LS and water
is continually streaming back into the sea. Empty shells were only found at HS and MS at the southern subsite.

(19) Bargara Beach (2nd Storm Drain) - S24°48.9’, E152°28.0’ A wide basaltic boulder field with a shallow slope. At MS there are two very large ponds. The second storm water drain on Bargara beach empties into the HS area towards the N. A wall of large boulders protects the shore and strewn boulders over the entire beach provide lots of refugia. Towards HS boulders decrease in size and become stones so that pools surrounded by medium boulders have stone and shell grit within. Few empty shells at MS and LS but many at HS.

(18) N. Bargara Beach - S24°48.8’, E152°27.8’ A wide boulder field composed of basaltic rock. Small pools are surrounded by small boulders with sand covered solid rock base. There are also many small rocks in and around all pools. At the lowest part of the intertidal several larger boulders reduce wave action to the eulittoral area, hence pools in the eulittoral and supra littoral areas are undisturbed.

(17) Burnett Heads (Middle) - S24°46.1’, E152°25.1’ A basaltic boulder field with three rocky juts that provide some protection to the higher boulder fields. Abundance of refugia and empty shells.

(16) N. Burnett Heads - S24°45.7’, E152°24.9’ A wide basaltic boulder field. At low tide the water is approximately 70 m from high tide mark. Numerous protected pools are present at HS. LS is protected by a boulder wall from severe wave action.
The Burnett river empties just N of this beach. Many empty shells at all levels of shore

(15) *Rules Beach* - S24°28.9’, E152°02.0’  A very exposed area made of a single rock wall at a slight angle out into the water which shelters a small, clay based rock area. No algae is present on the rock wall, but protected rocks have macro- and microalgae. No pooling of water.

(8) *Wreck Rock (DNP)* - S24°18.9’, E151°57.9’  Direct, heavy wave action from E on this very exposed site. Solid rock mounds are surrounded by sand. The top of most rocks are well above the sand and have small to large pools on them. See Plate 3A.

(9) *S. Middle Rock (DNP)* - S24°17.5’, E151°57.4’  Another exposed site with direct wave action on outer area. A solid, medium sized platform with sand substrate between solid boulders.

(10) *N. Middle Rock (DNP)* - S24°17.0’, E151°57.1’  A large area of solid outer rock that provides shelter for inner (western) area of the site. Area away from the water is strewn with unstable large and small rocks creating many large and small pools from mid to HS. Southern end of rock group receives more wave action than the northern end.
(11) *Flat Rocks (DNP)* - No latitude/longitude. A flat rock shelf that is completely covered at high tide and remains under severe, constant wave action, even at low tide. No protected areas or green algae present.

(12) *S. Red Rocks* - S24°15.3', E151°56.8’ A rocky headland with a steep slope. Small pools are up high (~2-4 m) in the rocks. South side of headland faces very strong wave action, while the area to the N has much less. Macro- and microalgae found in pools.

(13) *N. Red Rocks* - S24°14.7’, E151°56.6’ A flat, rocky outcrop of three distinct formations side by side, with numerous rocky pools, many of which are 3-5 m above water’s surface. Macro- and microalgae present in pools. At low tide the eastern end of this area continues to receive significant wave action.

(14) *Rocky Point* - S24°14.0’, E151°56.2’ A steep, rocky headland with heavy wave action on the SE end. The headland provides good protection on its NW face. To the SW of the point is a scattering of small boulders in sand substrate. These rocks contain only small pools at low tide. On the headland itself, solid deep crevices produce many large and small clear pools, which contain many macro- and microalgae.

(7) *Turkey Beach* - S24°04.4’, E151°39.1’ Flat, rocky shelf with much shell grit, beyond which a mud flat and mangrove forest extends. Many empty shells of poor
quality at this site. Many shells in good internal condition, but externally were encrusted with razor clams and algae. Most pools had many micro algae. See Plate 3B.

(6) Parsons Point - S23°51.2’, E151°17.4’ A flat, narrow rock shore composed of small, unstable boulders strewn atop very silty substrate. At very LS there are no rocks, only sandy mud out to the subtidal zone.

(5) Hamilton Point - S23°47.6’, E151°131.3’ This is a wide, relatively steep beach above a very silty, muddy subtidal area. The lower intertidal rocks are covered in this mud.

(72) Yellow Patch - S23°30.4’, E151°13.3’ A rocky headland with mangrove flats at the S end; small, unstable rocks covered with silty mud. Towards N there is a short, steeply sloping rocky area in which from LS - MS the rocks sit on sand, while from MS - HS is a short area of solid rock. Very few pools in LS - MS since water flows down through sand area. No pools at HS.

(71) Cape Capricorn - S23°29.1’, E151°13.9’ Rocky area on the eastern side of the bay. At LS small to medium sized unstable rocks are on sand substrate. At MS, medium sized boulders sit on solid rock, while HS is all solid rock. Numerous tide pools from HS - LS, many of which contain many algae.
(70) *Station Point* - S23°27.3’, E151°00.9’ A large sand beach leads up to this small clump of low lying rocks. Wave action is constant and medium. During high tide the rocks are completely covered. No algae and few sufficient tide pools present. Few empty shells, and very few snails present.

(73) *Hummocky Island Bay* - S23°24.0’, E151°09.4’ A narrow rock area, mostly of solid rock from HS - LS, with some small to medium unstable boulders at LS. From MS - HS is a fairly steep slope, while LS - MS is fairly flat. Constant, heavy wave action and pools do not form, but dissipate through sand substrate.

(74) *Emu Point* - S23°15.5’, E150°50.0’ A very wide, flat solid rock area at HS that drops down to MS. From MS - LS small to medium sized boulders are strewn atop solid rock substrate. Many pools, with little wave action along outer edges of rock flats.

(3) *S. Cooee Bay* - S23°08.5’, E150°45.7’ A very wide, gently sloping boulderzone. At HS - MS, boulders are unstable and medium size. At LS boulders are small and unstable, but some large clumps of solid rock occur. See Plate 4A.

(1) *Fisherman’s Beach* - S23°06.4’, E150°45.3’ The HS of this location has low-lying solid rock substrate with shallow, medium to large sized pools that are highly exposed to sun. At MS, flat solid rock leads to large, high mounds of solid rock, with some medium to small boulders strewn on solid and sand substrates. The large
rock mounds persist and drop off at the water’s edge. Many algae is present at LS, but less is present at MS and even less at HS.

(53) *E. Shellving Beach (Keppel Is.)* - S23°11.2’, E150°50.6’ A very steeply sloping, solid rock, short boulder zone. Most of beach is solid rock from HS to LS, with some medium sized boulders occurring in the water. Some pools exist along the upper part of HS. Some pools at lower HS have some algae, while almost all pools at MS and LS have algae. Little wave action due to outer rocks in the water. See Plate 4B.

(54) *W. Shellving Beach (Keppel Is.)* - S23°11.3’, E150°50.6’ Also a steeply sloping, solid rock zone. HS is wider than at E side, and drops down to MS and LS. Some large pools at HS and MS with algae cover. LS quickly becomes sand around LS rocks so pools are scant.

(55) *E. Long Beach (Keppel Is.)* - S23°11.6’, E150°50.8’ This is a very wide, relatively steep solid rock and boulder beach. At HS, solid rock substrate has several large pools with many algae. At MS and LS solid rock gives place to small to medium boulders to water’s edge.

(2) *Conical Island* - S23°03.0’, E150°52.7’ On the N side, the beach is composed of a medium width, large solid rock, moderately sloping beach. Solid rock at HS gives way to smaller boulders at LS. Pools occur from HS to LS. On the S. side, the
beach is a wide, intertidal zone of large to small, unstable boulders on solid rock substrate. Many pools form in this area.

(4) Five Rocks - S22°48.1’, E150°48.5’ The main rocky area of this beach is a steeply sloping, solid rock hill composed of solid rock with deep clefts. At LS, solid rock gives way to medium to small unstable boulders at the water’s edge. Pools form from HS to LS, with those at MS and HS containing many algae. There is moderate wave action driven by winds from the SE or NE.

(69) Clairview - S22°07.0’, E149°32.2’ A very wide boulder zone made of small rocks which begin at the lower edge of a sand zone. Boulder zone is flat, with many pools from HS to LS. At lower end of boulder zone stones give way to the sand flat. Some mangrove trees present in MS. Some seawater streaming from HS to MS.

(40) Zelma Beach - S21°21.6’, E149°18.7’ Very wide, somewhat steeply sloping boulder field of small to medium, unstable rocks from HS to LS. Most water drains to the sea, leaving very few pools and many wet, sandy (mud) areas amongst the rocks. Many rocks at LS covered with green (turf) algae. At very LS mangrove mud covers rocks and substrate. Mangroves are present throughout HS. Cabbage Tree Creek empties to the S of this site.

(40) S. Hay Point - S21°17.8’, E149°17.6’ A wide boulder field of small to medium sized unstable rocks from HS to LS with some stable, up-jutting rock. At
LS many turf algae are present on rocks and in some pools. Wave action is low to medium. HS butts up against built up road. See Plate 5A.

(39) Dudgeon Point - S21°14.8’, E149°15.2’ A very wide sand flat to the N and a boulder field to the S. From HS - MS, most of the area is medium to small sized unstable boulders. At LS this becomes solid rock with some boulders strewn on top of solid substrate. The LS is mostly covered with mangrove mud near the water’s edge. Just to the S the boulder field widens further and at LS solid boulders become much larger. Wave action is almost nil.

(38) Lamberts Beach - S21°03.8’, E149°13.5’ A solid rock boulder field from HS to LS, approximately 60 m wide. Minimal wave action. Some algae in pools at LS, but none at MS and HS.

(37) Mast (Slade Point) - S21°03.9’, E149°13.4’ Wide boulder field from HS - LS, S of a long sand beach. Wave action is minimal. Beach has medium slope and most water runs from HS and streams through pools from HS to LS.

(36) Slade Bay - S21°04.3’, E149°13.1’ Non-rocky, mangrove mud and sand area with several large pools containing coral rubble, shell grit and gravel. Freshwater drains from storm drain onto this site.

(35) Dolphin Heads - S21°02.1’, E149°11.1’ Very wide, medium sloping boulder field from HS - LS. Unstable rocks form small pools with stones in them.
Substrate is sand with boulders strewn on sand. Some wave action, but area protected by Whitsunday islands. No algae in HS and MS, but at LS some is present on rocks and very little in pools, which have sand substrate with stones.

(75) Finlaysons Point - S20°52.9’, E148°57.1’ A wide sand beach with small rocks at low shore. Slight wave action, but water does not pool. No algae present. No hermit crabs found.

(68) St. Helen’s Beach - S20°49.4’, E148°50.2’ A wide boulderzone of solid, mid-sized boulders from HS - LS. At LS, boulders give way to a solid rock platform that juts in and out roughly along the waters edge. A stream of fresh water streams down from high HS among mangroves and branches out and flows to LS in several spots.

(56) Midge Point - S20°38.9’, E148°43.6’ Short boulder zone of unstable, small rocks at LS and MS. HS is covered with mangrove among rocky substrate. Moderate wave action is broken by large sand bar before water reaches intertidal area.

(79) Conway (Proserpine) - S20°28.9’, E148°45.1’ This is mainly a sand beach at the base of a cliff with medium to large boulders strewn on top at the far south end. Little wave action here. Water does not pool. No hermit crabs found.
(80) *Wilson (Proserpine)* - S20°27.9’, E148°43.0’ A cement boat launch separates the slight wave action from the very narrow (~3-4 m) small-rock beach. This beach is at the base of a cliff. No hermit crabs found.

(58) *Pandanas Bay (Long Is.)* - S20°20.4’, E148°51.0’ Sand beach leads into short, unstable boulder zone from LS - MS. From MS - HS is solid rock with few pools. Above HS is a narrow strip of small stones. Slight wave action present.

(59) *Back Beach (Long Is.)* - S20°20.2’, E148°51.3’ Wide, unstable boulder zone with small unstable rocks from LS to MS and larger solid rock present at HS. Pools at LS are mostly contiguous with the sea. No real pools at MS as it is the most elevated area of shore, and only some very small pools are present at HS.

(78) *Shutehaven* - S20°16.9’, E148°47.0’ Small rocky area protected by built-up harbour. Solid rock-cement substrate. No sand is present.

(76) “*Airlie Bay*” - S20°15.8’, E148°43.4’ Just north of Shutehaven. A mostly man-made beach protecting an area of the harbour. Some pools form, but there are no algae and no wave action.

(57) *Bauer Bay (S. Molle Is.)* - S20°15.6’, E148°50.1’ A moderately sloping beach with sand base and small - medium sized unstable boulders strewn on top. The beach is approximately 30 m wide and is made of boulders from LS to HS. Due to
the slope of the beach, there are no pools at HS and almost none at MS, with a few, small pools present above the water’s edge.

(77) “Airlie Point” - S20°15.4’, E148°44.0’ This is a medium width (~ 25 m) beach that is below a built up area of park. Large boulders quickly give place to medium to small unstable boulders at MS then to stones at LS. Some pools. Almost no wave action.

(81) N. Port Denison - S20°01.3’, E148°15.8’ A narrow zone of large boulders, this area has been built up as part of the pier area. Very little wave action. Water pools on some large rocks, but not suitable for hermit crabs. No hermit crabs found.

(60) Horseshoe Bay - S19°58.7’, E148°15.7’ A short, closed in boulder zone made up of large to very large, solid boulders on a solid rock base covered by sand. Boulders occur from HS - LS. Outer boulders break constant, moderate wave action. Many pools on rock base have carpet algae through entire pool and shell grit and sand are found in almost all pools from HS - LS. Area is fairly flat and MS and HS pools do not stream to LS. See Plate 5B.

(82) Cape Pallarenda - S19°11.5’, E146°46.2’ This is a very short (~4 m), steeply sloping, man-made boulder zone directly down from the street. There is little wave action since the site is protected by Magnetic Island. No suitable habitat for hermit crabs. No crabs found.
(67) Toolakea - S19°08.7’, E146°34.9’ A low-lying, very flat, small-stone beach which begins at the bottom of a medium-width sand zone. The sand zone slopes down to the start of a medium width (~35 m) boulder zone. Many pools found from HS - LS. At the LS the end of the boulderzone is a sand flat that extends from there out to sea. Very few mangrove trees found at upper MS - HS and some water streams from the upper sand belt to HS and from there to LS.

(66) Bingil Bay - S17°50.1’, E146°06.0’ A wide boulder zone comprised of small, unstable boulders. Very little slope in this area, so pools occur at all levels. Some mangrove trees present at HS. At LS there is almost no wave action. Fresh water streams from supra littoral zone through a thin sand strip from the road to the HS rocks. A single storm water drain is present and fresh water streams toward the boat launch.

(83) Etty Bay (Innisfail) - S17°33.9’, E146°06.1’ Some fresh water streams down from under road through rocky beach area.

(84) Flying Fish Point - S17°29.9’, E146°05.0’ A very short sand beach leads to a rocky outcrop to the S where the river comes out. This rock is solid with no boulders. Some pools but no algae. Wave action is constant and moderate.

(62) Nudey Beach (Fitzroy Is.) - S16°56.2’, E145°59.0’ A short, small rock boulder zone. At HS solid rock base persists. At MS and LS mainly medium to small sized unstable rocks are found with many pools in the short width of LS. Some pools at
MS and only a few to none at HS. LS has some fine micro algae on rocks but not on substrate. Minor wave action broken by fringing reef and large boulders subtidally.

(61) *N. Welcome Bay (Fitzroy Is.)* - S16°55.9’, E145°59.3’ An area composed of sub-surface solid rock, but with much surface sand. It is a short boulder zone with very large boulders from HS - LS and with medium to small unstable rocks at LS. There are a few pools at HS and only a few at MS. LS is mostly at waters edge where most rocks and pools have some to many fine carpet algae.

(85) *N. Ellis Beach (Cairns)* - S16°42.9’, E145°39.1’ A highly exposed site with only a short boulder zone (~ 10 m) from LS to HS. Boulders are small to medium size and occur throughout zone. Boulders at LS (in water) are larger than those at MS - HS (stony type beach). Boulders at LS have algae on them below water surface, but none above.

(65) *Port Douglas* - S16°29.1’, E145°28.2’ A narrow (~ 15 m) wide boulder zone with large, solid boulders on solid rock base. There are several pools at LS and MS, but very few at HS. A large sand beach exists to the right of this site. At HS and near the sand beach area (just in to the start of the boulder zone) there are two large fresh water drains that empty onto this rocky area. Water flows from HS to LS and into the sea to the right of this site. To the left of the site no fresh water flows into the pools. Larger, solid rocks build up on far left of site at the bottom of a walkway. These storm water drains appear to be quite new.
(64) **Dayman Point (Mossman)** - S16°22.9’, E145°45.9’  Medium width (~ 30 m) boulder zone with unstable, small boulders, on solid rock base covered with sand. Rocks at LS and MS have some algae cover. Wave action is slight down by outer solid rock. Some empty shells at MS and HS.

(63) “**New Crab Point**” (Mossman) - S16°22.1’, E145°24.7’  A small area of rock beach mixed with sand. To the N there is some solid, upturned rock with areas between which are made up of small stones. In these stone troughs, fresh water is streaming down from above the highway. Beach is gently sloping. Between HS rocks and trees is a strip of ~ 8 m of sand, and from HS to LS is ~ 22 m. Many empty shells from HS to LS.

(86) **Cape Kimberley (Daintree)** - S16°16.7’, E145°29.1’  A wide sand beach leads to a rocky headland to the N composed of short, steeply sloping solid rock turning into large to medium boulders at LS. There is continual low level wave action but no pooling occurs.
Plate 1  A: The flat, stony beach at Woody Point (Site 32), Redcliffe where there is almost no wave action. B: The wide, flat rock shelf and highly exposed shore at Point Cartwright (Site 30), Mooloolaba.
Plate 2  A: The exposed, narrow rock beach at Alexandra Headlands (Middle) (Site 29). B: At Elliott Heads (Site 20), there is a wide, gently sloping boulder beach with tidepools extending very high up on the shore.
Plate 3  A: Wreck Rock (Site 8) (Deep Water National Park) is an exposed beach with variable rock substrate and a wide sand buffer above. B: Turkey Beach (Site 7) is calm and relatively flat. Mangroves are present to the north.
Plate 4  A: At S. Cooee Bay (Site 3), there are different types of substrate. The beach is a wide boulder zone with a gradual slope. B: The short, steep rock beach at E. Shellving Beach (Site 53) (Keppel Island) is well protected from wave action.
Plate 5  **A**: S. Hay Point (Site 40) is a wide, rugged, solid rock platform with boulders strewn on top. **B**: On the short beach at Horseshoe Bay (Site 60) boulders range from massive to small, with many sitting atop the sand beach substrate.