**Spatial dynamics and
life history characteristics
of an aggregating species,
*Petrolisthes elongatus***

by

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“The world and the universe is an extremely beautiful place, and the more we understand about it the more beautiful does it appear”.

Richard Dawkins

Abstract

Intertidal boulder fields are heterogeneous mosaics of different micro-habitat patches providing high structural complexity and spatial variability of environmental conditions that shape the heterogeneity of abundance of species. The influence of the spatial scale at which ecological patterns are measured has gained much attention over the last two decades. The adaptations to environmental conditions as well as the ability to disperse vary among species and, consequently, result in species-specific responses to heterogeneous environments. Understanding the causes and consequences of spatial patterns of abundance of organisms is a central problem in ecology and insight in underlying mechanisms may have important implications for fisheries management and conservation biology. The competing demands organisms are subject to require compromises to optimise fitness and facilitate the persistence of a population. Reproductive trade-offs, for example, may be largely the result of adaptive processes, constrained by phylogenetic effects. Generally, trade-offs are regarded as a key to understand the evolution of life history characteristics.

The present study investigates the spatial dynamics and life history adaptations of an aggregating species, the New Zealand half crab, *Petrolisthes elongatus*. This species has a biphasic lifecycle and occurs in geographically isolated benthic metapopulations that are associated with cobble beaches, where it reaches extremely high densities. Even though sampling was conducted exclusively in the Wellington region, sites at Cook Strait as well as within Wellington Harbour exhibited considerable differences in habitat structure and temperatures as well as wave exposure and food supply.

Cobble size was an excellent predictor of both population density and mean carapace width on almost every scale of observation and, therefore, appeared to be an important indicator of habitat quality for *P. elongates* because cobble size is closely related to availability and size of interstitial space between boulders the crabs utilize as shelters against predation and desiccation pressure.

Crab densities were significantly (6-fold) higher within the harbour compared to south coast sites, presumably due to 1) the different availability of shelter space, 2) lower settlement and recruitment rates at Cook Strait, and 3) higher food supply within the harbour.

Population structure was mainly influenced by settlement and recruitment, but also by rock size (i.e. shelter size), size selective predation and a higher mobility of larger crabs. Under laboratory conditions, predation rates among small crabs strongly depended on rock size, whereas large crabs were generally rarely to never preyed upon.

Migrated distances did not exceed 100cm over 25h in most cases but were different at different sites. While structural complexity could affect mobility (i.e. easier movement among larger rocks), local density and resulting levels of intraspecific competition were possibly the main drivers of limited mobility of adult crabs.

P. elongatus exhibits a high phenotypic plasticity of reproductive traits in response to the variable environmental conditions across sites. Female crabs at Island Bay (Cook Strait) showed the highest fecundity, higher percentage of ovigerous females, higher proportion of clutch to body weight (i.e. reproductive output) and higher egg numbers among large individuals compared to similar-sized individuals at other sites at the harbour entrance (Breaker Bay) as well as within the harbour (Hutt River mouth).

Larvae of *P. elongatus* strongly responded to waterborne settlement cues released by conspecific adults both in the laboratory and in the field. The average numbers of settlers was 4-fold higher in basket traps deployed in the field if conspecific adults were present. Therefore, settlement patterns are strongly influenced by conspecific density, even on a small spatial scale (tens of centimetres). Recently metamorphosed individuals may still respond to conspecific cues, presumably providing guidance to conspecific adults that protect juveniles from predation and desiccation pressure in addition to shelters between boulders.

Under laboratory conditions, individual growth rates as well as mortality depended on density but not on food level. Differences in density dependent growth rates and mortality varied with body size and were both more pronounced among smaller crabs.

Limb loss significantly influenced the increase in body weight over time, especially among small individuals; however, no differences could be detected regarding changes in body size due to few moults over the course of the experiment. Crabs with removed chelipeds gained more weight over 7 weeks relative to uninjured individuals, presumably due to the limb regeneration process. Reproductive output, however, appeared not to be affected by limb loss and the associated costs of regenerating chelipeds; however, sample sizes were low to reliably detect such differences.

The results of my thesis underline the importance of the consideration of spatial scale in ecological studies in order to meaningfully compare results with other studies. Additionally, the present study contributes to elucidate the influence of environmental conditions on density dependence and reproductive traits of mobile intertidal invertebrates.

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Chapter 1

General introduction

1.1 Introduction

Understanding the causes and consequences of spatial patterns of abundance of organisms is a central problem in ecology. For effective management of harvested marine species, for example, spatial patterns of harvest rates, reproductive output, population recruitment and growth rates of individuals must be considered (Hutchings, 2000; Walters & Kitchell, 2001; Conover & Munch, 2000; Tapella *et al.*, 2002). In conservation biology, the understanding how spatial structure influences metapopulation dynamics within single- and multispecies systems is crucial, especially for the management of endangered species living in fragmented habitats (Harding & McNamara, 2002). Much basic evolutionary theory invokes spatially explicit phenomena, e.g. local adaptation and speciation. Despite the central role of spatial patterns in population dynamics, effective resource management, and evolutionary biology, our understanding of mechanisms responsible for spatial patterns is far from complete.

Spatial variability and aggregation in nature

It is widely acknowledged that ecological communities exhibit heterogeneity and patchiness on a broad range of spatial scales (Kotliar & Wiens, 1990). The causes of this pattern may be different for different scales (Levin, 1992); hence, it is crucial for the comparison of scientific studies to consider the scale of observation (e.g. Archambault & Bourget, 1996; Chitarro, 2002). Besides a large number of definitions of patchiness (Blackwell, 2007), a population distribution is regarded as patchy or aggregated if the ratio variance / mean number of individuals in random samples taken in the same habitat area is larger than 1 (Lloyd, 1967; Perry, 1981; reviewed in McArdle *et al.*, 1990; McArdle & Gaston, 1992; Gaston & McArdle, 1993; Benedetti-Cecchi, 2003). This ratio is also called “index of dispersion” (see Perry & Mead, 1979, and calculations in appendix 2.10 of chapter 2). Generally, the observed spatial variability in abundance of animals (i.e. their “patchy” distribution) has been attributed to the heterogeneity in biological and physical factors including the differential availability of resources

such as food and shelter, as well as variability in predation, competition, disturbance, and recruitment (e.g. Dayton, 1971; Chapman *et al.*, 1995; reviewed in Underwood, 1992, 1996; Caley *et al.*, 1996). Especially in the rocky intertidal zone the resulting mosaic of patches with different sizes, shapes and habitat quality can exhibit high structural complexity with implications for patterns of abundance of species as well as for composition and diversity of communities. Individuals that group in response to resource availability and quality form patterns in which high quality patches have the highest densities (e.g. Fretwell & Lucas, 1970; Seitz *et al.*, 2003). However, the clumped (i.e. non-random) distribution of individuals does not always arise due to environmental heterogeneity but may also result from species-specific behaviour. Additionally, patterns of aggregation are not necessarily driven by functional purposes and evolutionary benefits and do not always result from the combined actions and interactions of many individuals. Currents, eddies and other hydrodynamic phenomena can result in highly clumped distributions of organisms (Levin & Segel, 1976; Mackas *et al.*, 1985). Once established, the properties of aggregations (e.g. group size and size frequency distribution) are influenced by biological factors including competition and predation. In addition to random aggregations that form temporarily due to physical effects or those that arise from individuals responding to external cues such as light or food there are “self organizing” aggregations (e.g. fish schools, colonies of bees and termites, as well as bird flocks), in which coordination and integration gives rise to swarm properties that are fundamentally different from properties of the individual (see Parrish *et al.*, 2002; Sumpter, 2012). In these types of aggregations, the benefits typically lead to increased fitness of individuals (i.e. increased survival and/or reproductive success) as well as to increased fitness of the group (i.e. population persistence and/or increased population growth). Generally, the aggregation of animals has been viewed as an evolutionary advantageous state in which individuals may benefit from protection from predators, facilitation, enhanced foraging, mate choice and cooperation, balanced by the costs of limiting resources and increased disturbance risk (Okubo, 1986; Ritz, 1994; Flierl *et al.*, 1999; Parrish & Edelstein-Keshet, 1999; Floater, 2001). In aggregating species, however, the costs of intraspecific competition are low even at high densities (Donahue, 2006). To understand how aggregations are formed it is important to

distinguish between the factors that trigger their formation and the effects arising from adaptive advantages (Miller & Hampton, 1989; Hofmann *et al.*, 2004).

Habitat quality and density dependence

The physical environmental conditions combined and interacting with biological factors at a particular location form a habitat, that could either be understood as space with relatively homogenous environmental conditions (micro-habitat) or, alternatively, as a certain biotope type that provides resources for its characteristic fauna and flora communities. Spatio-temporal variations in resource availability, resource quality and environmental conditions affect the fitness of individuals either directly or indirectly (Bernstein *et al.*, 1991; Pulliam 2000) and thus generate strong selective pressure for habitat selection (Cody 1985). However, reproduction, survival, and abundance of species may not all be positively correlated with habitat quality (Johnson, 2007) and cannot be assumed without supporting demographic data (VanHorne, 1983). In aggregating species such as *P. elongatus* and *P. cinctipes*, extreme population densities may lead to negative density dependence, affecting individual growth, reproductive output and survival, even though 1) these adverse effects could be outweighed by positive density dependence (i.e. Allee effects) at slightly lower densities and 2) aggregations were initially formed due to high patch quality (compare Donahue, 2004, 2006).

Life history characteristics and reproductive trade-offs

For any individual, available resources and energy uptake are limited. Hence, the available energy “budget” needs to be balanced by splitting the investment, for example in reproduction and survival. Consequently, higher resource allocation to growth, survival and maintenance often comes at the cost of lower fecundity (i.e. number of offspring per individual). Females facing similar energetic constraints can either have small numbers of large eggs, large numbers of small eggs, or any intermediate combination, provided that the proportion of resources invested in reproduction stays the same relative to the amount of material and energy that is spent for growth, maintenance and survival. Generally, the benefits of performing an ecological function come at a cost of performing another. Stearns (1989, 1992) described life history trade-offs as negative functional interactions between reproductive traits. Reproductive patterns in marine invertebrates have been

shown to be adaptive, in response to environmental conditions that select for maximum offspring survival and, therefore, population stability (Roff, 1992; Stearns, 1992). In decapods, life history traits such as egg size, number of eggs, reproductive output, and female body size may vary with temperature and latitude (Clarke, 1987; Lardies & Castilla, 2001; Ramirez Llodra, 2002; Lardies *et al.*, 2010). Fecundity, the quality of offspring and offspring survival are directly dependent on the nutritional state of the parent and its allocation of energy to reproduction (Olive, 1985; Eckelbarger, 1986; Jaekle, 1995, Bertram & Strathmann, 1998). For the porcelain crab *Petrolisthes granulosus*, Monaco *et al.* (2010) demonstrated that maximum body size and reproductive capacity are correlated with latitude; however, food availability and genetic factors may play an important role, as well. Shallow water benthic Crustacea in the polar regions commonly have a larger body size, larger eggs and a non-pelagic development compared to temperate and tropical species with a typically biphasic lifecycle that comprises a planktonic phase lasting several days to several months (Sastry, 1983, and literature therein). A larger maternal investment in individual eggs leads to larger “high quality” eggs and therefore to higher offspring survival (Stearns, 1992; Ramirez Llodra, 2002). However, larger eggs and higher offspring survival result in decreased fecundity and, due to hatching at a more advanced stage in development and shorter planktonic phase, lower dispersal capability. Environmental factors such as food availability and quality, temperature, competition, and predation select for an optimal egg size within certain limits that maximises parental fitness (Olive, 1985; Stearns, 1992; Ramirez Llodra, 2002). Smith & Fretwell (1974) proposed a model that suggests the selection for a single optimal level of parental investment in offspring for a given species. The variability of egg sizes observed in natural populations may be caused by temporal environmental effects during offspring development, affecting the ability of adults to allocate equal amounts of resources to each egg (McGinley *et al.*, 1987) as well as by morpho-functional constraints and adaptive phenotypic plasticity caused by variability in egg size and resulting offspring fitness (Einum & Fleming, 2000). The reproductive patterns of decapods are strongly influenced by the trade-off between body size and fecundity (Ramirez Llodra, 2002). Larger females carry higher numbers of eggs (Sastry, 1983; Ramirez Llodra, 2002 and literature therein). Likewise, egg mass weight is positively correlated with female

body weight (Corey & Reid, 1991). In addition to energetic and physiological constraints, the physical space for eggs that can be attached to pleopods is limited and depends on body size (Hines, 1982; Somers, 1991; Clarke, 1993). The age or size at first maturity is an important indicator for the life-history strategy of a species and is defined as the age or size at which the female produces the first batch of eggs (Ramirez Llodra, 2002). While early maturing species have shorter life spans and generation times, species with a later onset of sexual maturity live longer, grow larger and therefore have higher initial fecundity. A long lifespan also increases the probability of multiple spawning, thereby increasing lifetime fecundity. However, a delayed maturity also increases the mortality risk before reproductive capability is reached (Bell, 1980; Stearns, 1980, 1992). Additionally, the allocation of resources to reproduction may decrease parental survival and the probability of another reproductive event (Bell, 1980; Stearns, 1992; Gardner, 1999). To understand the demography and population dynamics of a species, the study of its life-history strategy is of great value. As a series of co-adapted and interdependent traits, the life history strategy of a species evolves in response to or in interaction with selective pressures of the biotic and abiotic environment, within limits of genetic, morphological, and physiological constraints.

Consequences of spatial structure on population dynamics and life-history traits

Spatial structure influences stability and organization of single and multispecies systems, both in nature and in theoretical considerations (Kareiva 1987; Tilman & Kareiva, 1997; Hanski, 1999). In fragmented landscapes the risk of extinction is usually increased, especially with increasing isolation of habitat patches or decreasing patch size (Burkey & Reed, 2006). Metapopulation dynamics crucially depend on the form of the relationship between recruitment rate (comprising both immigration and settlement) and the reduction in extinction risk (Levins, 1969; Harding & McNamara, 2002). However, not all patchy populations are metapopulations (Hanski & Simberloff, 1997), especially if subpopulations are not spatially separated but rather colonize a continuous or connected habitat with high spatial variability of environmental conditions. Metapopulations inhabiting isolated habitat patches may have extremely complex dynamics (Levins, 1969; Hastings & Volin 1989; Artzy-Randrup & Stone, 2010) due to large scale dispersal influenced by wind drift, currents and shoreline properties, leading to a differential connectivity (Pineda *et al.*, 2007; Trembl *et al.*, 2008; Carson *et al.*,

2011; Watson *et al.*, 2012). Additionally, larval settlement and recruitment rates in marine invertebrates are highly variable on several spatial and temporal scales (reviewed in Rodriguez *et al.*, 1993; Pineda, 2010). As a result of large scale dispersal, coastal marine species commonly exist in systems of interconnected subpopulations (e.g. Watson *et al.*, 2011a and b). Because gene flow between geographically isolated populations may increase fitness (Bossuyt, 2007; Vandewoestijne, 2008), pelagic larval development is of particular significance for benthic marine invertebrates, many of which have limited dispersal capabilities as adults. Dispersal also allows the colonization and recolonization of habitat patches (Hanski, 1985; Fahrig & Paloheimo, 1988; Adler & Nuernberger, 1994). On the other hand, dispersal effects are balanced by the costs of high losses of individuals due to failure to find suitable habitat and predation. In adaptation to geographically isolated metapopulations, species are more likely to exhibit high frequency of spawning, larger numbers of smaller offspring (due to the trade-off between size and number of offspring), prolonged pelagic larval development, and an ability to detect and respond to settlement cues. Additionally, the evolution of life history traits is influenced by habitat stability, disturbance rate, climate, food conditions, competition, and predation.

Settlement cues and conspecific attraction

Historically, it has become a paradigm that marine invertebrate larvae are passively transported by advection and diffusion (Johnson, 1939, Abelson & Denny, 1997), mixed in a “larval pool” (Pineda, 2000), and then randomly recruited to juvenile or adult habitat (Roughgarden *et al.*, 1988; Siegel *et al.*, 2003; Pineda *et al.*, 2007). However, in many species settlement occurs non-randomly due to the selectivity of larvae that is associated with a range of different settlement cues, many of which are species specific (for reviews, see Meadows & Campbell, 1972; Crisp, 1974; Burke, 1983, 1986; Pawlik, 1992; Rodriguez *et al.*, 1993; Rittschof *et al.*, 1998; Hadfield & Paul, 2001; Hay, 2009). A high specificity in detection of and responding to settlement cues in competent larvae may be correlated with their fitness and survival probability because settlement into sub-optimal habitat can be detrimental (reviewed in Levin & Bridges, 1995; Heyland *et al.*, 2011). Besides a range of physical substratum properties such as surface texture that may act as settlement cues, chemical waterborne cues either originate from substratum components or are released by

biofilms, coexisting species, predators or conspecifics; however, for most species, biological and chemical characteristics appear to be more important than physical properties (e.g. LeTourneux & Bourget, 1988). Conspecific cueing has been regarded as an adaptation of benthic marine invertebrates to a fragmented or widespread species distribution that increases the chance for a larva to find suitable habitat, facilitates dispersal, and ensures connectivity between geographically isolated metapopulations (Rodriguez *et al.*, 1993; Pineda *et al.*, 2007).

1.2 Study location

Hydrology

Wellington Harbour (Port Nicholson, Te Whanganui-a-Tara) is of tectonic origin, and a major earthquake fault lies along its western shore. While the entrance at its southern end is only 1.8km wide, the Harbour itself measures 11.1km at its widest point, has a surface area of approximately 85km², and is with an average depth of 20m (31m max.) relatively shallow (Booth, 1975) (Fig. 1.1). The semi-diurnal tides in the Harbour have a range of approximately 0.75m on average with a maximum of 1.5m during spring tides (Maxwell, 1956). On flood tide, water within the Harbour flows in a clockwise direction and anti-clockwise on ebb tide, leading to a net clockwise flow (Brodie, 1958; Heath, 1977). The major source of freshwater input is the Hutt River with a catchment of 630km² (Booth, 1975) and a discharge ranging from 2x10⁶ m³ to 180x10⁶ m³ (Maxwell, 1956). A freshwater lens with a thickness of ca. 1m extends out from the Hutt River mouth along the eastern shore and may reach as far south as well past Matiu-Somes Island after prolonged periods of rain (Helson, 2001). Other (minor) sources of freshwater input include three small streams: Kaiwharawhara, Ngauranga and Korokoro.

Cook Strait (Raukawa Moana), the strait between North and South Island of New Zealand, connects the Tasman Sea on the west with the South Pacific Ocean on the east (Fig. 1.2). With 23 kilometers at its narrowest point and an average depth of 128 meters it separates Cape Terawhiti in the North Island from Perano Head on Arapawa Island in the Marlborough Sounds. To the east, between the submarine plateaus of both islands lies the Cook Strait Canyon with steep walls descending eastwards into the Hikurangi Trench. The Narrows Basin to the north-

west is between 300 and 400 meters deep. The tidal flow through Cook Strait is unusual in that on each side of the strait ebb and high tides are almost exactly out of phase. Strong currents result, with almost zero tidal height change in the centre of the strait. Dependent on weather conditions, the tidal surge can be irregular. The direction of the flow is usually reversed every six hours but strong winds may partly negate reversed surge, resulting in unidirectional flow over longer periods (Carter, 2001; Foster, 2006). Moreover, water flow as well as variations in temperature and salinity within Cook Strait is influenced by three major currents: The Southland Current, moving northward along the east coast of the South Island, the (sub surface) East Cape Current, moving southward along the east coast of the North Island, and the D’Urville Current, travelling northward along the west coast of the South Island, entering Cook Strait from the north due to prevailing northerly winds (see Bowman *et al.*, 1983). These currents mix in Cook Strait in an area called the “Narrows”, west of Cape Terawhiti. In this area, flow velocities between 12.5 and 25cm s⁻¹ have been measured (Heath, 1971).

Fig. 1.1: Cook Strait with seafloor contours with Cook Strait Canyon and Hikurangi Trench (image credit: National Institute of Water and Atmospheric Research, NIWA, New Zealand). The boxed area, including Wellington Harbour, is represented in Fig. 1.2.

Fig 1.2: Map of main study sites in Wellington region at the southern tip of New Zealand's North Island in Wellington Harbour (Hutt River mouth (HRM), 41° 14'49.50" S, 174° 53'57.00" E), at the Harbour entrance (Breaker Bay – Reef Bay (BRB), 41° 20'17.90" S, 174° 49'26.60" E), and at Wellington South Coast (Island Bay – VUCEL (ISB), 41° 20'54.30" S, 174° 45'53.20" E).

Wind and wave exposure

Due to the funnel effect of Cook Strait, wind speeds are generally high in the Wellington area. Especially during the winter months Wellington's South Coast is regularly exposed to gale force southerly winds and swell heights of up to 6m have been frequently reported by MetService New Zealand (<http://metservice.com/marine/coastal/cook>). Maximum wave heights off Baring Head (10km south-east of Wellington), measured by buoys, peaked at 7 to 8 m (<http://www.niwa.co.nz/our-science/natural-hazards/research-projects>, 2010). The inner Wellington Harbour, by contrast, is a moderate wave energy environment, sheltered from swell from all directions except the narrow entrance to the south.

As a consequence, the Harbour is mainly subject to low energy waves generated by sea breezes, but is also influenced by ground swell from Cook Strait. On stormy days with southerly winds, wave heights may occasionally exceed 1m at the northern end of the Harbour (own observation).

Selection of study sites

Three intertidal cobble beaches in the Wellington area were selected as study sites, all of which were inhabited by porcelain crabs in high densities. The littoral zone at all three locations consists mainly of rough shingle and cobbles, interspersed with larger rocks. At Island Bay and Breaker Bay, large rocky greywacke outcrops fringe the boulder fields and form a reef-like barrier that partly protects the beaches from heavy surge. While the South Coast site, now situated within the boundaries of Kupe / Kevin Smith Marine Reserve, is characterised by high wave exposure, lower mean water temperatures, and generally smaller cobble sizes, the opposite was found at the Harbour site (Hutt River mouth). With overall intermediate features at the harbour entrance (Breaker Bay), the differential adaptations of *P. elongatus* individuals and population-responses could be examined within a broad range of environmental conditions.

A

B

C

Fig.1.3: Study sites, A) Hutt River mouth, B) Breaker Bay, C) Island Bay - VUCEL

1.3 Study species

The porcelain crab *Petrolisthes elongatus* (H. Milne Edwards, 1837) is highly abundant on intertidal boulder fields and cobble beaches throughout New Zealand including Auckland Islands as well as in Tasmania, Australia (Pellegrino, 1984). As these crabs appear to be restricted to this habitat type, it forms geomorphologically isolated metapopulations that are separated by uninhabited sandy beaches and stretches of rocky shores by hundreds of meters to several kilometers. Hence, the species exhibit a patchy distribution on a large scale in a naturally fragmented habitat. Field observations prior to this study revealed patchiness in local density also on a medium scale (several meters), as well as on a small scale (tens of centimetres), with high density aggregations under larger boulders. Besides an obvious negative phototaxis (Scott, 1958), Meyer-Rochow & Meha (1994) found, based on field studies, that during the day *P. elongatus* has a considerably higher tendency to conceal itself at low tide compared to high tide.

Ovigerous females occur from October to March (Jones, 1977). Compared to other decapods occurring in similar latitudes, the eggs are large (Gohar & Al-Kholy, 1957), whereby egg numbers are relatively small (Greenwood, 1965). Large females (14mm carapace length) have up to 900 (Jones, 1977), 1100 (Wear, 1965) or 1200 eggs (Greenwood, 1963), respectively. Like many other marine invertebrates, *P. elongatus* has a biphasic life cycle (Fig.1.3), with a planktonic larval phase and benthic juvenile and adult populations. The swimming and feeding larval stages remain in the plankton for several weeks; however, the exact duration of the planktonic phase of Porcellanidae is still unknown. According to laboratory-based rearing of *P. laevigatus* from a similar latitude in Chile (Mascetti & Wehrtmann, 1996), the larval development in *P. elongatus* (from hatching until metamorphosis into first instar juvenile) is likely to last for approximately 3-6 weeks and comprises six different stages, one or two of which may be frequently bypassed (Wear, 1964). Lower water temperatures typically result in considerably longer larval intermolt periods (Mascetti & Wehrtmann, 1996) and consequently in longer planktonic phases. Studies at Christchurch (Scott, 1958), Kaikoura (Jones, 1977), Wellington (Wear, 1965) and Auckland (Greenwood, 1965) suggest that breeding biology of *P. elongatus* varies with latitude. For a more comprehensive species description, see McLay (1988).

Fig. 1.4: Biphasic life cycle of *Petrolisthes elongatus*, comprising a pelagic larval and a benthic juvenile-adult phase. Eggs are attached to three pairs of pleopods in female crabs and carried between abdominal flap and sternum until hatching. Larval development via three to five planktotrophic zoea stages; the megalopa forms the last, meroplanktic stage that becomes competent and settles in rocky intertidal, approx. 3-6 weeks after hatching. Drawings of larval stages by Wear (1964); drawing of the adult stage by Jones (1977).

1.4 Objectives

Understanding the causes and consequences of population dynamics on various spatial scales and species-specific reproductive traits as adaptations to environmental conditions is crucial for both conservation and sustainable stock management. The identification of relevant habitat quality indicators for a species helps to understand its ecology and specific requirements for survival and fitness maximisation. Due to its high abundance and accessibility in intertidal boulder fields, its gregariousness, as well as its patchy distribution on a range of spatial scales *P. elongatus* was chosen as a suitable model organism to study the underlying mechanisms of observable distributional patterns within benthic populations, including habitat quality, settlement rates, and density dependence.

In this study, I examine the main drivers of patchiness of abundance in *P. elongatus*. Since these patterns are commonly influenced by habitat quality and the heterogeneous availability of resources I aim to identify the relevant environmental factors responsible for the patchy distribution of crabs within and between habitats. Because *P. elongatus* inhabits the interstitial space between boulders the availability of this cavity system serving as shelter and refuge is potentially crucial, providing protection from predation and excessive water movement. Therefore, I test the hypothesis that cobble size is a relevant habitat quality indicator for *P. elongatus*, directly or indirectly affecting patterns of settlement, migration, abundance and survival in this species. If we assume that the differences in shape or “roundness” of boulders are negligible, then the size-frequency distribution of boulders within a defined area determines the relative size of cavities, physically restricting the size and number of crabs that can inhabit a particular space between them. Hence, I aim to investigate whether rock size is a suitable predictor of local density and average size of crabs. The limiting factor of available interstitial space that may affect the size-frequency distribution of *P. elongatus* could also restrict or allow predation. I therefore aim to examine whether predation rates depend on rock size. Since structural complexity affects mobility, I investigate the impact of rock size on migratory activity. However, besides rock size other environmental factors may also influence local abundance; therefore, I aim to analyse spatio-temporal variations in temperature, food availability and larval supply.

The evolution of life history traits in marine invertebrates and other animals is shaped by environmental conditions that affect fitness. Additionally, reproductive traits, e.g. egg size and egg quality, may be altered by factors such as ambient temperature and food conditions (i.e. exhibit phenotypic plasticity). Against this background, I speculate whether extreme differences in habitat structure, wave exposure, temperature, predator abundance, and food supply between sites in Wellington Harbour and at the south coast influence or select for certain life history characteristics. In order to examine the probable site differences in reproductive traits in relation to environmental conditions, I measure and compare important life history characteristics in females from three geographically isolated metapopulations, e.g. body size versus number of eggs and egg mass weight,

female size at maturity, and egg mortality, in conjunction with temperature data and site differences in food availability and rock size.

Since conspecific cueing is common among marine invertebrates and *P. elongatus* is an aggregating species that is likely to settle gregariously (i.e. preferably in the presence of conspecifics) I hypothesize that competent larvae of this species are attracted to conspecific adults, mediated by a waterborne cue. If settlement was dependent on the presence of conspecifics, then higher cue densities due to higher local abundance of adults may be correlated with higher settlement rates. This assumption is tested with various field and laboratory experiments. Additionally, I investigate other potential sources of settlement cues such as crustose coralline algae and diatom biofilms that had been reported to affect swimming direction of other decapod larvae.

Living in aggregations involves a trade-off between fitness gains of in-group individuals and costs due to intraspecific competition for limited resources, especially at density levels close to the carrying capacity of a habitat patch. These costs and benefits depend on both life history and environmental conditions. To investigate how population density, combined with food availability, affects individual growth rates and feeding activity within different size classes of crabs I conduct a series of laboratory experiments similar to the work presented by Donahue (2002, 2004) on the density dependence in *Petrolisthes cinctipes*. Because crabs with autotomized limbs can be frequently found in the field it seems compelling to study the associated costs of limb loss by examining the effects of limb regeneration on individual growth rate and reproductive output. Additionally, I aim to determine whether frequency of limb loss can be predicted by local density (as an indicator for intraspecific competition) or whether autotomy is correlated with site-specific disturbance and predation rates, because shedding a limb is a strategy porcelain crabs utilize to escape predators or physical stress.

In summary, the aim of this study is to identify the main mechanisms and factors shaping the population structure of *P. elongatus* and the observable heterogeneity of abundance in the field.

1.5 Thesis layout

This dissertation comprises six chapters.

Chapter 2 discusses the role of cobble size as habitat quality indicator for *P. elongatus* on various spatial scales, ranging from single rocks within 0.25m² sample quadrats to different sites in the Wellington region, several kilometers apart. In a nested design the patterns of abundance as well as the mean carapace width of crabs are analysed in regard to rock size. In further experiments I examine the influence of cobble size on predation rates, migratory activity, and size frequency distribution of crabs in the field.

Chapter 3 investigates if and how the life history characteristics of *P. elongatus* differ between sample sites and discusses the underlying mechanisms driving the observed patterns. At all sample sites, temperature data are taken with data loggers placed among cobbles. Additionally, the analysis of spatio-temporal variations in food and larval supply is attempted, albeit without yielding usable datasets. Combined with conclusions drawn in chapter 2, the role of habitat quality in mediating life history characteristics is discussed.

Chapter 4 presents a comparative examination of a number of potential settlement inducing waterborne cues, both under laboratory conditions and in the field. With the help of a single option choice chamber the swimming behaviour of competent *P. elongatus* larvae in response to various potential chemical attractants, including those released by conspecific adults, is investigated. Settlement in response to presence or absence of conspecifics is examined using basket traps deployed among intertidal boulder fields.

Chapter 5 investigates the effects of density dependence on survival, individual growth rate, and feeding activity in *P. elongatus* across different size classes under laboratory conditions. Using a fully crossed factorial design combining two food levels and two crab densities, growth and mortality rates are monitored, while densities remain constant by replacing lost individuals. Adopting the same experimental setup and treatments, the effect of density and food level on frequency of filter-feeding is examined. To investigate the effect of limb loss on growth rate, changes in body mass and carapace width under laboratory

conditions are recorded over several weeks, which are then compared between injured and uninjured crabs across different size classes. Data obtained from a field survey complement these results.

Chapter 6 represents the integrated summary and general discussion of the findings of the various components of this study with regard to the previously formulated thesis aims.

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Chapter 2

Effects of cobble size on population structure, predation risk and movement of *Petrolisthes elongatus*.

2.1 Introduction

In the rocky intertidal spatial variability may be found in exceptionally high levels (Hartnoll & Hawkins, 1980; Miller & Ambrose, 2000). Intertidal boulder fields are heterogeneous mosaics of bedrock, gravel, pebbles and soft sediment and, therefore, provide a high structural complexity. The spatial and temporal variability of environmental conditions within a (macro-) habitat is linked to the heterogeneity of abundance of species (Sousa, 1979; McGuinness & Underwood, 1986; Davis & Wilce, 1987; Rios & Mutschke, 1999; Takada, 1999). Habitat variation exists at a broad range of spatial scales (Wiens, 1989); correspondingly, the same is true for the heterogeneity and patchiness of ecological communities (Kotliar & Wiens, 1990). The spatial distribution of krill populations in the Southern Ocean, for example, have been shown to be patchy an almost every scale of description (Levin *et al.*, 1989). The causes of this pattern may be different for different scales: While patches on a large scale are the result of water movement, small scale distribution is influenced by swimming behaviour (Levin, 1992). Hence, the identification of relevant scales is very important, as well as the consideration of the scale of observation when comparing the results of scientific studies (Levin, 1992; Archambault & Bourget, 1996; Azovsky, 2000; Bishop *et al.*, 2002; Chitarro, 2002).

Generally, the observed spatial and temporal variability in abundance of animals have been attributed to a multitude of ultimate and proximate factors, such as the distribution of suitable habitat, physical habitat structure and shelter availability (Hixon & Beets, 1993; Drolet *et al.*, 2004a; Shima *et al.*, 2008), food supply (Wildish & Kristmanson, 1979; Gardner, 2000; Helson *et al.*, 2007), predator abundance (Kneib, 1984; Alonzo & Mangel, 2001; Knight *et al.*, 2005), episodic disturbances (Dayton, 1971; Dayton & Oliver, 1980; Paine & Levin, 1981;

Dethier, 1984), hydrodynamic conditions (Shepherd & Partington, 1995; Menge *et al.*, 1997; Lapointe & Bourget, 1999; Pech *et al.*, 2002; Arkema, 2009), temperature (Stillman & Somero, 1996), and light (Spanier & Almogshtayer, 1992; Drolet *et al.*, 2004b), whereby each factor acts differently on a particular spatial scale. Thus, the identification of relevant habitat quality indicators across a range of spatial scales is crucial for the understanding of the differential population density and distribution of a species. Since levels of competition depend on both population density and availability of resources, the specific carrying capacity of a habitat (*sensu* Le Hir & Hily, 2005, “spatial area with homogenous environmental parameters on a given observational scale”) could be estimated based on habitat characteristics if habitat size and home range are taken into account (e.g. Thompson Hobbs & Hanley, 1990; Reid *et al.*, 2007; Downs *et al.*, 2008; Griffen & Drake, 2008). Not only patch quality, but also patch size and landscape context affect local population abundance (and dispersal rate) (Hanski, 1994; Andren, 1994; Ricketts, 2001; Thomas *et al.*, 2001; Haynes & Cronin, 2003, 2004; Haynes *et al.*, 2007). However, patchiness of abundance is also explainable by differential spatio-temporal larval supply, settlement and recruitment rates, differential mortality and predation, post-settlement migration, as well as aggregation and conspecific attraction.

Spatial structure influences stability and organization of both species and communities (Kareiva, 1987; Tilman & Kareiva, 1997; Hanski, 1999). Especially with increasing isolation of habitat patches or decreasing patch size, the risk of extinction in fragmented landscapes is usually increased (Burkey & Reed, 2006). Metapopulation dynamics depend crucially on the form of the relationship between recruitment rate (due to immigration and settlement) and the reduction in extinction risk (Levins, 1969; Harding & McNamara, 2002). Considerable efforts have been made to model the dynamics of metapopulations, taking into account the size, growth rate, and age structure of each subpopulation (Levins, 1969; Hastings & Volin 1989, Allen *et al.* 1993), patch quality (Hanski, 1994), and interactions with predators (Taylor, 1990; Holt, 1997). These and other studies revealed that metapopulations inhabiting isolated habitat patches (e.g. cobble beaches) with a differential connectivity due to large scale dispersal influenced by wind drift, currents and shoreline properties may have extremely complex dynamics.

Besides the large-scale variation of habitat structure, every habitat patch exhibits variation on a number of small scales. It is well known that habitat complexity strongly influences patterns of abundance of marine invertebrates (McCoy & Bell, 1991; Firstater *et al.*, 2011) as well as foraging success of predators (e.g. Bartholomew, 2002; Warfe & Barmuta, 2004). However, the drivers of spatial heterogeneity in population density and structure of a given species may be different on different scales of observation. While on a scale of tens of meters, for example, patterns of abundance of mobile invertebrates could be directly explained by actions and characteristics of the physical environment, the patterns on a smaller scale (e.g. tens of centimeters) could emerge due to behavioural traits. The irregular and structurally complex nature of rocky shores in general and cobble beaches in particular provides a multitude of habitat patches that vary in size and specific physical and biological characteristics that determine their quality for a particular species.

For *Petrolisthes* spp., cobble size (as a measure of interstitial space as a limiting factor for local population density) may be a relevant factor of habitat quality. Its variability could lead to patchiness on various spatial scales in terms of population density and crab size. Preliminary field observations indicated that high density patches and large individuals can be found mainly among larger boulders. Additionally, *P. elongatus* is restricted to intertidal cobble beaches and does not occur on sandy patches. Predation rates may also be influenced by rock size due to a varying degree of accessibility of prey. Despite their camouflaging colouration, firm carapaces and efficient defence mechanisms, *P. elongatus* juveniles and adults frequently fall victim to a variety of predators including fish (see Graham, 1938), birds, mammals and larger invertebrates (McLay, 1988), contributing to an increased post-settlement mortality. Moreover, larger and therefore heavier rocks provide “better” (i.e. more stable) shelters, whereas smaller ones are more prone to be shifted by water movement. Thus, individuals may be more frequently exposed to predators or injured or killed between tumbling rocks in heavy surge (Shanks & Wright, 1986). Furthermore, small-scale hydrodynamic conditions are influenced by physical habitat structure (Sanders, 1958; Boaden, 1968). Since porcellanids are filter-feeders, current velocity is crucial for filtration efficiency (Trager & Genin, 1993); *Petrolisthes* spp. may therefore aggregate at and compete for high quality feeding spots

(Molenock, 1976; Jensen, 1990). Hence, cobble size could be a relevant habitat quality indicator for *P. elongatus*. However, patterns of abundance and population structure of crabs may also be influenced by shelter-targeting and social behaviour as well as migration.

Mobile benthic crustaceans migrate between adjacent habitat patches for various reasons. Individuals may emigrate out of a patch to avoid high levels of competition in order to make use of substitutable or non-substitutable resources in neighbouring areas (Dunning *et al.*, 1992). Immigration into a habitat patch, on the other hand, could result from conspecific attraction. Other reasons for movement include active shelter seeking, flight behaviour to escape predators or competitors, aggressive pursuit of intruders, foraging behaviour, spatio-temporal variation in resource availability such as food, shelter, and mating partners, source/sink dynamics due to relative differences in patch productivity (e.g. Pulliam, 1988; Pulliam & Danielson, 1991), or (accidental) passive drift due to wave action.

In this chapter, I investigate the implications of a heterogeneous habitat structure on patterns of abundance and demography in *Petrolisthes elongatus*, based on the hypothesis that cobble size is an important factor of habitat quality for this species. Specifically, I examine how the spatial variability of rock size (as an approximate measure of the size and availability of interstitial space) affects local density and size-frequency distribution of crabs on a range of spatial scales. Another factor contributing to patterns of abundance in *P. elongatus* could be a differential predation rate which, in turn, may be related to cobble size. Hence, I examine whether predation rate depends on rock size. Further, I am interested in how migration rate is affected by spatial complexity, measured as size-frequency distribution of rocks. Additionally, crabs of different sizes are likely to be differently affected by predation and may exhibit different migration behaviour. Therefore, the heterogeneous distribution of rock sizes relative to body size could not only mediate the observable patchiness of abundance of crabs, but also influence local variations in population demographics that, traditionally, are primarily explained by spatio-temporal variations in rates of settlement and recruitment.

2.2 Materials and Methods

2.2.1 Field survey: *Petrolisthes elongatus* density and size relative to cobble size at different spatial scales

To understand how the heterogeneity in cobble size affects abundance and size frequency distribution of *P. elongatus*, local population density and average carapace width on three different spatial scales were measured, along with cobble size. In May 2006, a nested design with randomly chosen patches at three different sites (Hutt River mouth, Island Bay and Breaker Bay) was used, whereby each “nest” consisted of five sample quadrats (50cm side length), spaced between 1m and 2m apart. At each site (i.e. on the same cobble beach), three nests were sampled with a minimum distance of 10m in between (Fig. 2.1). Each sampling quadrat was delimited by a steel frame. Prior to sampling, all rocks within the frame larger than 2cm at their widest point were numbered with white crayon and a digital photograph of the sample patch was taken (Fig. 2.2). The image was later used for the calculation of the surface area of each rock using analytic imaging software (Image-Pro v5.1, Media Cybernetics, September 2004). The porcelain crabs were killed *in situ* with hot water (approx. 70-80° C) poured over the sampling patch. All rocks within the sampling area were removed one by one and the crabs found underneath collected and preserved in 70% ethanol. If there were several layers of rocks, another photo of the sample area was taken after removal of the top layer and consecutive numbering of rocks. To extract the crabs from these sediment samples, the material was transferred into a double sieve (5mm and 1mm mesh size) stacked on top of each other, and thoroughly rinsed with seawater. The residue from each sieve was washed into a shallow, white tray and all crabs were transferred into sample jars and preserved in 70% ethanol.

Fig. 2.1: Quadrat sampling: nested design. Three sites were sampled. A) Example of individual quadrat with rocks of different sizes and different numbers of crabs underneath, indicated by shades of grey where dark grey stands for higher local crab density. B) Example of 3 “nests” of quadrats at one site. Quadrats within nests were 1-2m apart from one another, nests approximately 10m.

Fig. 2.2: Examples of sample quadrats at each site. While site Island Bay has the smallest cobble size and highest wave exposure Hutt River mouth is characterised by large boulders and low wave exposure. Both factors are intermediate at Breaker Bay, located at the entrance of Wellington Harbour.

The patchiness of crab abundance as well as the variability in size frequency distribution of crabs and rock sizes on various spatial scales (i.e. site, nest, sample quadrat, and per single rock) were analysed separately by fully nested mixed model ANOVAs with site as fixed factor and all other levels as random factors. To determine if and how rock size influences the size frequency distribution of crabs as well as their local density, fully nested mixed model ANCOVAs on both

density and crab size were used with rock size as covariate and site as fixed factor. Additionally, the index of dispersion (ratio of *variance* in numbers of crabs under each rock to *mean* number of crabs per quadrat) was calculated as a measure of patchiness (see Appendix 2.9). Because crabs were generally found under larger rocks only, rocks sizes of occupied and unoccupied rocks, pooled across sites, were compared by t-test. Using linear regression, the relationships between rock size (i.e. surface area of occupied rocks) and frequency as well as mean carapace width of crabs found underneath each rock was calculated for each site. To determine whether the relationship between rock size and crab density could be generalized on the scale of the sample quadrat and whether there were differences between adult and juvenile density, mean rock size per quadrat was plotted against mean total crab density as well as against adult density (individuals/m²) for each site.

Apart from *Petrolisthes elongatus* there were mainly two other crab species found within the sample quadrats: *Hemigrapsus sexdentatus* (A. Milne Edwards, 1837) and *Heterozius rotundifrons* A. Milne Edwards, 1867. Because interspecific spatial concurrence may result in negatively correlated abundances of sympatric species, the frequency of *P. elongatus* per quadrat was plotted against the frequency of the second most abundant coexisting species (*H. sexdentatus* at Hutt River mouth and *H. rotundifrons* at Breaker Bay and Island Bay).

2.2.2 Field experiment: cobble size and colonization of *P. elongatus*

To examine the effect of rock size and the resulting interstitial space on mean carapace width of crabs inhabiting the cavity system within boulder fields, 30 baskets were deployed in the field in December 2005. The plastic baskets (30cm x 20cm x 15cm) had rectangular openings (10mm x 20mm) on either side, large enough to allow porcelain crabs of all sizes to colonise the cobbles inside. Greywacke rocks with a similar surface roughness were collected in the natural habitat of porcelain crabs, thoroughly rinsed with fresh water and dried on a clean concrete surface outside the laboratory. Three rock sizes (3-5cm, 5-10cm, and 10-20cm) were selected as treatments. Baskets were filled with rocks of the appropriate size and coarse PVC mesh (Netlon, 10mm mesh size) attached to the opening of each basket using cable ties to secure the rocks inside the baskets. For each treatment, ten replicates were deployed in a random distribution at Hutt

River mouth, the site with the highest known abundance of *P. elongatus* in the Wellington region, and anchored with two steel pegs each. The baskets were retrieved after four weeks in January 2006 and brought to VUCCEL. For transport and to prevent animals from moving out of the trap as well as to keep them moist for several hours, the baskets were slid into plaited, breathable plastic bags. At the laboratory, the crabs were extracted from the basket traps by thoroughly rinsing the content with running seawater on a double sieve (5mm and 1mm mesh size). The residue from each sieve was washed into a shallow, white tray and all crabs were transferred into sample jars and preserved in 95% ethanol. Later, the animals were sexed and measured with a dissecting microscope.

Number of crabs per basket as well as crab size (carapace width) in each treatment were analysed by one-way ANOVA with “basket” as random factor nested within treatment. Because there were fishes found in all basket traps (*Acanthoclinus fuscus*, the same species that was used for predation experiments, see Section 2.2.3), the effect of rock size treatments on mean head-to tail length of fish were also analysed by one-way ANOVA.

2.2.3 Laboratory experiment: Influence of cobble size on predation rate

The influence of cobble size on vulnerability to predation (i.e. mortality rate due to predation) was examined by exposing crabs to predators in a laboratory experiment. As described above (Section 2.2.2), three rock sizes were used as treatments with a maximum length of 3-5cm, 5-10cm, or 10-20cm. Greywacke rocks with a similar roundness were collected from the supralittoral zone of a cobble beach in Island Bay, measured and sorted by hand, thoroughly rinsed with fresh water and dried for 24h at 50°C in a drying oven. 1kg of rocks from each of the three cobble size treatments was then placed into a 30L seawater aquarium (eight per treatment) and piled up against one side wall of the tank in at least two layers to simulate the cavity system between rocks on natural boulder fields. Additionally, the rocks (and thus the photonegative porcelain crabs) were shielded from light by a non-transparent PVC sheet that was attached to the front side of each tank. Each aquarium was filled with 15L unfiltered seawater that was replaced every two days and had two air-stones. To reduce mortality related to factors other than predation, porcelain crabs were introduced first and the predatory fish 6-8 days later.

The olive rockfish, *Acanthoclinus fuscus* (Plesiopidae) (Fig. 2.3), native to New Zealand, appeared to be an ideal model predator species: these fish (with a maximum head-to-tail length of max. 30cm) live sympatrically amongst porcelain crabs in the intertidal zone and in rock pools at low tide, feeding mostly on small invertebrates, particularly crustaceans and molluscs. Predation of *A. fuscus* on *P. elongatus* was observed on several occasions in the field as well as in captivity. A specific characteristic of this species is its ability to breathe air when out of water; hence it can be found in the intertidal during low tide, hidden in moist cavities between rocks, often amidst an aggregation of crabs (for species descriptions, see Hardy, 1984; Francis, 2001). For this experiment, 48 fish in two size classes were collected: 3-6cm and 8-12cm head-to-tail-length ($4.56 \pm 0.19\text{cm}$, and $10.25 \pm 0.097\text{cm}$) to match the approximate size distribution found in the wild with large specimen (>15cm length) being rare. Two fish from each size class were placed into each tank.

A

B

Fig. 2.3: Olive rockfish, *Acanthoclinus fuscus*, live among boulders in the intertidal where they can be found even at low tide. These fish share their habitat with *P. elongatus* and prey upon smaller sized individuals of this species. A: size class 3 specimen with a head-to-tail-length of approx. 10cm, and B: several individuals in an aquarium; note the characteristic fleshy dorsal fin rays and the dorsal/anterior light brown stripe.

Porcelain crabs were collected at Hutt River mouth during low tide. To each aquarium 30 crabs in four size classes were added, in a ratio of 10:10:5:5 individuals per tank: (size class 1 = 3.5-4.5mm carapace width, size class 2 = 6.5-7.5mm, size class 3 = 9-11mm, and size class 4 = 12.5-14.5mm). After the fish were added to each treatment, the numbers of remaining crabs in each tank and size class were counted weekly for a period of 30 days by carefully removing all rocks and animals from the aquaria. Dead crabs were removed and replaced as soon as possible to keep numbers of available prey consistent with numbers of crabs placed into each tank at the beginning of the experiment minus those that had been eaten by fish. The decline of crab individuals due to predation was used to estimate predation rates dependent on cobble size. Treatment differences in the final number of surviving crabs after 30 days within each size class were analysed by two-way ANOVA (No. of survivors ~ Rock size + Crab size + (Rock size * Crab size)).

*2.2.4 Field experiment: Mobility and migration of *P. elongatus* among cobbles*

The mobility and migration rate over one day of *P. elongatus* was examined with a mark and recapture survey for different size-classes (compare Jensen, 1989; Jensen & Armstrong, 1991; Donahue, 2004). 100 uninjured crabs were collected at Hutt River mouth and subdivided into four size classes (same as described above) of 25 individuals each. The animals were tagged with coloured and numbered “Queen Bee” tags (manufacturer: E.H.Thorne Ltd., Beehive Works, Wragby, Market Rasen, Lincolnshire, U.K., <http://www.thorne.co.uk/index.htm>) glued onto the carapace (one colour per size class, see Fig. 2.4). At three sites (Island Bay, Breaker Bay, and Hutt River mouth), a larger boulder (approx. 20cm x 20cm) was chosen as a point of release in the mid intertidal zone with a reasonably homogenous distribution of boulders surrounding it. If such a boulder could not be found, it was moved to a suitable spot from an adjacent area. The patch under the rock was cleared of all crabs and the boulder itself was marked with a small dot of spray paint. Prior to the release of the tagged crabs, wire gauze was put around the boulder to prevent the immediate spread of animals as a result of flight behaviour. After release and a period of calming (2min.) the gauze was carefully removed. The crabs were recaptured after 25h in an area with a radius of 10m around the point of release. Each recaptured individual was recorded and notes were taken concerning size class, individual tag number, distance from

point of release and direction of movement (by compass bearing) from the release point. At each site, the mark and recapture survey was conducted three times with at least six weeks between two consecutive runs. Site differences of migration distance within all size classes of crabs were analysed by 3-way ANOVA $\text{Distance} \sim \text{Site} + \text{Size class} + \text{Run} + (\text{Site} * \text{Size class}) + (\text{Site} * \text{Run}) + (\text{Size class} * \text{Run}) + (\text{Site} * \text{Size class} * \text{Run})$ with stepwise desaturation.

Fig. 2.4: Tagged porcelain crabs in a seawater tank prior to release. Size classes of crabs are marked by differently coloured “queen bee tags”, glued onto their carapaces. The tags are numbered in order to distinguish individuals. Only uninjured crabs were used for the mark and recapture survey.

All statistical analyses (ANOVA, ANCOVA) in this chapter were calculated in JMP 4.0.4 (SAS Institute, September 2001). For regressions and graphs, SigmaPlot 10.0.1 (Systat, January 2007) as well as Microsoft Excel (2003) was used.

2.3 Results

2.3.1 Field survey: *P. elongatus* density and size relative to cobble size at different spatial scales

The size frequency distributions of *P. elongatus* at the three sample sites (Fig. 2.5) show a distinctive peak of smaller crabs between 1.5mm and 4.5mm carapace width (CW), especially at Hutt River mouth (HRM). These crabs largely represent settlers (*Megalopa* larvae, approx. 1.5-2.0mm CW) and recruits (juveniles, approx. 2.0-3.5mm CW) from the latest reproductive season. Another, much lower maximum comprises adult crabs from previous years between 6.0mm and 9.0mm CW at HRM, between 4.5mm and 8.0mm CW at Breaker Bay (BRB), and between 4.0mm and 7.0mm CW at Island Bay (ISB). Additionally, there were more large crabs at HRM compared to the other two sites. Despite a higher total number of crabs at ISB, there were more large crabs at BRB. According to the size frequency distributions of crabs split by size class of rocks (Appendix 2.1, 2.2, and 2.3), rock size did not influence size frequency distributions at HRM and BRB, but clearly has an effect on the relative frequencies of size classes of crabs at ISB. While there were (relatively and absolutely) more small crabs (0.5mm-3.5mm CW) under small rocks (<100cm² surface area), there were more larger crabs (6.0mm-7.0mm CW) under larger rocks (200-300 cm² surface area).

Crab densities were significantly higher at HRM (on average, approximately 6-fold) compared to the BRB and ISB (Fig. 2.6). This was confirmed by the nested mixed model ANOVA on crab density per rock (Table 2.1) and post-hoc tests. The overall differences between densities within nests were non-significant (Table 2.1); however, at all sites the mean densities within one nest (nest 3 at HRM, nest 1 at BRB, and nest 1 at ISB, respectively) were lower than within the other two (Fig. 2.6). Differences between quadrats within nests and sites were highly significant (Table 2.1 and Appendix 2.4), whereas differences between rocks, nested within quadrats, nests and sites were non-significant (Table 2.1).

Fig. 2.5: Size frequency distribution of *P. elongatus* (numbers of individuals) at all sites in May 2006. The high frequency of smaller sized crabs (1.5-4.5mm) largely represents settlers (*Megalopa* larvae, approx. 1.5-2.0mm) and recruits (juveniles, approx. 2.0-3.5mm) from the latest reproductive season. Numbers of settlers, recruits, and resident adult population were much higher at Hutt River mouth. Female crabs reach sexual maturity at a size of 3.4 ± 0.1 mm CW at all sites (see section 3.3).

Fig 2.6: Mean crab density per quadrat within nests at all sites (HRM = Hutt River mouth, BRB = Breaker Bay, and ISB = Island Bay) in May 2006. On average, total densities (including juveniles) were approx. 6-fold higher at HRM than at the other two sites. Error bars represent 95% confidence intervals.

Table 2.1: Fully nested mixed model ANOVA on crab density per rock, where site is a fixed factor and all others random factors. Crab density significantly varied with site and sample quadrat, but did not on the scale of nests and single rocks. This result indicates patchiness of abundance on the 1-5m scale and reflects site differences as shown in Fig. 2.6.

Source	SS	df	F	p
Site	371.68	2	7.4141	< 0.0239
Nest [Site]	325.08	6	2.1615	< 0.6990
Quadrat [Site,Nest]	2080.64	36	2.3057	< 0.0001
Rock [Site,Nest,Qu.]	142408.27	301	18.8750	< 0.1819
Error	312716.85	345		

Mean carapace width (CW) of adult crabs was significantly higher at BRB compared to the other two sites (Fig. 2.7, and Table 2.2). The overall differences between nests within sites were non-significant (Table 2.2), whereas the differences between quadrats within nests and sites (Table 2.2 and Appendix 2.5) and between rocks within quadrats, nests and sites (Table 2.2) were significant.

Fig 2.7: Mean carapace width of adult crabs per quadrat within nests at all sites. Error bars represent 95% confidence intervals. There were significant differences in mean crab size between sites and sample quadrats.

Table 2.2: Fully nested mixed model ANOVA on crab size, where site is a fixed factor and all others random factors. Crab size significantly varied with site, sample quadrat and rock, suggesting that population structure was heterogeneous on the small (5-50cm) and on the large scale (several kms).

Source	SS	df	F	p
Site	440.148	2	16.4891	< 0.0017
Nest [Site]	106.575	6	0.7971	< 0.5775
Quadrat [Site,Nest]	1271.69	36	5.2246	< 0.0001
Rock [Site,Nest,Qu.]	2708.69	301	2.0830	< 0.0001
Error	25264.795	5848		

The mean sizes of rocks occupied by crabs were significantly higher at HRM compared to BRB and ISB (due to larger rocks at HRM), whereas there was no difference between mean rock sizes at BRB and ISB (Fig. 2.8 and Table 2.3). The differences between nests within sites were non-significant (Table 2.3) but the differences between quadrats within nests and sites were significant (Table 2.3 and Appendix 2.6).

Fig. 2.8: Mean rock sizes (measured as rock surface area) of occupied rocks within nests at all sites. Error bars represent 95% confidence intervals. Rock sizes were, on average, largest at HRM, intermediate at BRB and smallest at ISB; however, overall differences between nests are non-significant.

Table 2.3: Nested mixed model ANOVA on rock size where site is a fixed factor, nest and quadrat random factors. Rock size significantly varied with sample quadrat and site.

Source	SS	df	F	p
Site	204138.01	2	19.1703	< 0.0001
Nest [Site]	363839.04	6	1.1286	< 0.0726<
Quadrat [Site,Nest]	334680.11	36	2.7461	< 0.0069
Error	1607949.0	302		

Crabs preferred larger boulders as shelters over smaller ones (Fig. 2.9) and occurred under boulders with a minimum surface area of approximately 30cm². Smaller rocks were hence unoccupied.

Fig. 2.9: Mean (dashed line) and median (solid line) rock size of occupied versus unoccupied rocks, pooled across sites. Whisker caps represent 2.5% and 97.5% quantiles. T-test: $p < 0.0001$; $T = 72.399$; $df = 2481$. Crabs chose larger boulders as shelters with a minimum surface area of approx. 30cm². Crabs were be found under all larger rocks (unless their bottom side was buried in fine sediments), whereas small rocks and pebbles were not used as shelters.

Individual rock size explained 20-43% of the variation in the number of crabs per rock at all sites (Fig. 2.10). However, mean rock size was not significantly related to mean total crab density (Appendix 2.7) or mean adult density (Appendix 2.8).

Rock size was significantly positively related to mean carapace width of adult crabs per rock at HRM and ISB, but not at BRB (Fig 2.11). However, the amount of variation in carapace width explained by rock size was very low (5-7%) indicating this relationship, although significant, was weak.

The densities of *P. elongatus* were positively correlated with those of *Hemigrapsus sexdentatus* (A. Milne Edwards, 1837) at HRM (Fig. 2.12) and *Heterozius rotundifrons* A. Milne Edwards, at BRB (Fig. 2.13) and ISB (Fig. 2.14).

A) Hutt River mouth ($R^2 = 0.4395$; $F = 94.0847$; $p < 0.0001$; $y = -9.6861 + 0.2956x$)

B) Breaker Bay ($R^2 = 0.1968$; $F = 17.8817$; $p < 0.0001$; $y = 3.0885 + 0.0443x$)

C) Island Bay ($R^2 = 0.2476$; $F = 30.2689$; $p < 0.0001$; $y = 1.29 + 0.055x$)

Fig. 2.10: Rock size (i.e. surface area) versus number of individuals under each rock at a) HMR, b) BRB, and c) ISB. Larger rocks offer more shelter space for more individuals. Please note the different scales on X- and Y-axis for site a) (HRM).

A) Hutt River mouth ($R^2 = 0.0448$; $F = 5.5776$; $p = \mathbf{0.0198}$; $y = 3.6795 + 0.0022x$)

B) Breaker Bay ($R^2 = 0.03$; $F = 2.3519$; $p = 0.1293$; $y = 4.6734 + 0.0036x$)

C) Island Bay ($R^2 = 0.0686$; $F = 6.9271$; $p = \mathbf{0.0099}$; $y = 4.4461 + 0.0059x$)

Fig. 2.11: Mean carapace width of adult crabs per rock versus rock size at a) HMR, b) BRB, and c) ISB. The average crab size was larger under larger rocks. Please note the different scales on the X-axis for site a) (HRM).

Fig. 2.12: Density of *P. elongatus* versus *Hemigrapsus sexdentatus* (A. Milne Edwards, 1837) per quadrat (0.25m²) at Hutt River mouth ($r = 0.3943$; $F = 23.1982$; $p < 0.0001$)

Fig. 2.13: Density of *P. elongatus* versus *Heterozius rotundifrons* A. Milne Edwards, 1867 per quadrat (0.25m²) at Breaker Bay ($r = 0.6424$; $F = 63.9552$; $p < 0.0001$)

Fig. 2.14: Density of *P. elongatus* versus *Heterozius rotundifrons* A. Milne Edwards, 1867 per quadrat (0.25m²) at Island Bay ($r = 0.4028$; $F = 23.6217$; $p < 0.0001$)

2.3.2 Field experiment: cobble size and colonization of *P. elongatus*

Mean density of adults that colonized experimental baskets was significantly different in all rock size treatments (Table 2.4 and post-hoc tests). Adult densities were highest in baskets with small rocks, intermediate among medium-sized rocks, and lowest among large rocks (Fig. 2.15). The relationship for juvenile densities was similar (Table 2.5 and Fig. 2.15), except there was no significant difference between small and medium-sized rocks according to Tukey's HSD. For juveniles and adults there were no significant differences between baskets nested within treatments.

Fig. 2.15: Mean density of *P. elongatus* adults (n=2005, dark grey) and juveniles (n=3955, light grey) as average number of individuals per basket trap within all treatments (i.e. three size classes of rocks: small: 5-10cm, medium: 10-15cm, and large: 15-20cm maximum length). Error bars represent 95% confidence intervals.

Table 2.4: One-way ANOVA results adult crab density per basket vs. rock size with basket as random factor, nested within treatment (rock size)

Source	SS	df	F	p
Rock size	19956.25	2	15.4826	< 0.0001
Basket no. [Rock size]	2211.726	3	1.1439	< 0.3582
Error	11600.524	18		

Table 2.5: One-way ANOVA results juvenile crab density per basket vs. rock size with basket as random factor, nested within treatment (rock size)

Source	SS	df	F	p
Rock size	142660.75	2	7.8948	< 0.0035
Basket no. [Rock size]	2133.70	3	0.0787	< 0.9707
Error	162631.55	18		

Mean body size of adults depended on rock size with significant differences between treatments (Fig. 2.16 and Table 2.6) with significantly smaller crab sizes among small rocks compared to the other treatments (Fig. 2.16). The differences in body size of crabs between baskets nested within treatments were non-significant (Table 2.6).

Fig. 2.16: Mean body size (carapace width, CW) of *P. elongatus* adults (n=2005) within all treatments (i.e. three size classes of rocks: small: 5-10cm, medium: 10-15cm, and large: 15-20cm maximum length). Juveniles were excluded due to identical carapace widths. Error bars represent 95% confidence intervals.

Table 2.6: One-way ANOVA results adult carapace width versus rock size with basket as random factor, nested within treatment (rock size)

Source	SS	df	F	p
Rock size	2.4677274	2	171.5264	< 0.0001
Basket no. [Rock size]	0.0086967	3	0.4030	< 0.7509
Error	10.617183	1521		

2.3.3 Laboratory experiment: Influence of cobble size on predation rate

Cobble size significantly influenced predation rates (i.e. number of survivors) (Table 2.7) with highest predation and, accordingly, lowest survival for the smallest 1 crabs among small rocks (Fig. 2.17). Predation rate also varied

significantly with crab size (Table 2.7 and Fig 2.17). Small crabs had much higher survival rates among medium and large rocks. Size class 2 crabs had intermediate survival, similar for all rock sizes, whereas large crabs (size class 3 and 4) were rarely to never preyed upon, regardless of rock size (Fig. 2.17).

Fig. 2.17: Cobble size (small = 2.5 - 5.0cm; medium = 5 - 10cm; large = 10 - 20cm maximum length) versus mean percent survivors within three size classes of crabs at the end of the predation experiment (exposure to *Acanthoclinus fuscus* for three weeks). Size class 4 crabs are not shown due to 100% survival in all treatments. Error bars represent 95% confidence intervals. In all treatments, smaller crabs were preyed upon more frequently than larger ones. For small crabs, predation rates were higher among small rocks compared to predation in the other treatments.

Table 2.7: Survival analysis (Cox's Proportional Hazard; nominal logistic fit) No. of crabs per census* ~ Rock size + Crab size. Tank as random factor was excluded from the model as it proved to be non-significant. Size class four (largest crab size) was excluded due to no predation over time. SE = Standard Error; CI = Confidence Interval. *Weekly count of survivors in each size class over 3 weeks.

Variable	df	Coefficient (SE)	CI (upper)	(lower)	P (Chi ²)
Rock size	20	1.0995 (0.4673)	2.0036	0.1651	0.0103
Crab size	20	-0.9163 (0.2929)	-1.5176	- 0.3616	< 0.0001

2.3.4 Field experiment: Mobility and migration among cobbles of *P. elongatus*

The interaction between site and size class was non-significant (Table 2.8). However, the distance the crabs had moved over 25h was significantly different among sites (Table 2.8). Post-hoc tests revealed that the mean distances at HRM were significantly different from those at BRB and ISB, but there was no significant difference between BRB and ISB. These results are reflected in Fig. 2.18: All size classes of crabs at HRM had moved significantly smaller distances compared to those at the other two sites. The differences among size classes were also significant (Table 2.8). Small crabs (size class 1) had moved significantly less than all larger crabs and size class 2 crabs moved significantly smaller distances than size class 3 and 4 crabs (post-hoc tests and Fig. 2.18). Tukey's HSD showed that the differences among all size classes were significant apart from size class 3 versus size class 4. Differences between runs were non-significant (Table 2.8 and post-hoc tests). In the fully saturated model (Appendix 2.10), all interactions with "run" were also non-significant and were thus removed from the final model.

Table 2.8 : 3-Way ANOVA results Distance ~ Site + Size class + Run + (Site * Size class). Migration rate significantly varied with crab size and site, whereas there were no differences between runs at each site.

Source	SS	df	F	p
Site	2.0045169	2	11.3423	< 0.0001
Size class	5.8203202	3	21.9557	< 0.0001
Run	0.0355214	2	0.2010	< 0.8180
Site * Size class	0.4812757	6	0.9077	< 0.4896
Error	25.183901	263

A) Hutt River mouth (HRM)

B) Breaker Bay (BRB)

C) Island Bay (ISB)

Fig. 2.18: Mark and recapture survey: Size class (carapace width) versus distance from position of crab to point of release after 25h at all sites. Carapace width is positively correlated with migration rate. Error bars represent 95% confidence intervals. Please note that scale of Y-axis varies among subfigures A-C.

2.4 Discussion

Population density and structure of porcelain crabs living in intertidal boulder fields are affected by a variety of factors such as larval supply, settlement and recruitment, predation, individual growth rates, migration in response to intraspecific competition, light conditions and desiccation stress, etc.; however, substratum characteristics and habitat structure appear to be highly relevant in shaping the observable patterns of abundance and size frequency distributions of crabs on different spatial scales.

Patterns of abundance

A patchy distribution of *P. elongatus* was found on the scale of 1-5 meters (between quadrats) as well as on the scale of several kilometres (between sites). On these scales of observation cobble size was a good predictor of local abundance of porcelain crabs. Similarly, Gebauer *et al.* (2007) observed that the high spatial variability in population density of *Petrolisthes laevigatus* in southern Chile may be attributed to the size and shape of rocks. In the present study, rock size was positively correlated with numbers of crabs found underneath since larger rocks, on average, provide more shelter space. Additionally, *P. elongatus* prefers larger rocks (min. surface area of approx. 30cm²) as shelters over smaller ones. This preference could be explained by visually guided shelter targeting behaviour (Meyer-Rochow & Meha, 1994) in conjunction with negative phototaxis (Scott, 1958). Generally, larger rocks provide better protection from predation (see discussion below), temperature stress, and desiccation (Stillman, 2002; Emperanza, 2007). In intertidal boulder fields in northern Chile, Emperanza (2007) showed that distribution patterns as well as mean size of *Petrolisthes granulosus*, *P. violaceus* and *Allopetrolisthes angulosus* is strongly affected by temperature and emersion gradients. Pellegrino (1984) reported that the vertical distribution of *P. elongatus* is mainly driven by increasing desiccation pressure with increasing height, combined with species specific levels of adaptation to water loss (compare Stillman & Somero, 1996), whereby small individuals are more vulnerable than larger ones (Jones & Greenwood, 1982). In addition to the responses to environmental factors such as light conditions and desiccation stress, the selection of shelters may be influenced by the sediment type below boulders.

In a randomized field experiment, Akins (2003) found that adult *P. cinctipes* strongly preferred rocks set on cobbles and pebbles, rather than rocks on sand or on a combination of sand and pebbles. The same appears to be true for *P. elongatus* (own observation).

Generally, mean crab density was significantly higher at HRM compared to BRB and ISB, presumably due to factors such as differences in larval supply and retention, recruitment and survival rates, food supply, availability of shelter space, and wave exposure. At HRM, local densities of up to 6,500 ind./m² per boulder and up to 843 individuals per quadrat (= 3372 ind./m²) were estimated or counted. To my knowledge, these are the second-highest recorded densities of porcelain crabs, surpassed only by *Petrolisthes cinctipes* living in the interstices of *Mytilus californianus* beds, reaching densities of up to 3933 ind./m² in the cool temperate north-eastern Pacific (Jensen 1990).

Population structure

Rock size does not only affect local abundance in *P. elongatus*, but also influences population structure with significant differences in mean carapace width (CW) between sites as well as on the scale of quadrats and single rocks. At two sites (HRM and ISB), mean CW was positively correlated with rock size: larger crabs were found under larger rocks, which is consistent with the mean CW of adults extracted from basket traps. While at ISB factors such as wave exposure and differential predation may have contributed to this pattern, a dominance hierarchy among *P. elongatus* in competition for the most suitable microhabitats could have been the main driver at HRM. Such hierarchical systems based on body size and agonistic interaction have been observed in *P. elongatus* (own observation), *P. cinctipes* (Molenock, 1976; Donahue, 2004; Rypien & Palmer, 2007), *P. cabrilloi*, *P. eriomerus* and *P. manimaculis* (Molenock, 1976), *Allopetrolisthes spinifrons* (Baeza *et al.*, 2002), as well as in the hermit crab *Pagurus longicarpus* (Winston & Jacobson, 1978) and other anururan crustaceans. Additionally, the physical space between boulders can delimit the body size of occupants. Populations of many crustacean species appear to be constrained by the availability of appropriately sized refuges in the substratum (Wahle & Steneck, 1992; Beck, 1995; Casariego *et al.*, 2004; Briones-Fourzán *et al.*, 2007) or in artificial substrates (Bartholomew & Shine, 2008). Juveniles of the

southern rock lobster *Jasus edwardsii*, for example, exhibit a close association with shelters that are conform to their body dimensions (Booth & Ayers 2005), as do other panulirid species (Jernakoff 1990; Eggleston & Lipcius, 1992; Dennis *et al.*, 1997). Shelter size also sets an upper limit to the body size of American lobsters, *Homarus americanus*, occupying the interstitial spaces among cobbles (Wahle, 1992). Hixon & Beets (1993) and Drolet *et al.* (2004a) demonstrated that the physical structure of subtidal reefs, particularly through the provision of refuges from predation, profoundly affects associated communities of fish and invertebrates. Willis & Anderson (2003) detected positive correlations between reef surface rugosity and the density and diversity of cryptic fish communities in and adjacent to the Cape Rodney-Okakari Point Marine Reserve in north-eastern New Zealand. By contrast, Alexander *et al.*, (2009) found reef structure (i.e. rugosity) to be a relatively poor predictor of invertebrate abundance and species richness on all spatial scales examined (5m, 50m, and 200m).

The size frequency distributions of crabs that were obtained by quantitative sampling in May 2006 (well after the reproductive season, lasting from July/August until March in the Wellington region, see Wear, 1965), clearly show frequency peaks for small crabs (1.5mm-4.5mm) which result from seasonal larval supply and recruitment into the benthic population. This pattern was especially pronounced at HRM, suggesting higher recruitment rates (and possibly larval supply) at this site.

Predation

Predation on *P. elongatus* varied with both crab size and rock size when exposed to *Acanthoclinus fuscus* under laboratory conditions. Small crabs were significantly more susceptible to predation than larger ones with higher predation rates among small rocks (2.5-5.0cm max. length) relative to larger rocks (5-10cm and 10-20cm). In juvenile blue crabs, *Callinectes sapidus*, the smallest crabs were eaten at a higher rate than larger crabs if algal cover was absent and therefore shelters unavailable (Wilson *et al.*, 1990). Rock size, available shelter space, and predation risk are related for a number of reasons. At wave exposed shores, pebbles roll and shift more frequently than larger boulders due to water movement, thereby increasing disturbance (see Shanks & Wright, 1986) as well as predation risk of small crabs among small rocks, whereas small crabs are more

easily dislodged by high current velocities than larger individuals. Larger predators are capable of moving smaller rocks. Larger individuals of *A. fuscus*, for example, wiggle into loose gravel to seek cover or prey on small crabs (own observation). However, larger cavities among large boulders may be more accessible for predators, whereas smaller rocks in the more stable ground layer of boulder fields provide physical refuge, possibly explaining the significantly higher densities of (on average) smaller crabs in basket traps with small rocks compared to densities and size frequency distributions among larger rock sizes. In addition to the importance of physical shelter, Jensen & Armstrong (1991) showed that adults of *P. cinctipes* protected settlers and juveniles from predation by intertidal fishes.

The effectiveness of autotomy in *Petrolisthes spp.* as an escape strategy has been demonstrated by Wasson *et al.* (2002); however, the crabs show a context dependent response and only employ the costly strategy of autotomizing a limb as a last resort if the success of struggle or flight is low (Wasson & Lyon, 2005). Furthermore, *P. elongatus* exhibits differential behavioural responses to food and alarm odours that are profoundly affected by autotomy of limbs (Hazlett, 2004).

The variability of coloration in *P. elongatus* adults appears to be an adaptation to the diversity of microhabitats (own observation) in order to be optimally camouflaged on differently coloured substrates such as rocks, biofilms and shingle (i.e. mollusc shells). By contrast, larvae (including the Megalopa stage) are unpigmented and thus appear transparent, almost invisible for predators in the water column and on most surfaces (e.g. Felder *et al.*, 1985). Future research may elucidate whether site-specific differences in colouration of adult crabs could be explained by differential visual predation, thereby selecting for better camouflaged phenotypes, or whether other environmental factors such as local variations in diet composition influence these patterns (see chapter 6).

Sympatric species

The positively correlated densities of *P. elongatus* and two relatively abundant sympatric crustacean species, *Heterozius rotundifrons* and *Hemigrapsus sexdentatus*, indicate that the level of interspecific competition is low and has consequently no effect on their local abundance. However, Hazlett & McLay

(2005) presented evidence for chemical communication (i.e. the perception of interspecific waterborne alarm odours) between *P. elongatus* and *H. rotundifrons*. Despite the fact that these species share the same habitat (i.e. the interstitial space among boulders), each of them occupies a different niche in terms of shelter use as well as regarding exploitation of food resources. While *P. elongatus* is a suspension feeder and seeks shelter in small cavities and crevices under and among cobbles, *H. rotundifrons* can be commonly found buried in the sediment under boulders (Bennet, 1964, and own observation), and is feeding on seaweed (McLay, 1988). *H. sexdentatus*, by contrast, is much larger and more mobile than the other two species, preys upon drift algae as well as molluscs (McLay, 1988), and is far less susceptible to desiccation (Pellegrino, 1984). These crabs do not live exclusively in the upper intertidal, but also in the supralittoral among large boulders.

Migration

Migrated distances did not exceed 100cm over 25h even for larger crabs and where up to 10 times smaller compared to those of other decapods, such as *Carcinus maenas* (Moksnes, 2002), *Cancer magister* (Holsmann *et al.*, 2006), and *Callinectes sapidus* (Johnson & Eggleston, 2010). In a mark-recapture survey Donahue (2004) conducted examining the mobility of *P. cinctipes*, most individuals moved very little (<0.5m) in 24h. At HRM, the mean travelled distances of crabs in all size classes were significantly smaller compared to the other sites. While a larger variation in (larger) rock sizes increases structural complexity, a higher complexity should decrease migration rate. Additionally, mean population density was significantly higher at HRM relative to BRB and ISB, presumably indicating higher patch quality and/or higher levels of intraspecific competition that may, in turn, influence migration rate. Donahue (2006) argues that conspecific density in *Petrolisthes* spp. is likely to reflect underlying microhabitat quality due to differential mortality of crabs in different quality patches, but also through immigration of resident conspecifics into high-quality patches. However, Hugie & Grant (1998) emphasize that animals will occasionally move between patches for reasons other than to simply maximize their resource payoffs. Both movement and aggregation of porcellanidae with intertidal distribution is probably related to the tidal cycle, similar to hermit crabs (Snyder-Conn, 1980; Gherardi & Vanini, 1992; Turra & Leite, 1999), even

though in *P. elongatus* and other porcellanidae no evidence was detected for vertical migration following the tidal rhythm. While clusters of mostly inactive individuals form primarily during low tide in response to environmental factors such as habitat heterogeneity, light, and desiccation, animals disperse more readily when submerged (own observation), e.g. adjusting their position to suitable locations and current velocities optimal for filter feeding.

In the present study, small crabs exhibited significantly lower migration rates than larger crabs, which is consistent with observations of size-dependent flight behaviour in *P. elongatus* (own observation) and in *P. cinctipes* (Jensen, 1990; Donahue, 2004). Adult crabs quickly escape after turning over a rock, whereas recruits do not move at all. Generally, *P. elongatus* as well as *P. cinctipes* appear to move more with increasing disturbance (Jensen, 1990; Jensen & Armstrong, 1991; Donahue, 2004, and own observation).

Sampling methods

A major drawback of methods using rock surface area (i.e. the area of a horizontal cross section of each rock as seen from above) as an indicator for shelter size and habitat complexity is that the surface area of rocks does not necessarily represent the amount of available interstitial shelter space, because shelter space depends not only on rock size but also on the shape (i.e. “roundness”) and packing density of rocks (for suggestions of a three dimensional measure, see Chapter 6). In some patches rocks were stacked in multiple layers, whereas in other areas boulders rested on bedrock and/or soft sediment, some of which were partially or entirely buried. However, in contrast to the standard method of measuring grain-size using the Wentworth scale (see Buchanan, 1984) based on the maximum diameter of particle fractions, I opted for a two-dimensional measure as a closer approximation to shelter space or cover area, almost identical to digital photography assisted quadrat sampling techniques applied by Warrick *et al.* (2009). A similar approach to the method chosen in the present study has been proposed by Bartholomew *et al.* (2000) who suggest to apply the ratio total area of cover within a habitat divided by the total area of the habitat (C_t/A_t) as a dimensionless index of habitat complexity (i.e. the amount of cover or shelter space available within a defined area). However, Bartholomew *et al.* (2000) propose a second index which measures the extent to which the structural

complexity interferes with a predator's ability to search or pursue prey, calculated as the average 'inter-structural space size' (i.e. the randomly chosen gap width between structures) divided by the size of the predator (Sp/Pr), e.g. the gill to gill width of a fish.

Conclusions

Because interstitial space among boulders is crucial for the presence of *P. elongatus* and directly or indirectly affects predation rate, local population densities and population structure, cobble size is an important indicator of habitat quality for this species that largely explained patchiness of abundance on a macro- (several kms) and microscale (5-50cm). By contrast, it remained elusive whether migration rate is affected by the size frequency distribution of rocks or whether movement is mainly driven by factors such as habitat quality, intraspecific competition, and disturbance. The underlying mechanisms of how habitat quality is influenced by rock size were difficult to quantify in detail (except for predation on *P. elongatus* by *Acanthoclinus fuscus*) and presumably acted differently in different habitat patches and at the sites examined in the present study. The effect of predation, for example, is far more complex in the field than the observed patterns in aquaria, where other predator species as well as abiotic factors such as wave exposure were excluded for simplification. The aim to identify relevant habitat quality indicators for mobile marine invertebrates living on intertidal boulder fields was only partially met. While patterns of abundance of *P. elongatus* are strongly affected by cobble size, future research should take a broad range of potentially relevant environmental factors (e.g. larval supply, differential mortality among and within habitats, predator abundance, and food availability) into account, as well, to better understand and predict patterns of abundance and demography in nature.

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Appendix 2

Appendix 2.1: Size frequency distribution of crabs at Hutt River mouth (numbers of individuals), split by size class of rocks

Appendix 2.2: Size frequency distribution of crabs at Breaker Bay (numbers of individuals), split by size class of rocks

Appendix 2.3: Size frequency distribution of crabs at Island Bay (numbers of individuals), split by size class of rocks

A Quadrats within Nests

B Quadrats within Nests

C Quadrats within Nests

Appendix 2.4: Mean crab density per rock within quadrats at A: Hutt River mouth, B: Breaker Bay, and C: Island Bay. Error bars represent 95% confidence intervals.

Appendix 2.5: Mean carapace width (CW) of adult crabs per rock within quadrats at A: Hutt River mouth, B: Breaker Bay, and C: Island Bay. Error bars represent 95% confidence intervals.

Appendix 2.6: Mean rock sizes of occupied rocks within quadrats at A: Hutt River mouth, B: Breaker Bay, and C: Island Bay. Error bars represent 95% confidence intervals.

Appendix 2.7: Mean rock size within each sample quadrat versus mean total crab density (individuals/m²), calculated from the number of crabs per quadrat.

(ISB: $R^2 = 0.0124$; $F = 0.163$; $p=0.693$; $y = 145.8606 + 0.25094x$)

(BRB: $R^2 = 0.2434$; $F = 4.1813$; $p=0.0617$; $y = 451.6296 - 2.0357x$)

(HRM: $R^2 = 0.0609$; $F = 0.8425$; $p=0.3754$; $y = 667.2818 + 3.5459x$)

Appendix 2.8: Mean rock size within each sample quadrat versus mean adult crab density (individuals/m²), calculated from the number of crabs per quadrat.

(ISB: $R^2 = 0.0049$; $F = 0.0634$; $p=0.8052$; $y = 123.4031 + 0.2444x$)

(BRB: $R^2 = 0.2616$; $F = 4.6050$; $p=0.0513$; $y = 285.0049 - 1.3139x$)

(HRM: $R^2 = 0.0574$; $F = 0.7916$; $p=0.3898$; $y = 316.7689 + 1.4092x$)

Appendix 2.9: Mean (dashed line) and median (solid line) index of dispersion (ratio between the variance in numbers of crabs under each rock and the mean number of crabs per quadrat) at sample sites Island Bay (IsB), Breaker Bay (BrB), and Hutt River mouth (HRM). Whisker caps represent 2.5% and 97.5% quantiles. Because all indices were > 1 , patchiness can be assumed on a between-quadrats level as well as between sites and is especially high at HRM, mainly due to a larger range of rock sizes and larger boulders. This reflects the results shown in table 2.1.

Appendix 2.10: 3-Way ANOVA results of the mark and recapture survey (fully saturated model): Distance $\sim$ Site + Size class + Run + (Site * Size class) + (Site * Run) + (Size class * Run) + (Site * Size class * Run)

Source	SS	df	F	p
Site	1.9920476	2	10.5034	< 0.0001
Size class	5.8164635	3	20.4455	< 0.0001
Run	0.0283584	2	0.1495	< 0.8612
Site * Size class	0.4829144	6	0.8487	< 0.5333
Site * Run	0.0411504	4	0.1085	< 0.9795
Size class * Run	0.0973556	6	0.1711	< 0.9844
Site * Size class * Run	0.1192880	12	0.1048	< 0.9999
Error	24.940004	263		

Chapter 3

Effects of habitat quality on life history traits

3.1 Introduction

Understanding the ecological factors that favour different life history strategies is a central goal in the study of life history evolution (e.g. Williams, 1966; Partridge & Harvey, 1988). Animal populations often exhibit considerable variation in life history traits due to their exposure to different environmental conditions within their natural range (reviewed in Roff, 1992; Stearns, 1992). Specifically, parental investment within a species varies with environmental factors (e.g. Morris, 1987; Roff, 1992; Stearns, 1992), largely attributed to phenotypic plasticity. Natural selection, on the other hand, rarely affects single life history traits but rather acts on suites of traits that respond to selection in a correlated manner (e.g. Endler, 1995; Badyaev & Ghalambor, 2001). The life history traits of a species such as size at sexual maturity, number of offspring and level of parental investment are interdependent, with differential resource allocations of an organism to reproduction, growth, maintenance metabolism and survivorship (e.g. Calow, 1979; Townsend & Calow, 1981). Due to energetic constraints as a result of limited availability of resources, the benefits of performing an ecological function come at a cost of performing another. Classic examples of life history trade-offs, generally defined as negative functional interactions between traits (Stearns, 1989a, 1992; Zera & Harshman, 2001) include 1) energy allocation to reproduction versus energy allocation to growth and maintenance (or relationship between body size and fecundity, respectively), 2) egg size and -quality versus numbers of eggs per female (or offspring survival versus dispersal potential, respectively), and 3) offspring fitness versus fitness of parent (or life span versus reproductive output and frequency of spawning, respectively).

Variations in life histories of marine invertebrates have attracted considerable research interest (e.g. Palmer & Strathmann, 1981; Grahame & Branch, 1985; Hines, 1986; Strathmann, 1986; Scheltema, 1998). The variability of life history strategies among and within species is commonly understood as adaptations to

specific physical and biotic environmental conditions, constrained by phylogenetic effects (e.g. Herrera, 1998; Niewiarowski *et al.*, 2004; Dudycha & Lynch, 2005). Phenotypic plasticity, as a within-lifespan response of organisms associated with environmental change, can be crucial for the persistence of animal populations (Gabriel *et al.*, 2005; Helmuth *et al.*, 2005) and is defined as the interaction of an individual's genotype with environmental factors (GxE interaction) in the sense of an individual's inherent, albeit limited, ability to change behaviour, physiology, morphology, or life history characteristics (e.g. Edgell & Hollander, 2011). Phenotypic plasticity is considered heritable, favoured by high environmental variability or unpredictability, and in certain conditions adaptive because induced phenotypes may increase individual fitness (reviewed in Stearns, 1989b; Via *et al.*, 1995; Ghalambor *et al.*, 2007). Life history evolution, by contrast, comprises the mechanisms that select for certain suites of interdependent life history characteristics (via fitness of the individual in relation to environmental factors and their stability or unpredictability) and how these characteristics manifest themselves, or fluctuate, within populations over time. While reduced adult survival, for example, will select for early maturation and increased reproductive effort, the increase in juvenile mortality will favour the opposite pattern (e.g. Reznick & Endler, 1982; Reznick *et al.*, 1990). "K" and "r" selection are extremes in a spectrum of possible patterns of life history adaptations to the degree of environmental stability or disturbance, that generally involve trade-offs between the costs and benefits of particular strategies of survival and reproduction (for reviews, see Pianka, 1970, 1972; Stearns, 1977; Parry, 1981; Getz, 1993). Coexistence within communities and niche differentiation between species, on the other hand, are frequently explained by trade-offs in species performances of different ecological functions (reviewed in Laland *et al.*, 1999; Kneitel & Chase, 2004). The existence of a larval phase in many aquatic organisms has been attributed to avoidance of intraspecific competition due to resource partitioning (i.e. of food sources and space) in larvae and adults (e.g. Felder *et al.*, 1985). Therefore, larval stages differ from juvenile and adult phases in characteristics such as morphology, nutrient requirements, behaviour, and habitat, whereby these differences can be subtle or more pronounced.

Approximately 80% of marine organisms, both vertebrate and invertebrate, have a biphasic life-cycle. The planktonic larvae spend a variable amount of time developing in the water column, ranging from minutes to months, before they settle into the benthos and metamorphose into the adult life-form (Thorson 1964). Since many benthic invertebrates are either sessile or have very limited dispersal capabilities as adults, the planktonic larval stages are of particular significance. In geographically isolated metapopulations, such as those of *P. elongatus*, the planktonic phase does not only facilitate dispersal, but also connectivity and hence gene flow, between patches. Moreover, meroplanktonic larvae are considered as principal components of benthic-pelagic coupling processes (Anger, 2006). The transition between planktonic and benthic phase implies a radical change of life style, typically involving metamorphosis of competent larvae into the benthic life form.

Petrolisthes elongatus is highly specific concerning their habitat choice (Jones, 1976) and is virtually absent on sandy beaches, mudflats and at rocky shores (own observation). Consequently, their suitable habitat is naturally fragmented, leading to relatively isolated benthic metapopulations that are separated from other patches of suitable habitat by hundreds of meters to tens of kilometers. For a successful colonisation of more distant sites and maintenance of persisting metapopulations, the geographic isolation, associated with higher extinction risk, has to be compensated by dispersal strategies (i.e. planktonic larvae with high dispersal potential), larval behaviour (i.e. ability to swim and respond to settlement cues), larval features that enable drift, improve buoyancy, and reduce sink speed (i.e. long rostral and posterior spines and oil droplets), as well as reproductive traits such as high egg numbers and high frequency of spawning. Due to the trade-off between size and number of offspring, however, the adaptation to geographically isolated metapopulations and/or recruitment limitation is likely to result in larger numbers of smaller offspring.

In Porcellanidae as well as in other decapods, growth rate and body size strongly varies with latitude, and therefore with temperature (Stillman & Somero, 2000; Stillman, 2002; Wehrtmann, 2005; but see Rivadeneira *et al.*, 2010). Locally, adult body size decreases towards the upper intertidal zone, where average temperatures are higher and desiccation risk more intense (Emparanza, 2007).

Reproductive effort depends on both body size and temperature (Clarke, 1987), and is commonly affected by food supply.

In this chapter, I compare life history characteristics of *P. elongatus* from three geographically isolated metapopulations and aim to identify the relevant environmental factors and habitat quality indicators mediating phenotypic plasticity. Specifically, I test whether there are site-differences in reproductive output, egg size, egg numbers, size at maturity, sex ratio, and percentage of ovigerous females. As discussed in the previous chapter, the chosen study sites differ largely in available refuge, and presumably in larval supply and food levels, which I aim to examine.

3.2 Materials and Methods

3.2.1 Sex ratio

In January and February 2006, *P. elongatus* adults were randomly sampled using 15 50x50cm quadrats to standardize sample area at each of three sites: Hutt River mouth: 41° 14'49.50" S, 174° 53'57.00" E, Island Bay (VUCCEL), 41° 20'54.30" S, 174° 45'53.20" E, Breaker Bay (Reef Bay), 41° 20'17.90" S, 174° 49'26.60" E (chapter 1, Fig. 1.1). All individuals were sexed (for morphological differences between genders see Fig. 3.1) and the numbers of males and females recorded. The sex ratios for all samples at all sites were calculated; site differences were tested by binominal logistic regression.

3.2.2 Female size at sexual maturity

For the size at sexual maturity estimate, only females were used (compare Annala *et al.*, 1980; Fransozo *et al.*, 2003; Xiao & Kumar, 2003) as their morphological characteristics visibly change over the transition between juvenile and adult phase. These characteristics comprise in females 1) three pairs of ramified pleopods (on abdominal segments three to five) which may be present but incompletely developed (i.e. unramified) in late stage juveniles or sexually immature females, respectively, and 2) oval shaped genital openings on both coxae of the third pereopods (Fig. 3.1). At the laboratory, particularly late stage juveniles and young females (3.0mm – 5.0mm carapace width, CW) were examined under a dissecting microscope with 25 x magnification and divided in immature or mature individuals. Size at maturity was estimated for each quadrat as the mean of the 20 largest immature and the 20 smallest mature individuals. Using the carapace widths of these selected animals, site differences in female size of sexual maturity were tested by ANOVA.

Fig. 3.1: a) Ovigerous *Petrolisthes elongatus* female, ventral view. Several eggs can be seen between sternum and abdominal flap (arrow); the genital openings are not visible (position marked by black circle). Scale in mm. b) Arrangement of pleopods in male (top) and female (bottom) (modified, after M.B. Jones, 1976).

3.2.2 Female life-history traits

a) Sampling

From February until March 2008, 100 - 150 *P. elongatus* females were collected fortnightly (five times) at each of three sites: Hutt River mouth, Island Bay (VUCCEL), and Breaker Bay (Reef Bay) (Fig. 1.1). Both ovigerous and non-ovigerous females were randomly collected, if 1) all limbs were present and 2) the carapace width, measured with digital callipers in the field, was between 5.0mm and 12.5mm at its widest point. For subsequent processing, the animals were kept in separate tanks (one tank per site), filled with filtered seawater (10µm mesh size) at the National Institute of Water and Atmospheric Research (NIWA) facility in Wellington, New Zealand.

b) Percentage of ovigerous females

At the laboratory, each female was checked for eggs by folding over the abdomen with a pair of fine tweezers. The females were subdivided into 3 size classes (1=5.0-7.5mm; 2=7.6-10.0mm; 3=10.1-12.5mm CW). For each size class, each sample and each site, the mean percentage of ovigerous females was calculated.

The error for each site and size class results from combining the values obtained for each sample. A binary logistic regression was used to test differences between sites and size classes (Logit no. ovig. females ~ Site + Size class).

c) Body size, clutch weight and proportion of clutch to body weight

Every individual was weighed on an electronic balance (wet weight, B_{WW}), and the carapace width (CW) measured with digital callipers. Ovigerous females were weighed after the removal of eggs. Before the clutch wet weight (C_{WW}) was determined, removed egg masses were placed on a dry paper towel for approx. five seconds to drain excessive interstitial water. To examine whether body weight predicts clutch weight, linear regressions on data from each site were used. Site differences were analysed by ANCOVA with body weight as covariate and site as categorical factor. Similar to the gonadosomatic index, the proportion of clutch to body weight (P_{CB}) was calculated by dividing clutch weight by body weight, multiplied by 100 ($P_{CB} = (C_{WW} / B_{WW}) * 100$). The relationship between body size and P_{CB} was tested by linear regression. Site differences in P_{CB} , and interactions between site and body size were analysed by ANCOVA with body size as covariate and site as categorical factor.

d) Number of eggs per female and egg volume

Under a dissecting microscope with 25x magnification the eggs of each clutch were counted and measured in three dimensions. The egg volume (E_V) was calculated by using the formula for an ellipsoid ($E_V = 4/3 \pi abc$ where a = egg length, b = width, c = height). Egg numbers per female were regressed against individual body size (CW), pooled across sites. The effect of body weight and site on egg volume was analysed as ANCOVA, with body weight as covariate and site as categorical factor.

e) Egg dry weight

For the estimate of clutch dry weight (C_{DW}), the clutches from 20 females from each sample site were dried separately in a drying oven at 75°C for 24h. The C_{DW} was then weighed on an electronic balance. Egg dry weight (E_W) was calculated as $E_W = C_{DW} / \text{no. of eggs}$. To minimise variance, eggs of developmental stages 1 and 2 (see below) were used only. Site differences in egg dry weight were tested by one-way ANOVA. The water content of eggs (C_{WC} , Appendix 3.1) was

calculated as the difference (D) between clutch wet weight and dry weight ($D = C_{ww} - C_{dw}$), expressed as percent wet weight ($C_{wc} = D * 100 / C_{ww}$).

f) *Developmental stage of eggs, and egg mortality*

Despite continuous development, the eggs of each clutch were assigned the following defined developmental stages (see Fig. 3.2):

Stage 1: newly deposited eggs, oval, no cleavage, dark red yolk in healthy eggs

Stage 2: Early cleavage, white tissue cap present

Stage 3: Small black eyespots present, yolk still present but reduced

Stage 4: Eyes large, yolk limited, red chromatophores and pre-hatch larva visible

Fig. 3.2: Developmental stages of *P. elongatus* eggs, still attached to near-transparent pleopods. Note the changes in colouration, yolk structure as well as the development and enlargement of eyespots. The scales represent mm.

To account for possible size differences, only females with a carapace width between 7.5mm and 10.0mm were sampled for this analysis ($n=60$ per site). The eggs per clutch were counted and assigned to one of the four developmental stages shown in Fig. 3.2. For each site, the mean number of eggs was calculated for pooled developmental stages 3+4 (eggs with eye pigment; i.e. further developed) as well as for stages 1+2 (eggs lacking eye pigment; i.e. newly deposited). Based on decreasing egg numbers with increasing development (due to mortality and dead eggs being actively or passively removed from the clutch)

the initial mean egg number (stages 1+2) was set to 100%, whereas the percentage of the difference between newly deposited and older, remaining eggs ($D = (1+2) - (3+4)$) represents the egg mortality ($D \cdot 100 / (\text{mean stage } 1+2)$) (compare Jones, 1977). Site differences were tested by one-way ANOVA.

3.2.3 *Female density and reproductive output per area unit*

In order to describe the differences in reproductive output not only per individual female but also per area unit (square meter) at each site at a given time within the reproductive season, the density of ovigerous females (D_{OF}) was calculated from a subset of data obtained by quadrat sampling (described in chapter 2, see 2.2.2). Taking the size frequency distribution of females into account, the average number of eggs per female (E_F) was calculated for each sample quadrat and site. The average number of eggs per square meter (i.e. the reproductive output per square meter, RO) was then calculated by multiplying the average density of ovigerous females by the average egg number per female ($RO = D_{OF} \cdot E_F$). The variability within each site was estimated by calculating 95% confidence intervals by comparison of densities and egg numbers from 15 sample quadrats per site. Site differences in RO were tested by one-way ANOVA. To visualise the significance of site differences, D_{OF} was plotted against RO for all sites with corresponding errors.

3.2.4 *Temperature-Loggers*

At each sample site for ovigerous females, two “StowAway® TidbiT®” temperature loggers (Onset Computer Corporation, 470 MacArthur Blvd., Bourne, MA 02532, USA) were deployed in the field from February until May 2008, covering the second half of the reproductive season of *P. elongatus* and the time ovigerous females were sampled. The loggers were programmed to record the temperature every 5min. Each device was attached to a cobble filled plastic basket that was anchored with steel pegs in the intertidal zone (near the low and high water mark); dug in to the extent that the top of the basket was level with the surrounding rocks. To measure the temperature between cobbles (i.e. the temperatures the crabs are exposed to in their natural habitat) the loggers were covered by 1-2 layers of medium-sized cobbles (8-16cm length) inside each basket. The time series plots are shown in Fig. 3.3.

a) HRM

b) BRB

c) ISB

Fig 3.3: Temperature logger readouts as time series plot for each site with the date of sampling on the x-axis. Shown are the data measured at the high water mark, only, for a) Hutt River mouth, b) Breaker Bay, and c) Island Bay. Note the steep rise in temperature during low tide and the change in amplitude influenced by weather conditions, coherent across sites.

3.2.5 Food supply

Water samples were taken weekly over a period of 4 months (from September until December 2009). At each of the study locations (Island Bay, Breaker Bay, and Hutt River mouth), five samples were taken 1-2h after high tide at the water line by filling 1l dark bottles with seawater just below the surface and at intervals of approx. 5m. To preserve active chlorophyll and phaeophytin, the samples were cooled on ice immediately in insulated containers (i.e. a Styrofoam boxes with lid) and transported to the laboratory. Not longer than 3hrs after sampling, in subdued light conditions, the water was filtered using 25mm GF/F Whatman ash free filters. After placing a filter onto the 25mm sieve base of a plastic filter funnel, 2x100ml well shaken sample water was poured into the funnel (three runs / filters per bottle). An electric suction pump, connected with a conical flask under the funnel, was used to create a vacuum pressure ($< 2\text{psi}$) to suck the water through the filter. The pump was switched off as soon as the water level inside the funnel reached the 20ml mark. Each filter was removed with fine tweezers and put into a labelled plastic zip-lock bag that was stored in a -80°C freezer. It was planned to spectrophotometrically determine levels of chlorophyll a, b, c and pheophytin (EPA Method 446.0, see Arar, 1997; Arar & Collins, 1997) in filtration residues.

3.2.6 Larval supply

To estimate settlement and recruitment rates as well as their spatial variability, three different types of larval collectors were used in the field: tube traps, donut-shaped nylon mesh pan scrubbers and basket traps. The design of the tube traps was based on the principle of sediment traps (see Yund *et al.*, 1991) and consisted of a series of PVC pipes (5cm diameter, 60cm length each) with a glued-on cap at the bottom end. 5 truck tyres were fitted with two U-shaped reinforcing iron rods each (in a cross pattern, forming two interlaced perpendicular loops) and filled with concrete, providing robust, heavy base frames. To the reinforced iron loops of each base 4 upright standing tube traps were lashed with strong 1cm wide and 30cm long cable ties, approximately 20-30cm apart from one another. To kill and preserve larvae, the tube traps were filled with buffered formalin-seawater solution while submerged in seawater. Theoretically, the formalin remains inside the tube due to its heavier specific weight. These plankton collectors were

deployed in approximately 10m depth at Evans Bay, Shelly Bay, Petone Wharf, Island Bay, and Breaker Bay in April 2006.

Nylon mesh pan scrubbers (“Tuffies”) had been successfully used to estimate larval supply of bivalves (Menge *et al.*, 1994, 1999; Phillips & Gaines, 2001; Rilov & Schiel, 2006), and amphipods (Rule & Smith, 2005). These artificial substrates were bolted to rocks at the lowest possible level in the intertidal, using a nested design similar to the one used for quadrat sampling (see section 2.2.1) with 5 sampling units per nest, 3 nests per site, at 3 sites (Island Bay, Breaker Bay, and Hutt River mouth). After an exposure of 1 week the traps were retrieved and replaced, put into labelled plastic bags and processed at the laboratory by carefully disentangling the nylon mesh of pan scrubbers, rinsing them in filtered seawater and systematically searching the residue with a dissecting microscope and a Petri dish with grid lines.

Further, 2 types of basket traps were tested; a larger trap (30cm x 20cm x 15cm) and a smaller and shallower version (15 x 15 x 10cm), filled with bare cobbles from the supralittoral zone (10cm to 15cm maximum length). At each site, five traps of each type were deployed between February and April 2007.

All statistical analyses in this chapter were calculated in JMP 4.0.4 (SAS Institute, September 2001). For regressions and graphs, SigmaPlot 10.0.1 (Systat, January 2007) was used.

3.3 Results

3.3.1 Sex ratio

Sex ratios varied among sites (Table 3.1 and 3.2) but no differences between sample quadrats and nests of quadrats were detected; hence, these factors were excluded from the model. According to the parameter estimates, difference between BRB and ISB were significant, with a higher proportion of females at BRB (Table 3.1).

Table 3.1: Mean percentage and sex ratios of *P. elongatus* with standard error at sites HRM = Hutt River mouth ($n_{\text{total}}=2080$); BRB = Breaker Bay ($n_{\text{total}}=421$), and ISB = Island Bay ($n_{\text{total}}=564$), based on 15 samples per site taken at one time. There was a higher percentage of females at Breaker Bay relative to the other two sites.

Site	Males [%]	Females [%]	Sex ratio (m:f)
HRM	50.3 $\pm$ 1.7	49.7 $\pm$ 1.7	1.15 $\pm$ 0.07
BRB	46.0 $\pm$ 2.0	54.0 $\pm$ 2.0	0.88 $\pm$ 0.06
ISB	55.9 $\pm$ 2.1	44.1 $\pm$ 2.1	1.36 $\pm$ 0.15

Table 3.2: Binominal logistic regression results site versus sex ratio. There was a significant difference in sex ratio between sites.

Source	R ²	df	-log likelihood (diff.)	Chi ²	p (Chi ²)
Site	0.0015	2	3.1300	80.76196	0.0437

3.3.2 Female size at sexual maturity

Female size at sexual maturity ($3.40 \pm 0.09\text{mm}$, standard error) was similar at all sites (Fig. 3.4); all differences were non-significant (Table 3.3).

Fig. 3.4 Female size at sexual maturity at all sites. The median is indicated as solid line; the mean as dashed line. Across sites, female size at sexual maturity is similar at $3.40 \pm 0.09\text{mm}$. Whisker caps represent 2.5% and 97.5% quantiles.

Table 3.3: One-way ANOVA results female size at sexual maturity versus site. No significant differences between sites were detected.

Source	SS	df	F	p
Site	0.427554	2	0.8939	0.4167
Error	10.044637	42		

3.3.3 Percent ovigerous females

There was no clear pattern of percent ovigerous females among size classes between sites (Fig. 3.5) with non-significant differences between size classes (Table 3.4). However, there were significant differences between sites (Table 3.4) with significantly higher percentages of ovigerous females at ISB relative to HRM and BRB (Fig. 3.5 and post hoc tests).

Fig. 3.5: Percent ovigerous females (in relation to total number of females) at all sites within three size classes (1: 5.0-7.5mm CW; 2: >7.5-10.0mm CW; 3: >10.0-12.5mm CW). The percentage of ovigerous females varies with sites, but no conclusive pattern emerges when comparing size classes within sites. Error bars represent 95% confidence intervals.

Table 3.4: Logistic regression results (Logit no. ovig. females ~ Site + Size cl.). There is significant variation between sites, but not between size classes within sites.

Source	R ²	df	Chi ²	p
Site	0.0538	2	80.76196	< 0.0001
Size class	0.0019	1	2.755193	< 0.0969

3.3.4 Body size versus number of eggs

a) Hutt River mouth ($R^2 = 0.43$; $F = 26.2130$; $p < 0.0001$; $y = -143.132 + 33.558x$)

b) Breaker Bay ($R^2 = 0.4172$; $F = 28.3161$; $p < 0.0001$; $y = -103.841 + 28.152x$)

c) Island Bay ($R^2 = 0.6724$; $F = 76.0672$; $p < 0.0001$; $y = -191.764 + 43.982x$)

Fig 3.6: Body size versus number of eggs at all sites; the body size is given as carapace width. At all sites egg number was strongly correlated with female body size with a steeper slope at Island Bay.

Table 3.5: ANCOVA results No. of eggs ~ Site + Body size + (Site * Body size)
Egg number varied with both site and body size.

Source	SS	df	F	p
Site	85472.61	2	17.1726	< 0.0001
Body size	327552.56	1	131.6191	< 0.0001
Site * Body size	10742.61	2	2.1583	< 0.1189
Error	390716.36	157		

3.3.5 Body weight versus clutch weight

a) Hutt River mouth ($R^2 = 0.3391$; $F = 16.4173$; $p=0.0003$; $y = 9.783 + 0.028x$)

b) Breaker Bay ($R^2 = 0.6018$; $F = 69.5130$; $p<0.0001$; $y = 7.574 + 0.035x$)

c) Island Bay ($R^2 = 0.6577$; $F = 147.9410$; $p<0.0001$; $y = -1.456 + 0.058x$)

Fig. 3.7: Body weight versus clutch weight at all sites. At all sites clutch weight was strongly correlated with female body size with a steeper slope at Island Bay. Note that the X-axis (body weight) differs among subfigures a) to c).

Table 3.6: ANCOVA results Cl. weight ~ Site + Body wgt. + (Site * Body wgt.) Clutch weight varied with site and body weight; however, body weight differs between sites.

Source	SS	df	F	p
Site	3421.820	2	16.5066	< 0.0001
Body wgt.	21041.245	1	203.0022	< 0.0001
Site * Body wgt.	2431.019	2	11.7270	< 0.0001
Error	15547.546	157		

Body size was an excellent predictor of egg number per female; predicting 42-67% of the variation in number of eggs per female (Fig. 3.6). There were significant differences between sites, with females from ISB having on average a higher number of eggs than the other sites (post hoc Tukey test, $p < 0.05$). Expectedly, body weight was significantly positively related to clutch weight (Fig. 3.7) and clutch weight varied with site (Table 3.6). However, the ANCOVA revealed that body weight also varied with site (Table 3.6) with heavier females at BRB compared to ISB, despite no significant differences in body size (Table 3.5). Additionally, the slope of the regression line for both body size versus number of eggs and body weight versus clutch weight at ISB was steeper compared to the other two sites, indicating higher individual reproductive output. At ISB, females had on average heavier clutches than at HRM or BRB (post hoc Tukey test, $p < 0.05$).

3.3.6 Proportion of clutch to body weight

The proportion of clutch to body weight did not vary by body size, but did vary with site (Table 3.7). Post hoc tests confirmed that the proportion of clutch to body weight was significantly higher at ISB than at the other two sites (Fig 3.8), which is consistent with results of the regressions body size versus number of eggs and body weight versus clutch weight shown above (Figs. 3.6 and 3.7).

Fig. 3.8: Mean proportion of clutch to body weight (P_{CB}) in percent body weight at all sites with a higher mean value at Island Bay compared to HRM and BRB. Error bars represent 95% confidence intervals.

Table 3.7: ANCOVA results $P_{CB} \sim \text{Site} + \text{Body size} + (\text{Site} * \text{Body size})$ While the mean proportion of clutch to body weight varied with site, there is no relation to body size.

Source	SS	df	F	p
Site	46.645486	2	7.7279	0.0006
Body size	7.184003	1	2.3804	0.1249
Site * Body size	5.364997	2	0.8888	0.1432
Error	473.822440	157		

3.3.7 Mean egg volume

The mean egg volume did not vary with female body weight but was significantly different between sites (Table 3.8). There were smaller eggs at ISB compared to HRM and BRB (Fig. 3.9, Tukey's HSD $p < 0.05$).

Fig. 3.9: Mean egg volume at all sites (developmental stages 1 and 2 only). At Island Bay, egg volume is significantly lower than at Hutt River mouth and Breaker Bay. Error bars represent 95% confidence intervals.

Table 3.8: ANCOVA results $E_v \sim \text{Site} + \text{Body weight} + (\text{Site} * \text{Body weight})$ Mean egg volume strongly varies with site, but not with body weight.

Source	SS	df	F	p
Site	1.3575472	2	12.3209	< 0.0001
Body wgt.	0.0107136	1	0.1945	< 0.6604
Site * Body wgt.	0.0161298	2	0.1464	< 0.8641
Error	4.6276526	84		

3.3.8 Mean egg dry weight

The mean egg dry weight was significantly different between sites (Table 3.9) with the highest value at Hutt River mouth compared to the other two sites (Fig. 3.10), largely related to egg volume (Fig. 3.9). While mean egg dry weight at HRM is significantly different from values at the other two sites, those for Breaker Bay and Island Bay were not significantly different from each other (Tukey's HSD $p < 0.05$).

Fig. 3.10: Mean egg dry weight of 100 eggs at all sites (developmental stages 1 and 2 only). At Hutt River mouth, mean egg dry weight is significantly higher compared to the other two sites. Error bars represent 95% confidence intervals.

Table 3.9: One-way ANOVA results egg dry weight versus site. Egg dry weight is significantly different between sites.

	SS	df	F	p
Site	0.00360944	2	144.9852	< 0.0001
Error	0.00070951	57		

3.3.9 Mean egg water content

Site differences in mean egg water content were significant (Table 3.10); however, Tukey's HSD revealed that only site differences between Hutt River mouth and Island Bay were significant with highest values at HRM (Fig. 3.11).

Fig. 3.11: Water content of eggs at all sites (developmental stages 1 and 2 only). Mean egg water content was highest at Hutt River mouth and lowest at Island Bay. Error bars represent 95% confidence intervals.

Table 3.10: One-way ANOVA results water content of eggs vs. site. Egg water content varied with site.

	SS	df	F	p
Site	318.42237	2	5.0502	< 0.0096
Error	1796.94960	57		

3.3.10 Egg wet weight versus developmental stage of eggs

The average egg wet weight increased with progressing egg development (Fig. 3.12) with significant differences between developmental stages (Table 3.11). According to post hoc tests, eggs in the earliest two developmental stages were significantly lower in weight than those in the more advanced two developmental stages (Tukey's HSD $p < 0.05$, Fig 3.12). While there was no interaction between site and developmental stage, differences between sites were significant similar to the above analysis where egg weights were higher at ISB than the other two sites (Table 3.11).

Fig. 3.12: Mean egg wet weight within clutch (single egg) versus developmental stage of eggs (see Fig. 3.2), pooled across sites. Egg wet weight increases with the development of the egg. Error bars represent 95% confidence intervals.

Table 3.11: ANCOVA results ($E_w \sim \text{Dev. stage} + \text{Site} + (\text{Dev. stage} * \text{Site})$) Mean egg wet weight varied with developmental stage and there were site differences, as well.

	SS	df	F	p
Site	0.03132505	2	5.7602	< 0.0039
Dev. stage	0.14135772	3	17.3291	< 0.0001
Site * Dev. stage	0.00450868	6	0.2764	< 0.9473
Error	0.40514301	150		

3.3.11 Egg mortality

Egg mortality in females with a carapace width between 7.5mm and 10.0mm was significantly different between sites (Table 3.12) with mortality at BRB significantly higher (approx. twice as high) as that of the HRM (Tukey's HSD, $p < 0.05$; Fig. 3.13). However, there were no significant differences between BRB and ISB, and HRM and ISB.

Fig. 3.13: Egg mortality in crabs with 7.5mm - 10.0mm CW varied with site and was with approx. 5% at HRM significantly lower than at BRB (approx. 11%). Error bars represent 95% confidence intervals.

Table 3.12: One-way ANOVA results egg mortality vs. site. There were significant differences in egg mortality between sites.

	SS	df	F	p
Site	103.60496	2	6.0040	0.0156
Error	103.53559	12		

3.3.12 Density of ovigerous females versus reproductive output per unit area

The average numbers of eggs per square meter were significantly different at the different sites (Table 3.13). Post hoc Tukey tests revealed that all sites were significantly different from one another, with highest RO at Hutt River mouth, intermediate at Island Bay and lowest at Breaker Bay (Fig 3.14, Tukey's HSD $p < 0.05$). Fig 3.14 shows that this pattern is linearly related to the density of ovigerous females at each site.

Fig. 3.14: Density of ovigerous females versus average numbers of eggs per square meter (reproductive output per area unit, RO) at all sites in January and February 2006. Female density (ovigerous only) was linearly positively correlated with mean number of eggs per square meter, which, in turn is dependent on female density. However, if intraspecific competition would affect individual egg numbers within the sampled density range, then the relationship would have resembled a saturation curve rather than being linear. Error bars for both factors represent 95% confidence intervals.

Table 3.13: One-way ANOVA results RO vs. site. Reproductive output per area unit strongly varied with site, as visualized in Fig. 3.14.

	SS	df	F	p
Site	465,356,684	2	15.6920	< 0.0001
Error	578,285,704	42		

3.3.13 Temperature data

Mean temperature varied significantly with site (Table 3.15) with a significantly higher mean temperature at BRB relative to HRM and ISB (Table 3.14 and post hoc Tukey test). Fig 3.3 shows the high temperature fluctuations due to tidal rhythm and periodic submersion (up to 17°C max. amplitude at HRM). Additionally, influences of weather changes are visible with generally warmer interstitial air temperatures at BRB, as well as the overall cooling with the shortening day-lengths in early autumn.

Table 3.14: Temperature data from all sites (HRM = Hutt River mouth, BRB = Breaker Bay, ISB = Island Bay; 1 = near high water mark; 2 = near low water mark), between 28/02 and 10/05/2008 (SE = standard error; sample size per temperature logger n=18,919). While mean temperature at ISB is lower compared to BRB and HRM, the amplitude (between temperature maxima and minima) is lower at ISB, as well. Both mean temperature as well as amplitude is generally lower at the low water mark compared to locations higher up on the beach due to differences in submersion time and exposure during low tide.

Site	Min.	Max.	Mean $\pm$ SE
HRM1	4.85	29.96	16.35 $\pm$ 0.05
HRM2	5.11	27.32	14.87 $\pm$ 0.04
BRB1	6.26	30.55	17.63 $\pm$ 0.08
BRB2	8.32	26.37	15.39 $\pm$ 0.06
ISB1	6.30	27.58	15.44 $\pm$ 0.03
ISB2	8.23	26.37	14.32 $\pm$ 0.03

Table 3.15: One-Way ANOVA results on mean temperatures (subsets 1&2 combined) at all sites revealed highly significant differences between sites.

Source	SS	df	F	p
Site	575.20639	2	61.8701	< 0.0001
Error	13931.563	2997		

3.3.14 Food supply

Both water sampling and filtration was completed for all samples and study sites; however, mainly due to time constraints the photometric analysis of filtration residues was not carried out and, therefore, yielded no results.

In addition to the analyses of water samples, continuous sampling with CTD instruments (Conductivity-Temperature-Depth recorder) and other sensors

deployed in the field may yield more detailed information on spatio-temporal variations of salinity, temperature, turbidity and phytoplankton densities (measured as fluorescence). Also, GIS assisted remote-sensing techniques have proven useful, although costly, for estimating plankton distribution (see Harding & Miller, 2009) and providing information on food supply for decapods (Salam & Ross, 2000; Salam *et al.*, 2003).

3.3.15 Larval supply

After 2-4 weeks of exposure, SCUBA diving revealed that both trap-base units of the sediment traps at Island Bay and Breaker Bay had disappeared or were destroyed by wave action. From sites within the harbour only the plankton collector at Petone wharf could be retrieved but contained large amounts of silt and almost no plankton. Despite repeated dives the remaining sample collectors could not be found due to low visibility, dense algal canopies, and no GPS coordinates to indicate the exact location.

Because most nylon mesh traps were found empty and only occasionally 1-5 *P. elongatus* megalopae were encountered, this experiment was terminated after 3 months, lasting from September until December 2006.

Basket traps were generally suitable (see settlement experiment, section 4.2.2) but very large in comparison to the tiny (1.5mm-2.0mm CW), near-transparent larvae. The extraction of larvae from traps proved to be more difficult and time consuming than presumed, since the very fragile megalopae are naturally very good at clinging to the surface of rocks, frequently in small cracks and nooks, only to be dislodged by a high pressure water-jet or exposure to ethanol or formalin-seawater solution. Even though steel pegs and cable ties were used to anchor the traps, most of them were either removed by curious or environmentally conscious people (personal communication; this problem was resolved by tags stating their purpose and origin in later experiments) or swept away after the first storm.

Yan *et al.* (2004) introduced a promising type of filter-cup trap that can be easily and cost-effectively assembled as a simplified version of a plankton trap designed and used by Castilla & Varas (1998) and Castilla *et al.* (2001). Deploying a similar trap, bolted to bedrock and placed among boulders, may be a useful method to estimate spatio-temporal variations in settlement of *P. elongatus* larvae.

3.4 Discussion

The reproductive traits of *P. elongatus* strongly varied with site. While at ISB the percentage of ovigerous females, as well as the proportion of clutch to body weight was significantly higher relative to females from HRM and BRB, mean egg volume mean as well as egg dry weight were significantly smaller at this site. Additionally, when comparing numbers of eggs per female with a similar body size across sites, egg numbers were significantly higher at ISB, especially among large individuals. Apart from the exception of elevated egg mortality at BRB, site specific characteristics of reproductive traits were generally similar at HRM and BRB. This high variability is consistent with large scale phenotypic differences in reproductive traits in *Petrolisthes armatus*, reported by Wehrtmann *et al.*, 2012.

Due to the close proximity of the study sites and prevailing current patterns (see chapter 1) it can be assumed that connectivity is high between metapopulations, maintained by larval transport and a pelagic phase lasting several weeks. Consequently, the observed pattern largely reflects phenotypic plasticity of crabs in response to the different environmental conditions at these sites. Roff (1992) argues that reproductive patterns in marine invertebrates are adaptive, related to environmental conditions, in order to maximise offspring fitness and, hence, population stability. Phenotypic plasticity in water fleas *Daphnia spp.* (i.e. their change in head morphology to reduce predation risk in response to waterborne cues) is not necessarily associated with high metabolic costs (Oda *et al.*, 2007). Generally, short-term phenotypic plasticity is one of the most significant responses of organisms to environmental change (West-Eberhard, 2003; Berrigan & Scheiner, 2004), and may determine whether a population will persist following an alteration in its conditions (Gabriel *et al.*, 2005; Helmuth *et al.*, 2005). Differences in phenotypic plasticity between introduced and indigenous species are likely to be particularly important in mediating responses to climate change (Walther *et al.*, 2002; Stillman, 2003; Chown, 2007).

Effects of temperature on reproductive traits

Generally, gonad growth and development are strongly affected by temperature in marine organisms (Nelson *et al.*, 1988). While total clutch production is commonly correlated with lifespan, clutch size and the timing of clutch

production varies with water temperature (Dickinson *et al.*, 2006, Darnell *et al.*, 2009). However, even though mean temperature was significantly higher at BRB relative to HRM and ISB during sampling (section 3.13), neither mean egg volume nor mean egg dry weight appeared to be positively affected by the generally higher rates of metabolism at higher temperatures (e.g. Gillooly *et al.*, 2001). However, elevated temperature could have been responsible for higher egg mortality at BRB. In *P. granulatus*, reproductive output is negatively correlated with environmental temperature and egg volume as well as body size and reproductive capacity increase with latitude (Monaco *et al.*, 2010). There is no evidence for a latitudinal gradient in egg size in *P. elongatus* (Jones, 1977).

The length of the reproductive season in *Petrolisthes spp.* depends on water temperature, and consequently varies with latitude (Wehrtmann, 2005; Gebauer *et al.*, 2007). While ovigerous *P. elongatus* females can be found over 12 months in Hauraki Gulf (Greenwood, 1965), and over 9 months between July and March in Wellington (Wear, 1965, and own observation), Jones (1976) reported that in the Christchurch area ovigerous females were found over 6 months between October and March, limited by the cyclic variations in water temperature (Jillett, 1971). Alternatively or additionally, Boolloothian (1959) suggested that species with annual breeding cycles have adapted to the seasonal differences in food availability for larval stages, whereas Ahmed & Mustaquim (1974) presented evidence that in decapods with tropical distribution timing of the breeding period may depend on food supply for adult crabs. Gebauer *et al.* (2007) reported that in *Petrolisthes laevigatus* from warm-temperate waters of southern Chile ovigerous females were present during 11 months, whereas species with tropical distribution, such as *Petrolisthes armatus* (Gibbes), usually exhibit continuous reproduction (Oliveira & Masunari, 1995).

P. elongatus female can have several broods during her lifespan (Jones, 1977). Most females with well developed eggs (i.e. developmental stages 3 and 4) carried a new batch of eggs in their ovaries. Therefore, it is likely that in the Wellington region most females carry at least two broods per reproductive season (Wear, 1965, and own observation). This is consistent with the findings of Scott (1958) in Kaikoura.

Stillmann (2002, 2004) suggested that the thermal acclimatisation capacity in *Petrolisthes spp.* involves an evolutionary and/or functional trade-off between the maintenance of plasticity in thermal tolerance and the achievement of extreme tolerance limits. Due to high variation in temperature (and desiccation stress) between high and low tide intertidal organisms generally exhibit adaptations to a wider range of temperatures compared to subtidal species, including specific life history characteristics.

Food conditions

The aim to estimate spatio-temporal variations in food supply as an important environmental factor influencing reproductive characteristics was not met in the present study. However, various authors (Gardner, 2000, 2002; Gardner & Thompson, 2001; Helson, 2001; Helson *et al.*, 2007) reported higher food levels (i.e. phytoplankton and particulate organic matter) within Wellington Harbour compared to south coast sites. Despite presumably much higher food supply at HRM, reproductive output per female of equal size is lower compared to ISB. The extremely high population densities found at HRM are likely to lead to high levels of intraspecific competition (see chapter 5) that may outweigh positive effects of high food levels (Donahue, 2004).

Density dependence and carry-over effects

Density dependent fitness loss to offspring may favour high variability in offspring size (McGinley *et al.*, 1987). If smaller egg size results in lower larval quality and performance that could be carried over into the benthic phase, then fitness (i.e. fecundity) of the adult may be reduced, as well (Williams, 1966; VanNoordwijk & DeJong, 1986), with further implications on offspring fitness in the following generation. If egg size affects the length of the larval phase, then dispersal potential would be altered, as well. However, Marshall & Keough (2005) indicated that small offspring may not necessarily exhibit lower performance and survival rates than larger offspring as suggested by many authors (reviewed in Moran & Emlet, 2001).

Salinity, turbidity, and parasite loads

Reduced salinity near the Hutt River mouth (Lachowicz, 2005) as well as high fluctuations in salinity (Maxwell, 1956; Hicks, 1973; Booth, 1975) should not

greatly affect *P. elongatus* because this species can tolerate salinities as low as 50‰ seawater over several days (Jones, 1976). However, egg size may be negatively correlated with salinity (Giménez & Anger, 2001), which could partly explain larger egg sizes and higher egg water content within the Harbour compared to south coast sites. Further, temporarily elevated turbidity after heavy rain, especially at HRM (own observation), may negatively affect filtration efficiency (and therefore energy uptake) of *P. elongatus* if the concentration of suspended sediment exceeds 100 mg/L (Steger & Gardner, 2007). Parasite loads were generally negligible and in all samples taken within the scope of this study, only two individual *P. elongatus* females were found with bopyrid infestations.

Larval supply

All attempts to estimate larval supply at the study sites were unsuccessful. For larvae of the mussels *Aulacomya maoriana*, *Mytilus galloprovincialis* and *Perna canaliculus*, Helson & Gardner (2004) found that planktonic larval densities were almost an order of magnitude greater within Wellington Harbour than at coastal sites and larval recruitment was also significantly greater at harbour sites. Hence, I speculate that the distributional patterns and settlement rates for *P. elongatus* larvae could be similar, even though fine scale settlement is strongly influenced by settlement cue density (chapter 4). The production of higher egg numbers as well as higher individual reproductive output at Cook Strait sites could be a strategy to compensate for the recruitment limitation reported by Helson & Gardner (2004). Higher larval retention rates, by contrast, that are likely to occur within the harbour (e.g. Wing *et al.*, 1995, Archambault & Bourget, 1999), combined with high densities of reproducing females at HRM, do not require, or allow, high individual reproductive output.

Reproductive output

Generally, reproductive output in decapods varies with age (Pianka & Parker, 1975), body size (MacDiarmid, 1989), temperature (Calow, 1979), and food supply (Calow & Woolhead, 1977). Even though the per-capita reproductive output appeared to be highest at ISB, the reproductive output per area unit, largely dependent on population density, was on average approximately twice as high at HRM. At BRB, the numbers of eggs per square meter were significantly lower than at the other sites (approx. 2300 eggs/m² at BRB as opposed to 6000 eggs/m²

at ISB and 12,000 eggs/m² at HRM). The number of eggs per square meter were positively correlated with density of ovigerous females and with total female density (not shown), but not with absolute density (compare section 2.3.1, Fig. 2.6), mainly due to variable relative densities of juveniles across sites. Because the relationship between number of eggs per square meter and female density appeared to be linear, intraspecific competition does not seem to affect individual fecundity within the sampled density range.

Egg number and size

Large *P. elongatus* females (14mm carapace length, CL) may have up to 400 eggs (own unpublished data for Wellington region), 900 eggs (Jones, 1977, for Kaikoura), 1100 eggs (Wear, 1965, for Wellington Harbour) or 1200 eggs (Greenwood, 1965, for Hauraki Gulf). Jones (1977) pointed out that larger ovigerous females from Kaikoura (>11.5mm CL) carried fewer eggs compared to other areas. However, egg numbers in *Petrolisthes* spp. do not seem to mainly depend on temperature, but rather vary with carapace width (CW), species, and location. Ogawa & Rocha (1976) report a maximum egg number of 260 eggs for *P. armatus* from Brazil (11mm CW), whereas Reid & Corey (1991a) counted 1050 eggs in a female of the same species from Florida (9.2mm CW). While *P. haigae* females (7mm CW) may have 711eggs (Reid & Corey, 1991a), *P. zaca*e females (7mm CW) carry up to 455eggs (Reid & Corey, 1991a). For the porcelain crab *Pisidia longicornis* Tapella *et al.* (2001) reported egg numbers of 265 ± 225 at 4.9mm CW and 600 ± 373 at 6.1mm CW. Wehrtmann (2005) compared the reproductive ecology of several Porcellanidae species from Costa Rica and Chile and found that species from the tropics had slightly elevated egg numbers but smaller eggs relative to those from temperate waters, resulting in a similar reproductive output in crabs from both locations. This indicates that crabs allocate a similar proportion of their body mass to egg production (Wehrtmann, 2005).

The eggs of *P. elongatus* are large in comparison with other decapods (Gohar & Al-Kholy, 1957) and the egg number per clutch is correspondingly small (Greenwood, 1965). In the galatheid crab *Munida subrugosa* sampled in Beagle Channel, Argentina, freshly released eggs had a mean diameter of 0.69mm (Tapella *et al.*, 2001). In the porcelain crab *Pisidia longicornis*, sampled in

Galicia, Spain, egg volume ranged between $0.025 \pm 0.005 \text{ mm}^3$ and $0.023 \pm 0.005 \text{ mm}^3$, and varied with site and depth (Sampedro *et al.*, 1997).

In reproduction of crustacea egg size is one of the main factors affecting fecundity (Corey, 1991; Steele & Steele, 1991). Due to resource constraints it is a common phenomenon among decapod species that small females with low egg numbers exhibit larger eggs compared to larger females of the same species (Mason, 1978, but see Huner & Lindqvist, 1991). Mauchline (1980), Corey (1987), Corey & Reid (1991) and Reid & Corey (1991b) reported strong linear relationships between carapace volume and volume of the egg mass for different crab species. López *et al.* (1997) showed that in *Petrolisthes granulosus* (Guérin, 1835), numbers of eggs and carapace length were positively linearly correlated. In sexually mature individuals, net growth is determined by resource allocation for adaptive survival and reproduction strategies (Stearns, 1989a). However, egg size might be highly variable among females of the same species with a similar size (Clarke, 1993). Additionally, egg size may vary with site (Mashiko, 1990) as well as across spawning events and can show seasonal fluctuations (Jones & Simons, 1983; George, 1990). Seasonal variations in egg size have been reported for some amphipods (Skadsheim, 1984) and isopods (Brody & Lawlor, 1984; Willows, 1987).

Whether egg size is a useful measure of egg quality has been hotly debated for many years (Jaekle, 1995). For many decapods, the energy content and biochemical composition of eggs, rather than egg size, are highly correlated with larval development (Jaekle, 1995), including *Petrolisthes laevigatus* (Lardies & Wehrmann, 1995), distributed at the west coast of South America. Consequently, Jaekle (1995) concluded that comparisons of the mean egg size within populations and species should be completed by the measurement of energy content and biochemical composition for a more solid estimation of the differences in reproductive effort and corresponding resource allocation.

Egg mortality

When estimating egg mortality by comparison of egg numbers with different developmental stages in similar sized crabs, a significant proportion of observed egg mortality (i.e. net loss) could occur due to a weak attachment of eggs to pleopods and, therefore, their dislodgement over time. Additionally, porcelain

crabs actively remove moribund eggs and clean their clutches with a pair of modified fifth pereopods (Förster & Baeza, 2001). Jones (1977) reported 15% mean egg mortality for the *P. elongatus* population at Kaikoura, using a similar method, compared to approx. 11% and 5% in the present study. The higher egg mortality at BRB relative to the other sites may be partly explainable by higher desiccation stress at elevated temperatures during low tide and potentially by extreme temporary increases of water temperature and salinity in shallow rock pools. Pinheiro & Fransozo (1995) presented evidence that in the porcellanid *Pachycheles haigae* Da Costa, 1960, exposure to higher water temperature may result in reduced fecundity.

Sex ratio

Despite the highest proportion of ovigerous females at ISB, there were more males than females at this site, as opposed to lower male to female ratios at BRB and HRM. Wear (1965) reported a seasonal fluctuation of sex-ratios with higher percentages of female crabs during the reproductive season, whereas in late autumn and during winter months (i.e. between April and June) sex ratios were approximately 1:1. This pattern may emerge due to the migration of females into the upper limit of the intertidal zone in order to expose their eggs to longer periods of warmer atmospheric temperatures (Wear, 1965; Lardies *et al.*, 2004). However, Gebauer *et al.* (2007) did not observe such migrations and argue that seasonal variations in sex ratio in *P. leavigatus* could arise from recruitment into the benthic population.

Size at maturity

Differences in female size at sexual maturity (3.42 ± 0.09 mm CW) were non-significant across sites. However, there is evidence for a latitudinal gradient, since smaller females (5.5mm carapace length, CL) became ovigerous at Kaikoura (Jones, 1977) compared to Wellington (8.5mm CL) (Wear, 1965) or 7.5mm CL, respectively (own unpublished data), and Hauraki Gulf (8.5mm CL) (Greenwood, 1965). Similar to the findings of many authors describing egg development in Porcellanidae (e.g. Jones, 1977, for *P. elongatus*, López *et al.*, 1997, for *P. granulatus*, and Hernaez & Palma, 2003, for *P. granulatus* and *P. tuberculatus*), mean egg wet weight increased with progressing egg development with significantly lower values for stages 1 and 2 compared to stages 3 and 4.

Hernaez & Palma (2003) suggested that size increase of eggs may be important especially for Porcellanidae species distributed in the lower intertidal with less desiccation pressure. For the porcellanid *Pisidia longicornis* Smaldon (1972) reported that females from the sublittoral are smaller and carry more eggs over shorter periods compared to females from the littoral.

Hatching process and larval development

Instead of 4 developmental stages, Lardies *et al.* (2004) and Gebauer *et al.* (2007) classified three categories for egg development in *P. laevigatus*: I) initial: red-purple colour, homogenous yolk, and no visible eyespot; II) intermediate: between 1/4 and 1/2 of the yolk consumed and slightly visible ocular spot; and III) final: 3/4 of the yolk consumed and a well-developed ocular spot of prezoaea. A detailed description of the hatching process in *P. armatus* has been given by Davis (1966). The swimming and feeding larval stages remain in the plankton for several weeks; however, the exact duration of the planktonic phase of Porcellanidae in the natural environment is still unknown, despite being critical in regard to connectivity between metapopulations. Larval development in Porcellanidae (hatching until metamorphosis of last larval stage) under laboratory conditions takes between 15-20 days in *Neopisosoma neglectum* (Werdning & Müller, 1990), 22-40 days in *Petrolisthes laevigatus* (Mascetti & Wehrtmann, 1996), significantly dependent on water temperature (Albornoz & Wehrtmann, 1996; Mascetti & Wehrtmann, 1996).

Conclusions

The significant variation between sites in nearly all reproductive characteristics examined suggests that *P. elongatus* exhibits high phenotypic plasticity. However, the responsible underlying mechanisms driving this pattern may be complex and remain unclear because the aim of this study to identify and characterise the relevant environmental factors has only been met in part. While temperature affects metabolic rate and may be positively correlated with egg mortality, other factors such as food supply, turbidity and salinity may play an important role in shaping site-specific reproductive traits, as well. Intraspecific competition could lead to a decreased fecundity and may be responsible for the lower individual reproductive output at HRM where the highest population densities were recorded (see Chapter 2), presumably due to available shelter space, related to rock size,

and abundant food. In ISB on the other hand, food levels could be a limiting factor, also affecting the amount of energy allocated to a single egg. This could explain the smaller egg volumes and lower egg dry weights measured at this site. Additionally, the production of higher egg numbers (compared to BRB and HRM) is traded off with smaller egg size.

Future research may shed light on the adaptive value of phenotypic plasticity in *P. elongatus* in the context of the natural fragmentation of its habitat and highly variable environmental conditions. It remains a challenge to explain how much local environmental conditions directly induce phenotypic variations in reproductive traits or, alternatively, how much of the observable individual phenotypic plasticity is related to gene expression.

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Chapter 4

Larval response to settlement cues

4.1 Introduction

The importance of larval settlement patterns and the effects of variable larval recruitment on community development and structure in marine systems are widely acknowledged (e.g. Raimondi, 1988b, 1991; Menge, 1991; Gaines & Bertness, 1993). While larval supply at a given site is determined by the number of larvae in the offshore “larval pool” and larval transport, the factors controlling settlement on a smaller scale closer to shore also include larval behaviour (i.e. response to settlement cues), micro-hydrodynamic processes, and substrate availability (Wetthey, 1983; Raimondi, 1990; Pineda, 2000). While approaching the shoreline and substratum, density-dependent factors as well as larval behaviour increasingly affect local settlement rate, survival, and the success of finding a suitable habitat.

For many species settlement occurs non-randomly and the selectivity of larvae is associated with a range of different settlement cues, some of which are species-specific (for reviews, see Pawlik, 1992; Rodriguez *et al.*, 1993; Rittschof *et al.*, 1998; Hadfield & Paul, 2001; Hay, 2009). When larvae become capable of responding to settlement cues, they are referred to as “competent” (Crisp, 1984). The zoea and megalopa stages of decapods generally correspond to the developmental (pre-competent) and searching (competent) phases of invertebrate larvae (Meadows & Campbell, 1972; Sulkin & Van Heukelum, 1982); the megalopa is transitional between the planktonic and benthic phase, in terms of both behaviour and morphology. After settlement, megalopae and juveniles may be subject to differential mortality or migration. Consequently, not only differential larval supply and settlement, but also post-settlement processes alter recruitment patterns and the often patchily distributed adult population (Keough & Downes, 1982; Osmann *et al.*, 1989).

Settling larvae often respond to chemical cues emitted from substratum and coexisting species (e.g. Crisp, 1974; Welch *et al.*, 1997; Forward *et al.*, 2003; Hadfield & Koehl, 2004), prey species (e.g. Barnes & Gonor, 1973; Morse *et al.*, 1979; Morse & Morse, 1984; Salierno *et al.*, 2003), hosts (Boone *et al.*, 2003), as well as conspecific adults (e.g. Knight-Jones 1953; Pawlik, 1986; Raimondi, 1988b, 1991; Boudreau *et al.*, 1993; Toonen & Pawlik, 2001a, b; Zito-Livingston, & Childress, 2009, but see Lecchini *et al.*, 2010). Cues originating from competitors and predators tend to repel competent larvae (“kairomones”) (Johnson & Strathmann, 1989; Boudreau *et al.*, 1993; Anger, 2006) but may work as settlement inducers if those cues are associated with enhanced fitness in the benthos and if the ability of dispersers to detect low-quality habitats is increased (Stamps & Krishnan, 2005).

Additionally, settlement preferences have been demonstrated for a variety of substratum characteristics such as surface texture (e.g. Meadows & Campbell, 1972; Keough & Downes, 1982; Raimondi, 1988a; Keough, 1986; Pawlik *et al.*, 1991; Hills & Thomason, 1996; Walters & Wetthey, 1996; Berntsson *et al.*, 2004), surface orientation (Gotelli, 1987), grain size of sediments (Gray, 1974), sediment cover (Hodgson, 1990), microbial films (e.g. Morse & Morse, 1984; Le Tourneux & Bourget, 1988; Todd, 1998; Tamburri, *et al.*, 1992; Keough & Raimondi, 1995), chemical cues from seagrass (Montfrans *et al.*, 2003), macroalgae (Botero & Atema, 1982; Krug & Manzi, 1999; Swanson *et al.*, 2007), water flow next to the substratum (Crisp, 1984; Wetthey *et al.*, 1988), sound of breaking waves (Phillips & Penrose 1985; Jeffs *et al.* 2003; Montgomery *et al.*, 2006), and visual cues (Thorson, 1964; Botero & Atema, 1982; Forward & Rittschof, 1994; Lecchini *et al.*, 2010). For most species, however, biological and chemical characteristics of the substratum appear to be more important than physical properties (e.g. LeTourneux & Bourget, 1988).

Specific substratum selection due to chemical settlement cues or surface properties may lead to aggregated (“gregarious”) settlement and can determine recruitment patterns (Gaines & Roughgarden, 1985; Minchinton & Scheibling, 1991; Hills & Thomason, 1996; Vermeij, 2005). It has been proposed that larvae respond to these cues differently, dependent on daytime: While moving offshore during the day to avoid reef-associated predators, onshore movement and

settlement predominantly occurs at night (Leis & Carson-Ewart, 1998). In many cases, larvae settle preferentially on substrata that provide high chances of survival (Knight-Jones *et al.*, 1971; Young & Chia, 1984; Davis, 1987; Jensen, 1989).

Conspecific attraction, the preferential settlement in habitat patches with individuals of the same species relative to equivalent patches without (Pawlik, 1992; Donahue, 2006), is common among marine invertebrates (reviewed in Burke, 1986; Pawlik, 1992; Rodriguez *et al.*, 1993; Kingsford *et al.*, 2002). This strategy, combined with a complex lifecycle including a pelagic, planktonic larval phase, has been viewed as an adaptation of benthic marine invertebrates to a fragmented distribution of adult habitats and metapopulations that facilitates or enhances dispersal, connectivity and gene-flow (e.g. Sastry, 1983; Young, 1990; Pawlik, 1992; Anger, 2006; Pineda *et al.*, 2006; Cowen & Sponaugle, 2009). Settlement cues do not only indicate the presence of conspecifics, but also the location of suitable habitat patches, as these patches have proved suitable for those individuals inhabiting them. The obvious benefit of this strategy is increased fitness, e.g. due to conspecifics that may provide benefits directly via positive density dependence (i.e. Allee effects) (Donahue, 2006), such as lower per capita predation rate when surrounded by conspecifics (Bertness & Grosholz 1985; Jensen & Armstrong 1991; Ray & Stoner 1994), higher post-settlement survival (Welch *et al.*, 1997), decreased environmental stress near conspecifics (Bertness 1989), and/or enhanced reproductive success after sexual maturity due to increased access to mates (Toonen & Pawlik, 1994). On the other hand, settlement into occupied habitat patches results in local populations of very high density (Jensen, 1989; Donahue, 2004), accompanied by costs of density dependence such as higher conspecific competition, e.g. for food (Crisp, 1979; Donahue, 2004) and/or space (Minchinton & Scheibling, 1993). In mobile organisms, the immediate costs of aggregation may be mitigated by migration. Juveniles and adults of *P. elongatus*, however, remain in high-density aggregations. Generally, post-settlement mortality may be particularly high if settlement rates are high (Hurlbut, 1991). Due to the prevalence of gregariousness in marine hard substratum communities it can be assumed that fitness gains in gregariously settling species must outweigh the costs of higher conspecific densities (Pawlik, 1992; Donahue, 2006).

Chemical cues from habitats and conspecifics have been shown to induce the metamorphosis of crustacean postlarvae (e.g., Gebauer *et al.*, 1997; Gebauer *et al.*, 2003b; O'Connor, 2007; Krimsby & Epifanio, 2008). In the absence of such cues, crab megalopae are capable of delaying metamorphosis until a suitable signal is detected (Cole & Knight-Jones, 1939; Thorson, 1950; Scheltema, 1961; Jensen & Morse, 1984; Gebauer *et al.*, 2003). This metamorphic plasticity increases their time spent in the plankton and thus the chance of finding a suitable habitat (for reviews, see Pechenik, 1990, 1999; Pawlik, 1992). Even though several authors (e.g. Scheltema, 1974; Butman, 1987; Fenaux & Pedrotti, 1988) reported that metamorphosis may occur before reaching the benthos, these findings are comparatively rare (Rodriguez *et al.*, 1993). Generally, larvae of different species have different degrees of dependence on and specificity to attractants that trigger their settlement and metamorphosis (Morse 1990).

In this chapter I investigate the conspecific attraction in *P. elongatus* between larvae and adults of both sexes, both in the field and under laboratory conditions. Specifically, I examine whether these cues influence swimming direction in a single option choice chamber and settlement preference (i.e. settlement rate in presence or absence of adult conspecifics) in the field. Additionally, I test a range of potential non-conspecific settlement cues, such as biofilms, crustose coralline red algae and two sympatric species of crabs. To examine whether crabs lose their ability to detect waterborne conspecific cues with metamorphosis (i.e. moult from swimming megalopa larva to benthic juvenile stage) I observe the behavioural response of juveniles of two different size classes, using the same experimental design and setup as for larvae. Generally, the response to settlement cues can have profound implications on the spatial distribution and demography of a benthic population, especially if individual migration rates are low.

4.2 Materials and Methods

4.2.1 *Attraction effects on larvae and juveniles caused by conspecific adults and other potential sources of settlement cues in a laboratory experiment*

A small and shallow seawater tank (28cm x 10cm x 3cm) made of grey, non-transparent PVC sheets joined together with a watertight sealant, served as single-option choice chamber (Fig. 4.1). Divided into two compartments by a fine-meshed transparent nylon gauze with a mesh size of 0.5mm by 0.5mm, a potential source of a waterborne cue (e.g. conspecific adults) could be placed into the smaller section of the choice chamber (3cm x 10cm x 3cm), a larva into the larger one. The gauze prevented the larvae from moving into the “source” compartment and adult individuals from moving into the “observation” compartment. The observation compartment was further subdivided into 10 numbered sections by thin black lines drawn on the bottom of the chamber every 2.5cm. The section adjacent to the “source” chamber was assigned a “+5”; the one at the opposite end a “-5” and the line exactly in between (i.e. the point of release of the larvae) was labelled “0”. In contrast to the typical setup of such experiments, such as wind tunnels used to test insect responses to pheromones (e.g. Stelinski et al., 2004) or laminar flow choice chamber experiments with marine invertebrate larvae (e.g. Boudreau *et al.*, 1993; Diaz *et al.*, 2003) I used a still water choice chamber (compare Snelgrove *et al.*, 1998) because flow is bidirectional and turbulent in coastal environments due to wave action and is highly variable. By recording the swimming behaviour of the larvae, which can be directed or undirected, the hypothesis of an attraction effect on larvae caused by conspecific adults or other potential sources of waterborne cues was examined.

Competent *P. elongatus* larvae (megalopae) as well as juveniles were tested in the experiment. The animals were collected from the field (an intertidal cobble beach directly in front of VUCCEL, 41° 20'54.30" S, 174° 45'53.20" E). At low tide near the low water mark boulders were turned over quickly and larvae and juveniles were washed into a bucket with seawater. All animals were used for the experiment immediately after sampling within 5 hours. The developmental stage of the specimens was verified with a dissecting microscope at 25x magnification. Megalopae differ from juveniles in that they still have four pairs of fully functional pleopods, arising from the ventral side of the second, third, fourth and

fifth abdominal segment (see Wear, 1965a), enabling the larvae to swim efficiently. Even though the pleopods are degenerated after the moult into the first postlarval stage, juvenile and adult porcelain crabs are still capable of swimming using their abdominal flap as a paddle.

Conspecific males and females as well as *Heterozius rotundifrons* of both sexes were collected in the mid and upper intertidal (for a species description see McLay, 1988) at the same site as the *P. elongatus* larvae and juveniles. Larger boulders were lifted up and put aside; the animals were then gathered by hand and put into buckets half-filled with seawater. At the lab, the adults of both species were transferred into separate tanks with filtered seawater (FSW; 10µm mesh size) and kept for at least 30min. Before any individuals were chosen for the experiment they were sexed, measured with a digital calliper (carapace width, CW), and weighed on an electronic balance (wet weight, WW, see table 4.1) after drying off excess water on a paper tissue. Disposable gloves were worn at all times.

Pebbles of a defined size (see table 4.1) were also collected in the intertidal and upper subtidal directly in front of VUCCEL. Two types of pebbles were selected: 1) those entirely covered with green micro algae and diatoms (which was later confirmed with a dissecting microscope) and 2) those that had at least 60% crust cover. All pebbles were measured with a digital calliper in all three dimensions. Using the formula for the surface area of ellipsoids (see below), the area of the biofilm and/or algal cover was calculated for each pebble.

$$\text{Surface area ellipsoid} \approx 4\pi \left(\frac{a^p b^p + a^p c^p + b^p c^p}{3} \right)^{1/p}$$

Where $p \approx 1.6075$ yields a relative error of at most 1.061% (Knud Thomsen's formula)

Thirty runs were conducted per treatment, with individuals and water replaced each time. After filling the choice chamber with 200ml filtered seawater (FSW; 10µm mesh size), a gradient of dissolved cues was allowed to build up for 20min. With a custom made Pasteur pipette a larva was then placed exactly into the

middle of the “observation” compartment (on the middle of line “0”), and after a calming time of 20sec. the 4min. observation was started. Every 4sec., the position of the larva (i.e. the section number) was recorded. Between runs larvae were removed, the choice chamber was thoroughly rinsed, first with tap water, then with FSW. Finally it was filled again with FSW and a new source of waterborne cues was placed into the “source” compartment. To avoid systematic errors due to a potential effect of negative phototaxis, the chamber was rotated clockwise for 22.5° to 45° after each run. Between different treatments, the choice chamber was submerged in seawater in a ventilated flow-through tank for at least 12h to remove any remaining traces of chemical cues from the previous treatment.

Fig. 4.1: Single-option choice chamber. The small compartment on the right served as “source” compartment, containing the tested potential source of a waterborne settlement cue, e.g. conspecific adults. The larva was placed into the middle of the larger compartment and its swimming direction within the concentration gradient recorded. Nylon gauze prevented the animals from moving into the adjacent compartment.

For each treatment, the probable location of the larva or juvenile, respectively, at the end of the observation (t_{240}) was calculated as the mean value of the recorded locations in all 30 runs. These were then plotted according to the subdivision of the choice chamber (X-axis), where “0” is the point of release of larvae at t_0 , “5” is directly adjacent to the compartment containing the source of a potential settlement cue, and “-5” marks the opposite side of the choice chamber (Figs.4.4 & 4.5), combined with the standard deviation. Additionally, the mean values for all time points recorded were plotted over time (Y-axis) and according to the subdivision of the choice chamber (X-axis) (see Appendix 4.1 & 4.2).

<p>1) Pre-settlement behaviour</p> <p>a) Conspecific waterborne cues:</p> <ul style="list-style-type: none"> - 4 conspecific adults: 2♀; 2♂ (5-12mm CW) ♀: 8.44±1.32mm CW; 589.07±279.71 mg WW ♂: 8.61±1.63mm CW; 732.90±470.51mg WW - 4 conspecific adults: 4♀ (5-12mm CW) ♀: 8.60±1.35mm CW; 606.69±278.77 mg WW - 4 conspecific adults: 4♂ (5-12mm CW) ♂: 8.76±1.64mm CW; 761.73±479.51mg WW
<p>b) Potential non-conspecific settlement cues:</p> <ul style="list-style-type: none"> - 4 adults sympatric sp. <i>Heterozius rotundifrons</i> 2♀; 2♂ (15-20mm CW) ♀: 17.87±1.71mm CW; 1563.23±439.22mg WW ♂: 16.34±1.86mm CW; 1518.63±693.67mg WW - 4 pebbles with biofilm (max. 30mm length) Mean total surface area of all pebbles used per run: 162.38±42.28cm² - 4 pebbles with biofilm and coralline crust (max. 30mm length, >60% crust cover) Mean total surface area of all pebbles used per run: 126.43±49.81cm²
<p>2) Post-settlement behaviour:</p> <ul style="list-style-type: none"> - 10 conspecific larvae (megalopae, 2.09±0.25mm CW) on larvae - 4 conspecific adults: 2♀; 2♂ (5-12mm CW) on juveniles size cl. 1: (3.0-5.0mm CW) ♀: 8.71±1.43mm CW; 637.51±313.38mg WW ♂: 8.47±1.54mm CW; 684.71±427.95mg WW Juveniles: 2.37±0.36mm* CW - 4 conspecific adults: 2♀; 2♂ (5-12mm CW) on juveniles size cl. 2: (5.0-7.0mm CW) ♀: 8.48±1.27mm CW; 550.43±236.43mg WW ♂: 8.23±1.32mm CW; 589.09±465.27mg WW Juveniles: 3.58±0.40mm CW
<ul style="list-style-type: none"> - Control 1 empty chamber vs. larvae - Control 2 empty chamber vs. juveniles

Table 4.1: Treatments used in the single-option choice chamber experiment, subdivided in cues relevant in pre- and post settlement behaviour. Settlement could be affected by a) conspecific cues and b) non-conspecific cues. The error is given as standard deviation.

The sets of responses to each chemical cue (i.e. the final position values) were subdivided in positive, neutral and negative response: A positive response corresponds to a position of the larva or juvenile directly adjacent to the source compartment of the choice chamber (section +5), and a negative response, when the larva or the juvenile had moved to the opposite end of the choice chamber (section -5). All positions in between (sections +4 to -4) were labelled as neutral response. The percent distribution of responses of larvae and juveniles at the end of the observation (t_{240}) was calculated for each treatment (Fig. 4.6). Additionally, the durations larvae spent in all sections of the choice chamber were calculated and presented as percent of total time (30 x 240sec. for each treatment) for three outcomes (negative, neutral, and positive; Appendix 4.3). Contingency tables display the frequency distribution of total counts of the responses within all treatments (the categorical variables) as well as the expected values (post hoc). Pearson's chi square statistic was used for pair wise comparisons between treatment and control, for both larvae (Tables 4.2 & 4.3) and juveniles (Tables 4.4 & 4.5).

Fig. 4.2: *Petrolisthes elongatus* megalopa, distinguishable from first instar juvenile only by four pairs of fully developed and functional pleopods on the ventral side of the abdomen. Note: fifth pereopods small, used as highly flexible “cleaning legs” in porcellanids.

4.2.2 Attraction effects on larvae caused by conspecific adults in the field

To confirm the results from the laboratory experiment, 16 basket traps were deployed in the field at the Hutt River mouth site (41° 14'49.50" S, 174° 53'57.00" E) spaced at intervals of at least 3m along the mean low water mark and with a random distribution of treatments. All baskets (30cm x 20cm x15cm) were filled with bare cobbles from the supralittoral zone of 10cm to 15cm length and were fitted with a mesh inlay (2mm by 4mm mesh size) that allowed settlement of larvae but prevented migration of juveniles and adults (Fig. 4.3 & 4.7). Furthermore, death of settlers by predation before sampling was unlikely because the enclosures excluded fish and crab predators. 8 baskets contained 30 adult crabs each (15 males, 15 females, 5mm CW minimum), resembling natural densities observed at this particular site (see chapter 2). For the other treatment, 8 baskets were left empty, the mesh preventing any juveniles and adults from colonizing the trap. After 4 weeks of exposure in the intertidal, the traps were retrieved and the contents carefully transferred into two sieves stacked on top of each other, a coarse (5mm mesh size) and a fine sieve (1mm mesh size). The rocks and other accumulated material were thoroughly rinsed with running seawater and the residue from each sieve was washed into a shallow tray. All crabs were transferred into sample jars and preserved in 95% ethanol on the same day. Later, settlers (megalopae and first instar juveniles) of *P. elongatus* in each basket were counted. The significance level of the difference between numbers of settlers in both treatments was determined by chi square statistic.

Fig 4.3: Basket trap in an intertidal boulderfield with a high abundance of *Petrolisthes elongatus* (at Hutt River mouth). The coarse mesh prevents cobbles inside the trap from falling out, while the fine mesh allows larvae to settle but prevents larger crabs from colonizing or escaping from the trap (in case of the “adults present”-treatment).

4.3 Results

4.3.1 Attraction effects on larvae and juveniles caused by conspecific adults and other potential sources of settlement cues in a laboratory experiment

4.3.1.1 Effect of potential settlement cues on larvae

Compared to the control where swimming direction appears randomly distributed around the point of release (within 2.5 cm on either side), *P. elongatus* larvae were attracted to conspecific adults (Fig. 4.4 a,b,c). At the end of the observation time (t_{240}), 57-70% of the larvae were sitting as close as possible to the 4 conspecifics in the source compartment (Fig. 4.6). The response was similar for the two treatments “4 conspecific females” and “4 conspecific males” (Fig. 4.4xb & c; Fig. 4.6) and all treatments involving conspecific adults were significant (Table 4.3). Biofilms as well as biofilms combined with coralline crusts (*Lithothamnion* sp., Rhodophyceae) did not attract *P. elongatus* larvae (Fig. 4.4 f & g; Table 4.3). However, in the presence of coralline crusts 43% of the larvae

were in section +5 at the end of the observation (Fig. 4.6) and the sample mean at t_{240} was positive (Fig. 4.4; Appendix 4.2.1), suggesting a possible weak attraction effect. Larvae were not attracted by 10 conspecific larvae (Fig. 4.4 d). The presence of a sympatric species, *Heterotius rotundifrons* (Fig.4.4 e), also had no effect on the swimming direction of *P. elongatus* larvae.

Fig. 4.4: Mean position of larvae within the choice chamber at the end of the observation time (t_{240}). The x-axis represents the subdivision of the choice chamber, where 0 is the point of release of larvae at t_0 , and 5 directly adjacent to the compartment containing the source of a potential settlement cue (empty in control). There is a positive response to the presence of conspecifics (a,b,c) and even though not statistically significant, to coralline crusts (f), as well. Error bars represent 95% confidence intervals.

In Appendix 4.1 – 4.3, the mean values (and standard errors) of the positions of larvae and juveniles are shown for all time points ($t_0 - t_{240}$) for all treatments, resulting in “probability paths” for the responses to potential cues over time. These results visualise the chronological sequence of the average position of larvae and juveniles within the choice chamber, their average swimming direction (i.e. towards the source of the cue, away from it or randomly distributed) and provide evidence that the chosen total observation time (240sec.) was sufficient for the determination of the final response.

4.3.1.2 *Effect of potential settlement cues on juveniles*

Juveniles showed no significant response to conspecific adults (Table 4.5). However, at the end of the observation time, 53% of both size class 1 and 2 juveniles showed a positive response as opposed to 7% that had moved to the far end of the choice chamber (Fig. 4.6). Additionally, juveniles spent 34% (s.cl.1) and 44% (s.cl.2) of the total time (i.e. the entire duration of the experiment) in section +5, as opposed to 10% and 15% at the opposite side (Appendix 4.3). Therefore, and despite non-significant results of Pearson's chi-square statistic, it is likely that recruits do not lose their ability to detect and respond to conspecific cues at metamorphosis.

Treatments:

- A 4 conspecific adults (2m, 2f) tested on juveniles of size class 1 (3.0-5.0mm CW)
- B 4 conspecific adults (2m, 2f) tested on juveniles of size class 2 (5.0-7.0mm CW)
- C Control juveniles (15x 3.0-5.0mm CW & 15x 5.0-7.0mm CW)

Fig. 4.5: Mean position of juveniles within the choice chamber at the end of the observation time (t_{240}). The x-axis represents the subdivision of the choice chamber, where 0 is the point of release of larvae at t_0 , and +5 directly adjacent to the compartment containing the source of a potential settlement cue (empty in control). Despite positive sample means there is no significant response of size class 1 and 2 juveniles to the presence of adults (see Table 4.5). Error bars represent 95% confidence intervals.

Treatments:

1) 4 conspec. adults (2m, 2f)	5) 4 <i>H. rotundifrons</i> (2m, 2f)	1a) 4 conspec. adults
2) 4 conspec. adults (4m)	6) Pebbles biofilm	Juveniles size class 1
3) 4 conspec. adults (4f)	7) Pebbles biofilm + crusts	2a) 4 conspec. adults
4) 10 conspec. Larvae	8) Control larvae	Juveniles size class 2
		3a) Control juveniles

Fig. 4.6: Distribution of responses of *P. elongatus* larvae (on left) and juveniles (on right) in percent at the end of the observation (t_{240}). A positive response was recorded when the larva or juvenile was located directly adjacent to the source compartment of the choice chamber (section +5), a negative response, when the larva or the juvenile had moved to the opposite end of the choice chamber (section -5), and a neutral response for all positions in between (sections +4 to -4).

	1 2m2f	2 4m	3 4f	4 10L	5 4H.rot	6 Pb	7 Pb+c	8 Contr	Row total
Positive	21 (12.38)	19 (12.38)	17 (12.38)	7 (12.38)	7 (12.38)	8 (12.38)	13 (12.38)	7 (12.38)	99
Neutral	8 (13.63)	7 (13.63)	11 (13.63)	17 (13.63)	16 (13.63)	18 (13.63)	15 (13.63)	17 (13.63)	109
Negative	1 (4)	4 (4)	2 (4)	6 (4)	7 (4)	4 (4)	2 (4)	6 (4)	32
Column total	30	30	30	30	30	30	30	30	240

$$\chi^2_{\text{Pearson}} = 38.0476; \text{df} = 14; p = \mathbf{0.00051}$$

Table 4.2: Contingency table for larval responses (rows) for all treatments (columns). Shown are the observed values (based on total counts) and, in brackets, the expected values (post hoc, based on the ratio of product of row total and column total to grand total, rounded). The Pearson chi-square statistic result indicates highly significant differences between larval responses in different treatments.

Treatment		Chi ² _{Pearson}	df	p
A	4 conspecific adults (2m, 2f)	13.8114	2	0.0010
B	4 conspecific adults (4m)	7.4524	2	0.0241
C	4 conspecific adults (4f)	10.1051	2	0.0064
D	10 conspecific larvae	0	2	1.0000
E	4 <i>H. rotundifrons</i> (2m, 2f)	0.1072	2	0.9478
F	4 Pebbles biofilm	0.4952	2	0.7807
G	4 Pebbles biofilm + coralline crusts	3.9250	2	0.1405

Table 4.3: Significance values for the final positions of larvae (at the end of observation, t_{240}) for each cue type compared to the control by Pearson's chi-square statistic with three outcomes (positive, neutral, and negative response; observed and expected values). For each treatment 30 runs with newly replaced larvae and cue sources were conducted. A significantly positive response of larvae regarding their swimming direction was detected for conspecific adults, only.

	1 S.cl. 1	2 S.cl. 2	3 Contr.	Row total
Positive	16 (13.33)	16 (13.33)	8 (13.33)	40
Neutral	10 (11.67)	10 (11.67)	15 (11.67)	35
Negative	4 (5)	4 (5)	7 (5)	15
Column total	30	30	30	90

Chi²_{Pearson} ~ 15.6161; df = 4; p = 0.2123

Table 4.4: Contingency table for juvenile responses (rows) for all treatments (columns). Shown are the observed values (based on total counts) and the expected values (based on the ratio of product of row total and column total to grand total, rounded) in brackets. The Pearson chi-square statistic result indicates highly significant differences between juvenile responses in different treatments.

Treatment		Chi ² _{Pearson}	df	p
A	4 conspec. & juv. s.cl. 1	0.9569	2	0.0882
B	4 conspec. & juv. s.cl. 2	0.9569	2	0.0882

Table 4.5: Significance values for the final positions of juveniles (at the end of observation, t_{240}) for both cue types compared to the control by Pearson's chi-square statistic with three outcomes (positive, neutral, and negative response; observed and expected values).

Pearson's chi-square statistic results on the relative frequency distribution of larval responses indicated highly significant differences between the observed

frequency distributions in all treatments (Table 4.4). For juveniles no overall differences were detected (Table 4.5). However, comparing the observed frequencies of responses (twice as many positive outcomes in the presence of conspecific adults than in the control) it is likely that juveniles are responding to conspecific cues, as well.

4.3.2 Attraction effects on larvae caused by conspecific adults (field experiment)

In the field, presence of conspecifics had a highly significant effect on larval settlement of *P. elongatus*. Densities of newly settled larvae were four times higher in basket traps that contained conspecific adults compared to those where adults were absent (Fig. 4.7).

$\text{Chi}^2 = 14.3872$; $\text{df} = 7$; $p < 0.0001$

Fig. 4.7: Mean number of *P. elongatus* settlers in absence or presence of conspecific adults in basket traps deployed in the field. There were approx. 4 times as many settlers in traps with encaged conspecifics in the field. Error bars represent 95% confidence intervals.

4.4 Discussion

The results from the choice chamber experiments provide strong evidence that adults of *P. elongatus*, both females and males, release a waterborne chemical cue that attracts conspecific settlement stage larvae and post-metamorphic juveniles. This evidence is supported by results obtained in the field, demonstrating that *P. elongatus* settlement was four times higher in baskets with conspecific adults compared to those without. These results are consistent with studies of conspecific attraction in other *Petrolisthes* species. Jensen (1989, 1991) demonstrated that larvae of *P. cinctipes* (Randall) and *P. eriomerus* Stimpson are attracted to conspecific adults both under laboratory conditions and in the field. Additionally, Jensen (1991) presented strong evidence for an extended period of competency for settlement: While newly moulted megalopae of *P. cinctipes* settled within 2-4 days when conspecific adults were present, those held without adults delayed settlement for 2-3 weeks. Field observations suggest that megalopae of two other porcellanids, *Pachycheles rudis* Stimpson and *P. pubescens* Holmes, also settle in response to conspecific adults and remain closely associated with them (Jensen, 1989). The protection-seeking behaviour in megalopae as well as in juveniles is possibly mediated by the persistent responsiveness to the waterborne settlement-inducing cue released by conspecific adults. Megalopae as well as juvenile instars gain protection by hiding among and underneath conspecific adults (Jensen, 1991 and own observation); this behaviour significantly reduced predation in a laboratory experiment (Jensen, 1991) and could reduce post-settlement mortality in *P. elongatus*.

Conspecific attraction of juveniles

Juveniles of the southern rock lobster, *Jasus edwardsii*, become increasingly attracted to conspecific adults as they grow larger (MacDiarmid, 1994), due to an ontogenetic change in the response to conspecific cues (Butler *et al.*, 1999). It is likely that a similar ontogenetic change takes place in *Petrolisthes* spp.; however, it is unknown whether earlier larval stages (zoea larvae) respond to conspecific cues. Baeza & Stotz (1998) demonstrated that juveniles and adults of the porcellanid *Allopetrolisthes spinifrons* (H. Milne Edwards, 1837) exhibit a high host specificity (to a sea anemone) that appears to be less pronounced in larvae at the time of settlement, possibly mediated by an increasing sensitivity to cues with advancing development. Similar to *J. edwardsii*, later stage juveniles of

Caribbean spiny lobsters, *Panulirus argus*, become attracted to conspecific odours (Ratchford & Eggleston, 1998). Zito-Livingston & Childress (2009) suggested that in this species postlarval settlement may be influenced by conspecific density. *P. argus* adults, both the males and females, shelter gregariously (Herrnkind *et al.*, 2001), whereby shelter choice is significantly influenced by chemical cues associated with conspecific urine of either sex (Horner *et al.*, 2006). Even though the American lobster, *Homarus americanus*, is non-gregarious, early juvenile stages are attracted to conspecific odours (Boudreau *et al.*, 1993) and frequently share shelters with adults (Lawton & Lavalli, 1995). Thus, conspecific cueing may play a role in site selection and induction of settlement in *H. americanus* (Childress & Jury, 2006).

Conspecific attraction among larvae

Under laboratory conditions, competent *P. elongatus* megalopa larvae were not attracted by 10 conspecific larvae of the same stage, indicating the crabs begin to produce the attractant after metamorphosis. This seems logical insofar that a self-released odour would obliterate the settlement cue gradients and densities guiding the larvae to inhabited coastal sites with high habitat quality. Alternatively, the 10 megalopae in the “source” compartment may not have been enough to release a sufficient amount of odour to successfully attract others. Several studies have demonstrated that some larvae are chemically attracted to other larvae or recently settled juveniles (Keough, 1984; Wethey, 1984; Marsden, 1991). Wear (1965b) reported that zoea larvae of *P. elongatus* were occasionally found in large numbers close to the shore in shallow water; however, it is likely that these distributional patterns partly arise from hydrodynamic processes. Jensen (1991) and Mascetti & Wehrtmann (1996) observed positive thigmotaxis of *Petrolisthes laevigatus* megalopae with floating objects, including other larvae, often forming ball-like aggregations. This behaviour has also been observed in early life history stages of other decapods (Wehrtmann & Dittel, 1990).

Effects of adult density on patterns of settlement and recruitment

Typically, the conspecific attraction results in gregariousness and is most likely density dependent because the density of conspecific individuals within a given habitat patch will in large part determine the local cue concentration. Donahue (2006) manipulated the density of *P. cinctipes* in field enclosures and found that

the number of settlers increased with conspecific density. Despite the turbulent flow conditions within the natural habitat of *P. elongatus* on one hand and the relatively small size of the basket traps on the other, the larvae settled “patchily” on a scale of tens of centimetres by showing a significant preference for inhabited traps. Since juveniles are attracted to adults, as well (Fig. 4.5), and tend not to migrate long distances (see chapter 2), settlement patterns are likely maintained for some time after settlement. Therefore, recruitment patterns of *P. elongatus* are likely influenced by local adult density due to differential cue concentrations even on a surprisingly small scale. In contrast to *P. elongatus* postlarvae (megalopae) and juveniles, the aggregating behaviour in adults appears to be mediated by shelter targeting behaviour (see chapter 2), combined with the use of vision for shelter seeking (Meyer-Rochow & Meha, 1994), and negative phototaxis (Scott, 1958), rather than by conspecific cueing.

Crustose coralline red algae as sources of settlement cues

In addition to conspecific cues, coralline crusts frequently found in intertidal boulder fields, composed of red algae of the genera *Lithothamnion* and *Lithophyllum*, also release an effective positive cue that attracts *P. elongatus* (Fig. 4.4 and 4.6). For Porcellanidae, this has not been reported to date. However, crustose coralline algae have been shown to release a potent chemical attractant for larvae of chitons (Barnes & Gonor, 1973), limpets (Steneck, 1982), abalone *Haliotis* ssp. (Morse *et al.*, 1980; Morse & Morse, 1984; Daume *et al.*, 1999), sea urchins (Pearce & Scheibling 1990; Swanson *et al.*, 2006; Scheibling & Robinson, 2008), as well as for planula larvae of reef building corals (Price, 2010). Swanson *et al.* (2006) found evidence that the settlement cue for larvae of the Australian sea urchin from crustose coralline algae may derive from bacteria thriving on their surface. Botero & Atema (1982) showed that late-stage larvae of *Homarus americanus* settle preferentially on rocks covered by macroalgae and delay metamorphosis when offered nothing but sand or mud. Pueruli of the spiny lobster *Panulirus argus* exhibit a preference for intricately branched red algae (Herrnkind & Butler, 1986). In contrast to the coralline crust, and despite the importance of microbial films in the settlement of many marine invertebrate pelagic larvae (Rodriguez *et al.*, 1993) *P. elongatus* megalopae did not respond to biofilms composed of diatoms and cyanobacteria (Fig. 4.4 and 4.6).

Sympatric species

The sympatric species *H. rotundifrons* is neither a predator for *P. elongatus* nor a competitor for food and space (see chapter 2, Figs. 2.13 and 2.14). This usually far less abundant species also occupies a different ecological niche: It buries itself in sand and gravel and feeds on brown algae such as *Hormosira* sp. (McLay, 1988). Additionally, *P. elongatus* (Anomura) and *H. rotundifrons*, a brachyuran crab, are not closely related. Therefore, it is not surprising that competent *P. elongatus* larvae were not attracted or repelled by odours from this coexisting species. Any other crustaceans, such as the purple rock crab, *Hemigrapsus edwardsi* (Hilgendorf, 1882), or *Elamena producta* Kirk, 1878, were relatively rare and were only found at one of the sample sites throughout the study.

Methodology: laboratory versus field conditions

Within the choice chamber, it is possible that larvae may not have responded to the cue despite perceiving it, e.g. due to high stress levels after handling procedures and concerning the non-natural conditions. The limited water volume could have lead to unnaturally high cue concentrations that may have influenced the larval behaviour due to habituation (see Trapido-Rosenthal & Morse, 1986; Morse 1991). In the field, turbulent flow results in complex fluctuating structure of the odour plume (Balkovsky & Shraiman, 2002), may provide and distribute waterborne settlement cues and mediates their concentration (Abelson & Denny, 1997). The resulting on/off response of larvae enhances their transport to high quality sites (Koehl *et al.*, 2007). Additionally, flow velocity and turbulence could also influence larval behaviour directly (Tamburri *et al.*, 1996). It was therefore crucial to verify the choice chamber results by a field experiment to confirm whether larvae actually settle dependent on presence and density of conspecifics in the eulittoral zone, under natural conditions.

Settlement patterns and substratum selection in the field

The search for suitable sites for settlement operates at several different spatial scales, with different biological and physical influences (LeTourneux & Bourget 1988). Chabot & Bourget (1988), for example, found that selection by larvae of the barnacle *Semibalanus balanoides* was related to the heterogeneity of the substratum at a large scale whereas at a smaller scale settlement was influenced by the presence or absence of conspecific individuals. Butman (1987) indicated

that while hydrodynamic processes and passive transport determine larval distribution at a large spatial scale, the patterns on a smaller scale could be the consequence of a subsequent redistribution that may be influenced by larval behaviour. Although many invertebrate larvae are weak swimmers (Chia *et al.*, 1984; Young, 1995), other pre-settlement forms should actually be considered as mikronekton rather than plankton due to their high level of mobility (Zeldis, 1985; Luckenbach & Orth, 1992). Megalopae of *Petrolisthes sp.* were measured at speeds up to 5 cm/s, and appeared capable of exploring an extensive area of the intertidal zone within a single flood tide (Jensen, 1991).

Meadows & Campbell (1972) hypothesised that a hierarchy of cues guides invertebrate larvae towards a generally favourable habitat and finally determines the selection of a specific site (for a review, see Kingsford *et al.*, 2002; for a more recent study, see Ettinger-Epstein *et al.*, 2008). While cues from coralline crusts that are common in intertidal boulder fields may work on a larger scale (hundreds of meters) and attract *P. elongatus* larvae to coastal sections with potentially suitable habitat, conspecific cueing appears to work on small scale (tens of centimetres), manifested in the preference of high density patches. There could even exist another hierarchical level on an even smaller scale (centimeters, single boulders), that has not been tested in this study: larvae may preferably settle on boulders with a high surface roughness that provides more friction in flow. If one of these biological or physical conditions is not met, the larva will most likely reject the site and continues its explorative behaviour. Compared to sessile barnacles, however, the selection of a suitable habitat seems to be less critical for motile crustaceans as the benthic post-settlement stages are able to emigrate to more favourable sites (Moksnes *et al.*, 2003; Moksnes, 2004).

Megalopae typically respond to odours from conspecifics (Forward *et al.*, 2003) or congenetics (Gebauer *et al.*, 2002). Some crab species moult sooner in the presence of odours from conspecifics (O'Connor & Gregg, 1998) and/or when exposed to environmental cues that are characteristic of the parental habitat (O'Connor & Judge, 2004). The ability of crustaceans to accurately respond to chemical cues is well documented and indicates a sophisticated chemosensory apparatus that can adapt to varying cue concentrations (Zimmer *et al.*, 1999;

Finelli *et al.*, 2000). Many crab larvae are highly selective and display dose-dependent responses to cues (e.g. Pawlik, 1992; Fitzgerald *et al.*, 1998).

Cue specificity and directions for future research

The waterborne settlement cue released by conspecific *P. elongatus* adults that has yet to be characterised is most likely a pheromone, e.g. a polypeptide isolated from arthropod cuticles, “arthropodin” (Pawlik, 1992 and literature therein), but could also be an excretory product (Burke, 1986). Settlement in barnacle cyprids, for example, is mediated by a suite of chemical cues originating from both larvae and adults (for a review, see Clare & Matsumura, 2000). While larvae release the cyprid antennular secretion pheromone (Clare *et al.*, 1994), cues from adults comprise a settlement-inducing protein complex (SIPC) (Crisp & Meadows, 1963; Matsumura *et al.*, 2000; Elbourne & Clare, in press). SIPC’s work as species-specific attractants for barnacles (Dreanno *et al.*, 2007) and have been characterised as cuticular glycoproteins (Dreanno *et al.*, 2006a,b). Other active compounds of attracting odours may be free fatty acids, phenols and polysaccharides (Burke, 1986; Pawlik, 1986). However, it can be expected that the biochemical properties of cue molecules lead to a species specific attraction, even if several different substances are involved. *Petrolisthes novaezelandiae* Filhol, 1885 and *P. spinosus* Miers, 1876 megalopae settle subtidally (Wear, 1964, 1965b), indicating that their conspecific adults may release cues that are biochemically different. Additionally, these larvae may respond differently to physical cues such as water pressure and light conditions.

Despite the fact that chemical cues have been widely considered in studies of settlement, few natural attractants and settlement inducers, other than from barnacles, have been identified, isolated and characterized (Pawlik 1986; Rodriguez, 1993). Knowledge about the species-specificity of the attractant and the level of dependency of the larva on one hand and patterns of distribution of settlement-inducing substrata as well as differential cue densities in the field on the other may help to more precisely predict population and community patterns (Rodriguez *et al.*, 1993). Hadfield (1986) pointed out that for the determination of the specificity of an inducer it is critical to know its physico-chemical structure as well as the nature of the inducers in related species. Gebauer *et al.* (2002), for example, demonstrated that not only odours from conspecific adults but also

those released by closely related species are effective for stimulating metamorphosis in a semiterrestrial grapsid crab, *Sesarma curacaoense*. These authors showed that with increasing phylogenetic distance the strength of the larval response decreased (see also Dreanno *et al.*, 2007). Thus, the knowledge of the chemical structure of settlement-inducing cues at different taxonomic levels could be a useful tool in the study of phylogenetic relations between taxa (Rodriguez *et al.*, 1993), implying that the response to species-specific cues represents a heritable trait which is subject to natural selection (Anger, 2006).

Conclusions

For *Petrolisthes elongatus*, the behavioural selection of high quality habitat patches using waterborne chemical cues from conspecifics on a small scale as well as from crustose coralline algae, presumably on a larger scale, likely reduces the risk of mortality and enhances connectivity between geographically isolated metapopulations. The significance of chemical communication for both larval survival and biotic interactions as well as their effects on marine ecosystems remains a challenge for future research. A characterisation of the settlement inducer released by *P. elongatus* on a molecular level and physiological studies of cue perception would help to understand the adaptive evolution of conspecific cueing as well as how chemical cues regulate critical aspects of the behaviour of marine organisms.

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Appendix 4

4.1 Potential conspecific cues (larvae)

a) 4 conspecific adults (2♀; 2♂)

b) Control

c) 4 conspecific adults (4♀)

d) 4 conspecific adults (4♂)

e) 10 conspecific larvae (megalopae)

Appendix 4.1.1: “Probability paths” of swimming *P. elongatus* larvae (megalopae) in a single-option choice chamber in presence of conspecific adults (a, c, d) as well as conspecific larvae (e). The x-axis represents the subdivision of the choice chamber, where 0 is the point of release of larvae at t_0 , 5 is directly adjacent to the compartment containing the source of a potential settlement cue (empty in control, b), and -5 marks the opposite side of the choice chamber. Error bars represent standard deviations.

4.1 Potential conspecific cues (juveniles)

a) 4 conspecific adults (2♀; 2♂)
on juveniles size class 1
(3.0-5.0mm CW)

b) 4 conspecific adults (2♀; 2♂)
on juveniles size class 2
(5.0-7.0mm CW)

c) Control for juveniles
(both size classes are equally represented)

Appendix 4.1.2: “Probability paths” of *P. elongatus* juveniles (after metamorphosis) in a single-option choice chamber in presence of conspecific adults. As above, the x-axis represents the subdivision of the choice chamber. Error bars represent standard deviations; p-values represent paired t-test results.

4.2 Potential heterospecific and habitat cues

a) 4 adults *H. rotundifrons* (2♀; 2♂)

b) Control

c) 4 pebbles with biofilms

d) 4 pebbles with biofilms & coralline crusts

Appendix 4.2.1: “Probability paths” of swimming *P. elongatus* larvae (megalopae) in a single-option choice chamber in presence of non-conspecific sources of potential settlement cues. As above, the x-axis represents the subdivision of the choice chamber. Error bars represent standard deviations; p-values represent paired t-test results.

4.3 Percent of total time spent in choice chamber sections

Treatments:

1) 4 conspec. adults (2m, 2f)	5) 4 <i>H. rotundifrons</i> (2m, 2f)	1a) 4 conspec. adults
2) 4 conspec. adults (4m)	6) Pebbles biofilm	Juveniles size class 1
3) 4 conspec. adults (4f)	7) Pebbles biofilm + crusts	2a) 4 conspec. adults
4) 10 conspec. Larvae	8) Control larvae	Juveniles size class 2
		3a) Control juveniles

Appendix 4.3: The total time *P. elongatus* larvae (on left) and juveniles (on right) spent in sections of the choice chamber in percent of total observation time (t_0 - t_{240}). Section +5 was located directly adjacent to the source compartment of the choice chamber, section -5 at the opposite end, and sections +4 to -4 were located in between (see Fig. 4.1). The overall durations of stay are similar to the distribution of responses of larvae and juveniles at the end of observation (t_{240}) shown in Fig. 4.6: Larvae as well as juveniles exhibit a positive response to conspecific cues.

Chapter 5

Density dependence: Effects of conspecific density on survival, individual growth, feeding efficiency and reproduction.

5.1 Introduction

Petrolisthes elongatus (Milne Edwards, 1837) lives in dense multi-size aggregations under boulders, within the interstitial space of cobble beaches as well as among mussel beds in the intertidal zone of rocky shores (Morton & Miller, 1973) throughout Tasmania and New Zealand (Haig, 1960, 1964; McLay, 1988). Even though density dependence is a ubiquitous phenomenon it has been widely acknowledged that aggregation may be associated with a number of benefits, especially at intermediate densities and in social species. The advantages of conspecific attraction and gregariousness comprise conspecific cueing (using conspecifics as an indicator of habitat quality) (Raimondi, 1988; Jensen, 1989), access to mates (Burke, 1986; Metaxas *et al.*, 2002), greater reproductive output (Wethey, 1984), improved feeding efficiency (Bertness *et al.*, 1998), increased survival (Bertness, 1989; Leslie, 2005), reduced predation risk (Jensen & Armstrong, 1991; Ray & Stoner, 1994), habitat amelioration (Bertness *et al.*, 1991; Bertness & Leonard, 1997), reduced desiccation risk as an aspect of facilitation (Bertness, 1989), as well as Allee effects (i.e., positive density dependence) (Allee, 1931; Allee *et al.*, 1949; Donahue, 2006). Due to these benefits, aggregation has been viewed as an evolutionary advantageous state, traded off against the costs of limiting resources (Parrish & Edelstein-Keshet, 1999). Because areas of suitable habitat for *P. elongatus* are limited and patchy on a wide range of spatial scales, competition for space seems inevitable. However, intraspecific competition but may be comparatively weak due to an apparent selection pressure towards gregariousness (Donahue, 2004). It is therefore likely that in aggregating species such as porcelain crabs the benefits of a clustered distribution outweigh the costs even at higher densities (Leslie, 2005; Donahue, 2006), dependent on the specific carrying capacity of a habitat patch.

As suspension feeders, porcelain crabs use their setose 3rd maxillipeds for active and passive filtration (Wicksten, 1973; Caine, 1975), dependent on flow speed (Trager & Genin, 1993; Achituv & Pedrotti, 1999). As an adaptation to hydrodynamic conditions of the surf zone to optimize feeding efficiency, feeding motions are synchronized with flow oscillations (Trager *et al.*, 1992; Valdivia & Stotz, 2006). Molenock (1976) and Jensen (1990) suggested that *Petrolisthes* ssp. compete for high quality feeding spots characterized by high flow velocities. Donahue (2004) found that porcelain crabs fed less frequently at high density which is consistent with exploitative competition due to an impact of density on food availability. Competition for food depends on both food availability and population density and may result in size-dependent agonistic interactions that have effects on feeding rate and, ultimately, on growth rate (Donahue, 2004).

Generally, growth rates of intertidal suspension feeders depend on local environmental factors such as hydrodynamic conditions, the degree of parasite infestation as well as on regional environmental factors such as water temperature, salinity, and richness in suspended nutrients (Crisp, 1960). In turn, carrying capacity and thus population density is regulated by physical conditions, availability of food and suitable habitat, as well as inter- and intraspecific interactions, all of which may spatio-temporally fluctuate. While the underlying mechanism of self-thinning, a concept traditionally proposed for plant populations (e.g. Odum, 1971; Westoby, 1981), is most likely density dependent mortality in sessile populations (e.g. barnacles, Whetthey, 1983), local density in mobile organisms (e.g. crabs, Pile *et al.*, 1996) may be regulated by migration.

Short-term and small-scale variation in seston availability and quality within nearshore environments has been documented by various authors (e.g. Fegley *et al.*, 1992; Wilson-Ormond *et al.*, 1996; Chaparro *et al.*, 2008). This variation of food conditions can have significant effects on individual and population characteristics of benthic suspension feeders such as reproduction (Hines, 1978; Soniat & Ray, 1985) and growth rates (Cahalan *et al.*, 1989; Lesser *et al.*, 1994), as well as productivity (MacDonald & Thompson, 1985; Brown, 1988) and spatial distributions (Wildish & Kristmanson, 1979). The dynamics of sessile suspension feeders, such as mussels, bryozoans, and zoanthids, are substantially regulated by density-dependent food consumption (Frechette & Lefaivre, 1990;

Frechette *et al.*, 1992; Okamura, 1992; Tanner, 2002), and not just by competition for space (Connell, 1961; Dayton, 1971; Paine, 1974). If growth is density dependent, reproductive traits are likely to be affected as well, since generally, female body size is the principal determinant of reproductive output (Annala, 1991; Hines, 1991; Corey & Reid, 1991; Reid & Corey, 1991).

The level of density-dependent intraspecific competition in *Petrolisthes* spp. may not only be reflected by growth rate but also by frequency of limb loss, due to claw use in physical contests during competitive interactions (Molenock, 1976; Jensen & Armstrong, 1991; Donahue, 2004; Wasson & Lyon, 2005; Rypien & Palmer, 2007). In turn, the energy allocation for limb regeneration is likely to affect individual growth rate (Donahue, 2004) and fitness. In *Petrolisthes* spp. in general (Wasson *et al.*, 2002) and *P. elongatus* in particular (Hazlett *et al.*, 2000, 2004) chelipeds and walking legs are autotomized as an important defence mechanism when attempting to escape mechanical (Scott, 1958; McLay, 1988) or physiological stress (own obs.). Rypien & Palmer (2007) found significantly higher proportions of puncture wounds on chelipeds of *P. cinctipes* at sites with higher densities and wave exposure. Autotomy, the reflex severance of an appendage at a predetermined breakage plane in the basi-ischium (Wood & Wood, 1932; Hopkins, 1993), is a strategy that may provide immediate survival benefits such as predator avoidance and wound limitation in many decapods (Bliss, 1960; McVean, 1982). However, the loss of one or more limbs can result in long-term functional and energetic costs that may have profound effects on the population and community (Juanes & Smith, 1995, and literature therein).

In this chapter, I use manipulative experiments to investigate the costs of gregariousness by examining the effect of conspecific density on size-dependent growth rates, mortality, feeding activity, and limb loss. Because of its ecology, *P. elongatus* is a good model organism to study the trade-offs between survival benefits and growth costs of aggregation. Further, I analyse the long term effects of resource allocation for limb regeneration on both growth rate and reproductive output.

5.2 Materials and Methods

5.2.1 Effect of population density and food availability on growth rate

Petrolisthes elongatus of various sizes and of both sexes were collected from the intertidal zone at the river mouth of the Hutt River (41° 14'49.50" S, 174° 53'57.00" E, Fig.5.1), the site with the highest population densities throughout the Wellington region (chapter 2). The crabs were transported to the Victoria University Coastal Ecology Laboratory (VUCEL, formerly Island Bay Marine Laboratory) where the experiments were conducted. Prior the start of any experiment, the animals were held for at least 24h in tanks supplied with unfiltered seawater.

For the examination of the effect of population density and food availability on growth rate of *Petrolisthes elongatus*, a laboratory experiment with a fully crossed factorial design was conducted, based on a design used by Donahue (2004) using *Petrolisthes cinctipes* as model species. Two food levels (FL) crossed with two density treatments (D) were tested: FL1/D1; FL1/D2; FL2/D1 and FL2/D2. For each treatment, 6 replicate tanks (30cm x 30cm x 30cm) were used, filled with 15 L filtered seawater (10µm mesh size) at 12-15°C. Ventilation, agitation and flow were ensured by airstones connected to air pumps via PVC tubing. As a food source, *Spirulina* spp. flakes were fed to the crabs, ground with mortar and pestle until a fine powder was obtained. Dried *Spirulina* (more correctly: *Arthrospira* spp.) was chosen due to its high contents of proteins and minerals (Belay, 1997; Othes & Pire, 2001) similar to the natural food sources of *P. elongatus* (i.e. detritus and phytoplankton) and recommended for feeding Porcellanidae by various aquarists (e.g. <http://reefkeeping.com/issues/2007-05/as/index.php>). The concentrations used in the two food level treatments were based on estimates of natural food levels at south coast sites as well as in Wellington Harbour investigated by various authors (Gardner, 2000; Gardner & Thompson, 2001; Helson *et al.*, 2007). For FL1, 100mg of *Spirulina* powder were added to 15 L filtered seawater; for FL2 800mg.

Density treatments were designed to match high and low density patches observed in the field (chapter 2): I used 12 (low density) or 36 (high density), crabs respectively, divided into four size classes: A) 3.5mm - 5.5mm, B) 6.0mm - 8.5mm, C) 9.0mm - 11.5mm, and D) 12.0mm - 15.0mm carapace width (CW).

Since in natural multi-size populations smaller individuals are more frequent than larger ones the distribution of size classes in both density treatments was 1): 4:4:2:2 (A:B:C:D) for the low density treatment, and 12:12:6:6 (A:B:C:D) for the high density treatment. All individuals were marked with coloured and numbered “Queen Bee” tags (manufacturer: E.H.Thorne Ltd., Beehive Works, Wragby, Market Rasen, Lincolnshire, U.K., <http://www.thorne.co.uk/index.htm>) glued onto the carapace. In order to reduce stress levels, provide a substrate for the crabs to hold on to, and shelter from light, each tank contained a number of cobbles taken from the natural habitat that were thoroughly rinsed with freshwater before.

The experiment commenced after an adjustment period of 3 weeks due to high initial mortality rates (>25%), and terminated after further 70 days. Twice per week, the crabs were fed, the tanks were cleaned and the seawater was renewed. The CW of each animal was measured weekly with a digital calliper, and individual wet weight determined by weighing on an electronic balance after quickly drying off excess water on a paper tissue. If necessary (i.e. after moulting), crabs were retagged; dead individuals were replaced to maintain initial densities. Due to different light conditions and performance of the airstones, the crabs were assigned to the tanks randomly each week after measurements were taken.

Individual growth rate (the response variable, IGR) was calculated as the daily wet body weight (BW) increase for each crab: $[\ln(BW_{final}) - \ln(BW_{initial})] / \text{no. of days}$. Only the 382 crabs that retained both chelipeds and had been in the experiment for at least 70 days between initial and final measurements were used in the analysis. A general linear model (GLM) was used to analyze the effect of density (D), food level (F), size-class (S), and aquarium (A) on IGR: $IGR \sim D + F + S + (D \times F) + (D \times S) + (F \times S) + (D \times F \times S) + A(D \times F) + \epsilon$, in which $A(D \times F)$ is the error term for D, F, and $D \times F$, and ϵ is the error term for S, $D \times S$, $F \times S$, and $D \times F \times S$. Since there was significant non-normality and heteroscedasticity in the data, S represents the natural logarithm of initial carapace width as a continuous variable instead of the categorical variable size class. The residuals of the transformed model met the assumptions of normality and homogeneity of variance. While I present significance levels of the transformed model, I plotted individual growth rates against categorized size classes to ease interpretation.

The average mortality rates over 10 weeks (in % of number of crabs within size class and treatment) were estimated by the frequency of first replacements of crabs. Similar to the GLM above I analyzed the effect of density (D), food level (F), size-class (as natural logarithm of initial carapace width) (S), and aquarium (A) on mortality rate: $M \sim D + F + S + (D \times F) + (D \times S) + (F \times S) + (D \times F \times S) + A(D \times F) + \epsilon$, where M is the square root arcsine transformed average mortality for each aquarium. Statistical analyses were calculated using JMP 4.0.4 (SAS Institute, September 2001).

5.2.2 *Effect of density and food level on frequency of filter-feeding*

For this experiment, the same setup including density- and food level treatments described in 5.2.1 were used, apart from a replacement of the natural boulders by a propped up concrete slab (one per tank) to facilitate observation and counting. Feeding activity of all crabs within 4 size classes and 6 replicate tanks was observed every two hours for 24h from 8am to 8am on the following day. During a 2 minute observation period the numbers of individuals per size class displaying feeding behaviour were recorded from each tank. This experiment was conducted three times spread over three months with different individuals for each run. A 3-way repeated measures ANOVA was performed to analyze the effect of density (D), food level (F), and size-class (S) on the frequency of filter-feeding (FF) (i.e. the proportion of crabs feeding at each time point), using the model $FF \sim D + F + S + (D \times F) + (D \times S) + (F \times S) + (D \times F \times S)$. Sphericity was assumed due to the non-significant result of Mauchly's test ($p = 0.2172$). Before post hoc tests were applied, α -levels of the results were Bonferroni adjusted. The proportion of crabs feeding within each tank, size class and treatment were arcsine transformed to meet the normality assumption. A one-way GLM ANOVA showed no significant difference between the three replicate observations ($p = 0.0716$). Further, no differences between density and food level treatments could be detected; hence, the datasets were combined for the analysis.

5.2.3 *Effects of limb loss on growth rate*

To investigate the effect of limb loss on growth rate of *Petrolisthes elongatus*, the changes in body mass and CW over time were recorded, with either removed chelipeds (by induced autotomy) or with all limbs present. The experiment was conducted at the National Institute of Water and Atmospheric Research (NIWA)

facility in Wellington, New Zealand. Per treatment, 8 replicate tanks (30cm x 30cm x 30cm) were used, each containing 32 crabs in four size classes 1) 3.5mm - 5.5mm, 2) 6.0mm – 8.5mm, 3) 9.0mm -11.5mm, and 4) 12.0mm - 15.0mm) with 8 individuals per size class. At the beginning of the experiment all crabs as well as removed chelipeds were individually weighed on an electronic balance after drying off excess water on a paper tissue. Crabs in the limb regeneration treatment were weighed after cheliped removal. The weighing was repeated every 3-4 days. Additionally, CW was measured with a digital calliper. In both treatments, dead animals as well as crabs with additional missing limbs were replaced by crabs of the same size that were marked with a tag glued onto their carapace. These individuals were solely used to retain initial densities and were not included in the estimate of differential growth dependent on limb loss. The tanks were filled with 15 L unfiltered seawater that was replaced every 2 days. At the same time, all aquaria were cleaned and the crabs re-randomized in position in order to avoid a confounding effect of aquarium. In addition to the organic matter and plankton naturally present in the seawater, 500mg ground *Spirulina* flakes were added to the water of each tank in order to ensure sufficient food resources at all times. The experiment was terminated after 70 days when 80% of the animals with initially autotomized limbs had chelipeds that had been regenerated to at least 75% of their original size. The individual growth rate (IGR) was calculated as daily wet body weight (BW) increase: $IGR = [(BW_{final}) - (BW_{initial})] / \text{length of the experiment in no. of days}$. For the individual body size increase (ISI), the difference between initial and final carapace width (CW) was used: $ISI = [(CW_{final}) - (CW_{initial})] / \text{length of the experiment in no. of days}$. The effects of treatment (chelipeds present vs. clipped-off), and size class as well as the treatment x size interaction were calculated according to the 2-way ANOVA models: $IGR \sim T + S + (T \times S)$, and $ISI \sim T + S + (T \times S)$. To highlight the comparatively large size of the claws and the associated amount of energy that must be allocated for their regeneration, I regressed body mass versus cheliped weight, as well as body size vs. body mass as allometric reference.

5.2.4 Population density, frequency of limb loss, and reproductive output in crabs from the field

The frequency of limb loss in relation to population density and body size was obtained using artificial substrates (i.e. basket traps) in the field. These sampling units were colonised by the crabs during exposure and consisted of plastic baskets (30cm x 20cm x 15cm) filled with greywacke rocks taken from the natural habitat of *P. elongatus*. To prevent rocks from getting washed out a PVC mesh (mesh size 10 by 10mm) covered the baskets, tied down with cable ties. The mesh size of basket and mesh cover allowed crabs to freely move in and out of the sampling unit. Each basket was anchored by two steel pegs made of sharpened waratah stakes (Y posts) cut into 50cm pieces with a welded-on, bent reinforcing rod to hold down the basket. At each of 5 sites (Hutt River mouth (HRM), 41° 14'49.50" S, 174° 53'57.00" E, Island Bay (ISB), 41° 20'54.30" S, 174° 45'53.20" E, Mahina Bay (MAB), 41°16'17.00" S, 174° 54'22.50" E, Baleana Bay (BAB), 41° 17'33.00" S, 174° 48'10.00" E as well as Breaker Bay (BRB), 41° 20'17.90" S, 174° 49'26.60" E, Fig.5.1) eight replicate artificial substrates were deployed in January 2006 and recovered after 4 weeks to allow an undisturbed colonization process under near-natural conditions. At ISB, all crabs were extracted from the sampling units by separately transferring the contents into a double sieve (5mm and 1mm mesh size). The rocks and other accumulated material were rinsed with seawater, washing all crabs into the fine sieve underneath. Crabs were transferred into labelled sample jars and preserved in 95% ethanol on the same day. Later, the animals were sexed and measured with a dissecting microscope at 45-fold magnification.

Due to the fact that *P. elongatus* individuals easily autotomizes its limbs (Hazlett *et al.*, 2000, and pers. obs.), especially when handling or during transport, the frequency of regenerating limbs was used as a reliable indicator of frequency of limb loss. Regenerating limbs (from visible budding stage to final hardening of exoskeleton; corresponding to approximately 5 to 75% regeneration of limbs) were recorded as well as their position (1st to 4th pereopod). Eggs of all ovigerous females were counted, subdivided into four developmental stages and the wet weight of each clutch as well as the body weight of the females was determined. The ratio of clutch weight to body weight as a measure of reproductive output (RO) was calculated using the formula: clutch wet weight / body wet weight *

100. Differences of this ratio in relation to the regeneration of limbs (Reg) as well as in relation to local density (D) were analyzed by ANCOVA: $RO \sim \text{Reg} + D + (\text{Reg} \times D)$, with density as covariate. Because egg size (and therefore clutch weight) strongly varies with developmental stage (see chapter 2), only clutches consisting of stage 1 & 2 eggs were taken for the analysis. Further, only females with a body size between 7.5mm and 9.0mm CW were included to avoid possible confounding effects of a strongly positive relationship between crab size and egg number (chapter 2). Sample sizes for ovigerous females with regenerating limbs that met the above conditions were generally low; hence, samples (i.e. animals from separate artificial substrates) and the associated densities were compared for one site only (ISB).

Fig. 5.1: Map of sample sites in Wellington Harbour and Cook Strait at Island Bay (at the Victoria University Coastal Ecology Laboratory, VUCEL), at the harbour entrance (Breaker Bay), and within Wellington Harbour at Baleana Bay, Mahina Bay and on the true left bank of Hutt River mouth.

5.3 Results

5.3.1 Effect of population density and food availability on growth rate

The significant 3-way interaction of density x food x size (Table 5.1) was mainly caused by a strong effect of density (as well as potentially a weaker effect of size): Tukey's HSD revealed significant differences of group means within density whereas the results for food level were non-significant. The interaction density x size was significant (Table 5.1). Individual growth rate (IGR) varied with density and crabs had higher IGR values at low density (Fig. 5.2). IGR was significantly different for different size classes (Table 5.1): Small crabs grew faster than large ones (Fig. 5.2). There was no effect of food level on IGR, density x food level, and food level x size (Table 5.1). However, there was a significant effect of aquarium ($p < 0.0001$) (Table 5.1).

Size classes (mm carapace width):

1: 3.5 - 5.5

2: 6.0 - 8.5

3: 9.0 - 11.5

4: 12.0 - 15.0

Fig. 5.2: Individual growth rate (IGR), measured as daily increase in wet weight of crabs in four size classes in a fully crossed design comprising two density and two food level treatments. At lower densities, crabs had higher individual growth rates (i.e. gained more weight). Smaller crabs (size class 1) grew faster than larger ones. Food level had no effect on growth rate. Error bars represent 5th and 95th percentiles; the solid line median values.

Table 5.1: GLM results for IGR of crabs within all size classes and treatments show that growth rate strongly varied with density and size but were not affected by food level. However, there were significant interactions between density and food level as well as density and size. Despite the efforts to re-randomize crabs over aquaria on a regular basis, the effect of aquarium within each treatment was highly significant.

All size classes combined Source	SS	df	F	p
Density	0.00007057	1	28.9545	<0.0001
Food level	0.00000347	1	1.4238	0.2336
Size	0.00011598	1	47.5876	<0.0001
Density * food level	0.00000007	1	0.0299	0.8628
Density * size	0.00001927	1	7.9072	0.0052
Food level * size	0.00000199	1	0.8148	0.3673
Density * food * size	0.00001501	1	6.1607	0.00136
Aquarium (density * food)	0.00014725	20	3.0209	<0.0001
Error	0.00081647	335		

Mortality varied with density and size (Table 5.2, Fig 5.3). The effect of density was highly significant (Table 5.2) and according to Tukey's HSD all group means for density were significantly different but non-significant for food level. Smaller crabs died more frequently than larger ones (Fig. 5.3): The mortality of size class 1 crabs (all treatments combined) was 2.1 to 3.6-fold higher than within other size classes.

Table 5.2: GLM results for mortality within all size classes and treatments show that mortality rate is strongly influenced by density and is different between size classes; however, the food levels used in this experiment did not affect survival.

All size classes combined Source	SS	df	F	p
Density	0.13405868	1	20.5656	<0.0001
Food level	0.01816064	1	2.7860	0.0999
Size	0.05043513	1	7.7371	0.0071
Density * food level	0.01212862	1	1.8606	0.1773
Density * size	0.01292819	1	1.9833	0.1638
Food level * size	0.00229549	1	0.3521	0.5550
Density * food * size	0.00019630	1	0.0301	0.8628
Aquarium (density * food)	0.19691304	20	1.5104	0.1082
Error	0.42370899	65

Size classes (mm carapace width):

1: 3.5 - 5.5

2: 6.0 - 8.5

3: 9.0 - 11.5

4: 12.0 - 15.0

Fig. 5.3: Average mortality over 10 weeks, shown as percent of crabs within each size class that had died over the course of the experiment at different densities and with different food supply. The mortality of size class 1 crabs is significantly higher compared to other size classes. Error bars represent 95% confidence intervals.

5.3.2 Effect of density on frequency of filter-feeding

The 3-way repeated measures ANOVA, analyzing the effect of density on frequency of filter-feeding, shows a significant time x food x size class interaction, as well as a highly significant time x size class interaction (Table 5.3). Consistent with a highly significant effect of size class ($p < 0.0001$) in the ANOVA results, post hoc analysis with Bonferroni adjusted α revealed that size class had the strongest influence on the significance level within those interactions, followed by the time effect. Due to the non-significant interactions between time and density, time and food level, time x density x food x size class, as well as non-significant effects of density and food level I conclude there were no treatment effects. In accordance with the 3-way repeated measures ANOVA results, feeding activity varies with body size and daytime (Fig. 5.4): The larger the crabs, the more individuals were observed feeding. Even though feeding activity was inconsistent across size classes on a 2-hourly basis, there was a 2 to 3-fold increase of individuals observed feeding at night time (between 6pm and 6am) compared to day time (Fig. 5.4 and Table 5.4).

Table 5.3: The 3-way repeated measures ANOVA results show that frequency of filter-feeding strongly varied with crab size and time of the day; however, food level and conspecific density had no effect. ¹Wilks' Lambda; all other values given as uncorrected F-test results. The Bonferroni adjusted α is 0.0125 for 'between subjects' results and 0.0071 for 'within subjects' results.

Between subjects				
Source	Value	df	F	p
All between	0.8872205	15	16.0883	<0.0001
Intercept	0.1115189	1	30.3332	<0.0001
Density	0.0015129	1	0.4115	0.5218
Food level	0.0064121	1	1.7441	0.1877
Size class	0.264044	3	23.9400	<0.0001
Density * food level	0.0071359	1	1.9410	0.1647
Density * size class	0.0187257	3	1.6978	0.1678
Food level * size class	0.00953	3	0.8641	0.4602
Density * food * size	0.019796	3	1.7948	0.1484

Within subjects				
Source	Value	df	F	p
All within ¹	0.2612141	180	2.1124	<0.0001
Time	0.0823161	12	1.7904	0.0498
Time * density	0.0217225	12	0.4725	0.9297
Time * food level	0.0268556	12	0.5841	0.8544
Time * size class ¹	0.6726501	36	3.0796	<0.0001
Time * density * food	0.0161893	12	0.3521	0.9780
Time * density * size ¹	0.8476566	36	1.2336	0.1659
Time * food * size ¹	0.7774879	36	1.9065	0.0012
Time * density * food * size ¹	0.8001615	36	1.6805	0.0081

Fig. 5.4: Feeding activity of crabs over 24h within 4 size classes, assessed in 2-hourly intervals. Due to an undetectable treatment effect and no differences between the 3 replicate runs, data were pooled. More crabs were observed feeding at night time than during the day. Larger the crabs exhibit higher feeding activity compared to small individuals. Error bars represent 95% confidence intervals.

Table 5.4: The percentages of feeding individuals within each size class allow the comparison of relative (average) frequencies of filter-feeding individuals within 2 time intervals. There was an increase of feeding activity from daytime (6am to 4pm) to night time (6pm to 4am) in all size classes of crabs. Pooled data of 3 replicate runs and all treatments were used for the calculation, including standard errors.

Size class	6am - 4pm Feeding individuals [%]	6pm – 4am Feeding individuals [%]	Increase x-fold Day vs. night
1	7.24 ±0.9	15.05 ±2.0	2.08
2	12.9 ±1.7	32.00 ±3.0	2.48
3	22.92 ±4.3	43.75 ±3.8	1.91
4	17.46 ±2.8	55.79 ±5.4	3.20

5.3.3 Effects of limb loss on growth rate

Table 5.5 2-way ANOVA results: individual growth rate IGR ~ T + S + (T x S)
The growth rate of crabs (i.e. the relative changes in individual wet weight over time) strongly varied with body size. There were significant differences between individual growth rate between uninjured crabs and those with regenerating limbs.

Source	SS	df	F	p
Intercept		1		<0.0001
Treatment	0.7774939	1	5.9608	0.0153
Size class	1.5869329	3	4.0555	0.0077
Treatment * size class	0.6891910	3	1.7613	0.1549
Error	34.695749	266		

Table 5.6 2-way ANOVA results: ind. body size increase ISI ~ T + S + (T x S)
The individual body size increase (i.e. the relative changes in individual carapace width over time) were significantly different between size classes of crabs; however, there was no effect of treatment.

Source	SS	df	F	p
Intercept		1		0.0938
Treatment	95.00	1	0.0051	0.9432
Size class	637661.92	3	11.3773	<0.0001
Treatment * size class	495117.98	3	8.8340	<0.0001
Error	4969487.2	266		

For the initial growth rate (IGR) the 2-way ANOVA results show no significant treatment x size class interaction (p=0.1549) (Table 5.5), with only one significant difference between size class 1 and 4 within treatment “all limbs present” according to Tukey’s HSD. However, the effect of treatment (p= 0.0153), as well as the effect of size class (p=0.0077) were both significant (Table 5.5). While post hoc tests showed that for the treatment effect all group means were significantly different, only the means for size class 1 and 4 were significantly different. Figure 5.5 reflects these results: crabs with removed chelipeds gained more weight over the entire duration of the experiment than those with all limbs present. While the

difference in weight change between the two treatments was small in size class 1 individuals, the increase in body mass of larger crabs (size classes 2, 3, and 4) was approximately 2 to 4 times higher among those individuals with clipped-off chelipeds after 7 weeks of observation (Fig. 5.5). For the weekly changes in % body mass see Appendix 5.1. Regardless of being injured or not, small crabs gain relatively more weight than larger ones (Fig. 5.5), which is consistent with the significant effect of size class on IGR.

In terms of body size (carapace width, CW), there was a highly significant treatment x size class interaction (Table 5.5) that can be mostly explained by 6 significantly different group means of size classes when comparing both treatments, followed by 4 significant differences within treatment “removed chelipeds” according to Tukey’s HSD. Within treatment “all limbs present”, however, there were no significant differences at all. The main effect of size class on individual body size increase (ISI) was highly significant (Table 5.6). Posthoc tests showed significant differences between size classes 1 & 3, 1 & 4, and 2 & 4. The effect of treatment, however, ($p=0.9432$) is not significant and, according to Tukey’s HSD, all group means for treatment effect on ISI are non-significant. However, when comparing mean and median values in Figure 5.6, there was a trend for size class 1 and 3 crabs to grow slower (i.e. their CW increased at a smaller rate) when regenerating limbs. Moulting may have occurred in only a few individuals. Consistent with the significant effect of size class on ISI, the average increase in body size over the duration of the experiment was dependent on initial body size (i.e. size class): the smaller the crabs the larger their increase in body size over time (Fig. 5.6). For weekly body size changes see Appendix 5.2.

An overview of the frequencies of developmental stages of limb regeneration within all size classes over the duration of the experiment shows that after 7 weeks, 80% of the animals with autotomized limbs had regenerated chelipeds with 75% of their original size (Appendix 5.3); small crabs regenerated limbs faster than large individuals. In the field, the chelipeds (1st pereopods) are the limbs most frequently regenerated; they were found replaced approximately twice more frequently than all other limbs (5.7 ± 0.91 vs. approx. 3%) (Appendix 5.4). In large crabs (size class 4 and 5) the highest percentages of limb regeneration were found (Appendix 5.5), whereas size class 1 crabs, the smallest individuals, were found more frequently with regenerated limbs than size class 2 and 3 crabs.

Fig. 5.5: Change in body mass [%] in uninjured crabs and individuals with removed chelipeds over 7 weeks within 4 size classes. Regardless of body size, crabs with removed chelipeds (grey) gain significantly more weight compared to uninjured crabs, mainly due to the regeneration process (i.e. cheliped growth). The dashed line represents the mean, the solid line the median values.

Fig. 5.6: Change in body size [mm] in uninjured crabs and individuals with removed chelipeds over 7 weeks within 4 size classes. The regeneration of chelipeds does not affect changes in body size over time (i.e. growth rate in mm CW); however, moulting may not have taken place in most individuals over the course of the experiment. The dashed line represents the mean, the solid line the median values.

Fig. 5.7: Early developmental stages of cheliped regeneration in *P. elongatus* at approx. 5%, 10% and 30% of its original size. Note the soft transparent tissue of early growth (“budding”) and the subsequent pigmentation and hardening of the exoskeleton that is independent of moulting.

In *P. elongatus*, as well as in other decapods, the time span between physical stress induced autotomy and beginning of cheliped regeneration depends on body size. While in small individuals (size class 1) initial growth became visible after 3 to 6 days, it took up to 20 days in large males and females (size class 4) (own obs., compare Appendix 5.3). The initial or basal growth is moult-independent and has been compared to a budding process (e.g. Hopkins, 2001) due to an initially cone shaped germinative protuberance consisting of soft, unsegmented and unpigmented, semi-transparent tissue (Fig. 5.7). At approximately 10% of its original size, the limb segments become visible and at approximately 25% of its original size, pigmentation of the tissue as well as epidermis hardening begins (Fig. 5.7).

For the body size / body mass relationship (Fig. 5.8) a cubic polynomial regression provided the best fit. A crab at 12mm CW, for instance, was 9 times heavier than a crab at 6mm. The body mass / cheliped weight correlation was best described by a quadratic regression (Fig. 5.9). A crab above a body weight of 800mg (without 1st pair of pereopods) had heavier chelipeds than cephalothorax, abdomen and walking legs combined; crabs with lower bodyweight had relatively lighter claws.

Fig. 5.8:
Body size
(carapace width)
versus total body mass
(wet weight)

$$R^2 = 0.989; p < 0.0001$$

Fig. 5.9:
Body mass (without
Chelipeds, wet weight)
versus cheliped weight
(both chelipeds,
wet weight)

$$R^2 = 0.984; p < 0.0001$$

5.3.4 Effects of population density on frequency of limb loss and limb loss on reproductive output

The percentages of individuals with regenerated limbs were negatively correlated with the total number of crabs per basket (i.e. the local density, Fig. 5.10). However, the results of a quadrat sampling experiment covering 15 times 0.25m² at three sites (see 2.2.4.1 in chapter 2 for a description of the method; due to the relevance within the present context these results are referred to here; see Appendix 5.6 and 5.7) indicate that the proportion of individuals with regenerating limbs did not vary with density (i.e. individuals per sample quadrat) and site (2-way ANOVA, Appendix 5.7), even though the slope of the regression line (Appendix 5.6) suggests a similar relationship to the one shown in Fig. 5.10. While in basket traps the relative frequency of injured crabs does not appear to be affected by intraspecific competition (i.e. the frequency of antagonistic behaviour), predation rate and environmental conditions (i.e. physiological stress, grinding rocks due to strong water movement) may lead to both lower densities and an increased risk to lose a limb.

$$R^2 = 0.989; p = 0.0387$$

Fig. 5.10: Number of individuals per basket trap (as a measure of local population density) versus percent values of individuals with regenerated limbs. The percentages of individuals with regenerated limbs were negatively correlated with the total number of crabs per basket, suggesting that limb loss is not affected by intraspecific competition, but may rather depend on environmental conditions and the rate of (attempted) predation that also affect density itself.

The reproductive output (RO), measured as the ratio of clutch weight to body weight, did not vary with density and was not different between females with regenerating limbs and uninjured animals (Fig. 5.11 and Table 5.7). However, the sample size of injured females with 7.5mm - 9.0mm CW and developmental stage 1 & 2 eggs was small (<5 per sample); therefore, this result should be viewed with caution. For a comparison of the proportion of clutch to body weight across sites see section 3.3.6.

Treatment 1: Uninjured females (all limbs present)
 Treatment 2: Females with regenerating limbs

Density 1: 79 adult crabs / basket
 Density 2: 118 adult crabs / basket
 Density 3: 173 adult crabs / basket

Fig. 5.11: Reproductive output (RO), measured as the ratio of clutch weight to body weight, in females with and without regenerating limbs. The clutches of females extracted from three basket traps (with corresponding adult densities) were analyzed, all of which were sampled at ISB. Samples from other sites were excluded due to low sample sizes. Further, only females with 7.5mm – 9.0mm CW and developmental stage 1 & 2 eggs were selected for the analysis. While there is a strikingly clear pattern on the first glance, differences between females with regenerating limbs and uninjured animals as well as between densities (i.e. samples) were non-significant (see below). Error bars represent 95% confidence intervals.

Table 5.7: ANCOVA results reproductive output: $RO \sim Reg + D + (Reg \times D)$ show no significant differences between females with regenerating limbs and uninjured animals (Reg). Reproductive output does not vary with density, either.

Source	SS	df	F	p
Reg.	112.22199	1	1.8070	0.1878
Density	83.926830	1	1.3514	0.2531
Reg. * density	1.5798900	1	0.0245	0.8742
Error	2310.5638	37		

5.4 Discussion

In the present study, individual growth rate (IGR) was highest among the smallest individuals at low density (Fig. 5.2). Similarly, daily growth was negatively correlated with body size in *Petrolisthes cinctipes* (Donahue, 2004) as well as in the freshwater prawn *Palaemon lamarrei* (Katre & Reddy, 1977). Body size determines growth for various reasons: Small individuals grow faster due to higher metabolic rates (Peters, 1983), higher growth efficiency (Klein-Breteler, 1975), higher moulting frequencies (López, 1997, Asakura, 1992, and own observation), as well as higher growth increments (Asakura, 1992, Hartnoll, 1982, 1985).

Effects of conspecific density on individual growth rate

Density was an excellent predictor of IGR (Table 5.1) with generally higher IGR at low density (Fig. 5.2). This is consistent with the findings of Donahue (2004) as well as studies examining the effects of culture density on growth in juvenile spider crabs (Domingues & Alaminos, 2008), red king crab juveniles (Daly *et al.*, 2009), and the Chinese mitten-handed crab (Wenkuan *et al.*, 2009). However, the effect of conspecific density on IGR was different among size classes without showing a clear pattern. Donahue (2004) found IGR more strongly affected by density in small *Petrolisthes cinctipes* individuals, indicating smaller individuals suffer more from agonistic interactions than larger ones. Leslie (2005) found that in the intertidal barnacle *Balanus balanoides* density was negatively correlated to growth and individual reproductive output, but positively correlated to survival, resulting in a positive net effect of increased fitness at high densities. In aggregating species, however, the trade-off between density dependent survival benefits and growth costs may result in optimal group sizes and densities well below theoretical maxima (Booth, 2004), e.g. due to competition for food.

Effects of food level on individual growth rate

In the present study, IGR did not vary with food level (Table 5.1) except for the largest size class of crabs (Table 5.2), indicating large individuals may be more affected by limited food availability than smaller ones. Gimenez & Anger (2005) demonstrated that early brachyuran crab larvae are well adapted to the temporary lack of planktonic food. On the contrary, Peters (1983) suggested that smaller organisms are potentially more sensitive to changes in food level due to higher

metabolic rates. Moreover, intraspecific competition is expected to decrease with increasing body size (Donahue, 2004). The seemingly reversed pattern in the present study as well as the non-significant interaction between density and food level (Table 5.1) remains elusive and may have been influenced by sufficient food resources even in the low food level / high density treatment. Additionally, higher filtration efficiencies among smaller crabs could have been caused by a relatively high proportion of very small food particles due to the grinding of freeze-dried spirulina fish flakes. In Porcellanidae, the third maxillipeds, densely fringed with plumose setae, are used as filter apparatus (Nicol, 1932). Since the spaces between these setae increase with body size (personal obs.) the resulting mesh size, particle size selectivity and filtration efficiency varies. The “specialisation” on different particle sizes, in turn, results in resource partitioning and hence minimizes intraspecific competition for food (Pinn *et al.*, 1998). Size selective suspension feeding has been demonstrated for many taxa, e.g. rotifers (Rothhaupt, 1990), cnidarians (Collin *et al.*, 2003), polychaetes (Ropert & Goulletquer, 2000), bivalves (Shumway *et al.*, 1985), barnacles (Harvey, 1937), calanoid copepods (Mullin, 1966), penaeid shrimps (Nunes & Parsons, 1998), thalassinid crabs (Pinn *et al.*, 1998), and fishes (Castillo-Rivera *et al.*, 1996). For a review on motile suspension feeders, see Bushek & Allen (2005). Trophic plasticity, in terms of food sources and feeding mechanisms, has been reported for Porcellanidae by Caine (1975); Kropp (1981); Stevcic (1988); Trager & Genin (1993), and Achituv & Pedrotti (1999). In the field, feeding efficiency in filter feeders is controlled by flow velocity (Trager & Genin, 1993), immersion time (Bertness & Grosholz, 1985; Depledge, 1989), the amount of particulate organic matter (POM) in the water column (Helson, 2001), as well as dissolved organic matter (DOM, particle size < 0.45 µm) (Gili & Coma, 1998), and seston quality (Helson & Gardner, 2007).

Feeding activity

Werner & Anholt (1992) showed the pivotal importance of food level on feeding activity if the activity level is linearly correlated with both growth and mortality rates. Feeding rates among filter feeders commonly decrease with decreased food availability (Sanford *et al.*, 1994). In the present study, however, neither food level nor density had a significant effect on feeding activity (i.e. the number of individuals within a particular size class feeding at a time) which may have been

related to sufficient food resources even in the low food level / high density treatment. It was therefore difficult to distinguish the relative effects of exploitative and interference competition as Anholt (1990), Fradkin (1995), and Schmitt (1996) were able to quantify. Under food scarcity, effects of exploitative competition should have been reflected as reduced feeding activity and eventually in lower growth rates, especially in small crabs. Donahue (2004) reported lower feeding activities at higher density, presumably due to depleted food resources within the aquaria she used as rearing system. In the field, Barange & Gili (1988) and Klimmerer *et al.* (1994) demonstrated substantial local declines in phytoplankton due to the feeding ability of highly abundant filter feeders that are likely to regulate primary production directly and secondary production indirectly.

Porcelain crabs may compete for good filter-feeding locations (Donahue, 2004) in the field as well as in captivity, since the animals tend to congregate in locations with high flow in aquaria (Jensen, 1990; Donahue, 2004, and pers. obs.). Within these aggregations, agonistic behaviours described by Molenock (1976) can be frequently observed. Zittin (1979) reported that *Petrolisthes cinctipes* forms dominance hierarchies even in captivity, often with a single male controlling access to prime feeding currents and protective shelter (Jensen, 1990).

Despite higher individual growth rates at smaller body sizes, feeding activity was significantly lower in smaller crabs. Similarly, Donahue (2004) found that the smallest *Petrolisthes cinctipes* individuals fed significantly less frequently than crabs from all other size classes. However, a lower rate in feeding activity of small crabs does not necessarily indicate lower food intake relative to body weight (e.g. in % body mass) since the size specific feeding efficiency is unknown. Due to higher metabolic rates small individuals are likely to have relatively higher consumption rates (e.g. Bertalanffy, 1957). Cammen (1980) reviewed the food intake of various species of benthic invertebrate deposit feeders and detritivores and found that relative organic matter ingestion was a function of body size. In the mangrove crab *Ucides cordatus* (L. 1763), the daily food intake was strongly correlated with body size ranging from 19.8% of body dry weight in small crabs to 6.0% in large individuals (Nordhaus *et al.*, 2006).

The generally higher feeding activity in *P. elongatus* at night has not been reported in earlier studies and may be an adaptation to higher predation risk at day time from visual predators such as fishes and birds. Gonor & Gonor (1973) observed a periodicity in feeding activity of megalopae of *Pachycheles pubescens* and *P. rudis* (porcellanidae); however, these authors did not demonstrate an effect of light conditions on feeding behaviour. Förster & Baeza (2001) reported a higher general activity of females in *Petrolisthes violaceus* at night compared to day time, even though embryo grooming was significantly higher during the day. However, Ziedins & Meyer-Rochow (1990) showed that unlike in crayfish (Arechiga & Wiersma, 1969) and rock lobster (Meyer-Rochow & Tiang, 1984) visual sensitivity in *P. elongatus* is not linked to a circadian rhythm.

Mortality

In captivity, mortality rates among small crabs were generally higher compared to larger size classes, but were not significantly affected by food level. The overall mortality pattern can be identified among the basic schemes suggested by Deevey (1947) and seems to resemble type III, where mortality is high among early life history stages with only a few survivors that have a greater life expectancy. The higher mortality rates at low density contrast with the significantly higher growth rates at low density and may be explained by adverse effects of food particle accumulation in aquaria between cleaning due to lower total consumption rates at low density. In addition to predation in the field, mortality may increase with frequency of limb loss (e.g. Figiel & Miller, 1995).

Effects of limb regeneration on growth rate and reproductive output

In contrast to the suggestion of Donahue (2004) that cheliped loss is a potentially important cost of agonistic interactions, the relative frequency of injured crabs did not appear to be affected by intraspecific competition in the present study. Most intraspecific competitive interactions in *P. elongatus*, and generally in crustaceans, are highly ritualized and do not result in autotomy (Molenock, 1975, Juanes & Smith, 1995, and literature therein). The percentages of crabs with regenerating limbs were higher at lower densities, suggesting that, rather than agonistic behaviour, the rate of attempted predation as well as environmental conditions may be related to an increased risk of limb loss. Habitat factors such as wave exposure and rock size (i.e. substrate stability) may simultaneously increase

the rate of limb loss and mortality by crushing extremities and individuals. In turn, mortality rates could negatively affect local density. In the common shore crab *Carcinus maenas*, McVean (2003) found a higher frequency of limb loss at an exposed shore compared to sheltered sites. Additionally or alternatively, the local predator abundance could explain this pattern, dependent on habitat structure (i.e. availability of refuges for crabs vs. interstitial space amongst boulders accessible to predator species).

Limb regeneration requires resource allocation for this process that may result in a decreased carapace growth (Donahue, 2004; for reviews, see Juanes & Smith, 1995, Mariappan *et al.*, 2000). In the present study, however, individuals with removed chelae gained 2 to 4 times more weight compared to uninjured crabs, probably due to the process of limb regeneration itself. Additionally, cheliped removal did not seem to affect growth rate in terms of body size, but molting may have occurred only in a few individuals within the limited duration of the experiment. The costs of limb loss in *Petrolisthes* may be compensated by an increase in food intake (Wasson *et al.*, 2002; Donahue, 2004) but may negatively affect individual growth rates under food scarcity. Compared to other limb types the replacement of chelipeds should divert the greatest amount of energy from growth due to their relatively large proportion of the total body weight (>50% in large adults). The more limbs are regenerating at a time, the more evident is the effect on increase in body size per moult (Juanes & Smith, 1995, and literature therein). In the fiddler crab *Uca pugilator*, regeneration of a number of limbs may even result in negative growth (Hopkins, 1982). In decapods, limb autotomy commonly affects the moult cycle: Depending on the number of limbs removed and the stage at which injury occurs, ecdysis can be either accelerated or delayed (Hopkins, 1982; Spivak, 1990; Smith, 1992).

The reduced size of regenerated appendages can affect animal performance at many levels (Maginnis, 2006). The effects of limb loss on growth are potentially important for individual fitness of decapods (Juanes & Smith, 1995) because differences in relative body size have been shown to be critical to reproduction and the outcome of various ecological interactions such as intraspecific competition and predator-prey encounters (Hyatt, 1983; Garvey *et al.*, 1994; Smith, 1995). Limb replacement may also decrease reproductive output directly

(Hines, 1992; MacDiarmid, 1986; Luppi *et al.*, 1997), the ability to attract mates (e.g. van der Meeren, 1994), or the reproductive potential of a crab population (Lysenko *et al.*, 2000). However, Juanes *et al.* (2008) suggest that for females, allocating energy to egg production and brood care may be more important than investment in increasing claw size. Comparing the ratio of clutch to body weight between *P. elongatus* females did not reveal a significant difference between injured and uninjured individuals; however, the power to detect such a difference was low due to low numbers of ovigerous females with regenerating limbs found in the field (n=9; 1.97% of all females). All of these females had only a single regenerating limb and in two cases a cheliped was regenerating, rather than a walking leg. Interestingly, 83.68% of the uninjured females were ovigerous whereas only 50.0% of the females with regenerating limbs carried eggs. While this result should again be treated with caution with regard to sample size, the significant difference in the relative frequency of ovigerous females between these two groups may indicate that limb loss impairs mating success in *P. elongatus* females. Juanes & Smith (1995) found that frequency of limb loss is generally independent of sex in most decapods.

A considerable number of studies on agonistic behaviour in decapods had shown that body or chelae size determines competitive capability (e.g. Garvey & Stein, 1993; Sneddon *et al.*, 1997). Body size determined the success in agonistic interactions between pairs of *Petrolisthes cinctipes* (Molenock, 1976) and *Allopetrolisthes spinifrons* (Baeza *et al.*, 2002). Contrary to my findings that large crabs had a higher frequency of limb regeneration in the field (Appendix 5.6), Donahue (2004) found that small crabs in captivity were more susceptible to limb loss at low food levels. Wasson & Lyon (2005) showed that in *P. cinctipes* and *P. manimaculis* small individuals and females autotomized their limbs more readily than larger ones and males. However, full limb regeneration is a considerably longer process in larger crabs and may therefore be found more frequently in larger individuals in the field. Additionally, since larger crabs are more mobile than smaller individuals, they may be more susceptible to predation and predation attempts.

In addition to claw use in agonistic interactions, the flattened chelae in *Petrolisthes* are thought to work as current deflectors (Werdning, B., pers. comm.).

The underside of crabs in this family forms a suction cup in which the extremities play a critical role concerning its adhesion efficiency (Molenock, 1976, and pers. obs.). Hence, in *P. elongatus*, missing chelipeds do not only limit individual defence from competitors and predators but may also impair the ability to cling to the surface of rocks in wave exposed areas (pers. obs.) and therefore further increase predation risk and mortality. Zimmer-Faust (1989) suggested that autotomy may be particularly important in aquatic environments, where waterborne chemical cues of injured individuals can attract predators. Hazlett (2000) and Hazlett *et al.* (2000) found that *P. elongatus* decreased locomotion and other movements upon introduction of an alarm odour released by crushed conspecifics. If this cue alerts predators is unknown to date. Based on relatively lower frequencies of regenerated than missing limbs found in the field McVean & Findlay (1979) and Shirley & Shirley (1988) suggested that injury may increase mortality in decapods. Harris (1989) emphasized the importance of non-lethal injury as a regulating factor of population size in some species if injury is density dependent and decreases reproduction.

The regeneration of autotomised limbs begins with moult-independent basal growth of soft, unsegmented and unpigmented, semi-transparent tissue (compare Fig. 5.7) that involves mitosis and differentiation, followed by a second phase of proecdysial growth that is partly under direct hormonal stimulation (Bliss, 1956; Hopkins, 1993, 2001). In crustaceans, total recovery of a limb following autotomy generally requires a minimum of two moults (e.g. Miller & Watson, 1976; Smith, 1990) but may require up to seven moults over seven years in the blue king crab, *Paralithodes platypus* (Lysenko *et al.*, 2000). Furthermore, limb recovery is dependent on the moult frequency as well as the proportion of limb length replaced at each ecdysis (Goss, 1969; Skinner, 1985). The time required to regenerate a limb to normal size may vary dramatically with temperature (e.g. Weis, 1976) as well as between life history stages and species of crabs (Juanes & Smith, 1995). Because in crustaceans moulting frequency typically declines with age (Hartnoll, 1982), regeneration takes longer in older individuals (Smith & Hines, 1991). In *Petrolisthes elongatus*, the complete regeneration of the chelipeds takes between 9 and 14 weeks (pers. obs.) at 15°C, with significantly faster rates in smaller crabs (Appendix 4.5). In the paddle crab *Ovalipes trimaculatus*, the complete regeneration of the 4th pereopod took between 9 and

10 weeks (Alvarez & Meruane, 2009); segmentation of the limb bud became visible after 4 weeks, pigmentation started after 6 and cuticle hardening after 7 weeks. Infestations with parasites such as bopyrids, entoniscids and sacculinids are known to affect the normal growth of chelipeds (O'Brian & Skinner 1990; Mariappan *et al.*, 2000, and literature therein); however, parasite infested individuals of *P. elongatus* can rarely be found in the Wellington region (own obs.).

Conclusions

In summary, *P. elongatus* grew faster in captivity at low density with generally higher mortality rates for smaller individuals, indicating that the costs of aggregation are more pronounced for juveniles than for adult crabs. However, there was no effect of food level, presumably due to a sufficient food supply even within the low density treatment. Donahue (2004) conducted a similar laboratory experiment with *P. cinctipes* and filtered versus unfiltered seawater as food level treatments and showed strong effects of density and food level on IGR. Future research may elucidate how growth rates in the field depend on local population density and long term food supply.

The frequency of limb loss appeared to be mainly affected by environmental conditions and attempted predation rather than by conspecific density and agonistic interactions as Donahue (2004) suggested. Besides predator abundance, habitat stability and disturbance that are related to rock size and wave exposure may determine the risk of limb loss in *P. elongatus*. However, further investigations are necessary to shed light on the costs of autotomy and limb regeneration in porcelain crabs and their implications on individual fitness and survival.

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Appendix 5

Appendix 5.1: Weekly changes in body mass [%] in uninjured crabs and animals whose chelipeds had been removed by artificially induced autotomy.

Appendix 5.2: Weekly size changes [mm carapace width] in uninjured crabs and animals with removed and regenerating chelipeds.

Appendix 5.3: Frequency of developmental stages of limb regeneration within 4 size classes over 7 weeks. The full limb regeneration takes between 9 and 14 weeks, independent of moulting but dependent on body size (pers. obs.). Chelipeds in smaller crabs are regenerating much faster than in larger individuals. Differences between sexes were not observed.

Appendix 5.4: Percentage of the total population at which a limb pair (1st to 4th pereopods) was found regenerating (i.e. in the process of regeneration). From all limb pairs, regenerating chelipeds (1st pereopods) were found most frequently. Error bars represent 95% confidence intervals.

Appendix 5.5: Percent individuals with regenerating limbs within 5 size classes. While size class 1 crabs shed their limbs more readily than larger animals and may be more prone to injury due to environmental conditions, the regeneration process in larger crabs takes longer and, therefore, could be more frequently observable. Additionally, adults may be more prone to injury due to attempted predation since migration rates are higher in larger crabs. Error bars represent 95% confidence intervals.

Appendix 5.6: Number of sexually mature individuals per sample quadrat versus percent values of individuals with regenerated limbs. (Results were obtained by quadrat sampling, described in chapter 3.)

Appendix 5.7: 2-way ANOVA results: proportion individuals with regenerated limbs PR ~ D + S + (D x S) (D = Density: individuals per sample quadrat; S = Site).

Source	SS	df	F	p
Intercept		1		< 0.0001
Density	79.6478	1	1.4392	< 0.2436
Site	37.6037	1	0.3397	< 0.7158
Density * site	75.7510	2	0.6844	< 0.5153
Error	1162.1836	21		< 0.2100

Chapter 6

General discussion

6.1 Summary of findings

The examined metapopulations of *P. elongatus* at the south coast as well as within Wellington Harbour exhibited a high variability in population density and reproductive traits across sites and had a patchy distribution on almost all scales of observation. The underlying mechanisms driving the heterogeneity of abundance on a larger scale could not be identified in the present study; however, it is likely that the significantly (6-fold) higher densities of *P. elongatus* within the harbour with up to 843 individuals per sample quadrat ($= 3372 \text{ ind./m}^2$) compared to south coast sites can be explained by the varied availability of shelter space as well as by probably significant differences in food and larval supply. Cobble size largely explained the heterogeneity of abundance of *P. elongatus* especially on small scales ($<50\text{cm}$ and $<5\text{m}$) but also on the large scale (between approximately 5 and 15km) and was generally a suitable predictor for mean carapace width with larger crabs under larger rocks, thereby influencing local population structure. Both, density as well as the mean size of adult crabs appeared to be strongly influenced by substratum constraints, specifically the availability and size of interstitial space between boulders that in turn depend on the size and size frequency distribution of rocks. Cobbles with a surface area smaller than 30cm^2 were not used as shelters at all sites due to a high local disturbance risk (i.e. movement of rocks) and insufficient protection from temperature and desiccation stress.

While the mobility of crabs strongly varied with site, differences in structural complexity did not have a major impact on migration rate. The underlying mechanisms responsible for approx. 50% shorter migrated distances at Hutt River mouth ($<70\text{cm}$ over 25h) compared to those recorded at the south coast remained unclear but were likely to be influenced by relatively higher levels of intraspecific competition due to significantly higher local densities. Generally, mobility of

P. elongatus is low compared to other decapods and depended on crab size with higher migration rates in larger crabs.

Conspecific density affected individual growth rate and mortality under laboratory conditions, especially among smaller individuals. Feeding activity, however, was not correlated with density but strongly varied with time of the day (2-4fold increases at night) and size, with higher frequencies of filter feeding in small crabs.

Settlement rates varied on a surprisingly small scale (tens of centimetres), dependent on the presence and density of conspecific adults. Similar to other *Petrolisthes* species, males and females of *P. elongatus* release a waterborne settlement cue that attracts conspecific larvae and influences settlement patterns via heterogeneous cue densities. Recruits may still positively respond to these cues, possibly guiding them to aggregations of protecting adults; however, the results in this aspect were inconclusive.

Under laboratory conditions, fish predation on crabs mainly depended on crab size with higher predation among smaller crabs. In the field, however, cobble size may also affect the frequency of predator-prey encounters and therefore predation rate, as well as the risk of limb loss due to predation attempts and shifting and grinding of smaller rocks in the surf. Limb loss was negatively correlated with conspecific density and is most likely related to disturbance rate, wave exposure, and predator abundance. The limb regeneration process is independent of moulting and was responsible for a higher wet weight increase compared to uninjured crabs. Whether the associated energetic costs of limb loss affect growth increment during moults and / or reproductive output remains to be tested.

The reproductive traits of *P. elongatus* were highly variable across sites, with the highest reproductive output per female (i.e. ratio clutch to body weight), and higher egg numbers in similar-sized females at Island Bay compared to other sites. This pattern is probably influenced by lower levels of intraspecific competition at this site compared to other sites, while temperatures at the south coast were generally lower compared to the harbour. However, females with the largest eggs with highest egg water content and highest egg dry weight were

found at HRM, presumably driven by abundant food and lower salinity. Generally, each of the examined metapopulations is exposed to different environmental conditions that may be responsible for the phenotypic plasticity *P. elongatus* exhibits. However, in the present study it could not be determined to what degree site specific phenotypic differences occurred as a result of plastic responses to environmental conditions or to what extent these differences were genetically determined.

Generally, *P. elongatus* appears to be well adapted to its patchy and naturally fragmented habitat over a wide range of environmental conditions. While population dynamics are largely driven by habitat structure and environmental conditions, life history traits such as high frequency of spawning, phenotypic plasticity, high dispersal capacity due to a long pelagic larval phase and conspecific cueing allow these crabs to thrive in sustained metapopulations reaching higher densities than any other species in intertidal boulder fields.

6.2 General discussion

The role of habitat structure in shaping patterns of abundance and population structure

Similar to aggregations of *P. cinctipes* (Donahue, 2004, 2006), *P. eriomerus* (Jensen, 1989, 1990) and *P. laevigatus* (Gebauer *et al.*, 2007) in intertidal boulder fields, the highly clumped distribution of *P. elongatus* on small scales is closely related to the availability and size of shelters, combined with shelter targeting behaviour especially during low tide. Ultimately, available shelter space depends on both rock size and habitat structure (i.e. layering, surface rugosity, and the presence or absence of fine sediment). Therefore, small scale variations in habitat structure and complexity are correlated with the patchiness of abundance of crabs inhabiting the interstitial space. It is widely acknowledged that refuge availability, shelter size, and habitat structural complexity can strongly affect the abundance and demography of crab populations (Howard, 1980; Wahle, 1992; Beck, 1995; Sosa-Cordero *et al.*, 1998; Allen *et al.*, 2006). Consequently, and because the degree of environmental heterogeneity varies with spatial scale, patterns of abundance are expected to vary with the scale of observation, as well (Wiens,

1989; Levin, 1992). *P. elongatus* prefers larger rocks as shelters over smaller ones, probably due to better protection from desiccation and temperature stress by larger rocks (Stillmann & Somero, 1996; Stillman, 2002; Emparanza, 2007) as well as from strong water movement and predation. Larger rocks in combination with lower wave exposure may additionally provide more stable microhabitats with lower mortality rates compared to smaller rocks that shift and grind in heavy surge. Because larger crabs (i.e. dominant competitors, see Molenock, 1976) were found under larger rocks, leading to a positive correlation between rock size and mean carapace width, population structure (i.e. the size frequency distribution) is closely associated with shelter size. Additionally, settlement and recruitment rates, in combination with conspecific cueing, strongly influence local population demographics as well as patterns of abundance. Density, in turn, affects individual growth rate (compare Donahue, 2004) and therefore reproductive output since egg numbers per female are strongly associated with body size. Local crab density may be mitigated by the (size dependent) movement of individuals competing for optimal feeding locations (Molenock, 1976; Jensen, 1990) during high tide (see below). The underlying mechanisms driving the heterogeneity of abundance on a larger scale were only partly identified in the present study; however, it is likely that the significantly higher densities of *P. elongatus* within Wellington Harbour compared to south coast sites can be explained by 1) more available shelter space at Hutt River mouth due to a larger range of rock sizes and multiple layers, 2) higher food supply within the harbour according to findings of Gardner (2000, 2002); Gardner & Thompson (2001); Helson (2001), and Helson *et al.* (2007), and 3) presumably relatively lower settlement and recruitment rates at Cook Strait due to prevailing currents and higher larval densities within the harbour as presented by Helson & Gardner (2004) for planktonic larval densities of the bivalves *Aulacomya maoriana*, *Mytilus galloprovincialis* and *Perna canaliculus*.

Influences of settlement and conspecific cueing on patterns of abundance

In many benthic marine invertebrates settlement crucially depends on the presence of conspecific adults and is delayed in absence of conspecific cues (Pechenik, 1990; Gebauer *et al.*, 2003). Because higher cue concentrations may trigger stronger attraction effects in larvae and waterborne cue density depends on local variations of abundance of adult crabs, settlement rates may vary even on a scale of tens of centimetres in areas with low wave exposure. Jensen (1989),

Donahue (2006), and Gebauer et al. (2011) presented evidence that megalopae of *P. cinctipes*, *P. eriomerus* and *P. laevigatus* also settle preferably in the presence of conspecific adults, suggesting that conspecific cueing may be common in *Petrolisthes* spp. Generally, conspecific cueing is common among marine invertebrates including many crustacean species (for reviews, see Meadows & Campbell, 1972; Crisp, 1974; Burke, 1986; Pawlik, 1992; Rodriguez *et al.*, 1993; Rittschof *et al.*, 1998; Hadfield & Paul, 2001; Hay, 2009) because it facilitates a higher probability of finding suitable or high quality habitat (Raimondi, 1988; Jensen, 1989). Gregariousness frequently leads to extremely high population densities (Jensen, 1989, 1991; Jensen & Armstrong, 1991).

Density dependence

Elevated density may negatively affect individual growth and feeding rates and could lead to increased mortality rates under laboratory conditions with more pronounced effects on smaller individuals of *Petrolisthes* spp. (compare Donahue, 2004). Hence, the costs of aggregation are higher for recruits than for adult crabs. However, intraspecific competition does not only depend on density but also on availability of resources such as food and shelters. In the field, interference competition for space could decrease individual fitness due to energetic costs of agonistic behaviour. Additionally, the occupancy of shelters by an aggregation of crabs whose larger individuals may be dominant competitors results in the decrease in availability of the critical resource shelter space. Exploitative competition for food in porcellanids, on the other hand, may only play an important role at sites with long term food limitation and low water movement, where the local depletion of food particles could lead to decreased individual growth rates and fitness. Highly abundant filter feeders may be responsible for substantial local plankton declines (Barange & Gili, 1988; Klimmerer *et al.*, 1994). However, variations in food supply may be partly attenuated by effects of water movement. While food levels are generally higher and wave exposure lower in shallow natural embayments such as Wellington Harbour, the open coast is commonly characterised by high wave exposure (involving constant water movement and mixing processes within the surf zone) but lower levels of particulate organic matter (e.g. Helson *et al.*, 2007). Additionally, similar to bivalves such as *Perna canaliculus* (Hawkins *et al.* 1999), porcelain crabs are able to adjust feeding rates over a wide range of plankton concentrations (Kropp,

1981; Števíć, 1988) and current velocities (Trager & Genin, 1993; Achituv & Pedrotti, 1999). However, despite evidence for Allee effects (e.g. decrease in predation on settlers in the presence of conspecific adults, Donahue, 2006) intraspecific competition appears to be generally an important feature in mobile filter feeders such as *Petrolisthes* spp. (compare Donahue, 2004) as well as in filter feeding sessile invertebrates (reviewed in Branch 1984).

The contribution of mobility to patterns of abundance

When undisturbed, movement and migration predominantly occurs during high tide, as soon as there is enough water for filter feeding (own obs.). Movement appears to be mainly motivated by the search for optimal feeding spots (Jensen, 1990; Donahue, 2004) at which microhydrodynamic conditions (i.e. small scale current velocities, laminar vs. turbulent flow) maximise feeding efficiency. Additionally, the search for mates as well as agonistic behaviour in *Petrolisthes* spp. described by Molenock (1976) may contribute to movement patterns. As soon as the intertidal boulder fields re-emerge with the outgoing tide, shelter targeting behaviour (Meyer-Rochow & Meha, 1994) in conjunction with a negative phototaxis (Scott, 1958) may become the main driver for migratory activity. The tide dependent variations in movement, short range dispersal and aggregation are very similar to those found in many intertidal hermit crabs (e.g. Gherardi & Vanini, 1993; Turra & Leite, 1999). While small individuals remain within crevices and cavities among rocks almost permanently, larger crabs move about during high tide. In addition to active movement, a combination of passive drift and swimming behaviour (by rapidly flapping their abdomen) may occasionally transport individuals to nearby locations after having been dislodged in heavy surf (own obs.). Population density appeared to be negatively correlated with mobility whereby high density patches may act as physical barrier involving agonistic interactions between “intruder” and “local” individuals. Similar to *P. cinctipes* (see Donahue, 2004), *P. elongatus* is relatively sedentary compared to other decapods.

The role of predation in relation to habitat structure

A number of studies suggest that predation effects on crab and reef fish populations are mediated by the protective capacity of a reef or vegetative benthic cover with high structural complexity (e.g. Eggleston & Lipcius, 1992; Eggleston

et al., 1997; Moksnes *et al.*, 1998; Thistle *et al.*, 2010). However, despite evidence for a negative correlation between rock size and fish predation rates on small crabs under laboratory conditions, the influence of habitat structure on predation rate and survival in natural conditions was difficult to quantify. In the field, predation effects are far more complex compared to the observed patterns in aquaria, where other predator species and site specific predator abundance as well as abiotic factors such as wave exposure were excluded for simplification.

Reproductive traits and phenotypic plasticity

P. elongatus exhibits a high variation in life history characteristics across sites that are likely to be influenced by environmental factors such as food supply, temperature and salinity. In turn, the variability of environmental conditions across and within habitat patches leads to a high degree of phenotypic plasticity that is not necessarily adaptive, but rather the physiological and biochemical response of organisms to variable environments. The naturally fragmented habitat that leads to geographically isolated metapopulations selects for an adequate dispersal potential, e.g. a long pelagic larval phase, to ensure connectivity (i.e. sustained gene-flow) and the ability of patch (re-) colonisation as an adaptation to minimize local extinction risk (Hanski, 1998). Additionally, conspecific cueing increases survival because the presence of a benthic population of conspecifics indicates habitat suitability. Generally, the investment in per-capita survival is high in *P. elongatus* that exhibits low numbers of large eggs relative to similar-sized decapods from temperate latitudes. Contrary to the traditional perception that dispersal capacity is closely related to large numbers of small eggs, porcelain crabs appear to have evolved an alternative strategy that compensates fewer eggs per female not only with higher investment in individual survival but also with high frequency of spawning and high reproductive output per female (in terms of the clutch weight to body mass ratio). Further, the egg production per m² habitat may be high due to commonly high adult densities. However, animals with biphasic life cycles, including porcelain crabs, often experience considerable losses during their early development in plankton due to predation (e.g. Pineda, 2000; Rilov & Shiel, 2006).

6.3 General conclusions

Clustered distributions of mobile invertebrates in intertidal boulder fields do not necessarily arise from social behaviour or conspecific cueing, but may also be strongly influenced by the response of individuals to structural complexity of the habitat, micro hydrodynamic conditions, and available shelter space. The resulting aggregation is associated with a number of benefits, such as increased reproductive success and the protection of juveniles by adults. However, while aggregating species may have evolved an elevated tolerance for high conspecific densities, intraspecific competition could have adverse effects on individual growth rate, reproductive output and ultimately fitness at densities close to the specific carrying capacity of a habitat patch. To some extent, levels of intraspecific competition could be mitigated by migration, dependent on densities and competition in adjacent patches (see Fig. 6.1).

Fig. 6.1: General conceptual model of mechanisms influencing local population density, demography (i.e. size frequency distribution), and reproductivity in intertidal marine invertebrates using the example of porcelain crab populations living in intertidal boulder fields.

VanHorne (1983) noted that population density may be a misleading indicator of habitat quality because intraspecific dominance interactions (e.g. territory

acquisition by dominant males) may lead to the displacement of less dominant individuals to low quality habitat patches. Within a “saturated” habitat, mortality regulates maximum population density. Both mortality and migration rate may be size (or age) dependent, shaping the local population structure. Additionally, individual growth rate is commonly influenced by intraspecific competition, leading to decreased individual reproductive output because, in decapods, female body size determines the number of offspring. Food limitation due to low food supply and / or exploitative competition may further reduce reproductive output, directly or indirectly. Gregarious settlement typically involves conspecific cueing that leads to higher settlement rates in patches with higher benthic populations of conspecific adults, thereby influencing local density and population demography (i.e. size structure). Predator abundance in conjunction with the availability of shelters influences predation rate that may be selective with regards to prey size (e.g. higher among small individuals). On the other hand, the frequency of predator-prey encounters that is dependent on habitat structural complexity may increase the risk of limb loss due to attempted predation and a successfully applied escape strategy (i.e. autotomy). Limb loss may also depend on disturbance rate, potentially leading to decreased individual growth and / or reproductive output due to resource allocation to limb regeneration.

Since habitat structure and specifically interstitial space among boulders is critical for the survival of mobile intertidal invertebrates, the availability of shelters (that is closely related to cobble size) is an important indicator of habitat quality for species such as porcellanids and hermit crabs. Interstitial space may strongly affect local population density and population structure either directly (shelter space as limiting resource) or indirectly (e.g. via the influence of cavity size on predation rate).

While high spatio-temporal variations in environmental conditions within and across habitat patches may lead to heterogeneous patterns of abundance and select for a high phenotypic plasticity in reproductive traits, many life history characteristics can be viewed as specific adaptations to environmental factors. If for example the natural fragmentation of suitable habitat requires a high dispersal potential there may be alternative stable states or strategies within and across species that successfully achieve persistence and fitness maximisation.

6.4 Future research

Further analysis of spatial distribution of individuals

Crowding represents the level of local density (and hence intraspecific competition) that the average individual experiences (Lloyd, 1967; Hartley & Shorrocks, 2002). The quadrat sampling data analyzed in section 2.3.1 may provide information on mean crowding per habitat patch (i.e. per quadrat, nest and site), since the size frequency distribution and number of crabs was recorded for each rock within each quadrat. Mean crowding is defined as the “number of other (i.e. non-self) individuals in a patch, averaged across individuals” including the relationship between variance and mean ($\bar{c} = M + (V/M) - 1$). In addition to mean crowding, the Index of Aggregation (IA), introduced by Ives (1988) could be useful to further analyse quadrat sampling data. This index measures “the level of within-patch density, averaged across individuals, relative to a random distribution of the same regional mean”, $IA = (V - M) / M^2 = (\bar{c}/M) - 1$ (see Hartley & Shorrocks, 2002). In aggregated populations mean crowding is significantly elevated compared to the mean number of individuals per patch, whereas for a random (Poisson) distribution no difference is detectable. However, Neuhäuser *et al.* (2010) pointed out that crowding data consist of values that are not statistically independent since, by definition, all individuals have the same number of neighbours within a certain patch and subpopulation. In order to avoid pseudoreplication according to the definition of Hurlbert (1984), classic statistical methods cannot be applied (see Reiczigel *et al.*, 2005, 2008). A different kind of statistical non-independence (i.e. spatial autocorrelation) could arise from the mobility and migratory activity of individuals. The number of crabs under a certain rock may be influenced by the number of crabs under a neighbouring rock, dependent on relative distance. Spatial autocorrelation statistics such as Moran’s I or Geary’s C could be used that, generally, analyse the degree of dependency among observations in a geographic space (see Getis & Ord, 1992; Perry, 1995; Fortin *et al.*, 2002). Such tests require a spatial weights matrix that reflects the intensity of the geographic relationship between observations in a neighbourhood, e.g. the distances between neighbours, the lengths of shared border, or whether they fall into a specified directional class. This information could be obtained by measuring the distances between all boulders within each quadrat on digital images of all sampling areas, using image processing software such as

“ImagePro” (Media Cybernetics). Additionally, gravity models may yield illuminating information on how individuals will distribute over time in a given landscape (e.g. with certain rock sizes), taking into account migration rates (see section 2.3.4), distance between patches (e.g. rocks), topology (e.g. surface roughness), negative phototaxis, conspecific attraction (e.g. of larvae by the presence of adults, influencing local settlement rates, see section 4.3.2), and tidal oscillation (i.e. alternation between submerged and emerged state).

An estimate of interstitial space

Rather than rock size, interstitial space between rocks provides a more accurate and relevant measure of available refuges within a defined habitat patch and therefore may be a more suitable predictor for local abundance of *P. elongatus*. Interstitial space could be estimated by using a plastic container with a known volume, ideally with volumetric scale and reasonably large in order to minimise errors due to edge effects. The container could be filled with all rocks found within a defined area of cobble beach (e.g. a sampling quadrat 50 x 50cm) down to the level where fine-grained sediment is clogging the cavities. Rocks should be stacked as densely as possible and similar to their three-dimensional position on the beach. The height of rocks within the container determines the total volume, whereas the interstitial volume is measured by filling the spaces between pebbles and boulders with water, using a bucket or large beaker with volumetric scale. The ratio between total and interstitial volume could then be plotted against average rock surface area to test whether mean rock size is a reliable measure of interstitial space.

Relative contribution of genetic & environmental factors to phenotypic plasticity

To examine to what degree site specific phenotypic differences occurred as a result of plastic responses to environmental conditions or whether they were mainly genetically determined, reciprocal transplant experiments of crabs have proven useful (e.g. Brazeiro, 2005; Pascoal *et al.*, 2012). Specifically, reproductive traits of female *P. elongatus* could be examined at the Wellington south coast and within the harbour compared to transplanted female subpopulations, e.g. using basket traps with mesh inlay similar to those described in section 4.2.2 of the present study. Further, the quantification of larval retention and connectivity between metapopulations on various spatial scales (e.g. within

Wellington region and across Cook Strait) may elucidate the level of gene flow between sites (for a review of methods, see Thorrold *et al.*, 2002).

Effects of limb loss on reproductive output

In the present study it could not be determined with certainty whether reproductive output (measured as the ratio of clutch weight vs. body weight, see section 5.3.4) is affected by limb loss and local density. This was mainly due to a low sample size of injured females. Additionally, none of the females used in the experiment to test growth rates in relation to cheliped loss (section 5.3.3) became ovigerous while in captivity. Hence, it remains unclear whether in *P. elongatus* energy allocation for the regeneration of limbs decreases fecundity directly as in many brachyuran decapods (see Hines, 1982, 1991, 1992; MacDiarmid, 1986; Norman & Jones, 1993; Luppi *et al.*, 1997), or whether egg production has priority over allocating energy to increasing claw size as suggested by Juanes *et al.* (2008). Additionally, fecundity may be affected indirectly via disadvantages in competition for mates (Smith, 1991; Abello *et al.*, 1994; reviewed in Juanes & Smith, 1995). A field experiment, conducted during the reproductive season, with encaged males and females with removed chelipeds may be useful to shed light on the trade-off between limb regeneration, somatic growth, and reproductivity (reviewed in Maginnis, 2006) under near-natural conditions.

Variability of colouration in P. elongatus adults

The role of colour morphs for predator avoidance on various substrates and predation rates in response to “matched” and “mismatched” colouration would be an interesting field for future studies (see p.52, Chapter 2). Similar to classic examples of phenotypic plasticity, such as the Peppered moth (*Biston betularia*) (e.g. Kettlewell, 1958; Grant, 1999) and the Grove snail (*Cepaea nemoralis*) (e.g. Cain & Sheppard, 1953; Silvertown *et al.*, 2011), *P. elongatus* adults exhibit a high variability of coloration which is presumably heritable and appears to be an adaptation to the diversity of microhabitats in order to be optimally camouflaged on differently coloured substrates such as rocks, biofilms and shingle (i.e. mollusc shells) (own observation). While the blue, black and grey types seemed to be relatively more abundant at HRM amongst dark grey rocks and purple-bluish shell fragments of *Aulacomya maoriana* and *Mytilus galloprovincialis*, the majority of *P. elongatus* individuals at BRB appeared to be red-brown and

greenish brown, amongst grey-brown boulders and many thallus fragments of green-, brown- and red macroalgae. A laboratory-based experiment testing predation (i.e. survival) rates dependent on carapace colour versus colour of the substrate could involve the spatial separation of certain colour morphs and exposure to the same predators (e.g. in a choice chamber type set-up) with standardised densities and sizes, e.g. spotty (*Notolabrus celidotus*), red cod (*Pseudophycis bachus*) (see Graham, 1938), and olive rockfish (*Acanthoclinus fuscus*). Additionally, it is relatively easy to collect porcelain crabs in sufficient sample sizes for a quantification of potential differences of frequencies of colour variations across sites. Alternatively to “destructive” sampling, digital images could be taken from a short-term disturbed habitat patch (i.e. with boulders being flipped over quickly before the image is taken and the put back into place). Since there are no distinct colourations but rather a continuous transition of shades, the determination of certain “types” may be somewhat arbitrary. The preservation of samples for processing at a later stage by other means than deep freezing, however, could be difficult as colour complexes are not stable in ethanol and formalin. A similar study has been conducted on juveniles of a freshwater isopod with habitat specific varied pigmentation that is only displayed during the juvenile phase (Hargeby *et al.*, 2004). Additionally, the associated genetic mechanism of colouration might yield valuable information on the biochemical basis of camouflage strategies.

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