Distribution and recruitment patterns of *Evechinus chloroticus* and other New Zealand echinoderms: the role of pre- and post-settlement events

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A thesis

submitted to Victoria University of Wellington

in fulfilment of the requirements for the degree of

Doctor of Philosophy

Victoria University of Wellington

2020

Abstract

Numerous environmental and biological processes are responsible for shaping community structure in temperate rocky reefs. Replenishment of most marine invertebrate populations is largely determined by recruitment success, but it can be highly variable at different spatial and temporal scales. Recruitment is a complex process that involves larval supply, settlement (attachment to a suitable substrate and metamorphosis) and survival and growth of settled juveniles. However, factors controlling recruitment of mobile invertebrates, such as sea urchins, remain largely unknown. This study examines the major biotic and abiotic processes affecting early life stages of the sea urchin *Evechinus chloroticus*, and to what extent these events control the size and distribution of adult populations. This thesis contributes to a better understanding of the processes shaping population structure of *E. chloroticus* and other echinoderm species.

In Chapter 2, I investigated the spatial and temporal variation in settlement of *E. chloroticus*, during the austral summer, at five sites in two locations of the Wellington region (Harbour and South coast) that differ in population structure and environmental conditions. The highest mean seawater temperature and lowest salinity were observed in the Harbour, while the South coast displayed higher chlorophyll and turbidity values. Density of adult sea urchins was significantly higher in the Harbour compared to the South coast and was significantly correlated to the predominant habitat type (shells). The mean size of urchins was larger in the South coast sites and juveniles (<20 mm) were only found at one site in the Harbour. Settlement was very infrequent and spatially variable. Pulses of settlement occurred in February 2018 and January 2019, in the Harbour sites and Breaker Bay (mouth of the Harbour), but not on the South coast. The presence of a young adult cohort (40 – 60 mm) at these sites suggests that there has not been a large episode of recruitment in 2 to 3 years. The low recruitment patterns observed here could be similar in other parts of New Zealand where sea urchin barrens are not very common.

In Chapter 3, I described the echinoderm assemblage in the Wellington region and their recruitment patterns. Echinoderms play important ecological roles in the benthic community, but the ecological processes that regulate species assemblages are still poorly understood. The aim of this study was to analyse variation in abundance,

settlement, and the correlation with environmental variables. Five echinoderm species were responsible for the assemblage variation within sites and their density was highly correlated with habitat composition. Cushion stars (*Patiriella regularis*) were highly abundant at all sites, while eleven-armed sea stars (*Coscinasterias muricata*) and snake brittle stars (*Ophiopsammus maculata*) were dominant in the Harbour and Moa Point respectively. Settlement of echinoderms was moderately correlated with temperature, and showed significant differences between the Harbour and the South coast. There was an important pulse of eleven-armed sea star settlers in 2019, while ophiuroid settlers were present in lower numbers but constantly during the studied period. These findings demonstrate how interannual variation in echinoderm recruitment can occur. One or more years of poor recruitment can follow a relatively good year for recruitment, and species-specific processes, as well as environmental variables, might be contributing to the observed differences.

In Chapter 4, I examined possible factors limiting larval development and settlement success of *E. chloroticus* in the Wellington region, which frequently experiences coastal runoff. I experimentally assessed the combined stress of low salinity and sediments, in a short-term exposure, similar to runoff after a major rain event, on *E. chloroticus* larval and juvenile performance. Larval development was reduced in the lowest salinity and suspended sediment treatments, but these differences were no longer visible near the end of larval development. Larval survival was not affected by the treatments. However, settlement success and juvenile development was reduced by both larval exposure to the lowest salinity and in the presence of deposited sediments. At 28 d post-settlement, there were no surviving juveniles that had been exposed either to the lowest salinity, or to the highest level of suspended sediment, early in larval life. These findings suggest that even short exposure to runoff stress during early development can have strong consequences for later larval settlement and juvenile performance, which could compromise recruitment to adult populations.

Predation is an important source of mortality of young marine invertebrates. In Chapter 5, I highlighted predation as a potential factor affecting recruitment success of *E. chloroticus*. I experimentally assessed mortality due to predation of new settlers (<1 mm) and juveniles (10 – 40 mm), as well as the role of sea urchin size and the availability of refuges on their survival. Predation on *E. chloroticus* new settlers had not been investigated before, and I identified hermit and decorator crab juveniles as

the most effective micropredators. The availability of refuges reduced mortality of settlers and juveniles by half. Adult decorator crabs were also effective predators of sea urchin juveniles, and only lobsters were able to prey on individuals >42 mm. Although the role of macroinvertebrate predation in shaping sea urchin populations remain unclear, these findings suggest that micropredation (especially by crabs) should be considered as an important factor driving recruitment success.

Together, this research provides insights on the distribution and recruitment patterns of echinoderms, which have been rarely studied in New Zealand (and not at all in the Wellington region), and attempts to elucidate the role of pre- and post-settlement events in determining recruitment to the adult population, using *E. chloroticus* as a model species. Findings suggest that stressors such as runoff and predation largely contribute to post-settlement mortality, and that carry-over effects of larval experience can have important consequences for juveniles. In addition, the infrequent settlement pulses and low densities of sea urchin juveniles indicate that recruitment might occur every 2 to 3 years in the Harbour, and every 3 to 4 years on the South coast. The differences in population structure observed between the two locations might be largely due to differential recruitment patterns and environmental conditions. For relatively long-lived species, even if recruitment is sporadic populations can be sustained if adult mortality is low. However, *E. chloroticus* is subject to exploitation in the Wellington region and across the country. This research contributes not only to a better understanding of the processes that shape population structure, but also to a better management of the fishery of *E. chloroticus*, as well as other invertebrate species subject to exploitation.

Acknowledgements

I would like to thank my supervisor Nicole Phillips for her endless support, great feedback and encouragement, even when kina babies were nowhere to be found! Thanks a lot to my second supervisor James Bell for his comments and feedback to improve this manuscript and data analyses. To Victoria University of Wellington Doctoral and Submission Scholarships for the financial support over these 3+ years and the FSRG for funding to present my work overseas.

To all the people involved in the fieldwork, thank you! Especially Daniel McNaughtan, Dan Crossett and John van der Sman, for the long hours spent underwater, advice and good disposition. Cheers to my dive buddies Maren, Megan, Becky and shore persons Yile, Caitlyn, Edith, Sergio, Olivia, Phoebe, Pauline, Ali, Albi, etc. Thanks to Paul for the larval culture induction. Huge thanks to Yile, Caitlyn and Andy who helped me in the lab rinsing hundreds of bio-balls and counting thousands of larvae!

I am immensely grateful to Maren and Joe Zuccarello who helped me with the DNA bit of this thesis, from getting the primers and covering the sequencing, to carrying me by the hand to do the extractions and PCRs. Also, thanks to Alice Rogers and Norbert Englebert for their advice and support in the field. Thanks to Sarah, Kim, Maren and Ali who read my manuscripts and helped improve them! Thanks to Lisa Woods for statistical advice in Chapter 4.

To my friends in New Zealand and back in Mexico for sharing a bit of their lives with me during this journey: Maren, Edith, Kim, Sergio, Balam, BAMAs, the VUCEL crew and Phillips lab. Especial thanks to my flatties Charlie, Clau and Nacho for creating such a lovely home and for always cheering me up! Thanks to my family, Anto, Julio, Vale and Áruna, for their endless support and love.

Publications

Chapters 2 and 3 were combined as a single manuscript and published as:

Glockner-Fagetti and Phillips (2020) Species assemblage and recruitment patterns of echinoderms on shallow rocky reefs in central New Zealand. New Zealand Journal of Marine and Freshwater Research: 1-9. DOI: 10.1080/00288330.2020.1718715

Chapter 4 is formatted as a stand-alone manuscript based on the published study:

Glockner-Fagetti and Phillips (2019) Low salinity and sediment stress on sea urchin *Evechinus chloroticus* larvae has latent effects on juvenile performance. Marine Ecology Progress Series 619:85-96. DOI: 10.3354/meps12951

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Chapter 1

General Introduction

Adult *Evechinus chloroticus* on the South coast

Chapter 1

1.1 Complex life cycles

Most benthic marine organisms have complex life histories, including a larva that develops in the water column after fertilisation (McEdward 1995, Huggett et al. 2006). The larvae inhabit the pelagic environment for a period of time, after which they return to adult habitats to complete their life cycles (Pineda 2000). However, mortality of larvae in the plankton is extremely high, due to predation, starvation, offshore transport and the inability to find suitable substrata for settlement (Rumrill 1985, 1990, Booth & Brosnan 1995, Bohn et al. 2013). Thus, larval stages are considered a critical period, since the preservation of populations and connectivity between them depend on the dispersal and survival of larvae, and their recruitment success (Miron et al. 1995, Clark et al. 2009, Cowen & Sponaugle 2009).

When the dispersal phase is over, the abundance of larvae ready to settle can be highly variable, both spatially and temporally (Hughes et al. 2000). The variable larval input and subsequent survival of new individuals can determine the size of the adult population (Hutchinson & Williams 2001, Bohn et al. 2013). Supply-side ecology highlights the role that variations in larval supply and recruitment play in the population dynamics of open systems (Underwood & Fairweather 1989, Caley et al. 1996, Hughes et al. 2000). Previous research has demonstrated that variation in settlement and post-settlement events affecting recruitment can lead to oscillations in adult population size (revised by(Gosselin & Qian 1997). Hence, settlement and recruitment are key processes that shape the community structure of marine invertebrates with planktonic larvae (Gaines & Roughgarden 1985, Balch & Scheibling 2000).

Settlement can be defined as the transition from a planktonic phase to a benthic phase, and involves the search for and attachment to a suitable substrate, triggering the metamorphosis to acquire the appropriate features for adult life (Rodriguez et al. 1993). Pre- and post-settlement processes include larval production, development, mortality and transport on the one hand, and growth and mortality of juveniles on the other hand (Lamare & Barker 2001). In contrast, recruitment, which is not a distinct biological event, involves a certain period of time after settlement (Rodriguez et al.

1993) and can be defined as the incorporation of new individuals to a population after a period of survival on the new substrate (Booth & Brosnan 1995). While recruitment involves both larval and juveniles stages, settlement only considers larval stages (Keough & Downes 1982).

Many physical and biological factors can influence settlement and recruitment rates in a population (Hutchinson & Williams 2001). The availability of larvae in the water column can be affected by adult reproductive cycles, and changes in larval mortality as a result of longer retention in the plankton or predation (Rodriguez et al. 1993, Miron et al. 1995). Furthermore, wind and current patterns can determine larval transport and dispersal (Rodriguez et al. 1993, Hunt & Scheibling 1997). Hence, it is crucial for recruitment that when suitable conditions for settlement occur, there are enough competent larvae in the environment (Hutchinson & Williams 2001).

1.2 Echinoderm recruitment

Most of the studies on settlement and recruitment of invertebrates have involved sessile species, such as barnacles and mussels (Connell 1985, Connolly et al. 2001, Broitman et al. 2008). In contrast, studies focusing on mobile species, such as echinoderms, have only began to increase in the last few decades (Rowley 1989, Ebert et al. 1994, Balch & Scheibling 2000). However, the relative importance of post-settlement events in determining patterns of recruitment in echinoderms is not fully understood (Jennings & Hunt 2010), and the study of settlement on natural substrata has been challenging and difficult to assess, mainly due to the small size of the settlers and their cryptic habitat (Balch & Scheibling 2000).

Settlement patterns of echinoderms vary spatially, from scales of tens to thousands of meters, and temporally, from days to years (Hereu et al. 2004, Jennings & Hunt 2010). As a result, recruitment is often highly variable, and years of successful recruitment can be followed by years of poor recruitment (Ebert 1983, Tomas et al. 2004). Settlement rates also vary seasonally. In temperate regions, settlement usually occurs during summer, but it can be extended through the autumn or be patchy throughout the year (Balch & Scheibling 2000). The study of variation in settlement and

recruitment are key to understanding the role of these processes in regulating and shaping echinoderm adult populations, and the accuracy of these predictions will ensure the proper management of stocks, especially if they are subject to exploitation.

Echinoderms are well known for their large density variation, in the so-called boom and bust cycles, which can lead to important changes in community structure (Uthicke et al. 2009, Byrne 2011). For example, population outbreaks of the crown-of-thorns starfish *Acanthaster planci* have had catastrophic effects on coral reefs across the tropical Pacific (Chesher 1969, Birkeland & Lucas 1990). Rapid population increases have been related to widespread dispersal of larvae and successful recruitment (Benzie 1992, Fisk 1992, Johnson 1992). However, researchers have failed to find *A. planci* juveniles in the field, which suggests that recruitment occurs in deep waters (Zann et al. 1987, Johnson et al. 1991). Another keystone predator, the temperate sea star *Pisaster ochraceus*, is well known for controlling the abundance and distribution of mussels in the intertidal (Paine 1974, Hoffman 1989). This species is widely spread in the North Pacific, and its high abundances have been related to mass spawning events, triggered by oceanographic processes like El Niño, and to continuous recruitment throughout the years (Sewell & Watson 1993, Blanchette et al. 2005).

Similarly, outbreaks in echinoid populations can cause considerable changes in rocky and coral reefs alike (Harrold & Reed 1985, Hutchings 1986, Watanabe & Harrold 1991). In temperate habitats, grazing activity of sea urchins can lead to change in stable states, from macroalgal-dominated ecosystems to sea urchin barrens (Hagen 1995, Flukes et al. 2012, Ling et al. 2015). This shift from highly complex macroalgal habitats to encrusting algae dominated systems represent a loss of diversity and productivity (Stewart & Konar 2012, Filbee-Dexter & Scheibling 2014, Schiel & Foster 2015, Krumhansl et al. 2016). The main cause of over-grazing of macroalgal beds by *Centrostephanus rodgersii* on the Tasmanian rocky reefs has been identified as the interaction between the effects of climate change and fishing pressure on the rock lobster, a key sea urchin predator (Ling et al. 2009b, Johnson et al. 2011). Oscillations in sea urchin populations have been attributed to high recruitment success due to favourable environmental conditions, such as increased seawater temperature (Hart & Scheibling 1988, Agatsuma et al. 1998, Hernández et al. 2010), availability of suitable substrate (Cameron & Schroeter 1980, Dworjanyn & Pirozzi 2008), and other oceanographic variables (Ebert et al. 1994, Prado et al. 2012). Therefore, the study of

settlement and recruitment of echinoderms are important, since they are part of the crucial processes affecting population dynamics, and can be limiting factors on the size of the resulting adult populations.

1.3 Quantifying recruitment in the field

Natural settlement patterns are difficult to measure in the field. Newly-settled larvae are often too small to be seen, or they settle in cryptic habitats, such as crevices and algal fronds (Booth & Brosnan 1995). Their abundance can be estimated a few days or weeks after settlement, but this period is also characterised by high mortality rates (Gosselin & Qian 1997, Bohn et al. 2013). Post-settlement mortality can occur immediately following settlement, due to abiotic disturbances, and biotic interactions, such as predation (Rodriguez et al. 1993, López et al. 1998). When recruitment is measured over a scale of weeks to months, it is an integration of settlement and post-settlement processes and is crucial to understand the dynamics of a population.

Settlement rates of echinoderms in the field have been estimated using different techniques. For example, Rowley (1989) removed small slabs off the reef to collect newly settled *Strongylocentrotus purpuratus* and *S. franciscanus*. López et al. (1998), on the other hand, scraped off the basal layer of crustose algae within a quadrat to sample newly settled *Paracentrotus lividus*. Other studies have used different types of artificial collectors, such as plastic pipes (Harrold et al. 1991, Balch et al. 1999), light diffusers (Bak 1985, Rogers & Lorenzen 2016), scrub brushes (Ebert et al. 1994, Hereu et al. 2004), artificial grass (Balch & Scheibling 2000, Lambert & Harris 2000, Jennings & Hunt 2010) and plastic bio-balls, originally used as biofilters in aquaria (Keesing et al. 1993, Hernández et al. 2006, Balsalobre et al. 2016). In general, artificial collectors have the advantage of quantifying settlement at frequent intervals, and reducing the effect of predation and migration (Balch & Scheibling 2000, Jennings & Hunt 2010). They also have the benefit of being standardised so that comparisons can be made over space and time. However, echinoderm settlers in collectors should be considered as an index of settler supply, and not as an indicator of settlement intensity on the natural substrate (Harrold et al. 1991, Jennings & Hunt 2010).

Few studies investigating echinoderm settlement in the field have included more than one class other than echinoids (e.g.(Keesing et al. 1993, Balch & Scheibling 2000, Jennings & Hunt 2010). Interestingly, the different groups showed distinctive settlement patterns that varied in space and time. For example, during their study on the Great Barrier Reef, Keesing et al. (1993) observed that asteroids had a poor year of recruitment, but that was not the case for echinoids or ophiuroids. Similarly, Balch and Scheibling (2000) observed that the magnitude of settlement varied between species and years, and that asteroids settled in higher numbers in kelp beds, while ophiuroid settlers were more abundant in barrens.

Most past studies on echinoderms have focused on sea urchin recruitment, revealing different patterns across a range of spatial and temporal scales. For example, *Paracentrotus lividus* in the Mediterranean has been extensively studied. Over a period of three years, Hereu et al. (2004) observed a single peak of settlement, which was correlated with the gradient of exposure to waves and currents. Tomas et al. (2004) found that settlement was higher on a rock wall compared to seagrass meadow, and that interannual variation was strong, of over one order of magnitude. In addition, the abundance of sea urchin adults and predatory fish, as well as depth and habitat complexity, have been identified as determinants of recruitment patterns of *P. lividus* (Ouréns et al. 2014, Oliva et al. 2016).

Similarly, settlement peaks of two species of sea urchins (*Strongylocentrotus purpuratus* and *S. franciscanus*) have been monitored in California kelp beds (Harrold et al. 1991, Ebert et al. 1994). Harrold et al. (1991) concluded that the abundance of settlers in artificial collectors combined with oceanographic data, provide a broad understanding of population dynamics of sea urchins. Furthermore, Ebert et al. (1994) suggested that long-term studies are needed to better understand the life history of the species, since settlement and recruitment can be unusual and very infrequent events.

Probably the most extensive study on asteroid recruitment is that of Loosanoff (1964), who estimated settlement of *Asterias forbesi* over a period of 25 years. The author observed strong interannual variation, but no pattern between good and bad years of recruitment (Loosanoff 1964). Balch (1999), on the other hand, observed that settlement of *Asterias* spp was higher in kelp beds compared to barrens. In contrast, continuous recruitment throughout the years has been observed for *Pisaster*

ochraceus in the Atlantic coast of Canada and the United States (Lubchenco-Menge & Menge 1974, Sewell & Watson 1993). Several studies have focused on the corallivore *Acanthaster planci*. However, even though the population outbreaks have been common in the tropical Pacific, observations of massive recruitment events have been sporadic (Zann et al. 1987, Fisk 1992).

1.4 Factors influencing settlement

Competent larvae available for settlement can determine the number of individuals recruiting within a population (Cameron & Schroeter 1980). However, larval availability can be subject to numerous abiotic and biotic factors, which interact at different spatial and temporal scales (Rodriguez et al. 1993). Patterns of wind, current, changes in climatic conditions, upwelling, and cold water plumes, among other oceanographic conditions, can affect the quantity of echinoderm larvae in the water column (Rodriguez et al. 1993, Hunt & Scheibling 1997), and minor oceanographic fluctuations can determine major settlement events over a scale of days (Balch et al. 1999).

Advective transport is responsible for the arrival of planktonic larvae to a suitable settlement site, since larvae have little control over their horizontal movement (Balch & Scheibling 2001). It has been observed that settlement rates of sea urchins are lower in sites with more intense offshore advection, and are higher with more stable oceanographic conditions, such as water retention (Ebert et al. 1994). Enclosed bodies of water, such as bays, can act as sources of recruitment of sea stars when larvae are retained after spawning, and settle at the same site of origin (Sewell & Watson 1993). Variation in settlement rates of sea urchins have also been positively correlated with the level of exposure to waves and currents, suggesting that coastal topography can explain variation in settlement (Hereu et al. 2004). Coastal circulation appears to be related to spatial variability of sea urchin settlement patterns, since larval supply, and subsequent settlement rates, have been found to be higher during the upwelling relaxation in the California Current (Morgan et al. 2000).

There is evidence of a positive relationship between temperature and settlement rates in the field (Ebert 1983, Hart & Scheibling 1988). Hernández et al. (2010) found that

the settlement of *Diadema africanum* was higher during warm years and temperatures >24°C induced important settlement pulses. This may be driven in part by accelerated development or other factors correlated with temperature. However, temperature alone cannot explain recruitment patterns, as other factors such as salinity, food availability and predation, may also play a role (Balch & Scheibling 2001). For example, although López et al. (1998) found a positive relationship between temperature and spawning for *P. lividus*, larval abundance and recruitment were more strongly correlated with planktonic primary production. A limitation in food supply can prolong the developmental period of larvae and delay metamorphosis, exposing them to further sources of mortality in the plankton, such as predation (Olson & Olson 1989, Vaïtilingon et al. 2001). Changes in food availability can have strong effects on the number of larvae reaching competency. For example, outbreaks of the corallivore sea star *Acanthaster planci* have been correlated with increasing chlorophyll concentrations (Birkeland 1982, Fabricius et al. 2010, Uthicke et al. 2018b).

Small scale hydrodynamic processes and larval behaviour are also key determinants of the settlement process (Rodriguez et al. 1993). An important factor affecting settlement is the presence, or absence, of specific inducers, which trigger metamorphosis of larvae, such as chemical signals (Pawlik 1992). Substrate selection for settlement occurs in response to environmental cues, such as surface texture, microbial films and even the presence of conspecifics (Cameron & Schroeter 1980, Pearce & Scheibling 1991). However, most of the evidence on the importance of settlement cues is based on laboratory studies, and very few studies have examined their role in the field.

1.5 Multiple stressors and carry-over effects

In addition to the natural biotic and abiotic factors that affect the larval stages, and hence settlement and recruitment rates, there are anthropogenic stressors that can affect larval development in the field, and their settlement success. The effects of climate change, such as increasing sea temperature (Sewell & Young 1999, Nguyen et al. 2012, Delorme & Sewell 2014) and ocean acidification on calcifying larvae are well documented (Dupont et al. 2010, Hofmann et al. 2010, Byrne 2012, Doo et al.

2012). However, other human activities that have a more direct impact on coastal areas have received less attention. For example, the effects of urban and storm water runoff on early life stages of marine invertebrates have been poorly described (Brodie et al. 2012, Fredston-Hermann et al. 2016).

Runoff carries terrigenous sediments that reduce light penetration from turbidity and can cause eutrophication from enrichment of organic matter and nutrients (Hessen et al. 1997, Fabricius et al. 2014). This can be advantageous for some coastal larvae like *Acanthaster planci*. Outbreaks of this corallivore species have been correlated with terrestrial runoff from heavy rains, which provide enough nutrients for the phytoplankton to bloom and thus, there is more food available for larvae (Birkeland 1982, Fabricius et al. 2014). Furthermore, river discharges also reduce salinity in nearby areas, where the superficial layer of low salinity can reach up to 5 m depth (Booth 1975). Thus, a storm event can be an important stressor for larvae in the water column that are ready to settle (Phillips & Shima 2006, Bessell-Browne et al. 2017). There is increasing evidence that terrestrial runoff can have deleterious effects on corals, reducing fertilisation success and disrupting the settlement process (Fabricius 2005, Larsen & Webb 2009). However, fewer studies have focused on the consequences that it has on the larval stages of other invertebrates, such as echinoderms (King & Riddle 2001, Bielmyer et al. 2005).

The effects of sediments and reduced salinity on marine invertebrates have generally been analysed separately (Gilmour 1999, George & Walker 2007, Carballeira et al. 2011, Miller et al. 2014). Even though they are likely to occur simultaneously, only Humphrey et al. (2008) have examined the combined effects of sediments and hyposaline conditions, which reduced fertilisation success of the coral *Acropora millepora*. Synergetic effects are more common in nature, as the interaction of two or more stressors occurs frequently (Crain et al. 2008). However, the combined effects of multiple stressors have received less attention (Breitburg et al. 1998, Przeslawski et al. 2015).

Besides the stressors that cause larval mortality, there are other anthropogenic factors that can have sub-lethal effects on larvae or that appear only after metamorphosis (Chiu et al. 2007, O'Connor et al. 2014, Pechenik 2018). Carry-over effects have been identified for several marine invertebrate juveniles after exposure to different stressors

as larvae. Ocean acidification had a negative effect on growth rates of juvenile oysters (Hettinger et al. 2012) and survival of green sea urchin juveniles (Dupont et al. 2012) when exposed as larvae to lowered pH. Interactive effects of increased temperature and UVB on embryos of an intertidal gastropod showed carry-over effects on growth and survival of larvae (Fischer & Phillips 2014).

Furthermore, latent effects of low salinity have also been identified. For example, hyposaline conditions caused smaller size at settlement and slower growth rate of the gastropod juveniles, when larvae were briefly exposed during development (Montory et al. 2014). Similarly, short exposure to reduced salinity had a strong sub-lethal effect on polychaete larvae that resulted in lower post-settlement survival and juvenile growth rates (Pechenik et al. 2001). Altogether, these studies demonstrated that the effects of stressors could be greatly underestimated if only a single life stage is examined.

1.6 Post-settlement events affecting recruitment

Post-settlement events that modify initial settlement patterns, are critical to recruitment success, since early mortality limits the size of the resulting adult population (Rowley 1990). During early juvenile life, mortality can be particularly high, even exceeding 30% in the first day (Gosselin & Qian 1997, Phillips 2017). Environmental stress, delayed metamorphosis, predation, and disease can cause mortality of newly settled individuals (Hunt & Scheibling 1997). However, the relative importance of these events is not fully understood, and the behaviour of post-metamorphic juveniles in determining survival rates remains largely unknown (Scheibling & Robinson 2008).

Predation is probably the most important cause of mortality of newly settled invertebrates (Gosselin & Qian 1997, Osman & Whitlatch 2004). Small predators, such as gastropods and crustaceans, are voracious and efficient consumers of newly settled sea urchins, and can have great impacts on their abundance (Bonaviri et al. 2012). Newly settled sea urchins usually occur in cryptic microhabitats (Raymond & Scheibling 1987), and the juveniles of some species take shelter under the canopy of adults, which provide protection to their conspecifics (Nishizaki & Ackerman 2007, Zhang et al. 2011). However, if they settle in exposed areas, they are more vulnerable

to predation and can be even damaged or killed by bulldozing grazers (Scheibling & Robinson 2008). Thus, the behaviour of the larvae at the time of settlement is key to their survival and can determine recruitment rates.

The availability of physical refuges, and the spatial heterogeneity and complexity, have been shown to reduce predation and increase the survivorship of small sea urchin juveniles (Hereu et al. 2005, Clemente et al. 2013). Algal assemblages provide refugee, and reduce predation on small juveniles (2-10 mm) from predatory fish (Hereu et al. 2005). Substrate refugees increase survival of juveniles, however the size of the predator is an important factor structuring intertidal communities (Clemente et al. 2013). Small juveniles are able to move into coralline algae, attracted by chemical cues, which provides refuge and reduces predation by crabs (Yiu & Feehan 2017).

Even though the highest mortality rates occur during the first days to weeks after settlement, settlers still must face the pressure of competition and availability of food and space resources. Chitons, limpets, and gastropods are potential competitors of sea urchin juveniles, while conspecifics, shrimps, worms, and whelks are likely competitors for sea star juveniles (Jennings & Hunt 2010). When echinoderm juveniles attain a certain size that can be observed in the field (>5 mm), they have generally overcome the major limitations of growing into adulthood (Pearse & Hines 1987).

1.7 New Zealand and the Wellington region

New Zealand, located in the southwestern Pacific Ocean, comprises two main landmasses: the North and the South Islands, and around 700 smaller islands. It spans from 29ºS to 52ºS of latitude, ranging from subtropical to sub Antarctic biomes. New Zealand's Exclusive Economic Zone is one of the largest in the world, but most of it remains unexplored (Gordon et al. 2010). The marine ecosystem is highly diverse, with about 12,780 described species of which at least half are endemic (Costello et al. 2010). The subtidal reef communities, dominated by large brown algae, are typical of temperate marine ecosystems (Schiel & Foster 1986, Shears & Babcock 2007).

In Wellington, located at the southern end of the North Island, two distinctive habitats with different hydrological and topographical patterns can be identified: the Wellington Harbour and the South coast. The Harbour (41°16' S, 174°51' E), is an enclosed and sheltered body of water, of about 80 km^2, and an average depth of 20 m (Booth 1975). It has a continual input of freshwater coming mainly from the mouth of the Hutt River, with maximum daily discharges of 180×10^6 m^3 (Maxwell 1956). Freshwater runoff can significantly affect surface seawater temperature and salinity to a depth of about 5 m (Booth 1975). Semi-diurnal tides prevail in the Wellington Harbour, with a mean amplitude of 0.75 m, and a maximum of 1.5 m (Maxwell 1956). Even though it is relatively isolated from oceanic conditions, the channel that connects the Harbour with the open sea is large enough to ensure a good mixing (Gilmour 1960), and the total flushing time is approximately 10 days (Heath 1971).

The South coast (41°20' S, 174°48' E), on the other hand, is highly dynamic and has a complex hydrology compared to the Harbour. It is located within the Cook Strait, which separates the North and the South Islands and has a maximum depth of 150 m (Heath 1971). The dynamics of the Cook Strait are driven by tides and wind forced currents and circulation (Walters et al. 2010), which also makes it a highly active sedimentary environment (Carter 1992). Subtropical and subantarctic waters converge in the Cook Strait, bringing warm and saline waters to the surface, or cold deep upwells during frequent periods of southerlies, respectively (Walters et al. 2010).

1.8 Previous studies in the Wellington region and New Zealand

Observations of the distinctive intertidal invertebrate assemblages between the Wellington Harbour and the South coast have motivated earlier investigations on the correlation between recruitment and the hydrological conditions. The absence of mussels from the South coast compared to the high abundances observed in the Harbour, led researchers to think that different oceanographic processes between these locations affected recruitment patterns. Helson and Gardner (2004) observed that larval supply and recruitment of mussels were in fact higher in the Harbour. However, the absence of mussels in the South coast could not be only attributed to a limitation in recruitment, but to higher post-settlement mortality (Helson & Gardner

2004). Later, Helson et al. (2007) suggested that the absence of mussels on the South coast was due to the quantity and quality of particulate food supply in the Cook Strait.

Other studies have shown that mussels and barnacles have different recruitment patterns in the Harbour compared to the South coast (Phillips & Hutchinson 2008, Demello & Phillips 2011), which was likely due to the distinctive circulation and water flow patterns between the two locations (Demello & Phillips 2011). Furthermore, Shima and Swearer (2009a) showed that the nutrient enriched waters of the Harbour were favourable for larval quality traits of the common triplefin *Forsterygion lapillum*. A positive correlation between recruitment intensity and settler condition in the Harbour suggested that populations might be self-recruiting and even exporting triplefin recruits to nearby areas, including the South coast (Shima & Swearer 2009b). Likewise, several studies have used the distinctive oceanographic characteristic of the region as a model system to study the connectivity among marine populations (Apte & Gardner 2002, Waters & Roy 2004, Nagel et al. 2015).

Very few studies have quantified settlement and recruitment of echinoderms in New Zealand (Barker 1977a, 1979, Stewart & Mladenov 1997), and none in the Wellington region. Settlement behaviour of two sea stars, *Coscinasterias muricata* and *Stichaster australis*, was investigated using both laboratory experiments and field sampling (Barker 1977a). *C. muricata* had low recruitment rates in the field, while numerous newly settled *S. australis* were found in offshore boulders covered with coralline algae (Barker 1977a). Most studies have focused on the endemic sea urchin *Evechinus chloroticus* (Walker 1984, Andrew 1988, Lamare 1998). It has been shown that there is a linear relationship between settlement and recruitment of *E. chloroticus* in the field (Lamare & Barker 2001). However, more studies focusing on the processes that determine recruitment rates are needed.

Most of the field studies on *E. chloroticus* recruitment have been conducted in New Zealand's southern fiords, and in the early 1990s, with no additional studies since that time. There is a need to study the settlement and recruitment patterns of *E. chloroticus* in other habitats and locations, as the abiotic processes that govern them likely vary. It is also essential to assess the recruitment of other echinoderm species, such as sea stars, which has not previously been conducted in New Zealand, because these species also play important roles in benthic communities, acting as predators; for

example *Astrostole scabra* and *S. australis*, and the highly abundant omnivore *Patiriella regularis*. The success of management strategies, conservation efforts, and exploitation regimes, will depend on the accuracy of predictions on population variability.

1.9 Focal species: *Evechinus chloroticus*

The sea urchin *Evechinus chloroticus*, locally known as kina, has been widely studied in New Zealand, because of its ecological and economical importance. This endemic species has been historically harvested by Māori people, and more recently for commercial fisheries (Barker 2007). Its grazing activities have important consequences for algal assemblages (Andrew 1988, Villouta et al. 2001). In fact, sea urchin barrens are a common habitat in northern New Zealand and Fiordland, in the South Island, but not in central and southern parts of the country (Schiel 1982, Shears & Babcock 2007).

Despite being a dominant species in most rocky reefs in New Zealand, little is known about the reproductive and recruitment patterns of *E. chloroticus* across the country. Most of the studies have been carried out in the fiords, which are unique environments that are not representative of New Zealand's entire coast. However, we know from these studies that kina reproduces during summer, and larvae complete development in 3 to 6 weeks from November to April (Lamare & Barker 2001). Synchronous spawning has also been observed in the southern fiords, where there is a high retention of larvae and high recruitment rates (Lamare 1998). Doubtful Sound, in Fiordland, appears to have higher settlement and recruitment rates compared to Tory Channel, in Marlborough Sounds. However, there was a strong interannual variation in the magnitude of these events (Lamare & Barker 2001).

Some laboratory studies have focused on the development of *E. chloroticus* exposed to different stressors (e.g. temperature, salinity, metal pollutants and sediments). It has been shown that low salinity affects fertilisation and early development (Delorme & Sewell 2014), while suspended sediments reduce fertilisation success (Miller et al. 2014) and increase mortality rates for early larval stages (Phillips & Shima 2006).

Moreover, settled sediments inhibit settlement of larvae and reduce survivorship of juveniles (Walker 2007). Altogether, these studies suggest that stressors associated with runoff can have important consequences at different life stages of *E. chloroticus* through immediate effects. However, further studies are needed to determine to which extent these factors, in combination, regulate recruitment success through carry-over effects.

The growth of *E. chloroticus* has been studied in the laboratory and in the field by calcein tagging and recapture. Walker (1984) found that newly settled individuals and small juveniles (0.5 – 3 mm) collected from the field and maintained in aquaria, had growth rates of 1 mm per month. Lamare and Mladenov (2000), on the other hand, observed that after one year, newly settled urchins grew to a mean size of 8 and 10.5 mm in the laboratory and in the field, respectively. Effects of fish predation on *E. chloroticus* juveniles has been studied in northeastern New Zealand through exclusion cages (Andrew & Choat 1982). The presence of adults did not affect the densities of juveniles, and despite the high densities of fish, the juveniles escaped predation (Andrew & Choat 1982). However, the behaviour of newly settled echinoderms has not been investigated and their predators are still unknown.

1.10 Aims and thesis structure

The aim of this research is to provide a comprehensive understanding of some of the pre- and post-settlement factors influencing echinoderm recruitment in New Zealand, with an emphasis on the sea urchin *Evechinus chloroticus*.

In Chapter 2, I estimated the spatial and temporal variation in settlement of *E. chloroticus* at sites around the Wellington Harbour and the South coast that differ in population structure and habitat composition. Moreover, abundance of settlers in the artificial collectors was correlated with environmental variables.

In Chapter 3, I described the echinoderm community composition in the Wellington region, with emphasis on the differences between the Harbour and the South coast, as well as relationships between density and habitat composition. I also examined

temporal and spatial variation in echinoderm recruitment and the correlation with environmental variables. This chapter and Chapter 2 have been combined and accepted for publication in New Zealand Journal of Marine and Freshwater Research as “Species assemblage and recruitment patterns of echinoderms on shallow rocky reefs in central New Zealand” (DOI:10.1080/00288330.2020.1718715).

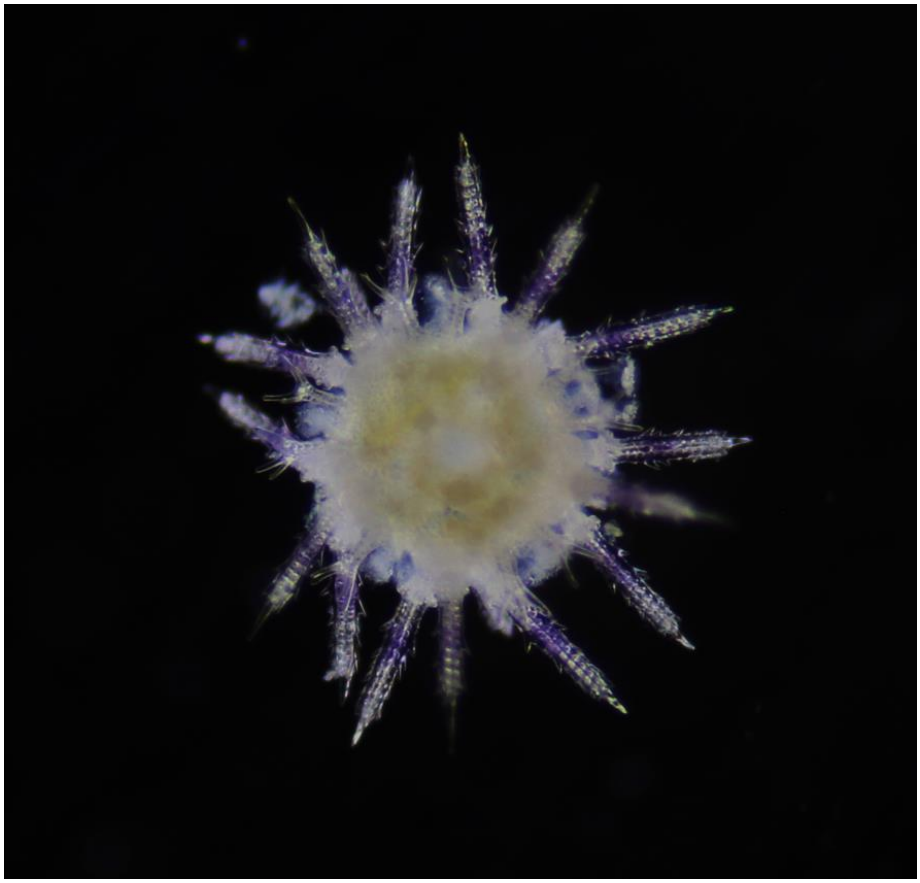
In Chapter 4, I investigated possible factors limiting larval development and settlement success of *E. chloroticus* in the Wellington region, which frequently experiences coastal runoff. This chapter has been published as Glockner-Fagetti and Phillips (2019) Low salinity and sediment stress on sea urchin *Evechinus chloroticus* larvae has latent effects on juvenile performance. Marine Ecology Progress Series 619:85-96.

In Chapter 5, I examined predation as a potential driver affecting juvenile survival and recruitment. I experimentally assessed mortality due to predation on new settlers and juveniles of *E. chloroticus*, as well as the role of their size and the presence of refuge on their survival.

Finally, in Chapter 6, I summarised the main findings and drew the general discussions and conclusion.

Chapter 2

Density and recruitment of *Evechinus chloroticus* and the correlation with environmental variables



Evechinus chloroticus settler from the artificial collectors

Glockner-Fagetti A, Phillips NE (2020) Species assemblage and recruitment patterns of echinoderms on shallow rocky reefs in central New Zealand. New Zealand Journal of Marine and Freshwater Research:1-19

Chapter 2

2.1 Introduction

Marine invertebrate populations can be highly variable at local scales and depend on recruitment for replenishment (Caley et al. 1996, Hughes et al. 2000, Broitman et al. 2008). However, for relatively long-lived species with biphasic life cycles, good recruitment years can be sporadic (Keough 1983, Hutchinson & Williams 2001). One of the reasons is the complexity of recruitment process, which involves larval supply, settlement (attachment to suitable substrate and metamorphosis), and survival and growth of settled juveniles (Cameron & Schroeter 1980, Harrold et al. 1991). Different biotic and abiotic factors affect each of these components, which can cause recruitment to vary both spatially and temporally (Lagos et al. 2005, Broitman et al. 2008).

Larval supply can be affected by environmental variability in the water column, such as temperature and salinity (Delorme & Sewell 2014, Crisp et al. 2017), food availability (Basch & Pearse 1996, Chiu et al. 2007, Brundu et al. 2016), and oceanographic factors controlling dispersal of larvae (Levin 2006, Cowen & Sponaugle 2009, Anadón et al. 2013). The abundance and quality of larvae in the water column mediate settlement rates, along with physical factors like habitat features and settlement cues (Hadfield & Paul 2001, Bohn et al. 2013, Brundu et al. 2016, Freckelton et al. 2017). The availability of suitable substrate for settlement is probably a key determinant for survival of settlers and successful recruitment to the adult population (Booth & Brosnan 1995).

Habitat features are important determinants, not only for the abundance and distribution of adult populations, but also for recruitment processes (Barry & Dayton 1991, Bell et al. 2012). Recruitment of invertebrates with complex life cycles can be highly variable between contrasting habitats, and at scales from ten to hundreds of meters (Andrew 1993, Labbé-Bellas et al. 2016). Herbivore species, such as the sea urchin *Evechinus chloroticus*, are key to understand the processes occurring in the benthic communities of temperate rocky reefs. In northern parts of New Zealand, *E. chloroticus*, or kina, is well known for contributing to the formation of urchin barrens and have an important top-down control over algal assemblages (Andrew & Choat

1982, Villouta et al. 2001). However, with the exception of Abel Tasman and Fiordland, where *E. chloroticus* can aggregate up to 30 in m^{-2} (Davidson & Chadderton 1994, Villouta et al. 2001), urchin barrens are not very common in central and southern parts of the country (Shears & Babcock 2007). Nevertheless, this species sustains a recreational fishery in the Wellington region, where the harvest was almost equivalent to the total allowable catch (TAC) which was estimated to be 102 t for the 2008 – 2009 fishing year (Miller & Abraham 2011).

Even though *E. chloroticus* plays an important ecological role in the benthic community, little is known about its patterns of distribution and recruitment in habitats other than New Zealand's southern fiords. There was a strong interannual variation in settlement rates observed in Doubtful Sound, and the abundance of recruits in the field were positively correlated with settlers in artificial collectors (Lamare & Barker 2001). However, the factors driving its abundance, such as habitat features and recruitment patterns, are still poorly understood. Recruitment of sea urchins can be seasonally predicted (Ebert et al. 1994, Garcia-Sanz et al. 2014), but it may not happen every year (Agatsuma et al. 1998, Tomas et al. 2004). Good years of recruitment, usually distinguishable by the presence of a juvenile cohort in the population size structure, may be followed by long periods of poor recruitment (revised by(Ebert 1983, Balch & Scheibling 2001).

Distinctive intertidal invertebrate assemblages have been previously recognised in the Wellington region, between the Harbour and the South coast (Gardner 2000, Helson & Gardner 2004, Demello & Phillips 2011). Mussel populations, for example, are highly abundant in the Harbour, but almost absent from the South coast. Several studies have aimed to explain the differences in adult population density through the study of larval supply, settlement and recruitment (Gardner 2000, Helson 2001, Lachowicz 2005). Larval supply and settlement were higher in the Harbour sites compared to the South coast. However, the absence of mussels was probably due, not only to a recruitment limitation, but also to post-settlement mortality (Helson & Gardner 2004). Furthermore, the availability and quality of food may also be a limiting factor for the development of mussel larvae on the South coast, which might also explain the low settlement rates (Helson et al. 2007). Recruitment patterns of barnacles also differed between the two locations, which were likely related to differences in circulation and water flow patterns (Demello & Phillips 2011). Similarly, populations of the common triplefin (*Forsterygion*

lapillum) in the Harbour were observed to be self-recruiting, and might be even exporting recruits to nearby areas, including the South coast (Shima & Swearer 2009a).

The study of spatial and temporal variation in a species' abundance can provide insights on the processes that shape population structure and ultimately influence benthic communities. Settlement and recruitment are key to understand the processes that shape community structure of sea urchins and other marine invertebrates with planktonic larvae. In this chapter, settlement was defined as the appearance of recently metamorphosed sea urchins in artificial collectors, while recruitment as the presence of sea urchin juveniles (<20 mm test diameter) that had survived in the field approximately one year after they settled. The aims of this study were: 1) to analyse the spatial variation in sea urchin *E. chloroticus* density and size structure, and correlate this with the habitat composition in the Wellington region; and 2) to estimate the spatial and temporal variation in sea urchin settlement, and correlate any patterns with environmental variables.

2.2 Materials and methods

2.2.1 Study area

Five sites were selected within the Wellington region: Princess Bay and Moa Point, located along the South coast, Breaker Bay near the mouth of the Harbour, and Kau Bay and Shelly Bay situated inside the Harbour (Fig. 2.1). All sites are located inside small bays, and relatively sheltered from wave exposure. They are separated from each other by 2 – 3 km (linear distance).

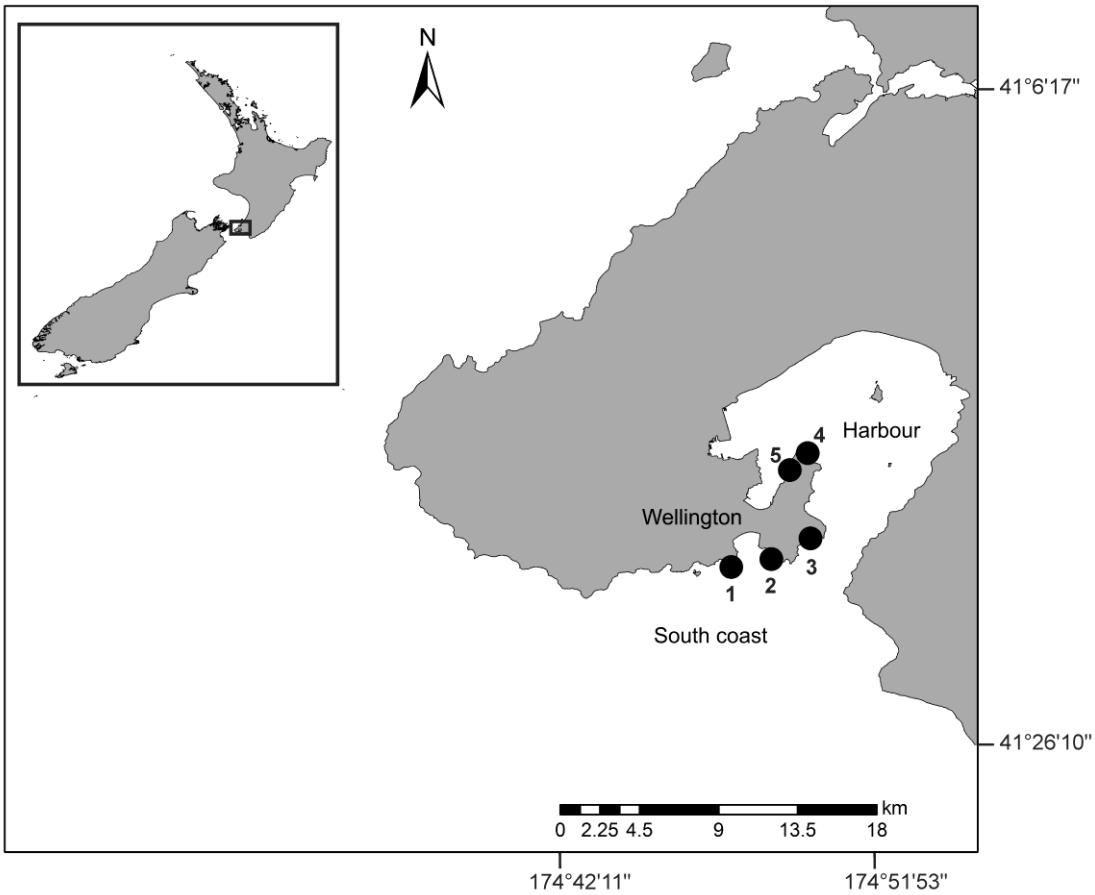


Fig. 2.1. Map of the sampling sites on the South coast: 1) Princess Bay and 2) Moa Point, in the mouth of the Harbour: 3) Breaker Bay, and inside the Wellington Harbour: 4) Kau Bay, and 5) Shelly Bay.

2.2.2 Environmental variables

Daily variation in seawater temperature, salinity, chlorophyll and turbidity in the Wellington region was estimated using CTD loggers (model XR-420). The instruments were deployed at ~5 m depth and suspended 2 m above the bottom, in the South coast (Island Bay Harbour, 41°20'37"S 174°46'24"E) from December 2016 to April 2017 (year 2017) and November 2017 to April 2018 (year 2018), and in the Wellington Harbour (Kau Bay, 41°17'14"S 174°49'45"E) in 2018. The instruments took measurements every hour. Extreme values were removed from the database and monthly averages were estimated (see Appendix 1). Monthly averages of seawater temperature from December 2018 to February 2019 (year 2019) were taken from

Environmental Monitoring and Research (Greater Wellington 2018), when the CTDs were not deployed.

Habitat composition was estimated yearly (2017 – 2019) at each site using three 25 × 2 m belt transects, at 4 to 8 m depth. The percentage of cover of abiotic and biotic variables was recorded in 5 × 2 m blocks along the transect, based on the New Zealand Marine Habitat Classification Scheme (NZMHCS) (Snelder et al. 2005). Abiotic variables included the categories sediments (mud, sand, pebbles, shells) and rocky reef (cobble, boulder, bedrock), while biotic variables included the macroalgae type cover (patch, bed, canopy) and the dominant group (Dohner 2014, Ladds et al. 2018).

2.2.3 Sea urchin density and size structure

The abundance of adult and juvenile sea urchins was quantified once a year (2017 – 2019) at each site using three 25 × 2 m belt transects at each site at 4 to 8 m depth. First, the number of adults was estimated at each transect, and their test diameter was measured using callipers (± 0.1 mm). Second, the surface along the transect was carefully inspected, turning stones upside down and searching in crevices in order to find juveniles <50 mm, whose test diameter was also measured. One-year-old *E. chloroticus* were considered to be <20 mm (test diameter), while juveniles older than one year were larger than 20 mm, and less than 50 mm (Walker 1984, Lamare & Mladenov 2000). Due to the low densities of juveniles, further effort was put on surveying different depths at Shelly Bay and Breaker Bay. Additional transects were laid during high tide at 2 and 5 m at each site during the three sampled years.

Density of adults and juveniles was calculated as the number of urchins found per transect, divided by the surveyed area (50 m^2). Variation in density was analysed separately between years and among sites using the non-parametric Kruskal-Wallis test, since the data did not meet ANOVA assumptions (assessed with Kolmogorov-Smirnov and Levene's tests). A post-hoc Dunn test was used to compare medians when factors were significant ($p < 0.05$). Pearson's correlation was used to analyse the strength of the relationship between sea urchin density and habitat composition. Size structure of sea urchins was estimated each year at each site (see Appendix 2).

After assumptions were verified, size of adults was analysed using two-way ANOVA, with years and sites as fixed factors. A post-hoc Tukey test was used to compare means when factors were significant ($p < 0.05$). All analyses were conducted using STATISTICA 10.0 (StatSoft) and R v3.2.4 (www.r-project.org).

Juveniles that were found in Shelly Bay in 2017 were kept at the facilities of VUCEL in a 200 l tank with flowing filtered seawater (FSW 15 µm). Juveniles were fed once a week with fresh kelp *Macrocystis pyrifera* or green algae *Ulva* sp. Measurements of the test diameter were taken using callipers (± 0.1 mm) every four months. Since individuals were not tagged, growth was estimated based on size structure frequencies.

2.2.4 Sea urchin settlement in artificial collectors

The use of artificial collectors has been a useful technique to monitor settler supply at frequent intervals and to isolate settlement from other components of recruitment (Harrold et al. 1991, Keesing et al. 1993). Plastic bio-balls have shown to be efficient collectors of newly settled sea urchins (*Diadema africanum*) at the Canary Islands (Hernández et al. 2006). The samplers collected up to 26 newly settled individuals during the settlement peak, which occurred in late summer (Hernández et al. 2006). More recently, Balsalobre et al. (2016) assessed the suitability of artificial collectors to measure settlement rates of *Paracentrotus lividus* and *Arbacia lixula*, with the authors recommending the use of plastic bio-balls for future studies on the quantification of settlement rates (Balsalobre et al. 2016).

Settlement of sea urchin was estimated during summer using artificial collectors. These consisted of one hundred highly rugose plastic bio-balls (36 mm in diameter), inside a nylon net (Fig. 2.2). The collectors were deployed at Princess Bay, Moa Point, Breaker Bay, Kau Bay and Shelly Bay. They were suspended 1 m above the seafloor, at 4 to 7 m depth, and anchored to the bottom with a heavy weight (75 kg). Three replicate collectors were placed at each site by SCUBA diving, and recovered every month, from November 2016 to April 2017 (2017), November 2017 to April 2018

(2018), and December 2018 to February 2019 (2019). The collectors were placed in a plastic bag, to avoid losing any organism, before bringing them to the surface.

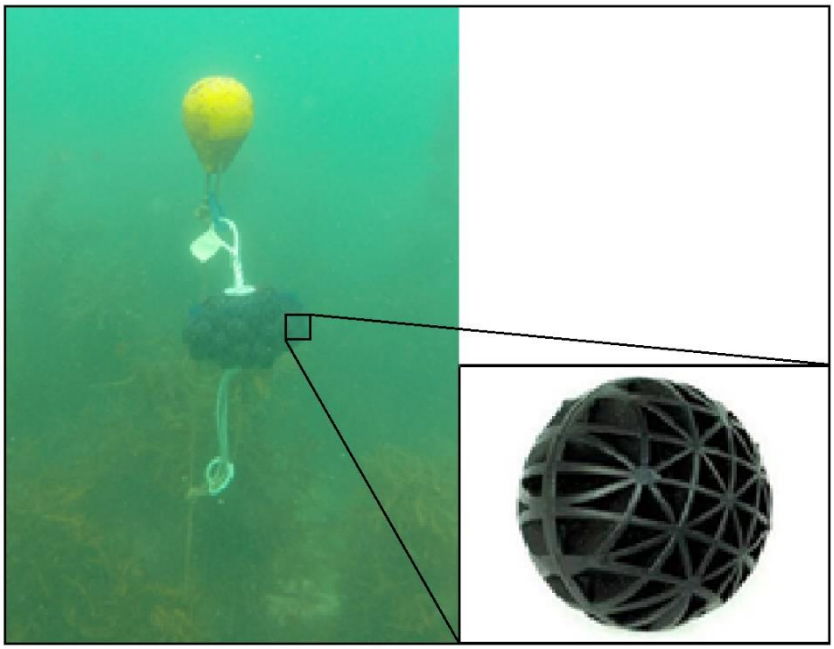


Fig. 2.2. Artificial collector deployed at the sampling site (left) and detail of the plastic bioball (right).

The plastic bags with the collectors were transported to the facilities of the Victoria University Coastal Ecology Lab (VUCEL) for washing (Keesing et al. 1993, Hernández et al. 2006). Each collector was placed in a bucket with freshwater to cause osmotic shock to the organisms. Then, the bio-balls were vigorously shaken and rinsed individually with pressurized water to ensure the release of all organisms. Each bioball was examined for remaining individuals and removed with forceps if needed. The water from the washing was collected in the same bucket and then, passed through 700 and 250 µm coupled sieves. The material retained in the sieves was preserved in 96% ethanol in Petri dishes until their examination under a dissecting microscope (25x magnification). Sea urchin settlers and potential predators and bulldozers, that were thought to have settled in the collectors, because of their small size (<5 mm), were quantified in each collector (for predator/bulldozer abundance see Appendix 3). The bio-balls were reused after being soaked overnight in 5% sodium hypochlorite, and the

collectors were left in running seawater for 10 days prior to their deployment, to allow the growth of biofilm.

Spatio-temporal variation of sea urchin settlement in artificial collectors was modelled as a function of year and site. Generalized linear model with negative binomial distribution and a zero-inflated negative binomial regression were used to account for the over-dispersion of the data ($z = 3.3099$, $p = 0.0004$, alpha = 0.049), and the large proportion of zeros. The two models were compared using the Vuong likelihood ratio test. Year, site, and their interaction were included as fixed factors in the full model. Akaike Information Criterion (AIC) was used to select significant factors. Pearson's correlation was used to quantify the strength of the relationship between sea urchin settlement and seawater temperature, salinity, chlorophyll and turbidity, and the adult density and habitat composition in the sampled sites. Analyses were conducted using R v3.2.4 with 'pscl' and 'MASS' packages (Jackman et al. 2017).

Due to the low settlement rates of urchins observed in the first year, another two types of artificial collectors were tested. However, sea urchins settlers were not observed in either of the collectors (see Appendix 4 for the results). Substrate samples were taken with the aim of finding recent settlers and one-year-old recruits (<20 mm) that were not easily visible during the dive. The superficial layer of substrate, including sand, algae and rocks, was sampled inside five 50 × 50 cm quadrats randomly placed inside a 25 × 2 m transect at 2 and 5 m depth, using a suction device. This consisted on a 15 cm diameter PVC tube, 1 m long, connected to an additional diver's air source. When the air source was open, bubbles flowed through the tube creating vacuum. A mesh bag was attached to the end of the tube, allowing the air to flow and collecting the sediments and small organisms. The mesh bags were transported in buckets with seawater to the laboratory, where the substrate samples were sorted using 1.2, 0.7 and 0.25 mm sieves. The 0.25 mm section was observed under the dissecting microscope (25x magnification) in search for recent settlers. Substrate samples were taken twice per year (January and March) in 2017 and 2018.

2.3 Results

2.3.1 Environmental variables

Seawater temperature varied between the years (Fig. 2.3). Mean (± SE) seawater temperature was significantly higher in the Harbour, 17.1 ± 0.03 ºC, compared to the South coast, 16.2 ± 0.04 ºC ($F_{(1, 24)}$ = 5.83, p = 0.024). The warmest months were February 2018 (19.1 ± 0.03 ºC) and December 2018 (18.5 ± 0.03 ºC) for the Harbour and the South coast, respectively. Overall, temperature increased from 15.7 ºC in 2017, to 16.7 in 2018, and to 17.4 in 2019 ($F_{(2, 24)}$ = 6.02, p = 0.008).

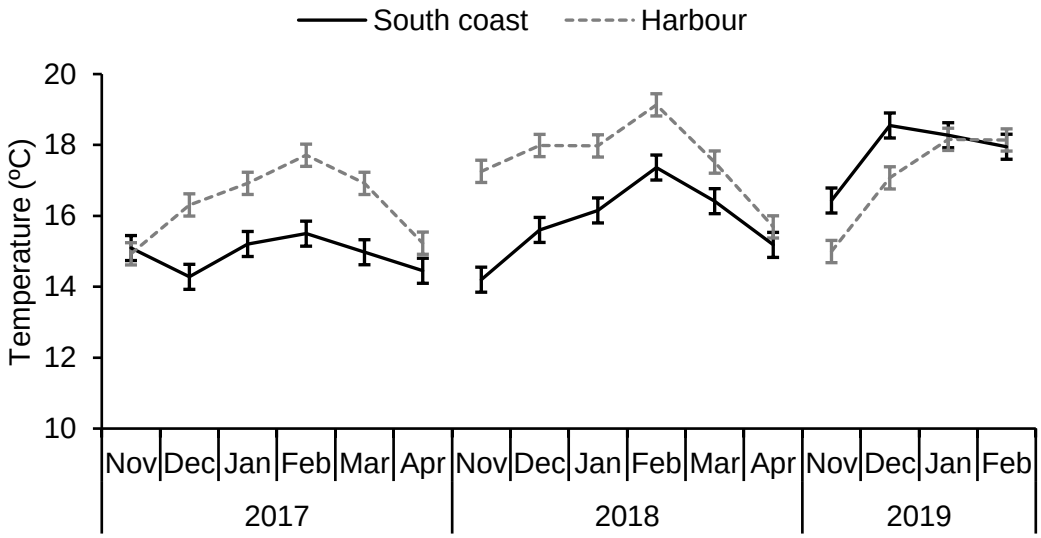


Fig. 2.3. Time series of seawater temperature (ºC) recorded by the CTDs in the South coast and the Wellington Harbour, from November 2016 to April 2017 (2017), November 2017 to April 2018 (2018) and November 2017 to February 2019 (2019). 2019 data at both sites was obtained from Environmental Monitoring and Research (Greater Wellington 2018). Bars represent mean values (± SE).

Salinity of seawater had different patterns at the two sites (Fig. 2.4). It was almost constant in the South coast during both sampled years, with a mean (± SE) of 34.5 ± 0.02 ppt. The lowest value (33.8 ± 0.02 ppt) was observed in March 2018, and the highest (34.8 ± 0.03 ppt) in February 2017 and November 2017. In contrast, salinity in the Harbour had considerably more variation, and the mean value (32.5 ± 0.06 ppt)

was lower compared to the South coast. Salinity in the Harbour displayed two peaks of high salinity observed in November 2017 and February 2018 (34.4 ± 0.11 and 34.2 ± 0.06 ppt, respectively), followed by a drop in January and April 2018 (29.6 ± 0.06 and 31.2 ± 0.06 ppt, respectively).

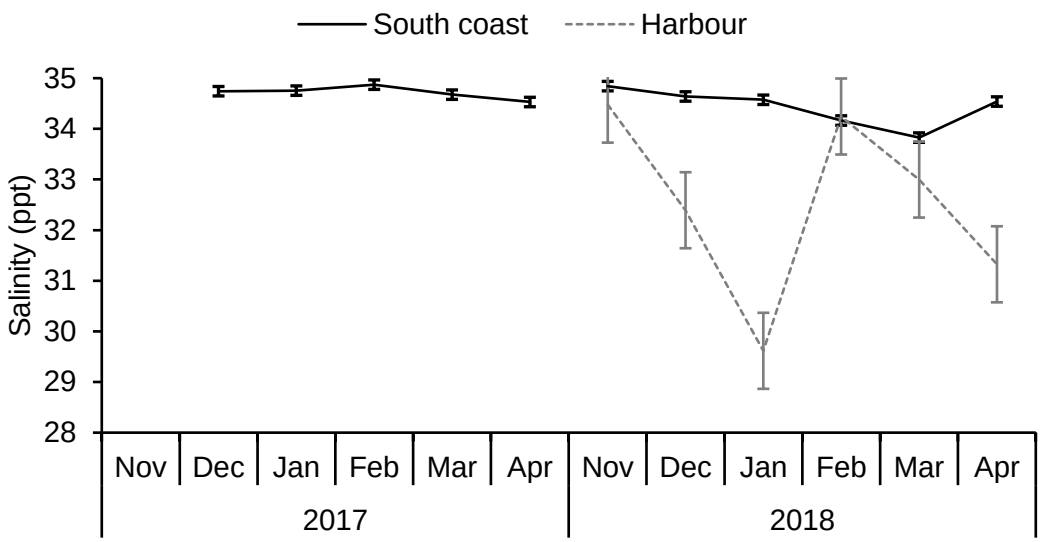


Fig. 2.4. Time series of mean (± SE) monthly salinity (ppt) recorded by the CTDs in the South coast and Wellington Harbour, from December 2016 to April 2017 (2017), and November 2017 to April 2018 (2018).

Chlorophyll (Relative Fluorescence Units – RFU) was highly variable in the South coast during the two sampled years. The maximum mean value was observed in February 2017 (50.2 ± 1.02 RFU), and in March 2018 (25.0 ± 0.98 RFU). The mean (± SE) chlorophyll value on the South coast (14.3 ± 1.18 RFU) was significantly higher compared to the mean value in the Harbour (0.98 ± 0.03 RFU). Chlorophyll at this site displayed less variation than at the South coast site, and the monthly values were significantly lower (Fig. 2.5). Finally, turbidity (Formazin Nephelometric Unit – FNU) displayed different patterns among years in the South coast (Fig. 2.6). Mean values were relatively low in 2017, compared to 2018, when two peaks were observed, in December (135.8 ± 4.43 FNU) and February (172.7 ± 2.18 FNU). In contrast, only one peak was observed in the Harbour in January 2018 (98.4 ± 1.44 FNU).

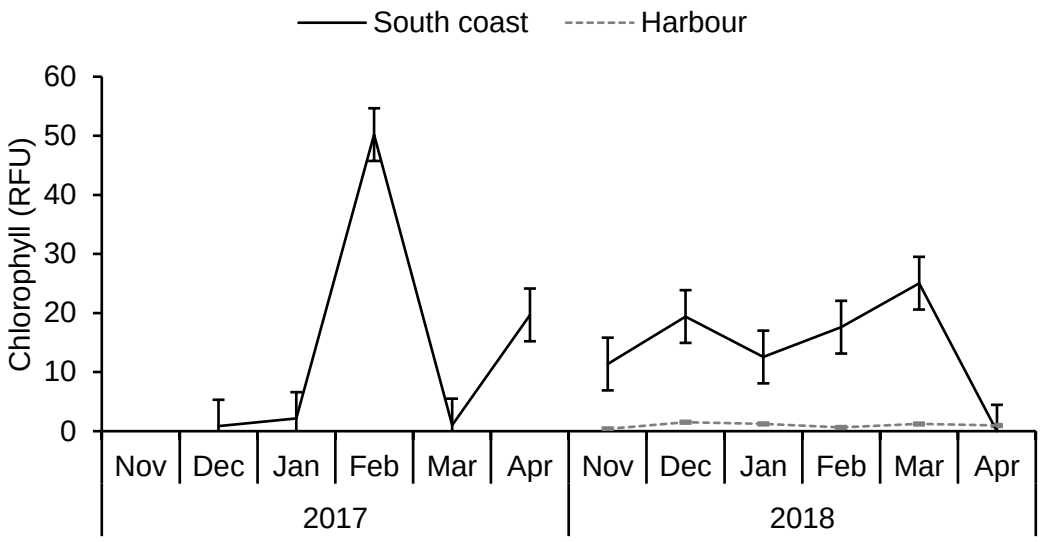


Fig. 2.5. Time series of mean (± SE) monthly chlorophyll (RFU) recorded by the CTDs in the South Coast and Wellington Harbour, from December 2016 to April 2017 (2017), and November 2017 to April 2018 (2018).

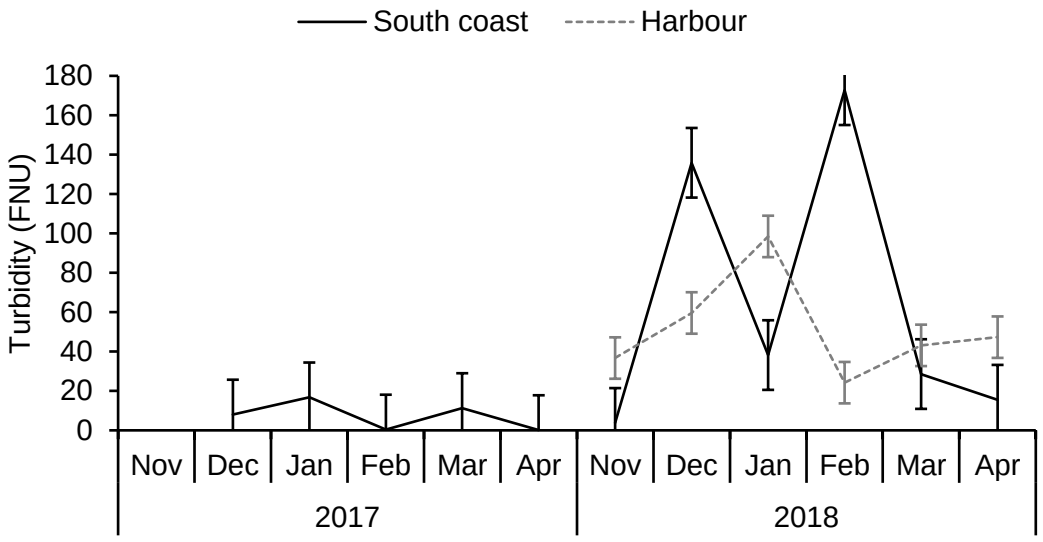


Fig. 2.6. Time series of mean (± SE) monthly turbidity (FNU) recorded by the CTDs in the South Coast and Wellington Harbour, from December 2016 to April 2017 (2017), and November 2017 to April 2018 (2018).

Habitat composition significantly varied amongst the sampled sites (Fig. 2.7). The Harbour sites were very similar to each other, mainly composed by shells (77% and 88% cover for Kau Bay and Shelly Bay, respectively) with smaller amounts of sand and cobble. Macroalgae cover was extremely patchy in Shelly Bay, and restricted to the shoreline in Kau Bay. The macroalgal species present in these two sites were the brown algae *Carpophyllum* spp and the invasive *Undaria pinnatifida*. In contrast, the sites on the South coast had macroalgal cover from 30 to 70% in Breaker Bay and Princess Bay, respectively. However, macroalgal cover in Breaker Bay and Moa Point was patchy, and dominated by *Macrocystis pyrifera*, while Princess Bay had a macroalgal bed of mixed species, including *Ecklonia radiata*, *Lessonia* spp, and *Marginariella* spp. Moa Point was predominantly a sandy bottom with smaller amounts of cobble, Breaker Bay had mostly cobble and boulders, and Princess Bay had largely a macroalgal bed with cobbles under the canopy and boulders were also present.

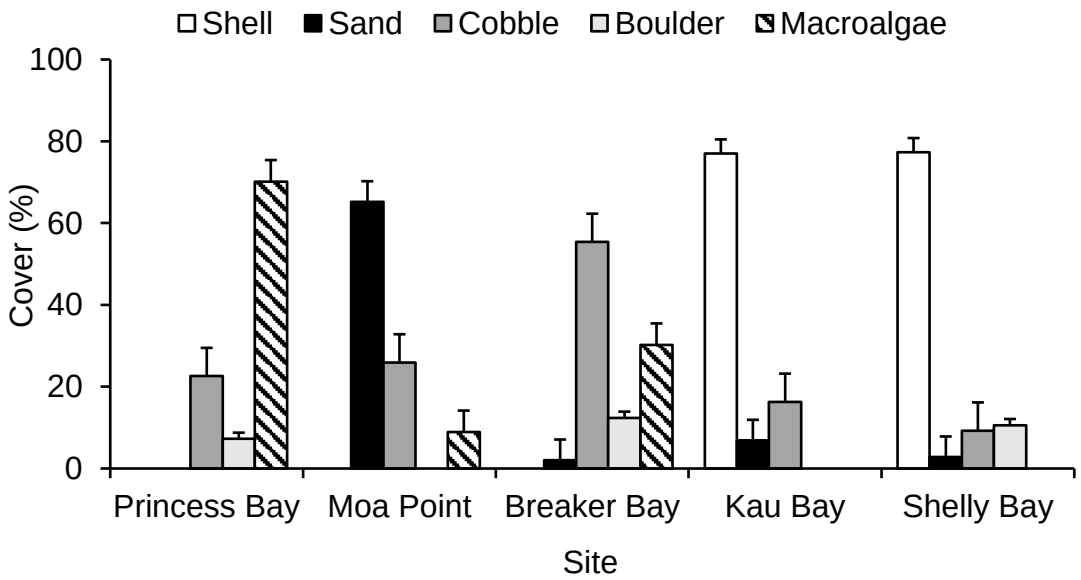


Fig. 2.7. Habitat composition cover (%). Bars represent mean ± SE.

2.3.2 Sea urchin density and size structure

Density of sea urchin adults did not vary significantly among the three sampled years, but they were significantly different among sites (Table 2.1). The highest mean values (± SD) were observed in Kau Bay (1.08 ± 0.59 ind m^{-2}) and Shelly Bay (0.73 ± 0.27 ind

m^{-2}), followed by Breaker Bay (0.10 ± 0.11 ind m^{-2}). However, mean density at the South coast sites was lower than 0.05 ind m^{-2} (Fig. 2.8). Furthermore, density of adult sea urchins had a moderate positive correlation with the habitat type shells (R = 58%, $p < 0.001$) and a weak negative correlation with macroalgae (R = -35%, p = 0.018) and cobble (R = -30%, p = 0.045) (Fig. 2.9).

Table 2.1. Results of the non-parametric Kruskal-Wallis test for sea urchin *Evechinus chloroticus* density between years and sampling sites. Kruskal-Wallis statistic (H), degrees of freedom (df), and p value (p) are given. Significant effects ($p < 0.05$) are highlighted in **bold**.

Source	H	df	p
Year	1.581	2	0.208
Site	14.94	4	**0.004**

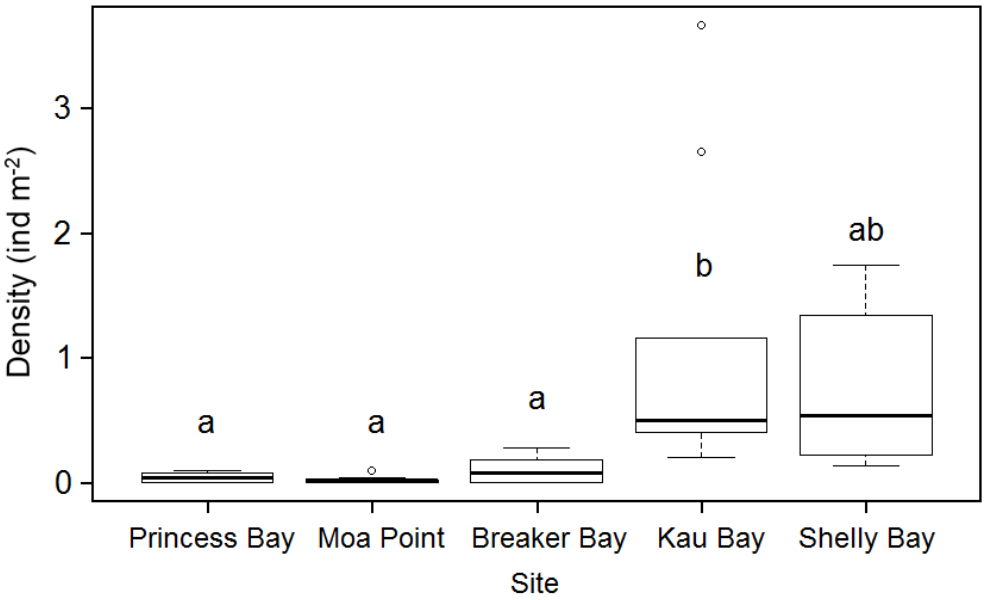


Fig. 2.8. Density of the sea urchin *Evechinus chloroticus* among the sampling sites. Boxes and whiskers represent mean (± SE). Letters above bars indicate significant differences in means based on post-hoc Dunn test.

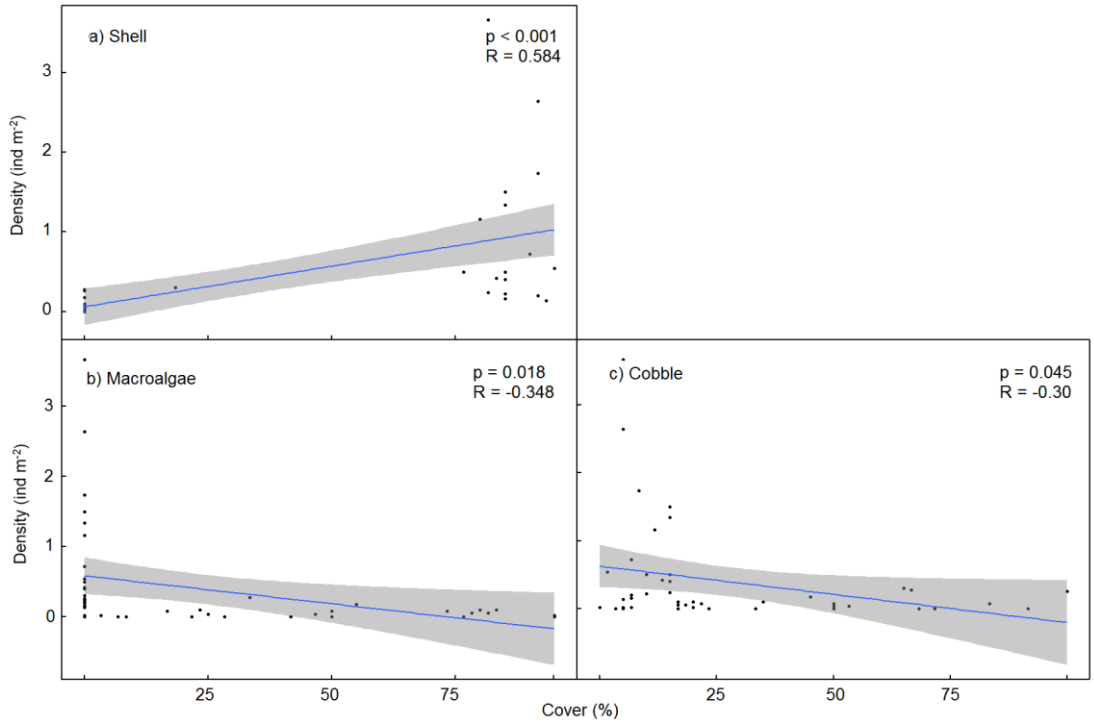


Fig. 2.9. Correlation between sea urchin *Evechinus chloroticus* density and habitat composition: a) shell, b) macroalgae, and c) cobble cover (%). Only significant interactions were plotted. Individual p and R values from Pearson's correlation are shown. Shaded area corresponds to 95% confidence interval.

Size structure of sea urchins varied amongst the sampled sites. No sea urchins <60 mm were observed either in Princess Bay (Fig. 2.10) or Moa Point (Fig. 2.11). The largest mean size (± SD) and maximum size were observed in Breaker Bay (88.7 ± 16.5 mm and 127 mm, respectively). Interestingly, only one juvenile (<30 mm) was found at this site in 2017, while young adults (<50 mm) were only observed in 2019 (Fig. 2.12). Very large individuals (>100 mm) were only found in the South coast sites. In fact, mean size in the Harbour was considerably smaller compared to the South coast. A very low percentage of individuals <50 mm was observed in Kau Bay (Fig. 2.13). The lowest mean and minimum size were observed at Shelly Bay (54.3 ± 19.3 mm and 11.1 mm). A relatively high percentage of juveniles <20 mm was found at this site in 2017 (Fig. 2.14), but were not very abundant in 2018, and completely absent in 2019. No recent settlers or juveniles were found in the substrate samples.

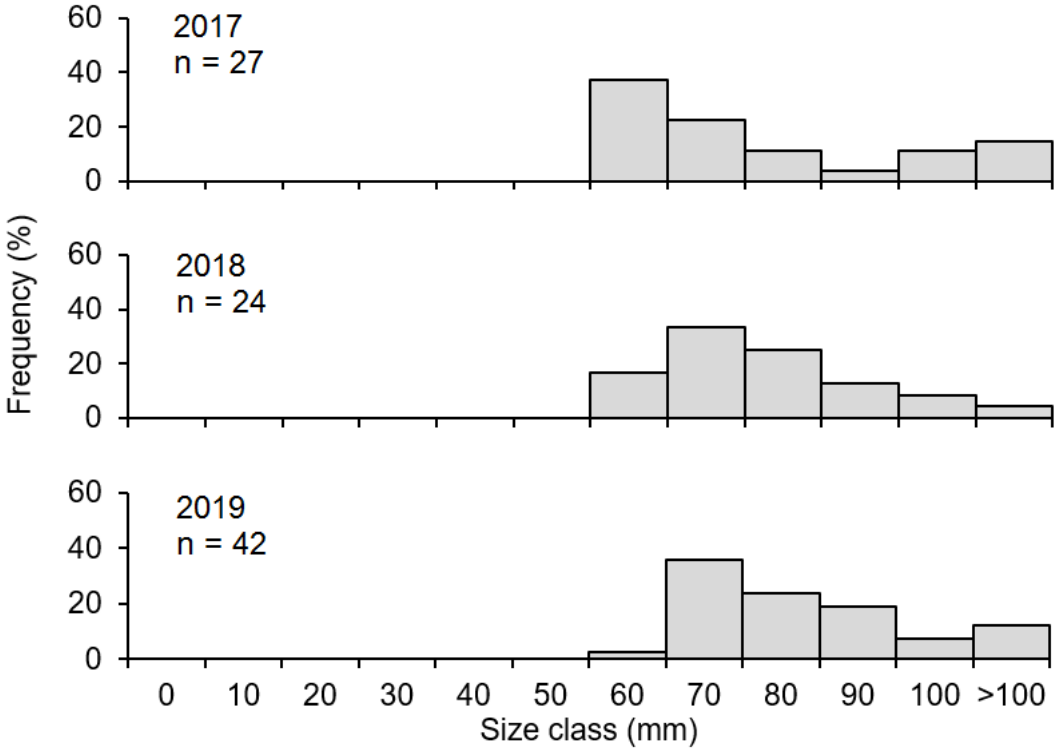


Fig. 2.10. Size structure of sea urchin *Evechinus chloroticus* at Princess Bay.

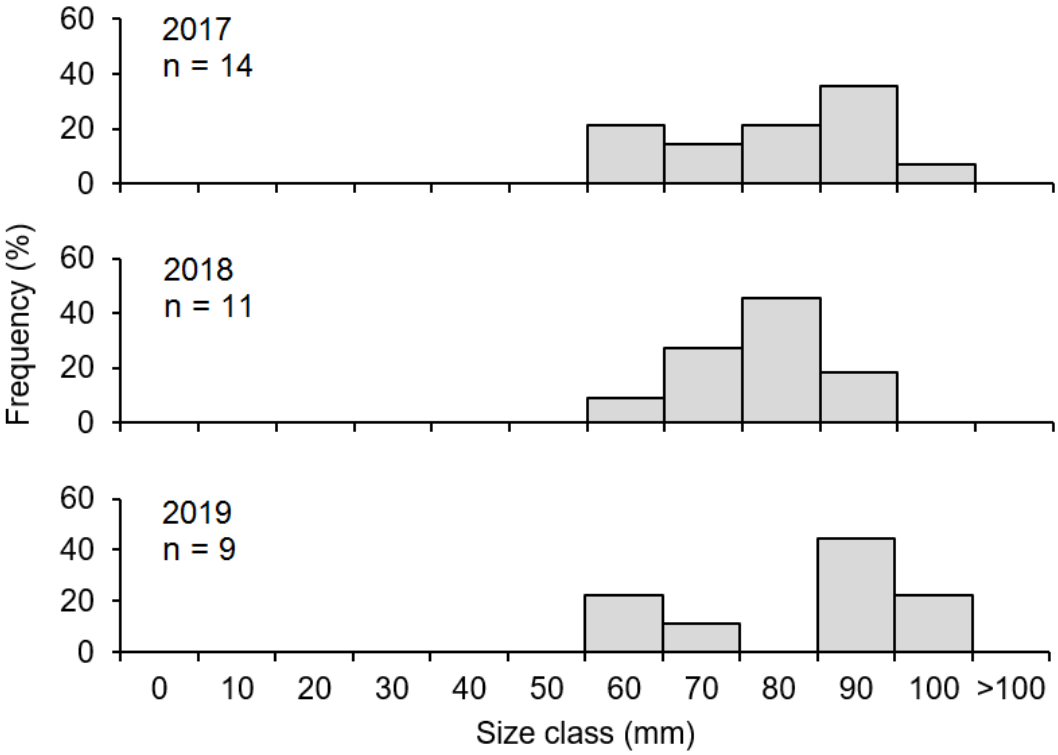


Fig. 2.11. Size structure of sea urchin *Evechinus chloroticus* at Moa Point.

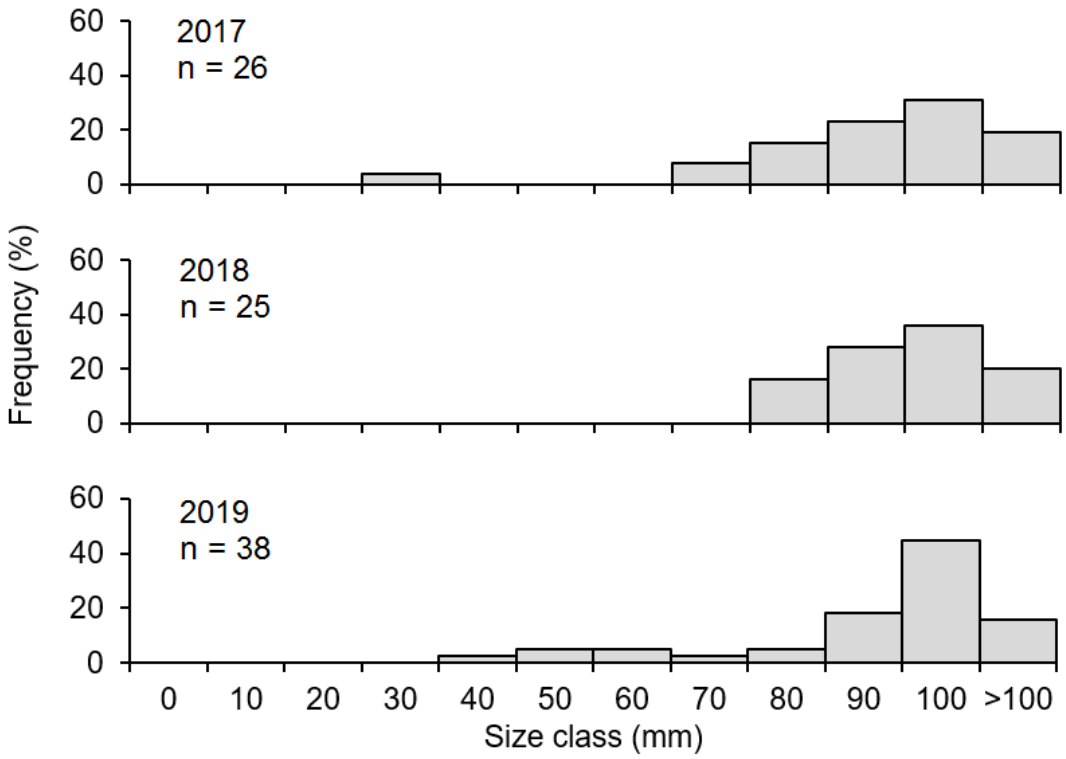


Fig. 2.12. Size structure of sea urchin *Evechinus chloroticus* at Breaker Bay.

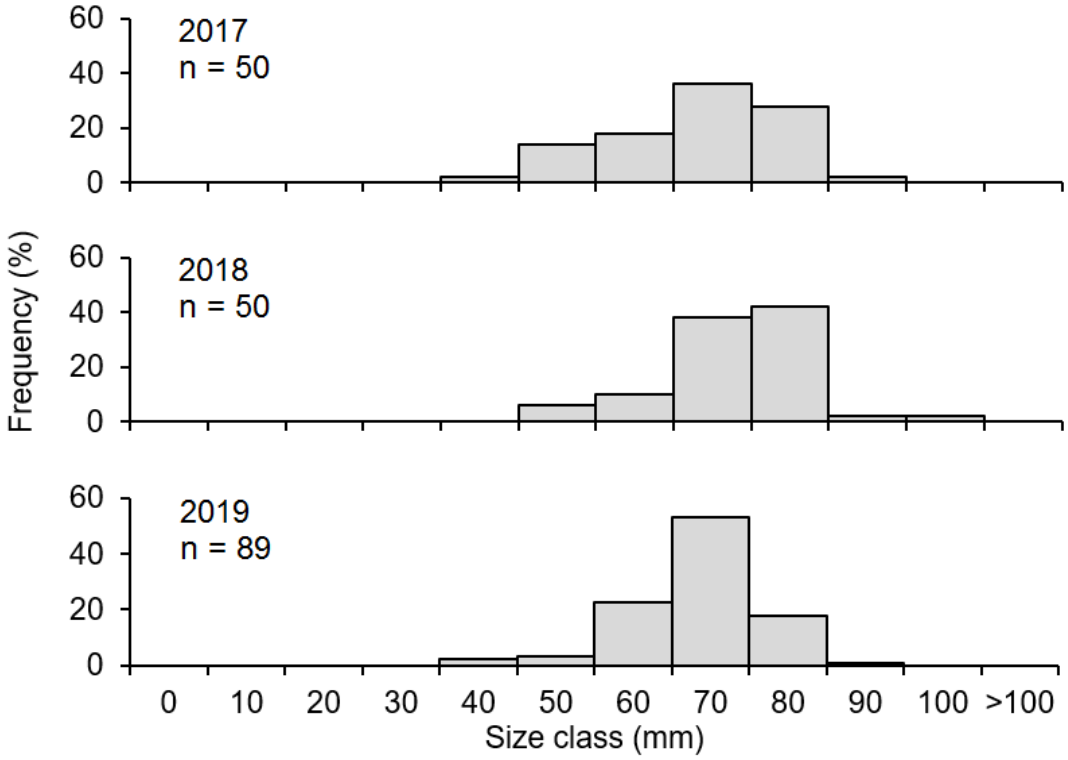


Fig. 2.13. Size structure of sea urchin *Evechinus chloroticus* at Kau Bay.

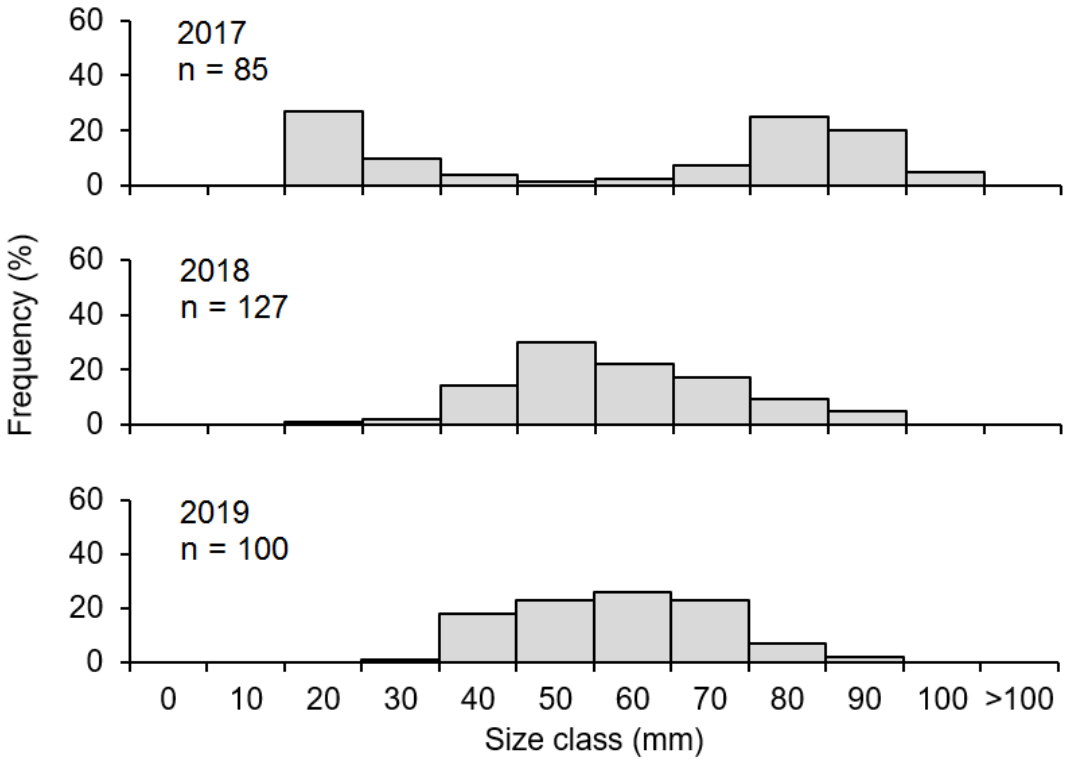


Fig. 2.14. Size structure of sea urchin *Evechinus chloroticus* at Shelly Bay.

There was no effect of year on the mean size of sea urchins. However, it was significantly different among the sampling sites (Table 2.2). Mean size was significantly larger at Breaker Bay compared to the rest of the sites, while the lowest values were observed in Shelly Bay (Fig. 2.15). There was a moderate negative relationship between mean sea urchin size and density (R = -57%, p = 0.27). Higher densities >1 ind m^{-2} were correlated with smaller sizes (Fig. 2.16).

A total of 79 juveniles were collected in Shelly Bay in 2017. Initial sizes ranged from 11 to 54 mm. Sixteen months later, the smallest individual was 19.5 mm, while the largest was 68 mm. Mean growth was estimated to be 13.8 mm per year. However, small juveniles (initial size of <20 mm) had lower growth rates than larger individuals, of only about 2.1 mm per year. In contrast, individuals >30 mm grew an average of 12.4 mm per year.

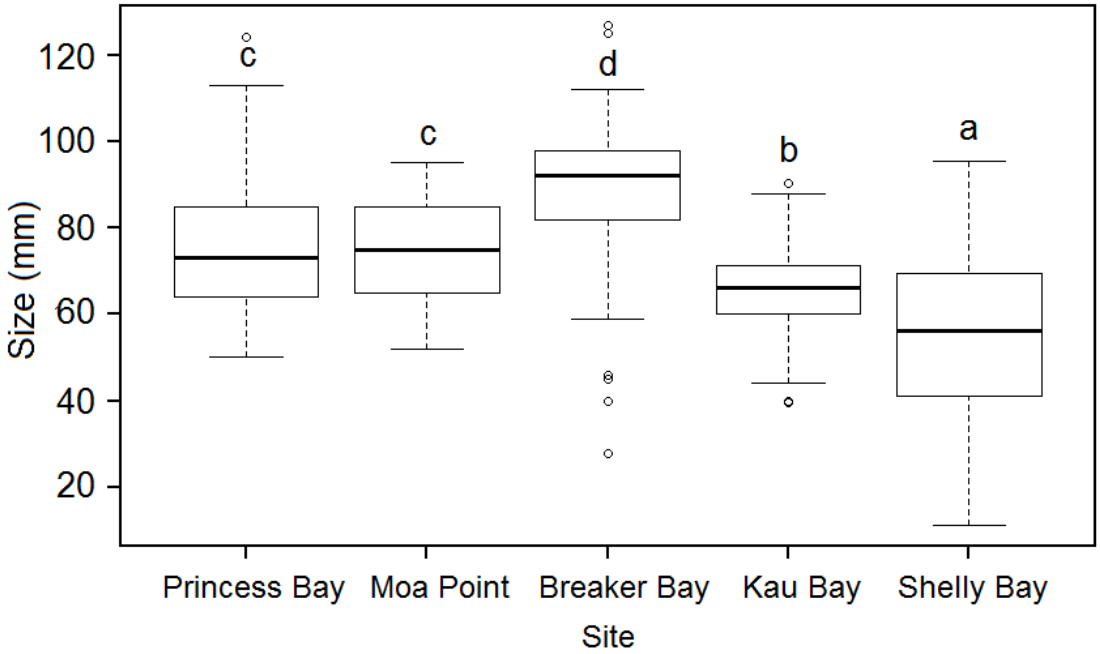


Fig. 2.15. Size of the sea urchin *Evechinus chloroticus* at the sampling sites. Boxes and whiskers represent mean ± SE. Letters above bars indicate significant differences in means based on post-hoc Tukey test.

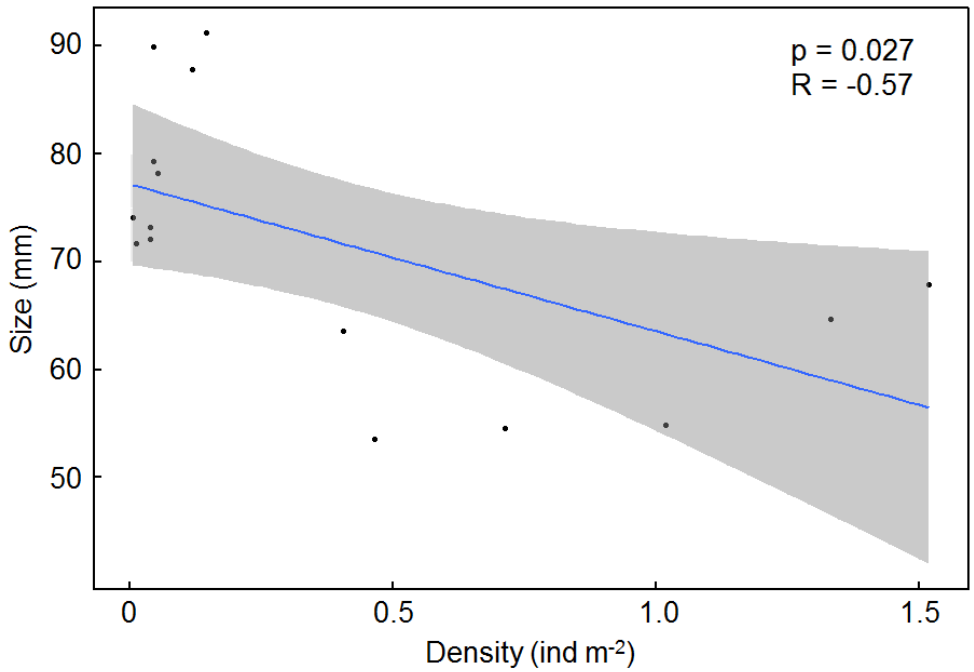


Fig. 2.16. Relationship between mean size (mm) and density (ind m^{-2}) of the sea urchin *Evechinus chloroticus* at the sampled sites. p and R values from Pearson's correlation are shown. Shaded area corresponds to 95% confidence interval.

Table 2.2. ANOVA results for sea urchin *Evechinus chloroticus* size between years and sampling sites. Sums of squares (SS), degrees of freedom (df), ANOVA statistic (F) and p value (p) are given. Significant effects ($p < 0.05$) are highlighted in **bold**.

Source	SS	df	F	p
Year	247	2	0.474	0.623
Site	97148	4	93.274	**<0.001**
Year * Site	1429	8	0.686	0.704
Error	182789	702		

2.3.3 Sea urchin settlement in artificial collectors

Sea urchin settlers were observed in the artificial collectors in February 2018 and January 2019 (Fig. 2.17). Sea urchin settlers were observed at Kau Bay only in 2018, at Shelly Bay only in 2019, and in both years at Breaker Bay. The highest settlement was in Shelly Bay with a mean of 2.3 settlers per collector. The spatial and temporal variation in sea urchin settlement was modelled as a function of year and site using negative binomial regression to account for the large proportions of zeros, and there was a significant effect of the interaction of these two factors (Table 2.3). There was a moderate positive correlation between settlement of sea urchins in the artificial collectors and seawater temperature and turbidity logged by the CTD (Fig. 2.18). The correlation between sea urchin settlement and habitat composition was not significant, but there was a moderate positive relationship with shells ($R = 33\%$, $p = 0.72$). Likewise, density of sea urchin adults was positive correlated with settlement but the relationship was not significant ($R = 25\%$, $p = 0.09$). Only one juvenile (13 mm test diameter) was found in Shelly Bay in the substrate samples, but no recent settlers or older juveniles were found in any other site during the sampled period.

Table 2.3. Spatial and temporal variation of sea urchin settlement, modelled as a function of year and site using negative binomial regression with a log-link function (theta = 0.73 ± 0.51, log-likelihood = -65.80). Chi-square (chi^2), degrees of freedom (df) and p value (p) are given. Significant effects ($p < 0.05$) are highlighted in **bold**.

Source	chi^2	df	p
Year	15.65	2	**<0.001**
Site	21.21	4	**<0.001**
Year * Site	15.87	8	**0.044**

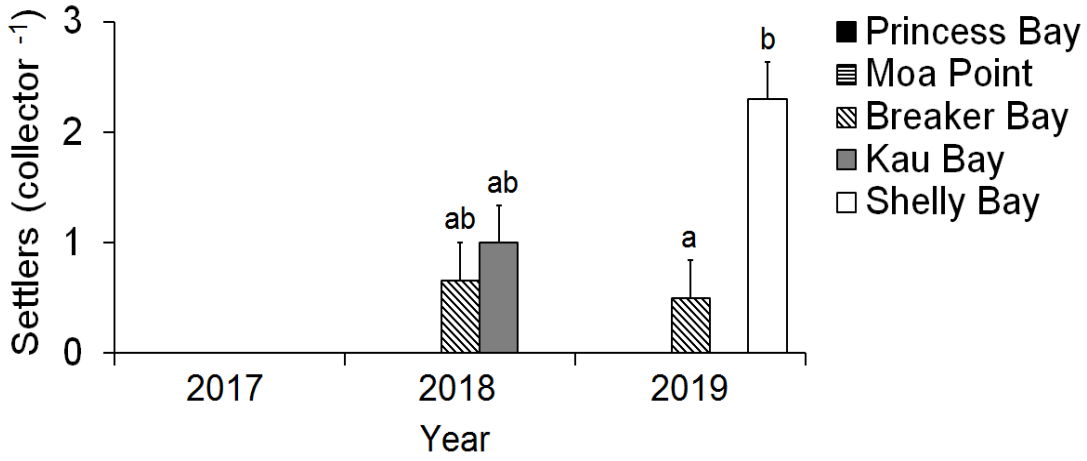


Fig. 2.17. Sea urchin settlement at each site pooled per year 2017 (Nov 2016 – Apr 2017), 2018 (Nov 2017 – Apr 2018) and 2019 (Dec 2018 – Feb 2019). Bars represent mean number of settlers per collector (± SE), and letters above bars indicate significant differences in means based on post-hoc Tukey tests on the interactive effects. Princess Bay and Moa Point not shown.

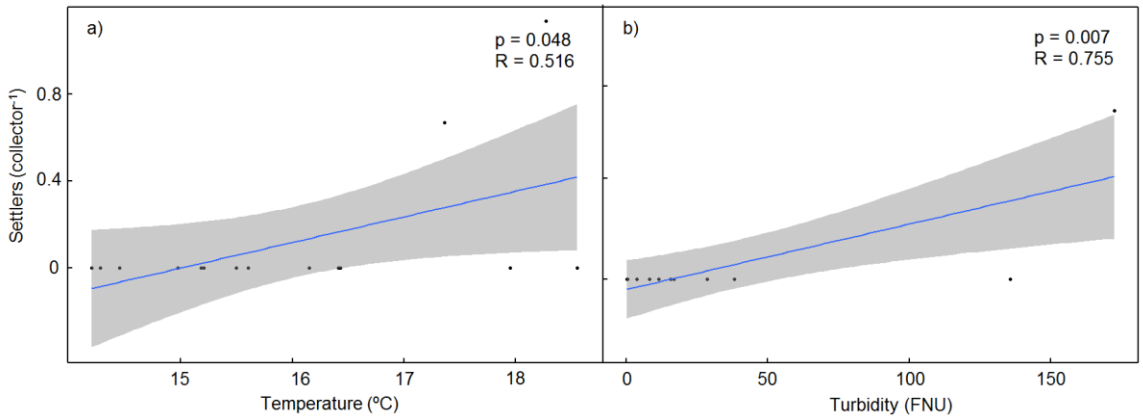


Fig. 2.18. Correlation between sea urchin *Evechinus chloroticus* settlement and environmental variables measured by the CTD: a) temperature (ºC), and b) turbidity (FNU). Individual p and R values from Pearson's correlation are shown. Shaded area corresponds to 95% confidence interval.

2.4 Discussion

Notable differences were observed in the population structure of the sea urchin *Evechinus chloroticus* around the Wellington region. Variation in density and size structure between the Harbour and the South coast was closely related to habitat features, and likely due to processes shaping the population structure, such as recruitment. While sea urchin densities in the Harbour were higher compared to the South coast, the mean sizes were smaller, mainly due to the presence of a young adult cohort (<50 mm) at Shelly Bay and Breaker Bay.

Habitat composition was the most distinctive feature between the Harbour and the South coast. While the substrate at Kau Bay and Shelly Bay consisted in a combination of shells and sand, the sites on the South coast were predominantly rocky reefs with a much higher macroalgal cover. In contrast, Breaker Bay, located near the entrance of the Harbour, was the most heterogeneous site, characterised by a complex rocky reef, with boulders and patches of macroalgae. It has been shown that habitat features can play an important role in controlling the size of sea urchin populations (Freeman 2003, Chiantore et al. 2008, Prado et al. 2012). In the present study, density was moderately correlated with the predominant habitat type in the Harbour, and displayed

a negative relationship with macroalgal cover. Previous studies have shown that at sites dominated by kelp, densities of *E. chloroticus* are usually low (Andrew 1989).

Density of *E. chloroticus* has been previously estimated in the Wellington region (Pande 2001), and the values were similar to those reported in the present study. Pande (2001) reported densities of approximately 0.033 ± 0.008 ind m^{-2} at Princess Bay and Breaker Bay. These values are relatively low compared to other sites across New Zealand. For example, in Fiordland, the maximum mean density was 2.47 ± 0.93 ind m^{-2} in Doubtful Sound (Witman & Grange 1998), and between 1.6 ± 0.1 and 2.6 ± 0.2 ind m^{-2} in Dusky Sound (McShane et al. 1993, Villouta et al. 2001). However, dense aggregations have been observed in the sounds (McShane & Naylor 1991, Wing et al. 2001), and in the northernmost parts of the country where densities can reach up to 30 ind m^{-2} (Choat & Schiel 1982, Shears & Babcock 2004).

In the present study, the spatial distribution of *E. chloroticus* also varied across the two adjacent systems of the Wellington region. At the South coast sites, sea urchins aggregated in small patches of five to ten individuals around small rocks (~50 cm). In contrast, sea urchins in the Harbour were found exposed on the substrate, as the habitat complexity was very low, but sometimes they aggregated to feed on drifting algae in groups of more than 20 individuals (A. Glockner-Fagetti personal observation). Dense aggregations of sea urchins are thought to be advantageous to resist wave action (Pearse & Arch 1969, Tuya et al. 2007), and as a mechanism to prevent predation (Valdez & Villalobos 1978, Vega & Romero 2011).

Larger sizes of *E. chloroticus* were found in the South coast sites, where the mode was usually 90 mm. In contrast, the mode in the Harbour sites was 70 mm, and at least 10% of the individuals were young adults <50 mm. Sea urchins are thought to reach larger sizes at low-density habitats, as growth is mainly determined by resource availability and the energy intake by the individuals (Levitan 1988, 1989). In the present study, test diameter and density were inversely correlated. Sea urchins reached larger sizes at sites where density was low, while smaller organisms were predominant at denser sites. This negative relationship has previously been observed for the sea urchins *Diadema antillarum* (Hunte et al. 1986, Levitan 1988, Rogers 2011), *Paracentrotus lividus* (Vega & Romero 2011, Ouréns et al. 2013), and for *E. chloroticus* in northern parts of New Zealand (Shears & Babcock 2007).

When food resources are limited, sea urchins are capable of slowing down their individual growth in order to maintain a continual reproductive effort, so the population can reach higher densities (Andrew 1989, Levitan 1989). Adult *E. chloroticus* reach larger sizes at sites with abundant kelp, which is probably the preferred element of their diet (Choat & Schiel 1982, Wing & Wing 2015). However, this species, similar to other sea urchins, can shift their diets and prey on other invertebrates and bacterial films (Vanderklift et al. 2006, Wing et al. 2008). This might explain how the populations of *E. chloroticus* are sustained in the Harbour, where the macroalgal cover is so very low and thus there is a possible food resource limitation.

The size structure of *E. chloroticus* in the Wellington region was unimodal, with a low percentage of young adults (<50 mm) present mainly at the Harbour sites and Breaker Bay. Young adults at Breaker Bay were usually found in crevices of large boulders, while they were found on the substrate but covered with shells and pebbles in Shelly Bay. Previous studies on the South coast showed a mode of 100 mm, where individuals <50 mm represented less than 10% of the population (Byfield 2013). Unimodal size-frequencies of *E. chloroticus* have been observed in northern New Zealand (Choat & Schiel 1982), Abel Tasman (Davidson & Chadderton 1994) and Tory Channel (Lamare & Barker 2001), where juveniles <20 mm were also very scarce. However, contrary to my findings, many previous studies have found bimodal populations, as evidence of the recruitment of a new cohort of 40 – 60 mm (McShane & Naylor 1991, McShane et al. 1993, Cole & Keuskamp 1998, Lamare & Barker 2001, Freeman 2006). Test diameter ranged from 12 to 190 mm (McShane & Naylor 1991) at Dusky Sound, and from 3 to 112 mm at Cape Rodney (Cole & Keuskamp 1998), but individuals <50 mm were usually cryptic.

The absence of juveniles and young adults in the South coast sites might indicate that there has not been a large episode of recruitment in the area, and populations are being maintained from migration of individuals from adjacent areas. In contrast, the presence of juveniles <20 mm at Shelly Bay in 2017, might be due to a large pulse of settlement in the previous year. Freeman (2006) observed a <20 mm-cohort at two non-reserve sites in Gisborne and pointed out that it was a good year for recruitment. However, such a size cohort was not observed the following year, which is also evidence that recruitment can be sporadic and infrequent (Freeman 2006). Here, the absence of individuals <5 mm, even in the Harbour sites, coincides with other studies

that were also unable to find recent settlers, even at high density populations (Dix 1972, McShane & Naylor 1991).

Sea urchin settlement can be temporally variable, restricted to only a few months during the year (Dix 1972, McNaught 1999, Garcia-Sanz et al. 2014) and years of successful recruitment can be followed by multiple years of poor recruitment (Lozano et al. 1995, Agatsuma et al. 1998, Tomas et al. 2004). Here, settlement of *E. chloroticus* occurred once during the summer and did not occur during the first sampled year. Spatial variation was also observed. Settlement occurred only in the Harbour sites and in the mouth of the Harbour, but not on the South coast. Similarly, Rowley (1989) and Balch and Scheibling (2000) found that settlement of *Strongylocentrotus* spp was higher in barrens, compared to kelp beds. These differences were attributed to different kinds of predators and competitors between the two habitats, which may lead to differential survival rates of sea urchin juveniles (Rowley 1990). Here, abundance of crab and snail recruits in the collectors were significantly higher in the Harbour (see Appendix 3), which may pose an additional pressure on survival of sea urchin settlers in this location, as will be discussed further in Chapter 5. However, other factors might be responsible for the absence of settlers on the South coast during the studied period.

Different settlement patterns of other invertebrates have been observed between the Harbour and the South coast. The most well described example, which has been subject of several studies, is the absence of mussels on the South coast, compared to the large populations that prevail in the Harbour (Gardner 2000, Helson 2001, Demello & Phillips 2011). Helson and Gardner (2004) found that larval densities in the plankton and settlement rates of mussels were significantly higher in the Harbour, compared to the South coast. However, the differences in adult populations between the two adjacent systems could not be only attributed to a limitation in recruitment, but to other factors such as post-settlement mortality (Helson & Gardner 2004), the quality and quantity of particulate food, which was significantly lower on the South coast (Gardner 2000, Helson et al. 2007), and to distinctive circulation patterns between the two systems (Demello & Phillips 2011).

In the present study, the environmental variables showed distinctive patterns between the two systems during the sampled period. Mean seawater temperature was

significantly higher in the Harbour compared to the South coast. This was likely due to the mixing of subantarctic waters that occurs in the Cook Strait and cools down the shores of the South coast, while the enclosed waters of the Harbour can warm up during the summer due to the low flow circulation (Walters et al. 2010). Although temperature was not a significant variable explaining differential patterns in mussel settlement in the Harbour (Helson & Gardner 2004), in the present study it was moderately correlated with the presence of sea urchin settlers in the artificial collectors.

Even though settlement of *E. chloroticus* might be occurring very sporadically in the Harbour, it was still detected during the course of this study, whereas on the South coast, no sign of settlers or juveniles was observed. Oceanographic features might be largely contributing to shape the population structure in the Wellington region. Enclosed bodies of water with a low flow system, like the Harbour, could contribute to the retention of the larvae in the water column, and the consequent recruitment in nearby areas. It has been observed that recruitment of fish (Shima & Swearer 2009a), and settlement of mussels and barnacles (Hoffmann et al. 2012), sea stars (Sewell & Watson 1993), and sea urchins (Rogers & Lorenzen 2016), are higher in enclosed habitats like bays. Similarly, high levels of retention of *E. chloroticus* larvae have been observed in New Zealand southern fiords (Lamare 1998). Field observations coupled with environmental modelling suggested that the fiords are composted by source and sink areas, where the highest abundance of sea urchins coincided with highest larval supply and settlement (Wing et al. 2003). Furthermore, settlement rates of sea urchins have been observed to increase during events of upwelling relaxation, which contributed to retention of larvae near coastal areas (Ebert et al. 1994, Morgan et al. 2000, Morgan et al. 2012), while offshore advection caused by wind transported larvae away from a suitable substrate for settlement (Balch & Scheibling 2001). The predominantly strong currents in the Cook Strait might be dispersing larvae offshore. In fact, this highly dynamic region is acting as barrier to gene flow of *E. chloroticus* between the North and the South Islands (Nagel et al. 2015).

The use of artificial collectors has been a convenient technique to study spatial and temporal variation in the settlement of sea urchins. However, data should be interpreted as an index of settler supply rather than an indicator of settlement intensity in the field (Jennings & Hunt 2010, Pineda et al. 2010). In this sense, the source of settlers in the Harbour might be higher compared to the South coast, which coincides

with the low densities of sea urchin adults observed in the latter. However, there was no direct relationship between adult density and larval settlement. Similar results have been found for *P. lividus* (Hereu et al. 2004, Prado et al. 2012) and *D. antillarum* (Rogers & Lorenzen 2016), where the relationship between density of adults and settlement estimated in the field was not significant. Nevertheless, the absence of juveniles and settlers on the South coast might be enough evidence to explain the low adult densities prevailing in this system and suggests that populations may be maintained by sporadic or infrequent recruitment pulses.

Two different population dynamics were observed in the Wellington region. The Harbour was characterised by higher sea urchin densities, smaller mean size mainly due to presence of a juvenile cohort, and sporadic but subtle pulses of settlement, all strongly correlated to habitat type. Settlement data in combination with size structure suggest that recruitment might happen every 2 to 3 years. However, post-settlement mortality might be so high that the magnitude of settlement needs to be greater than the observed here, so enough surviving juveniles can be detected the following year. The South coast, on the other hand, was characterised by low sea urchin density that was negatively correlated with macroalgal cover, where individuals reached larger sizes and recruitment was not observed during the three-year study. These results suggest that recruitment pulses are very infrequent and that juveniles might be recruiting in deep waters or in nearby areas. In fact, Breaker Bay might be a source of juveniles that migrate to adjacent sites on the South coast. This was the only site were settlement was observed during two consecutive years, and the presence of a young adult cohort (40 – 60 mm) suggests that recruitment might occur every 3 to 4 years.

Populations depend on recruitment for replenishment. The present study demonstrates that recruitment of *E. chloroticus* can be very infrequent. For relatively long-lived species, even if recruitment is sporadic populations can be sustained if adult mortality is low. However, kina is subject to exploitation, not only in the Wellington region, but across the country. The low recruitment patterns observed here could be similar in other parts of New Zealand where sea urchin barrens are not very common. This study contributes to a better understanding of the processes that shape population structure of *E. chloroticus*.

Chapter 3

Species assemblage and recruitment patterns of echinoderms in central New Zealand

Reef starfish *Stichaster australis* on the South coast

Glockner-Fagetti A, Phillips NE (2020) Species assemblage and recruitment patterns of echinoderms on shallow rocky reefs in central New Zealand. New Zealand Journal of Marine and Freshwater Research:1-19

Chapter 3

3.1 Introduction

Temperate rocky reefs are highly productive ecosystems that support a diverse marine community (Dayton 1985, Jones & Andrew 1992) and provide ecosystem services for local human populations (Holmlund & Hammer 1999, Smale et al. 2013). The structure of the community in rocky reefs is shaped by a wide range of environmental and biological processes that fluctuate in space and time (Barry & Dayton 1991, Sebens 1991). Increasing habitat complexity, and other abiotic factors, can lead to higher species richness and diversity (Tylianakis et al. 2008, Pierre & Kovalenko 2014). For example, fish abundance and number of species have been positively correlated with structural complexity of the reef and macroalgal cover in temperate systems (Parsons et al. 2016, Cheminée et al. 2017). However, fewer studies have focused on the relationship of habitat composition and mobile invertebrate assemblages, such as echinoderms (Entrambasaguas et al. 2008, Iken et al. 2010).

Patterns of distribution and abundance of species within a community also vary depending on their reproductive cycles and survival strategies (Hughes et al. 2000, Vanderklift & Kendrick 2004). The heterogeneity in echinoderm assemblages has been attributed not only to habitat features (Entrambasaguas et al. 2008, Hermosillo-Nuñez et al. 2015), but also to variation in recruitment rates (Balch & Scheibling 2000, Hereu et al. 2004), predation (Tegner & Dayton 1981, Sala & Zabala 1996), anthropogenic disturbance (Uthicke et al. 2009) and other broader scale environmental factors (Iken et al. 2010). However, the ecological processes that regulate patterns of distribution of echinoderm assemblages are still poorly understood (Pérez-Ruzafa et al. 2001).

Recruitment might be one of the most important factors controlling echinoderm abundance and distribution patterns (Balch & Scheibling 2001, Ling & Johnson 2009). It is usually determined by a number of variables affecting survival of the juvenile stages, including settlement and post-settlement processes such as predation and competition (Connell 1985, Turon et al. 2000). Settlement patterns can be unpredictable events that vary from year to year and at scales of tens to thousands of meters (Fisk 1992, Johnson 1992, Agatsuma et al. 1998). The magnitude and timing

of echinoderm settlement pulses also differ between species, which has been attributed to species-specific processes rather than environmental variables (Balch & Scheibling 2000, Jennings & Hunt 2010). Most of the previous studies have focused on recruitment patterns of sea urchins (Cameron & Schroeter 1980, Ebert et al. 1994, Morgan et al. 2000, Balsalobre et al. 2016). Less attention has been paid to recruitment patterns in the field of other echinoderm groups (Barker & Nichols 1983, Black & Moran 1991, Turon et al. 2000), with the exception of the corallivore sea star *Acanthaster planci* (Zann et al. 1987, Fisk 1992, Keesing & Halford 1992) and the temperate starfish *Asterias* spp (Loosanoff 1964, Barker & Nichols 1983).

Outbreaks of the crown-of-thorns sea stars (*Acanthaster* spp), attributed to dispersal of larvae and successful recruitment (Birkeland & Lucas 1990) have caused significant degradation to coral reefs in the Indo-Pacific (Chesher 1969, Faurea 1989). The study of dispersal of larvae has been key to the understanding and management of outbreaks in the Great Barrier Reef (Uthicke et al. 2015, Uthicke et al. 2018b). DNA techniques have been used to identify *A. cf. solaris* larvae from plankton samples and monitor the dispersal of larvae (Uthicke et al. 2018a, Uthicke et al. 2019). Similarly, identification of *Asterias amurensis* larvae from plankton samples using PCR-based tests has been useful to monitor the distribution and possible dispersal of this invasive species in Tasmania (Evans et al. 1998, Deagle et al. 2003).

Echinoderms play important ecological roles in the benthic community, occurring in all marine habitats, and across all climatic zones (Harrold & Pearse 1987, Uthicke et al. 2009). Sea stars, for example, are keystone predators that are able to modify the diversity, abundance and distribution of the prey species through top-down control (Menge & Lubchenco 1981, Day et al. 1995). Sea cucumbers, on the other hand, are detritivores that recycle and release nutrients back to the substrate, making them available for other species and increasing productivity in benthic ecosystems (Uthicke 2001, Wolkenhauer et al. 2010).

The echinoderm fauna in New Zealand is diverse, with roughly 623 recorded species (Gordon et al. 2010), many of which are endemic (Mills et al. 2014). However, basic information on the ecology and recruitment of many species is lacking from different areas around the country (Barker 1977a, Byrne & Barker 1991, Sköld et al. 2002). Probably the most well studied species are the cushion star *Patiriella regularis*, and

the eleven-armed sea star *Coscinasterias muricata*, both of which are commonly found from the intertidal to 100 m depth, and are widely distributed across New Zealand (Crump 1969, Byrne & Barker 1991). While the cushion star is an endemic species, that has been introduced in Tasmania, the eleven-armed sea star is widely distributed in the Indo-Pacific, but usually restricted to harbours and wave-sheltered shores (Barker 1977a, Byrne & Barker 1991).

Patiriella regularis has indirect development through a planktotrophic bipinnaria and brachiolaria larvae (Crump 1971). Larval development takes 9-10 weeks, and competent larvae swim close to substrate for metamorphosis, which can take up to six days (Byrne & Barker 1991). In contrast, larval development of *C. muricata* can take up to 30 days, and metamorphosis around 5 days (Barker 1978). However, this species is also capable of reproducing asexually through fission (Sköld et al. 2002). Reproduction of both species has been observed to occur during summer (Georgiades et al. 2006). Larval development and parental history has also been examined in the apricot sea star *Sclerasterias mollis* (Poorbagher et al. 2010a) and in the white sea urchin *Pseudechinus huttoni* (Kirby et al. 2006, Poorbagher et al. 2010b). The sea cucumber *Australostichopus mollis* is probably the most conspicuous and widely distributed holothurian in the shallow waters of New Zealand (Mills et al. 2014). This deposit feeder species displays an annual reproductive cycle, where spawning occurs during the austral summer (Sewell 1992). In contrast, there is little information on the ecology or reproductive biology of the large ophiuroid *Ophiopsammus maculata*, whose information is restricted to taxonomic data (Gould et al. 2001, Mills & O'Hara 2013).

The study of species composition and how their abundance changes through space and time is key to understanding the ecological processes that shape community structure. It also provides insights to identify crucial areas of protection for a better management of coastal areas. The aims of this study were: 1) to describe the echinoderm assemblage and estimate density and correlate these variables with habitat composition and 2) to evaluate the spatial and temporal variation of echinoderm settlement and recruitment in the Wellington region.

3.2 Materials and methods

3.2.1 Echinoderm assemblage composition and density

The abundance of adult echinoderms was estimated once a year (2017 – 2019) at Princess Bay and Moa Point (South coast), Breaker Bay (mouth of the Harbour), Kau Bay and Shelly Bay (Wellington Harbour). At each site, three 25 × 2 m belt transects were laid parallel to the shoreline at 4 to 8 m depth. All echinoderms inside the transect were counted. Density was estimated as the number of adults found per transect, divided by the surveyed area (50 m^2). Variation in density between years and among sites was analysed per species using the non-parametric Kruskal-Wallis test, since the data did not meet ANOVA assumptions (assessed with Kolmogorov-Smirnov and Levene's tests). A Dunn post-hoc test was used to compare observations when factors were significant ($p < 0.05$). Mean species richness (S), relative abundance (RA), Shannon's diversity (H') and Pielou's evenness (J) indices were calculated for each site as indicators of echinoderm assemblage structure.

Variation in echinoderm assemblage composition was analysed between years and among sites (fixed factors), using permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis similarity of square-root transformed abundance data. A two-way similarity percentage (SIMPER) analysis was used to compare the contribution of each species between the sampling sites and a canonical analysis of principal coordinates (CAP) to better visualise these results. Finally, resemblance matrices and distant based linear models (DistLM) were used to determine the correlation between echinoderm assemblage and habitat composition based on Euclidean distances of the log-transformed environmental data. Sea urchin density analyses were excluded in this chapter, but the values were included in the indicators of community structure. All analyses were carried out using STATISTICA v10.0 (StatSoft) and PRIMER 6 & PERMANOVA+ v 1.0.3 (Anderson et al. 2008).

3.2.2 Settlement in artificial collectors

Settlement of echinoderms was estimated at the sampling sites during summer from November 2016 to April 2017 (year 2017), November 2017 to April 2018 (year 2018), and December 2018 to February 2019 (year 2019). Deployment of collectors and washing technique were the same as described in Chapter 2. Spatio-temporal variation of echinoderm settlement in artificial collectors was modelled as a function of year and site. A generalized linear model with negative binomial distribution was used to account for the over-dispersion of the data and the large proportion of zeros. Year, site and their interaction were included as fixed factors in the full model. Akaike Information Criterion (AIC) was used to select significant factors. Pearson's correlation was used to quantify the strength of the relationship between echinoderm settlement and seawater temperature, salinity, chlorophyll and turbidity, and the habitat composition in the sampled sites (as described in Chapter 2). Analyses were conducted using the software R v3.2.4 with 'pscl' and 'MASS' packages (Jackman et al. 2017).

DNA was extracted from sea star spp1 and spp2 settlers with the aim to identify the species, following a modified CTAB method (Zuccarello & Lokhorst 2005). Samples were incubated at 60 ºC for one hour before extraction. The following primer combinations were used to amplify ~657 bp from the 5' region of the COI gene from mitochondrial DNA: forward primer EchinoF1–5'-TTTCAACTAATCATAAGGACATTGG-3' and reverse primer EchinoR1–5'-CTTCAGGGTGTCCAAAAAATCA-3' (Ward et al. 2008). Polymerase chain reactions (PCR) were performed with the following final concentration: 1x buffer, 0.2 mM dNTP's, 2.5 nM $MgCl_2$, 0.04% BSA, 0.25 pmol of each primer, 1 U *Taq* polymerase and 1 µl of DNA. Amplifications were carried out in a gradient thermal cycle, which consisted in a denaturation step of 94 ºC/3 min, followed by 35 cycles of 94 ºC/30 s, 50 ºC/90 s and 72 ºC/1 min, with a final extension step at 72 ºC/10 min. PCR products were then visualised on 1.5% agarose gels stained with 10% ethidium bromide. Successful amplifications were purified using ExoSAP-IT and commercially sequenced (Macrogen Inc., Seoul, Korea). New sequences were assembled in Geneious 8.0.5 (http://www.geneious.com,(Kearse et al. 2012) and BLAST searched for the closest match. GenBank sequences of the three closest BLAST hits and genera within the family Asteriidae were added to the alignments (Waters & Roy 2003, Preuss &

Zuccarello 2018). Genes were concatenated by codon and RAxML 7.2.8 was used to construct a maximum-likelihood tree (see Appendix 5).

3.2.3 Recruitment

Recruitment was defined as juveniles that had survived approximately one year after they settled. Age of recruits was determined based on size-frequency distributions (Balch & Scheibling 2000). One-year-old recruits, like the asteroids *Patiriella regularis* and *Coscinasterias muricata*, were considered those <20 mm (arm to arm length), and ≤ 2 mm (disc diameter) for ophiuroids, such as *Ophiocentrus novaezelandiae*. Juveniles older than one year were considered individuals from 20 to 30 mm. One-year-old recruits and juveniles were sampled at each site in 2017 and 2018, using 25 m belt transects and collecting substrate samples, as described in Chapter 2. Density of juveniles was estimated and all individuals were measured to the nearest mm using callipers (± 0.1 mm). Variation in density between years and among sites was analysed using the non-parametric Kruskal-Wallis test, since the data did not meet ANOVA assumptions. A Dunn post-hoc test was used to compare observations when factors were significant ($p < 0.05$). Analyses were conducted using STATISTICA v10.0 (StatSoft).

3.3 Results

3.3.1 Echinoderm assemblage composition and density

Nine species of echinoderms were observed in the Wellington region. One species of the class Ophiuroidea, six species of the class Asteroidea, one of the class Holothuroidea, and one of the class Echinoidea (Table 3.1). Density of echinoderms was not significantly different between years, except for *Patiriella regularis*, while differences in density amongst sites were significant for all echinoderm species except for *Stichaster australis* (Table 3.2). The least abundant species were the three-and-three starfish *Allostichaster insignis*, which was present only at Shelly Bay (mean

density ± SD: 0.03 ± 0.06 ind m^{-2}), the biscuit star *Pentagonaster pulchellus*, observed at all the sampled sites but in low densities (0.01 ± 0.01 ind m^{-2}), the seven-armed *Astrostole scabra* (0.01 ± 0.01 ind m^{-2}) and reef starfish *Stichaster australis* (0.003 ± 0.005 ind m^{-2}), which were only present at Princess Bay and Breaker Bay, respectively. These species were excluded from further analysis due to their low densities.

Density of the brittle star *Ophiopsammus maculata* was significantly higher at Moa Point, compared to the rest of the sampling sites, and was absent from Kau Bay (Fig. 3.1). In contrast, density of the eleven-armed sea star *Coscinasterias muricata* was significantly higher in Shelly Bay and Kau Bay, compared to Moa Point and Breaker Bay, and no individuals were observed at Princess Bay (Fig. 3.2). The most abundant species observed at the sampling sites was the cushion star *Patiriella regularis*, whose densities were significantly higher in 2018, compared to 2017. The highest density of *P. regularis* was observed at Princess Bay and the lowest at Shelly Bay (Fig. 3.3). Finally, the sea cucumber *Australostichopus mollis* was highly abundant at Princess Bay, compared to Breaker Bay and Kau Bay, while density in Moa Point was very low (Fig. 3.4).

Table 3.1. Taxonomic classification of echinoderms in the Wellington region

Phylum Echinodermata
- Class Ophiuroidea
  - Order Ophiurida
    - Family Ophiodermatidae
      - *Ophiopsammus maculata* (Verrill, 1869)
- Class Asteroidea
  - Order Forcipulatida
    - Family Asteriidae
      - *Astrostole scabra* (Hutton, 1872)
      - *Coscinasterias muricata* Verrill, 1867
    - Family Stichasteridae
      - *Stichaster australis* (Verrill, 1867)
      - *Allostichaster insignis* (Farquhar, 1895)
  - Order Valvatida
    - Family Asterinidae
      - *Patiriella regularis* (Verrill, 1867)
    - Family Goniasteridae
      - *Pentagonaster pulchellus* Gray, 1840
- Class Holothuroidea
  - Order Aspidochirotida
    - Family Holothuriidae
      - *Australostichopus mollis* (Hutton, 1872)
- Class Echinoidea

Order Camarodonta
Family Echinometridae
Evechinus chloroticus (Valenciennes, 1846)

Table 3.2. Variation in echinoderm adult densities during the sampled years and amongst sites. Kruskal-Wallis statistic (H), degrees of freedom (df) and p values (p) are shown. Significant effects ($p < 0.05$) are highlighted in **bold**.

Source	Year			Site		
	df	H	p	df	H	p
Ophiopsammus maculata	2	0.454	0.796	4	29.151	**<0.001**
Astrostole scabra	2	4.131	0.126	4	12.462	**0.014**
Coscinasterias muricata	2	0.633	0.728	4	36.710	**<0.001**
Stichaster australis	2	3.892	0.142	4	6.444	0.168
Allostichaster insignis	2	0.004	0.997	4	43.351	**<0.001**
Patiriella regularis	2	9.765	**0.007**	4	12.659	**0.013**
Pentagonaster pulchellus	2	0.639	0.726	4	13.072	**0.011**
Australostichopus mollis	2	0.246	0.884	4	24.122	**0.001**

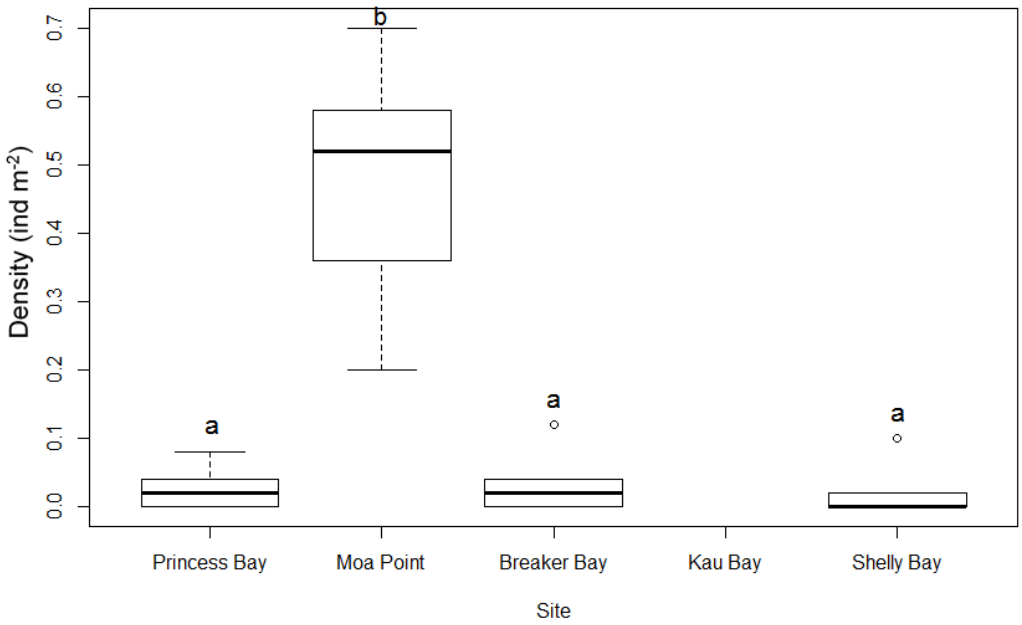


Fig. 3.1. Density of the brittle star *Ophiopsammus maculata* at the sampled sites pooled across years. Boxes represent the mean and quartiles, and bars the standard error. Letters above bars indicate significant differences in means based on Kruskal-Wallis test.

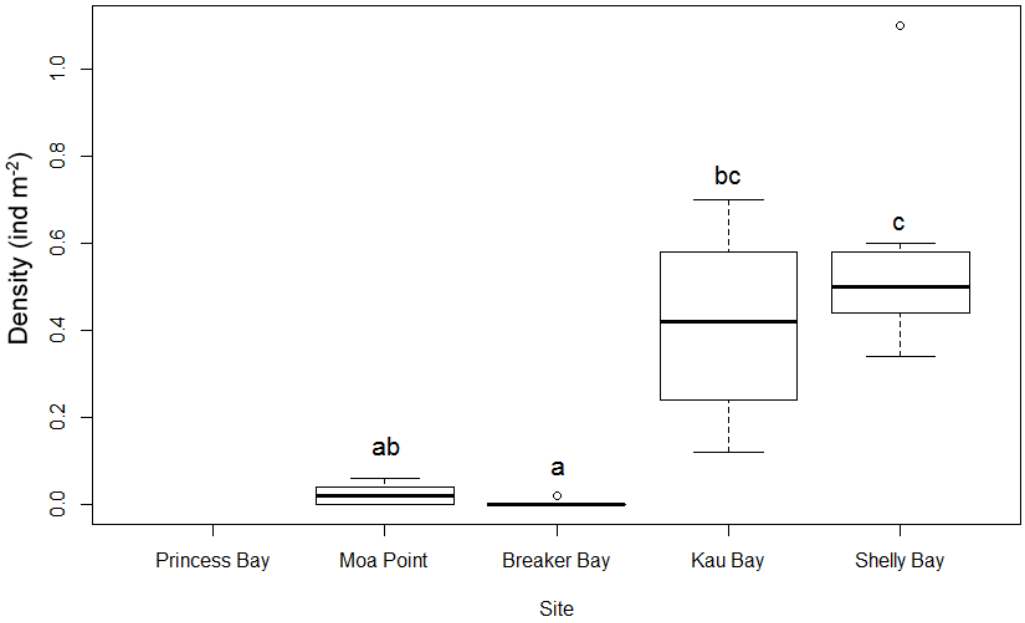


Fig. 3.2. Density of the eleven-armed sea star *Coscinasterias muricata* at the sampled sites pooled across years. Boxes represent the mean and quartiles, and bars the standard error. Letters above bars indicate significant differences in means based on the Kruskal-Wallis test.

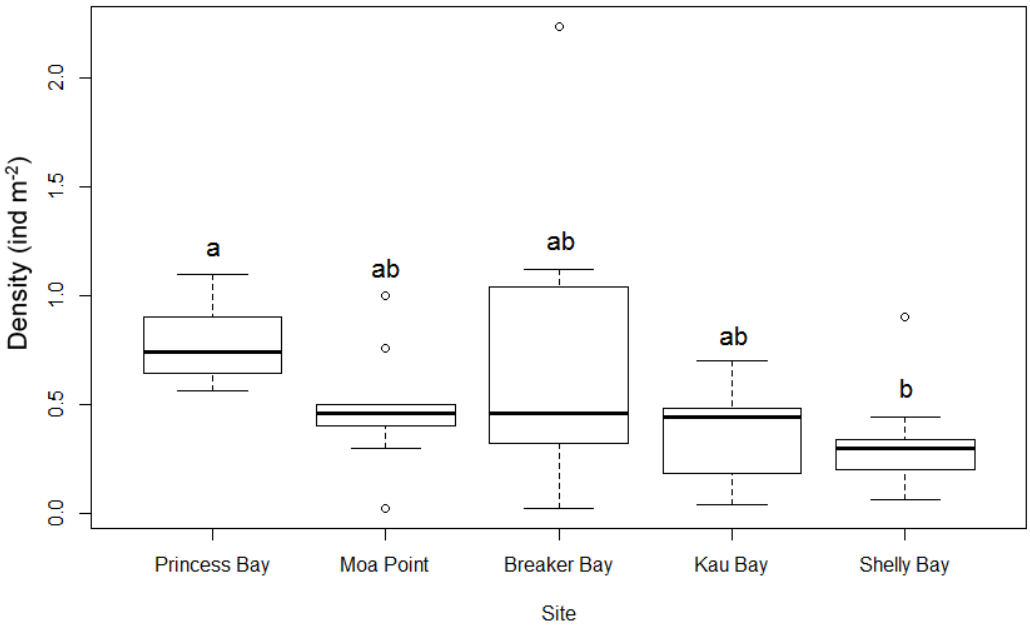


Fig. 3.3. Density of the cushion sea star *Patiriella regularis* at the sampled sites pooled across years. Boxes represent the mean and quartiles, and bars the standard error. Letters above bars indicate significant differences in means based on Kruskal-Wallis test.

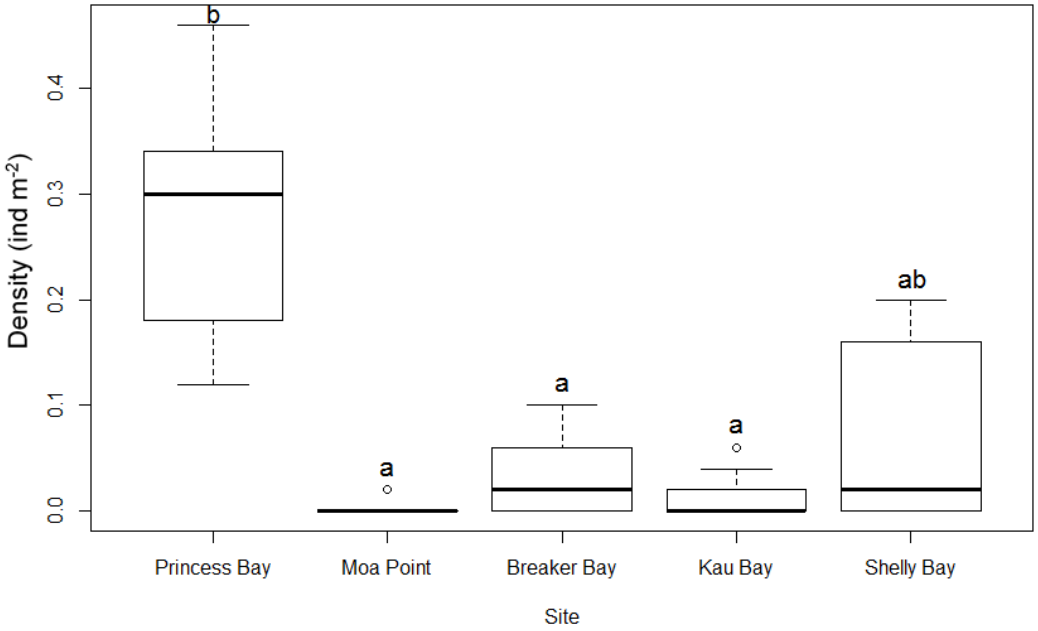


Fig. 3.4. Density of the sea cucumber *Australostichopus mollis* at the sampled sites pooled across years. Boxes represent the mean and quartiles, and bars the standard error. Letters above bars indicate significant differences in means based on Kruskal-Wallis test.

Breaker Bay was the site with the highest echinoderm species richness, closely followed by Shelly Bay, while Kau Bay and Moa Point had the lowest values (Table 3.3). Shelly Bay had the highest diversity value, where *E. chloroticus* and *C. muricata* were the species with the highest relative abundance (39.3% and 30.3%, respectively) followed by Breaker Bay, where P. regularis was the dominant species (68.7%). The highest evenness was also observed in Shelly Bay, followed by Kau Bay. The highest relative abundance was recorded for *E. chloroticus* in Kau Bay (Table 3.4).

Table 3.3. Indicators of echinoderm community structure: species richness (S), Shannon's diversity index (H') and Pielou's evenness (J). Mean (± SD) values are given per site across all sampled years.

	S	H'	J
Princess Bay	5.0 ± 0.01	0.88 ± 0.12	0.54 ± 0.07
Moa Point	4.7 ± 0.58	0.83 ± 0.13	0.54 ± 0.06
Breaker Bay	7.0 ± 1.0	1.01 ± 0.51	0.51 ± 0.25
Kau Bay	4.3 ± 0.58	0.94 ± 0.07	0.65 ± 0.03
Shelly Bay	6.7 ± 0.58	1.39 ± 0.11	0.73 ± 0.06

Table 3.4. Mean (± SD) relative abundance of echinoderm species (%) per site.

	Princess Bay	Moa Point	Breaker Bay	Kau Bay	Shelly Bay
O. maculata	2.2 ± 1.4	48.7 ± 16.9	5.2 ± 5.2	0	0.8 ± 0.8
A. scabra	0.7 ± 0.8	0	2.0 ± 1.7	0	0
C. muricata	0	1.9 ± 1.4	0.8 ± 0.7	27.5 ± 24.2	30.3 ± 13.0
S. australis	1.0 ± 1.7	0	0.5 ± 0.5	0	0
A. insignis	0	0	0	0	7.7 ± 1.8
P. regularis	67.8 ± 6.3	46.9 ± 18.1	68.7 ± 20.8	18.0 ± 8.0	17.5 ± 5.2
P. pulchellus	0	0	3.8 ± 2.9	0.1 ± 0.1	0.7 ± 1.0
A. mollis	24.4 ± 4.4	0.5 ± 0.5	5.3 ± 4.3	0.8 ± 0.2	3.7 ± 0.6
E. chloroticus	3.9 ± 0.3	2.1 ± 1.8	13.8 ± 9.7	53.7 ± 16.1	39.3 ± 11.9

The echinoderm assemblage was significantly different between years and among sites, but the interaction between the two factors was not significant (Table 3.5). The two-way SIMPER analysis showed that *P. regularis* and *E. chloroticus* made the largest contributions to the average dissimilarity within years, while *P. regularis*, *E. chloroticus*, *C. muricata*, *O. maculata* and *A. mollis* contributed the most to the average dissimilarity within sites. The CAP analysis showed a distinctive aggregation of species in relation to the sampled sites. Brittle stars were dominant in Moa Point, while eleven-armed sea stars and sea urchin dominated in the Harbour, and sea cucumbers and cushion stars clustered in Breaker Bay and Princess Bay (Fig. 3.5).

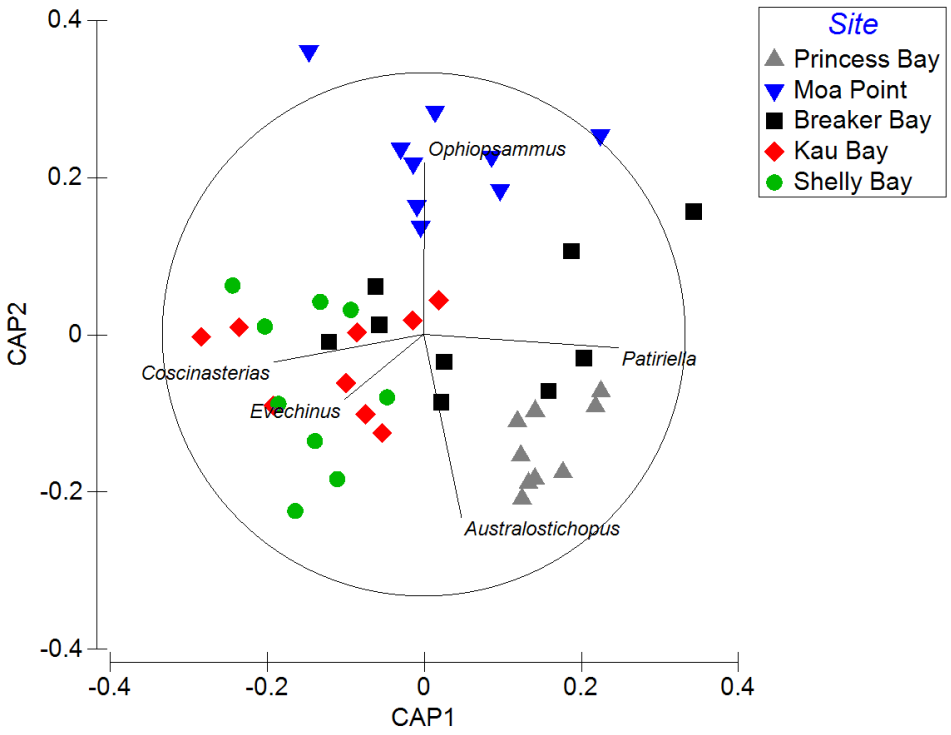


Fig. 3.5. Canonical analysis of principal components (CAP). Resemblance matrix based on Bray-Curtis similarity of square-root transformed data. Species that did not contribute to average dissimilarity between sites were removed for a better visualisation of the data.

The resemblance analysis showed that habitat composition and echinoderm assemblage were significantly correlated (Rho = 0.457, p = 0.001). Habitat features, except cobble, significantly explained the spatial variation in echinoderm abundance (Table 3.6). Shell and sand cover explained 94.6% of the total variation. However, the best model included the four variables as explanatories of the spatial variation of echinoderm assemblage (Fig. 3.6).

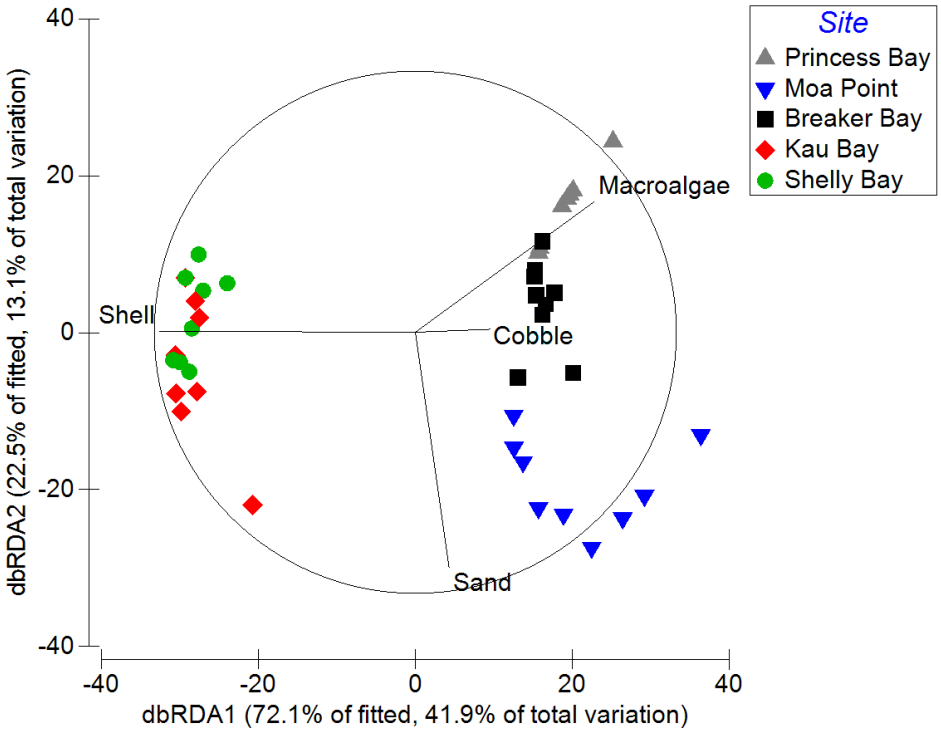


Fig. 3.6. Distance-based redundancy analysis (dbRDA) of echinoderm assemblage overlaid with normalised habitat composition variables.

Table 3.5. PERMANOVA results for the variation in echinoderm assemblage between years and amongst sites. Sums of squares (SS), degrees of freedom (df), Pseudo-F values and p values (p) are shown. Significant effects ($p < 0.05$) are highlighted in **bold**.

Source	SS	df	Pseudo-F	p
Year	2631.1	2	2.417	**0.026**
Site	41577	4	19.097	**0.001**
Year * Site	4764.1	8	1.094	0.344
Error	16329	30		

Table 3.6. Distant based linear model (DistLM) results for the interaction between echinoderm assemblage and habitat composition. Sums of squares (SS), Pseudo-F values and p values (p) are shown. Significant effects ($p < 0.05$) are highlighted in **bold**.

Source	SS	Pseudo-F	p
Shell	24011	29.128	**0.001**
Sand	6880.2	5.627	**0.003**
Cobble	2823.8	2.144	0.079
Macroalgae	13975	13.212	**0.001**

3.3.2 Settlement in artificial collectors

Four classes of echinoderms settled in the collectors, three species of sea stars, multiple species of ophiuroids, one sea cucumber and one sea urchin (Fig. 3.7). Sea star spp1 was successfully identified through DNA sequencing as *Coscinasterias muricata* (see Appendix 5). However, preservation methods of the low numbers of sea star spp2 prevented identification through PCR amplifications.

The abundance of echinoderm settlers varied significantly between years and amongst sites. *C. muricata* settlers were highly abundant in January 2019, at Shelly Bay and Kau Bay, reaching a mean of 63 settlers per collector. However, another important pulse of settlement was observed in 2017, at the same sites, reaching a mean of 9 settlers per collector. Settlers of this species were also observed at Breaker Bay, but not at Princess Bay or Moa Point. Sea star spp2 settlers were observed in 2018 and 2019, but only at Breaker Bay and Princess Bay, and its abundance did not exceed a mean of 2 settlers per collector. Only one sea star spp3 settler was observed at Princess Bay in 2019. Different species of ophiuroids were observed over the sampled period, but only in the South coast sites. The highest abundance of ophiuroid settlers was observed in April 2018 at Princess Bay, and January 2017 at Breaker Bay. Finally, only three sea cucumber settlers were present in the collectors during the sampled period, all of them in Shelly Bay (Fig. 3.8).

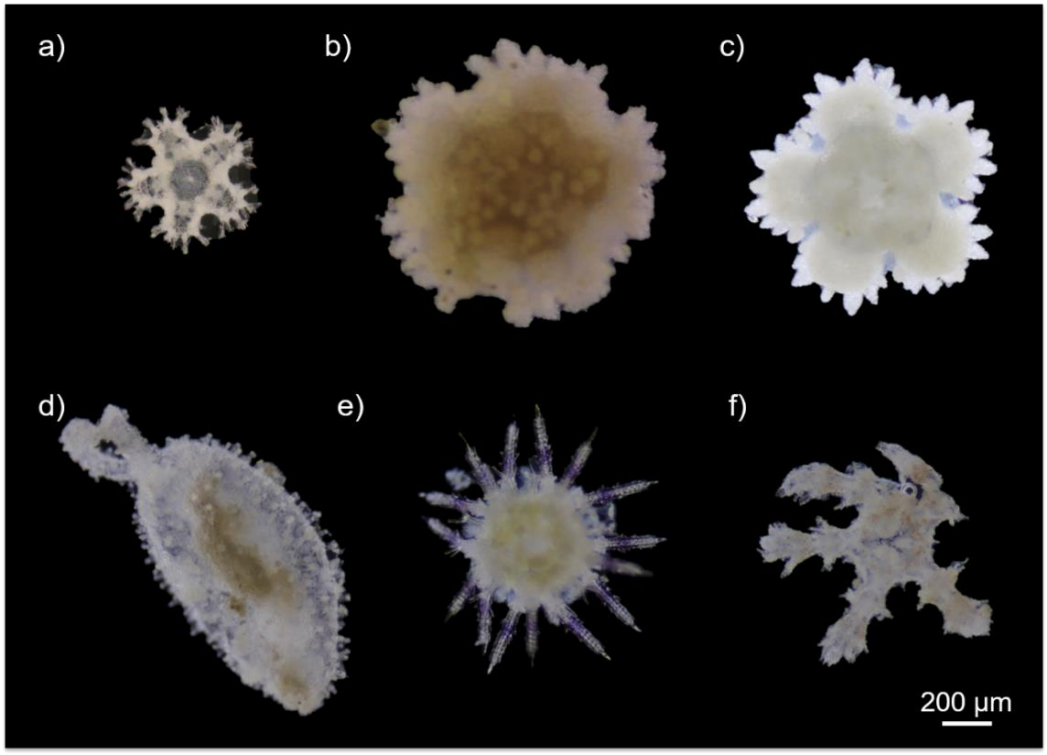


Fig. 3.7. Echinoderm settlers found in artificial collectors. a) Eleven-armed sea star *Coscinasterias muricata*, b) Sea star spp2, c) Sea star spp3, d) Sea cucumber *Australostichopus mollis*, e) Sea urchin *Evechinus chloroticus* and f) Example of ophiuroid settler.

The spatial and temporal variation of echinoderm settlement was modelled as a function of year and site using negative binomial regression, which appeared to be superior to the zero-inflated approach, according to the Vuong likelihood ratio test ($z = 2.498$, $p = 0.006$). The interaction between the two factors was statistically significant (Table 3.7). The number of settlers found in the collectors was significantly higher at Shelly Bay and Kau Bay in 2019, reaching a mean of 23 and 20 settlers per collector, respectively (Fig. 3.9). The mean number of settlers per collector (± SD) in Breaker Bay and Princess Bay was similar between the sampled years (0.87 ± 1.65 and 0.57 ± 1.19, respectively), while settlement in Moa Point was only observed in 2017 and the mean was very low (0.05 ± 0.16). Overall, settlement of echinoderms per month was significantly higher in January and February, while very low number of settlers were observed in November and December.

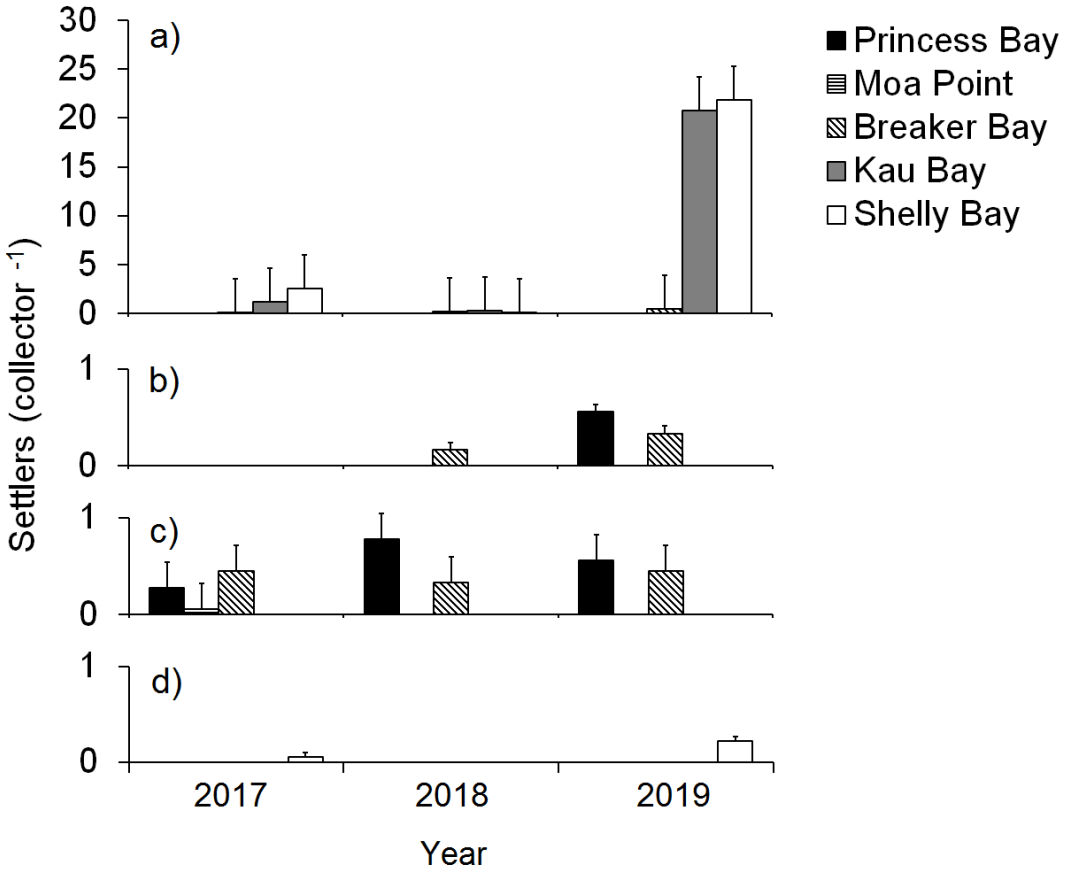


Fig. 3.8. Settlement of a) Eleven-armed sea star *Coscinasterias muricata*, b) Sea star spp2, c) Ophiuroids, and d) Sea cucumber *Australostichopus mollis*, at each site and pooled per sampled year: 2017 (Nov 2016 – Apr 2017), 2018 (Nov 2017 – Apr 2018) and 2019 (Dec 2018 – Feb 2019). Bars represent mean settlers per collector (± SE).

Table 3.7. ANOVA results for the variation in echinoderm settlement, modelled as a function of year and site using negative binomial regression with a log-link function. Chi-square (chi^2), degrees of freedom (df) and p value (p) are given. Significant effects ($p < 0.05$) are highlighted in **bold**.

Source	chi^2	df	p
Year	10.41	2	**0.005**
Site	46.21	4	**<0.001**
Year * Site	27.66	8	**<0.001**

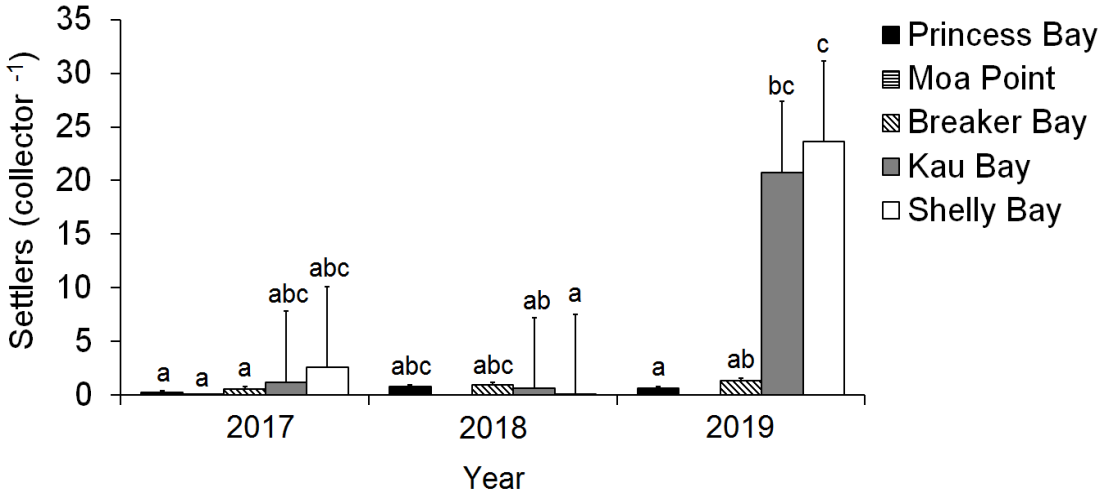


Fig. 3.9. Echinoderm settlers at each site pooled per sampled year: 2017 (Nov 2016 – Apr 2017), 2018 (Nov 2017 – Apr 2018) and 2019 (Dec 2018 – Feb 2019). Bars represent mean number of echinoderm settlers per collector (± SE). Letters above bars indicate significant differences in means based on post-hoc Tukey tests.

Settlement of echinoderms in the collectors showed a moderate correlation with shells (R = 54%, p = 0.038). This was type of substrate exclusively found in the Wellington Harbour, where the highest number of settlers were observed. During the sampled period, the months with highest mean seawater temperatures (January and February) had the highest number of settlers in the artificial collectors. Interestingly, pulses of settlement in the artificial collectors were moderately correlated with seawater temperature (R = 77%, p < 0.001). Furthermore, *C. muricata* settlers were positively, but not significantly correlated with adult densities (R = 23%, p = 0.13).

3.3.3 Recruitment

One-year-old echinoderm recruits and older juveniles were found at Shelly Bay, Kau Bay, and Breaker Bay in 2017 and 2018. No echinoderm recruits or juveniles were found at Moa Point and Princess Bay. Cushion stars, eleven-armed sea stars and different species of ophiuroids were more abundant in Shelly Bay, compared to the

other sites. Only cushion stars and a few ophiuroids were observed at Kau Bay, and cushion stars and ophiuroids were observed at Breaker Bay (see Appendix 6).

Recent settlers (≤5 mm) of *P. regularis* were found in substrate samples in 2017, at the three mentioned sites. The size structure of juveniles was different between years and amongst sites (Fig. 3.10). In Shelly Bay, smaller *P. regularis* individuals were found in 2017, where 5 mm was the size mode, while 20 and 30 mm were the modes in 2018. In Kau Bay, the size mode was 15 mm in 2017, and 20 mm in the following year. Finally, at Breaker Bay all individuals were <10 mm in 2017, while they were all >15 mm in the following year.

One-year-old recruits of the eleven-armed sea star were found at Shelly Bay and Breaker Bay in 2018, but in very low numbers. However, juveniles >10 mm were more abundant in both years at Shelly Bay, but they were not found either at Kau Bay or Breaker Bay. The size mode in 2017 was 30 mm, while it was 20 mm in 2018 (Fig. 3.11).

Density of echinoderm recruits did not vary significantly between the two sampled years or amongst sites (Table 3.8). However, density of ophiuroids was significantly higher in Shelly Bay, compared to Kau Bay and Breaker Bay.

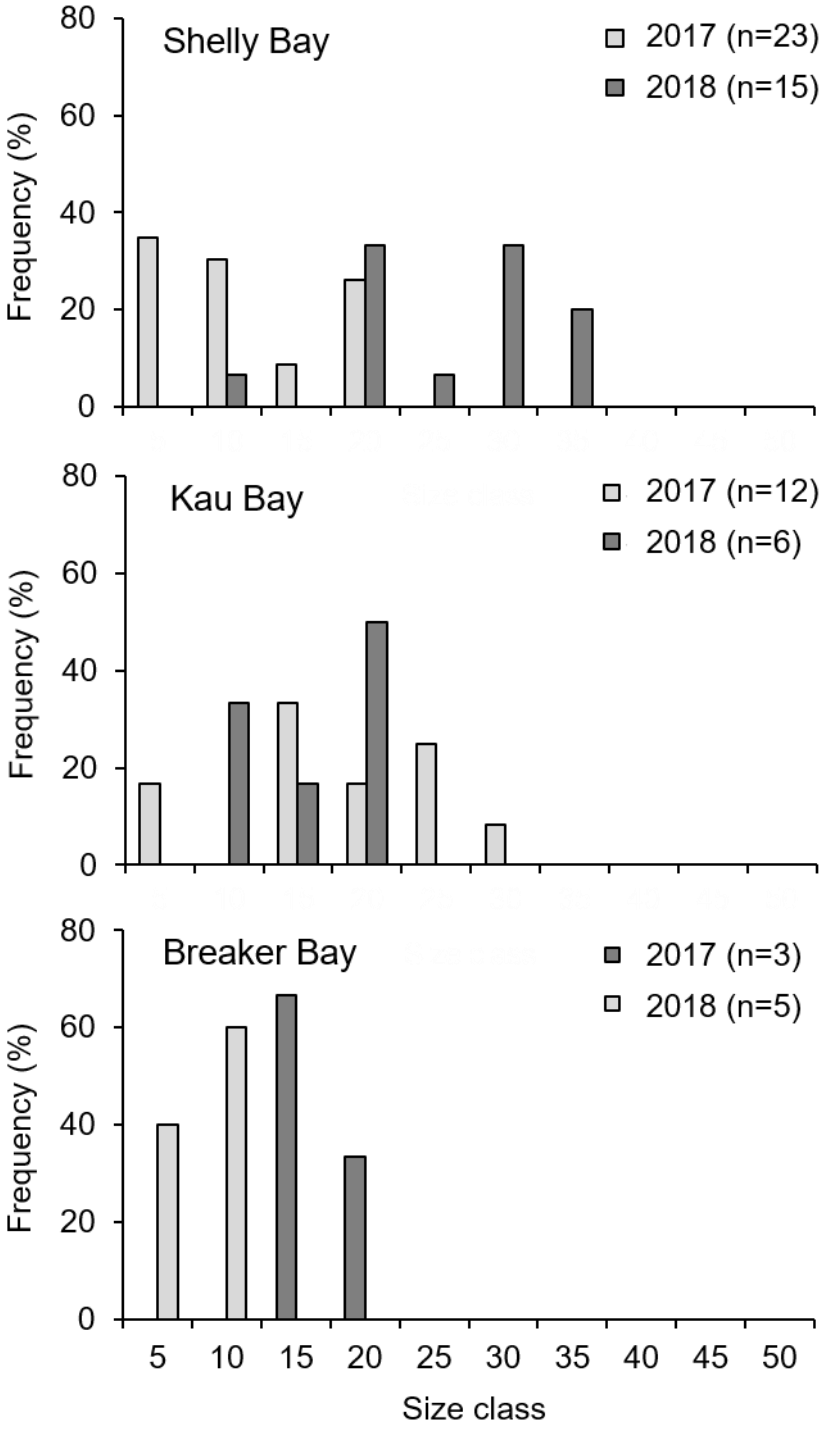


Fig. 3.10. Size structure of cushion sea star *Patiriella regularis* juveniles in Shelly Bay, Kau Bay and Breaker Bay, during the sampled years.

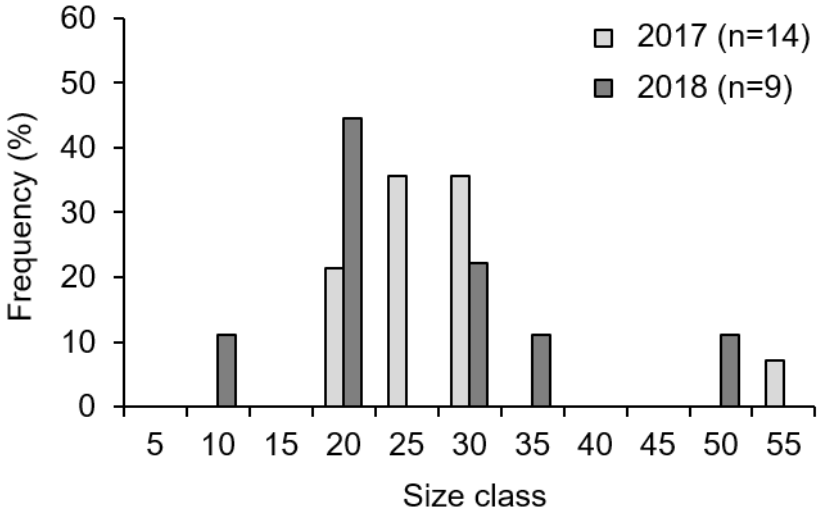


Fig. 3.11. Size structure of eleven-armed sea star *Coscinasterias muricata* juveniles in Shelly Bay, during the two sampled years.

Table 3.8. Variation in echinoderm recruit densities during the sampled years (2017 – 2018) and amongst sites (Shelly Bay, Kau Bay and Breaker Bay). Degrees of freedom (df), Kruskal-Wallis statistic (H) and p values (p) are shown. Significant effects ($p < 0.05$) are highlighted in **bold**.

Source	Year			Site		
	df	H	p	df	H	p
Patiriella regularis	1	2.396	0.122	2	2.710	0.258
Coscinasterias muricata	1	0.828	0.363	2	4.595	0.101
Ophiopsammus maculata	1	2.117	0.146	2	4.235	0.120
Ophiuroids	1	0.151	0.698	2	8.535	**0.014**

3.4 Discussion

The present study described the echinoderm composition and their spatial variation in density, as well the temporal patterns of settlement in the shallow rocky reefs of the Wellington region, in central New Zealand. Nine species of echinoderms were conspicuous and relatively abundant in the sampled sites, and at least six species of echinoderm settlers were identified in the artificial collectors. This is the first study in

New Zealand to have identified echinoderm settlers using artificial collectors, besides Lamare and Barker (2001), who estimated settlement rates of *Evechinus chloroticus* in the southern fiords, and the first one in the Wellington region.

There is increasing evidence that habitat composition is an important factor shaping echinoderm assemblages and community structure at different spatial and temporal scales (Pérez-Ruzafa et al. 2001, Entrambasaguas et al. 2008, Iken et al. 2010, Hermosillo-Nuñez et al. 2015). Distribution patterns of echinoderms are highly associated with specific characteristics of the habitat (Hermosillo-Nuñez et al. 2015). In the present study, densities were greatly correlated with habitat features specific to each sampled site. For example, the sea cucumber *Australostichopus mollis* and the brittle star *Ophiopsammus maculata* were abundant only at Princess Bay and Moa Point, respectively, where macroalgae and sand were the predominant substrates.

The cushion star *Patiriella regularis* was the most abundant species and was present in all the sampling sites. Even though it was negatively correlated with shells, densities were high in the Harbour compared to other species. Conversely, the eleven-armed star *Coscinasterias muricata* was highly abundant in Harbour sites. These two species play important ecological roles in the benthic community. *C. muricata* is an active predator capable of regulating the abundance and composition of other invertebrate species through top-down control (Day et al. 1995, Barker 2013), while *P. regularis* is an active and highly abundant scavenger (Crump 1971). However, there are not many studies on their abundance and distribution patterns around New Zealand.

Witman and Grange (1998) estimated densities of *C. muricata* and *P. regularis* in Doubtful Sound in relation to their predation pressure on mussels. Crump (1971) and Palmer (2010), on the other hand, estimated the abundance of cushion stars in the Otago peninsula and the Wellington region, respectively. Palmer (2010) did not find significant differences in density between the Harbour and the South coast, which ranged between 4 to 12 ind m^{-2}. However, the surveys were done in the intertidal (Palmer 2010). Furthermore, Byfield (2013) estimated maximum densities of *O. maculata* (20 ind m^{-2}), *P. regularis* (90 ind m^{-2}), *Astrostole scabra* (2 ind m^{-2}), *Pentagonaster pulchelus* (4.5 ind m^{-2}) and *A. mollis* (15 ind m^{-2}) at different sites on the South coast, including Princess Bay and Breaker Bay. Interestingly, *A. mollis* was

not particularly abundant at Princess Bay, like in the present study, but similar densities were observed for *P. pulchelus* at Breaker Bay (Byfield 2013).

Echinoderm fauna in the Wellington region was not particularly diverse compared to other parts of New Zealand. Edgar et al. (2013) reported 24 echinoderm species from the northeast coast of the country, where usually the sea urchin *E. chloroticus* is the dominant species. Six out of the ten most abundant mobile invertebrates were echinoderms, including three species of echinoids, one crinoid, one asteroid and one ophiuroid (Edgar et al. 2013). Shears and Babcock (2007) on the other hand, recorded 12 species of echinoderms across New Zealand bioregions, where *E. chloroticus*, *P. regularis* and *A. mollis* were amongst the ten most abundant species. The species richness found in the present study was similar to that found in South Australia, where only eight echinoderms were identified (Benkendorff 2005). However, echinoderm diversity is usually high in tropical (Pérez-Ruzafa et al. 2001, Entrambasaguas et al. 2008, Hermosillo-Nuñez et al. 2015) and Antarctic regions (De Domenico et al. 2006, Souto et al. 2014).

Species richness and diversity are usually related to locations with great habitat complexity (Pérez-Ruzafa et al. 2001). Surprisingly, in the present study, Shelly Bay was the site with the highest diversity, where *E. chloroticus* and *C. muricata* were the dominant species, while Breaker Bay had the highest richness of species. Both sites had in common the presence of boulders that contributed to the habitat complexity, providing substrate and refuge for the different species. Contrary to what was expected, the South coast sites did not show high richness or diversity, despite the higher macroalgal cover. However, another factor that might contribute to echinoderm assemblages in relation to habitat complexity is the habitat preference for settlement (Chia et al. 1984, Entrambasaguas et al. 2008).

Many echinoderm species have preferences for different substrates for settlement, including sea cucumbers (Mercier et al. 2000), sea stars (Barker 1977a, Johnson et al. 1991, Metaxas et al. 2008) and ophiuroids (Turon et al. 2000). In the present study, echinoderm settlement had a positive correlation with shells, which explained 54% of the total variation. Overall, the highest echinoderm settlement was observed at the two Harbour sites, where shells were the primary constituents of the substrate. However,

additional factors other than habitat composition may be contributing to higher number of settlers observed in the Harbour, compared to the South coast sites.

Different recruitment patterns of other invertebrate species have been observed between these two adjacent systems. Differential pulses of mussel and barnacle settlement have been related to distinctive circulation and water flow patterns (Demello & Phillips 2011). While the Harbour is a semi-enclosed body of water with low water flow, the South coast is a highly dynamic system, strongly influenced by winds and tides (Walters et al. 2010). It has been observed than in bays and enclosed bodies of water, such as harbours and fiords, larvae can be retained after spawning, and it is likely that they settle at the same site of origin (Sewell & Watson 1993, Lamare 1998). In contrast, offshore advection caused by wind can transport larvae away from a suitable substrate for settlement, since they are unable to control their horizontal movement (Ebert et al. 1994, Balch & Scheibling 2001). The Cook Strait is characterised by its fast-flowing tidal currents that can export a parcel of water through the strait in a single tidal period and the northward current influences the nutrient supply to the Marlborough Sounds (Stevens & Smith 2009, Stevens 2014). In fact, it has been suggested that the hydrology of Cook Strait can act as a barrier to gene flow for mussels (Apte & Gardner 2002) and *P. regularis* (Waters & Roy 2004), and that the upwelling zone represents a barrier for larval dispersal (Ayers & Waters 2005).

In the present study, settlement of echinoderms showed not only significant spatial differences between the Harbour and the South coast, but also between the sampled years. Interannual variation in echinoderm settlement has been previously recognised and correlated to variation in environmental factors such as seawater temperature (Agatsuma et al. 1998, Balch et al. 1999). There is evidence that increasing seawater temperatures can contribute to larger settlement rates in the field (Ebert 1983, Hart & Scheibling 1988). For example, significant settlement pulses of *Diadema africanum* were observed during warmer years (Hernández et al. 2010). Here, the highest echinoderm settlement occurred in January 2019, which was also the month with the highest mean seawater temperatures, for both the Harbour (18.2 ºC), and the South coast (18.3 ºC). However, temperature alone cannot explain the settlement patterns, as other factors such as salinity, food availability and predation, may also be influencing settlement the field (Balch & Scheibling 2001).

Food availability might be one of the most important factors limiting larval stages (Helson et al. 2007, Jennings & Hunt 2011). A limitation in food supply can extent the time that larvae spend in the plankton due to a delay in development and metamorphosis, exposing them to further sources of mortality (Olson & Olson 1989, Vaïtilingon et al. 2001). Changes in food availability can have strong effects on the number of larvae reaching competency, which can be reflected as low recruitment rates in the field (Booth & Brosnan 1995). Chlorophyll has been used as a proxy for phytoplankton biomass (Huot et al. 2007, Roesler & Barnard 2013), which can be interpreted as food available for larvae developing in the water column. Larval abundance and recruitment of the sea urchin *Paracentrotus lividus* were highly correlated with planktonic primary production (López et al. 1998). In the present study, chlorophyll peaked in February 2017 and March 2018, the same months when settlement pulses were observed.

Studies on echinoderm settlement in the field have mainly focused on sea urchins (Rowley 1989, Harrold et al. 1991, Lamare & Barker 2001, Tomas et al. 2004). Only a few studies have included the other echinoderm classes (Keesing et al. 1993, Balch & Scheibling 2000, Jennings & Hunt 2010), and differential patterns of settlement have been observed between them (reviewed by Ebert 1983, Balch & Scheibling 2001). In the present study, the presence and abundance of settlers varied depending on the species. Abundance of *C. muricata* settlers was significantly higher in 2019. This was the highest settlement pulse observed during the study and occurred mainly in the Harbour sites. In contrast, settlement of sea star spp2 was patchy, and limited to Breaker Bay and Princess Bay.

Interannual variation in asteroid settlement is common. Loosanoff (1964) observed only one major settlement event of the temperate sea star *Asterias forbesi,* over a period of 25 years. Abundance of settlers varied from year to year, up to four orders of magnitude, but there was no clear pattern of a poor recruitment year being followed by a good recruitment year or vice versa (Loosanoff 1964). Later, Balch and Scheibling (2000) and Jennings and Hunt (2010) observed that significant pulses of settlement of *Asterias* spp did not occur every year, and the timing varied from late June to early October. Miller (1995) observed that settlement of asteroids from the North Pacific doubled in the second compared to the first year of study. Similarly, Keesing et al.

(1993) observed a poor year of recruitment for asteroids but not for echinoids or ophiuroids in the Great Barrier Reef.

In the present study, ophiuroid settlers were relatively abundant across the three sampled years. This group, unlike asteroids and echinoids, has been observed to recruit continuously from year to year (Balch & Scheibling 2001). Two species from Nova Scotia were found to settle on artificial collectors during three successive years (Balch 1999). Regarding the spatial distribution of ophiuroid settlers, Keesing et al. (1993) did not find differences between two habitats on a coral reef. However, Balch (1999) observed that settlement was higher in barren grounds than in kelp beds, which is the opposite of what I found in the present study. Here, ophiuroids did not settle in the Harbour sites, but were abundant in the South coast sites, which are mainly dominated by macroalgae. In contrast, ophiuroid juveniles (<5 mm) were found in the substrate samples in Shelly Bay and Kau Bay, but not in the South coast sites.

It has been observed, especially for sea urchins, that the abundance of settlers in either the artificial collectors or in the natural substrate, is not positively correlated to the abundance of juveniles in the field (Tomas et al. 2004, Prado et al. 2012). This has been attributed to high post-settlement mortality, where only a few individuals survive the first year (Sewell & Watson 1993). Juveniles of the crown-of-thorns sea star *Acanthaster planci*, were difficult to find despite the population outbreaks observed across the Indo-Pacific (Johnson 1992). Zann et al. (1987) and Fisk (1992) observed a single large episode of recruitment in nine-year and five-year studies, respectively. This lead to develop the hypothesis that recruitment occurs in deep water, and that juveniles migrate to adult habitats after a period of survival (Johnson et al. 1991).

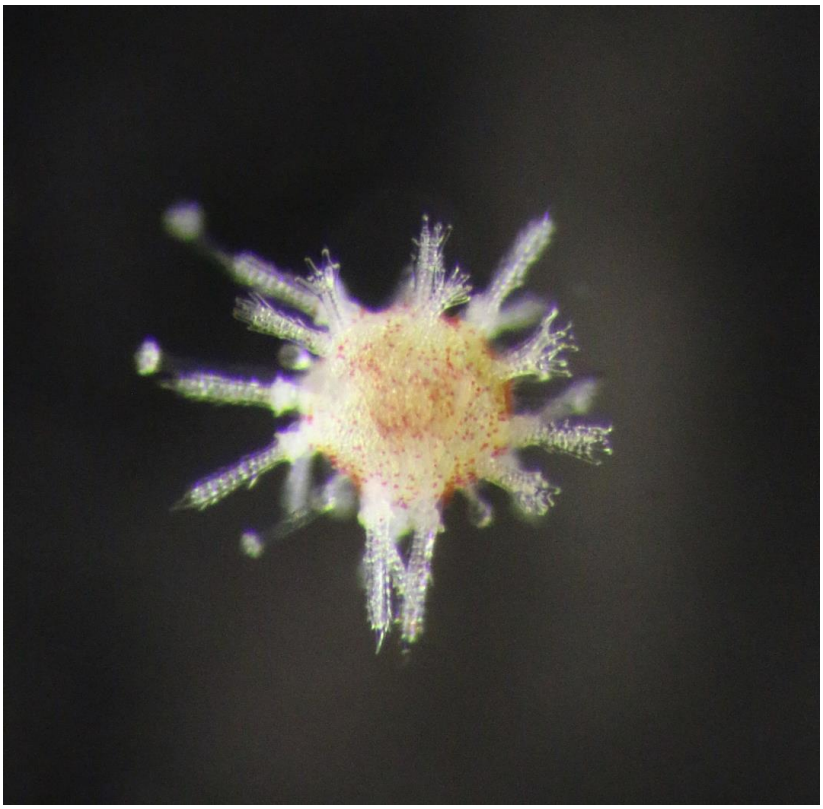
A study on settlement of *C. muricata* suggested that the lack of recent settlers in the field was due to low recruitment from the plankton (Barker 1977a). Recent settlers were never found, however young adults (30 – 60 mm total diameter) were reasonably common (Barker 1977a). In the present study, *C. muricata* juveniles (<30 mm) were found in 2017, but not the following year, which may indicate that a large pulse of settlement occurred the previous year. The high abundance of settlers observed in 2019 may contribute to good recruitment next year, which may be observed by the presence of a juvenile cohort. Interestingly, even though *C. muricata* was highly abundant in the Harbour, where the main pulses of settlement were observed in 2017

and 2019, the abundance of settlers was not significantly correlated with the density of adults. In contrast, recent settlers (≤5 mm) of *P. regularis* were observed only in 2017. It is hard to determine the age of those juveniles, but they might be a few months old. The lack of *P. regularis* settlers in the collectors suggests that settlement of this species might be occurring at a different depth (i.e. in the intertidal) or in a season other than summer. However, there are no studies on recruitment patterns in the field for this species, so it is difficult to know.

The present study showed that the spatial variability in echinoderm assemblages is highly correlated with habitat composition. In addition, species-specific processes may be limiting the size of adult populations. Important pulses of settlement observed during the study period might be contributing to the dominance of *C. muricata* in the Harbour, while the presence of *P. regularis* juveniles but the lack of settlers, might indicate that this species does not recruit every year or in a season other than summer. This study demonstrates how interannual variation in echinoderm recruitment can occur. A relatively good year for settlement can be followed by one or more years of poor settlement, and that environmental conditions such as temperature and chlorophyll may influence the timing and magnitude of the settlement pulses.

Chapter 4

Low salinity and sediment stress on sea urchin *Evechinus chloroticus* larvae has latent effects on juvenile performance



Newly settled *Evechinus chloroticus* from larval cultures

Glockner-Fagetti and Phillips (2019) Low salinity and sediment stress on sea urchin *Evechinus chloroticus* larvae has latent effects on juvenile performance. Marine Ecology Progress Series 619:85-96.

Chapter 4

4.1 Introduction

Marine ecosystems are increasingly being affected by both natural and anthropogenic stressors (Adams 2005, Hewitt et al. 2016). Although natural disturbances are important for structuring communities, the increasing anthropogenic pressure may compromise the ability of ecosystems to respond to disturbances occurring simultaneously (Darling & Côté 2008). In nature, stressors are more likely to occur at the same time and often interact with each other (Crain et al. 2008). When acting simultaneously, the effect of multiple stressors can be greater in combination than the sum of individual effects (Folt et al. 1999, Gunderson et al. 2016). A better understanding of the effects of multiple stressors would elucidate ecosystem functioning (Breitburg et al. 1998), and allow for the prioritization of management strategies that minimize the most severe interactions (Ban et al. 2014).

Coastal areas are among the most threatened habitats affected by human land-based activities, such as industrial and domestic discharges, deforestation, agriculture and other land use practices (Halpern et al. 2007). River runoff is the main transport mechanism of products from terrestrial human activities to coastal areas (Fredston-Hermann et al. 2016). Runoff not only reduces seawater salinity, but also carries terrestrial sediments and nutrients, and increases suspended particulate matter and turbidity (Humphrey et al. 2008). Low salinity has long been recognised as one of the most important abiotic factors that affects abundance and distribution patterns of marine organisms (Kinne 1971, Russell 2013). Sedimentation, on the other hand, has been identified as one of the greatest threats to coastal marine ecosystems globally (Halpern et al. 2007), as well as to particular regions such as New Zealand (Morrison et al. 2009, MacDiarmid et al. 2012).

River discharges can increase considerably after a rain event, and can contribute with high sediment loads to coastal areas (Airoldi 2003, Hicks et al. 2004). Precipitation patterns are likely to change dramatically by the turn of the century, with storms being more frequent and stronger (Harley et al. 2006). In New Zealand, the number of rainfall events is projected to increase by 32% in the next few decades (Renwick 2013). The

abiotic conditions after a storm, where reduced salinity and sediments can occur in combination, may last for several days and can have deleterious effects on early life stages of marine organisms (Humphrey et al. 2008, Larsen & Webb 2009).

Although hyposaline conditions typically have a negative effect on early life stages of marine organisms, the response varies depending on the species (Carballeira et al. 2011). Low salinity can inhibit fertilisation and hatching of corals (Humphrey et al. 2008) and sea stars (Allen et al. 2017), and delay larval development of gastropods (Diederich et al. 2011). Suspended sediment, on the other hand, can cause high mortality rates in fish larvae (Griffin et al. 2009), and increase their susceptibility to diseases (Hess et al. 2015). Problems associated with sedimentation include smothering and burial of organisms, and physical changes in the sea floor that can lead to loss of suitable substrate for settlement (Airoldi 2003).

Larvae developing in coastal areas can be exposed to both low salinities and sediments during their development (Phillips & Shima 2006). Usually, larval stages are more sensitive to environmental stressors than later life stages (Pechenik 1999, Przeslawski et al. 2015). As a result, high mortality rates in the plankton can lead to a failure in recruitment rates and depletion of the adult population (Hutchinson & Williams 2001). Besides the direct effects on larval stages, some stressors can affect performance in later life stages (Pechenik 2006). Latent and carry-over effects can occur across life-history stages, where an individual's current performance can be explained by previous experiences or situations of stress (O'Connor et al. 2014). The response to stress experienced during larval development is delayed, and only appears after metamorphosis (Pechenik 2018), which can also increase vulnerability to further stressors (Fischer & Phillips 2014).

The sea urchin *Evechinus chloroticus* (Valenciennes, 1846), locally know as kina, plays an important ecological role in the benthic community, and also sustains traditional and commercial fisheries (Barker 2007). It has been widely studied in New Zealand for its ecological and economic importance. Latent effects have been observed in this endemic sea urchin, where juveniles exposed to copper as larvae, began to show impaired growth and were smaller than controls from 8 d post-settlement (Rouchon & Phillips 2017). *E. chloroticus* is also sensitive to reduced salinity and sediments. Low salinity causes detrimental effects on larvae (Antonie

2003, Delorme & Sewell 2014), and sediments can inhibit fertilisation (Miller et al. 2014) and cause high mortality rates in both larvae and juveniles (Phillips & Shima 2006, Walker 2007). However, most of these studies focussed on a single stressor during one life stage. Therefore, there is a need to study the interactive effects of multiple stressors and to investigate potential effects that may only be detectable in a subsequent life stage. *E. chloroticus* represents a good model system to study developmental biology, and the fertilisation and larval rearing protocols are well established.

Environmental stressors in combination with increasing anthropogenic pressure, such as discharges of rivers to coastal areas, may ultimately impact the community structure affecting different life stages. Larval experiences and the negative latent effects on juvenile performance, may compromise recruitment to the adult population. Here we examined the combined effects of low salinity and suspended sediments, in a short-term exposure, similar to a runoff after a major rain event, on larval and juvenile performance of the sea urchin *E. chloroticus*.

4.2 Materials and methods

4.2.1 Sea urchin collection and fertilisation

Adult *Evechinus chloroticus* were collected from Kau Bay, Wellington, New Zealand (41.2881º S, 174.8308º E), in November 2017. They were kept at the Victoria University Coastal Ecology Lab (VUCEL) in a 200 l tank with flow-through filtered seawater (FSW, 15 µm) and fed once a week with fresh kelp *Macrocystis pyrifera* for one month before spawning. Spawning and fertilisation followed the procedure described in detail by Rouchon and Phillips (2016). Briefly, sea urchins were induced to spawn by intracoelomic injection of 4 ml of KCl (0.5 M). Eggs were collected by inversion over beakers with 500 ml FSW (0.2 µm), while sperm were collected ‘dry’ and placed on ice until fertilisation. Gametes from three females and two males were pooled to reduce inter-individual variation (Delorme & Sewell 2014). Sperm motility and egg roundness were checked under a compound microscope (50x magnification). Fertilisation occurred at densities of 30 eggs ml^{-1} and a high concentration of sperm

(approximate egg:sperm ratio 1:1000). Fertilisation rate was >95%. Embryos were rinsed twice with fresh FSW and incubated for 72 h in beakers with 500 ml FSW.

4.2.2 Larval exposure to low salinity and suspended sediments

Larvae reached the pluteus stage (when feeding begins) at 3 d post-fertilisation, and were transferred to 1.5 l treatment jars at densities of 1 larva ml^{-1}. We used a fully factorial design with three levels of salinity (28, 32, control: 36 ppt), and three levels of suspended sediments <63 µm grain size (control: 0, low: 40, high: 80 mg l^{-1}). Each treatment was replicated three times (n = 27 jars). Salinity values were based on the observations logged by a CTD deployed midwater at 5 m depth in the Wellington Harbour after rain events from November 2017 to April 2018 (see Appendix 7 for salinity, turbidity and rainfall data for the Wellington Harbour). Low salinity water was obtained by diluting FSW with distilled water. Salinity in each jar was monitored every day with a refractometer (± 0.1 ppt). Suspended sediment concentrations were based on ambient levels estimated for the Wellington Harbour several days after heavy rainfall (Phillips & Shima 2006). To obtain small-particle sediments (<63 µm), which usually remain in suspension for several days, ~20 l of seawater collected after a major rain event were left undisturbed for 14 d and then decanted. Deposited sediments were rinsed and dried at 60°C for 24 h, and the size fraction was separated (see Phillips & Shima 2006).

Jars were kept in a water table with running seawater at ambient temperature of 18 ± 1 ºC. Larvae were fed with *Dunaliella primolecta* (8000 cells ml^{-1}) after every water change, which occurred 3 times wk^{-1}. Jars were continuously stirred by a motorised paddle system at 10 rpm to maintain the larvae, food and sediments in suspension (Strathmann et al. 1992). Exposure to salinity and suspended sediment treatments lasted four days, after which (at 7 d post-fertilisation) the surviving larvae were transferred back to control conditions (36 ppt, 0 mg l^{-1}) until most larvae had become competent to settle (i.e. 8-armed pluteus larvae with large rudiments and protruding spines), at 23 d post-fertilisation.

Larvae from each culture jar were sampled immediately before and after the treatment (3 and 7 d post-fertilisation, respectively), and at 21 d post-fertilisation, near the end of the larval development period. To sub-sample the larvae, first the water volume in each jar was reduced to 750 ml using a reverse filtration system, and then, while the remaining water was well-stirred, three 15 ml aliquots were taken. The developmental stage, number of live larvae and proportion of normal larvae were recorded from each sample using a dissecting microscope (45x). Larvae lacking arms or with clear asymmetry (one arm >50% larger than the other), were considered abnormal. Samples were fixed in 3% buffered formalin in seawater for 24 h, and preserved in 40% ethanol. Ten normal larvae from each sample were photographed using a digital camera mounted on a compound microscope (50x), for further morphological measurements, following Lamare and Barker (1999), and Sewell et al. (2004). Measurements were done using the software Image J, and included larval size based on the post-oral arm length (PO) and body length (BL). All measurements were done blind with regard to the treatment.

4.2.3 Effect of larval experiences on juvenile performance

To investigate the latent effects on settlement and juvenile performance of larvae exposed early in development to low salinities and suspended sediments, we estimated settlement success, size at settlement, proportion of normal juveniles and survival and growth of juveniles. Replicate jars from each treatment were pooled, and 25 competent larvae were placed in glass bowls with 200 ml of FSW. The bowls had been inoculated with benthic diatoms (mixed species) beforehand, to provide food for the juveniles, and contained two crustose coralline algae (CCA) encrusted rocks (~2 cm long) as a settlement cue. These rocks were collected from the field on the same day of the experiment and rinsed with FSW to remove epibionts. Bowls were placed in a tray with running seawater at ambient temperature (18 ± 1 ºC). We used three replicate bowls for each of the nine treatment combinations of salinity and suspended sediments.

Competent larvae were left undisturbed, and assessment of settlement success (i.e. larvae had completed metamorphosis) was done after 48 h. Both CCA-encrusted rocks

and larvae that had not metamorphosed were removed at this point, and the surviving juveniles were kept in the bowls. Complete water changes were done 3 times per week, and at the end of the week, juveniles were transferred to bowls with a 7 d old diatom culture, in order to maintain a constant diatom cover over a period of four weeks. Juveniles were photographed using a digital camera mounted on a dissecting microscope (45x), and body length was estimated using the software Image J. Size at settlement, proportion of normal juveniles at 3 d post-settlement, and survival and growth of juveniles at 28 d post-settlement were estimated. Normal juveniles were considered those that developed feet and/or spines by 3 d post-settlement (Fig. 4.1). The experiment was ended at 28 d post-settlement.

4.2.4 Effect of deposited sediments on juvenile performance

In addition to looking at the effects of larval experience on settlement and juvenile performance, we also wanted to examine the effects of deposited sediments on juvenile growth and survival. Therefore, we had an additional three replicate bowls, as described above, for each of the nine larval treatments, but in this case we added 10 mg cm^{-2} of fine sediments (<63 µm). Sediments were left to settle on the bottom of the bowl and over the CCA-encrusted rocks, prior to adding the competent larvae. Settlement success was assessed after 48 h. Both CCA-encrusted rocks and larvae that had not metamorphosed were removed at this point, and the surviving juveniles were transferred to bowls with no sediments. Maintenance of the bowls and estimations of size at settlement, proportion of normal juveniles, and survival and growth of juveniles were performed exactly as described above.

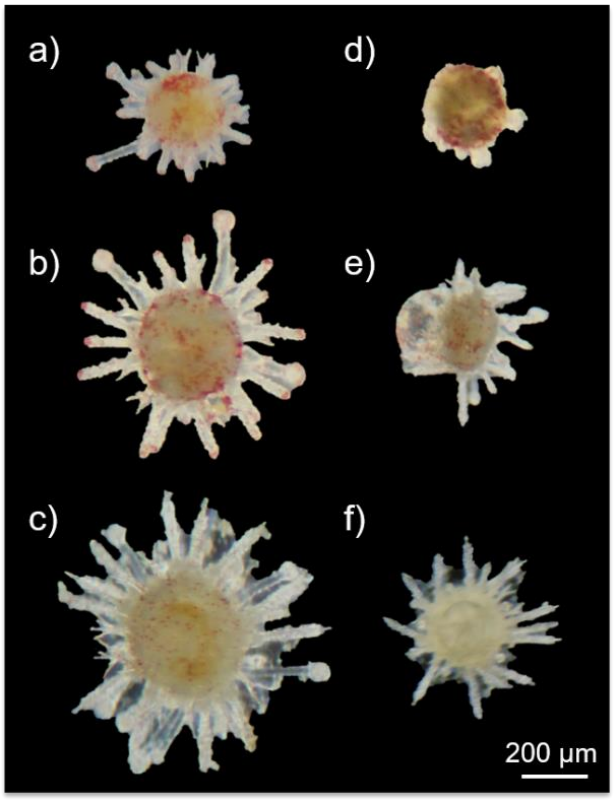


Fig. 4.1. Developmental categories of *Evechinus chloroticus* juveniles under control conditions at a) 3 d post-settlement, b) 14 d post-settlement and c) 28 d post-settlement. Abnormal juveniles at 3 d post-settlement from d) 28 ppt treatment and no sediments added, and e) 36 ppt and high suspended sediments. f) Newly dead juvenile at 28 d post-settlement from 32 ppt and high suspended sediments.

4.2.5 Statistical analyses

Larval size and morphometrics (PO, BL, PO:BL ratio), proportion of normal larvae, and larval survival were each analysed using nested ANOVAs, separately at 7 d (immediately after the 4 d treatment), and at 21 d post-fertilisation (near the end of development). Salinity (three levels) and suspended sediments (three levels) were fixed effects, while jar was a random effect nested within the main effects. Larval length was log-transformed, while proportion of normal larvae and survival were arcsin square root-transformed to meet ANOVA assumptions (assessed with Kolmogorov-Smirnov and Levene's tests). A post-hoc Tukey test was used to compare means when factors were significant ($p < 0.05$).

The effects of larval experiences on settlement success, size at settlement, proportion of normal juveniles at 3 d post-settlement, and survival and juvenile growth at 28 d post-settlement were analysed using general linear models with multiple fixed effects estimated by least squares. All variables were arcsine square root transformed to meet normality assumptions. Salinity and suspended sediments, and deposited sediments added during settlement, were included as categorical predictor variables. PO, BL, PO:BL ratio, proportion of normal larvae, and larval survival and growth were included as independent continuous variables in the full model. Akaike's information criterion (AIC) was used as the criterion for the selection of significant variables. A post-hoc Tukey test was used to compare means across treatment combinations when interactive factors were significant ($p < 0.05$). All statistical analyses were conducted with Statistica 10.0 (StatSoft) and the software R v3.2.4 (www.r-project.org) using the packages 'lmtest' (Zeileis & Hothorn 2002) and 'lsmeans' (Lenth 2016).

4.3 Results

4.3.1 Larval exposure to low salinity and suspended sediments

There were significant interactive effects between low salinity and suspended sediments on larval development both immediately after the treatment, and two weeks later (Table 4.1). Rearing larvae for 4 days at the lowest salinity (28 ppt) significantly reduced their size by 7 d post-fertilisation (Fig. 4.2). The mean post-oral (PO) arm length was reduced in the 28 ppt treatments with the smallest size in the no suspended sediment treatment. The effect of suspended sediments was not apparent for larvae at salinities 32 and 36 ppt. At 21 d post-fertilisation (Fig. 4.2), these patterns were reversed, where larvae in 28 ppt in low and high suspended sediments, had significantly longer arms compared to the control, which tended to have shorter arms than the rest of the treatments. There was no effect of salinity on PO arm length for larvae not exposed to suspended sediments (Table 4.1).

There were also interactive effects of low salinity and suspended sediments on the proportion of normal larvae at 7 d post-fertilisation and near the end of development, but these effects were more complex than on larval size. The individual effect of salinity

on the proportion of normal larvae was significant, while that of suspended sediments was not (Table 4.1). Immediately following the 4 d treatment, the lowest proportion of normal larvae was, again, in the 28 ppt treatment with no suspended sediments (Fig. 4.3). However, there were also fewer normal larvae in 28 ppt in both low and high suspended sediments, and in 32 ppt and no suspended sediments, compared to the control. At 21 d post-fertilisation, the differences in proportion of normal larvae were reduced across treatment combinations, compared to day 7. There was greater normal development in the 32 ppt treatment in both low and high suspended sediment compared to other treatment combinations (Fig. 4.3).

The interactive effects of low salinity and suspended sediments on body length (BL) were significant both at 7 and 21 d post-fertilisation, and the results were similar to those for PO. By contrast, the interactive effects on the PO:BL ratio were only significant at 21 d post-fertilisation. Finally, exposure to low salinity and suspended sediment had no effect on larval survival (Table 4.1).

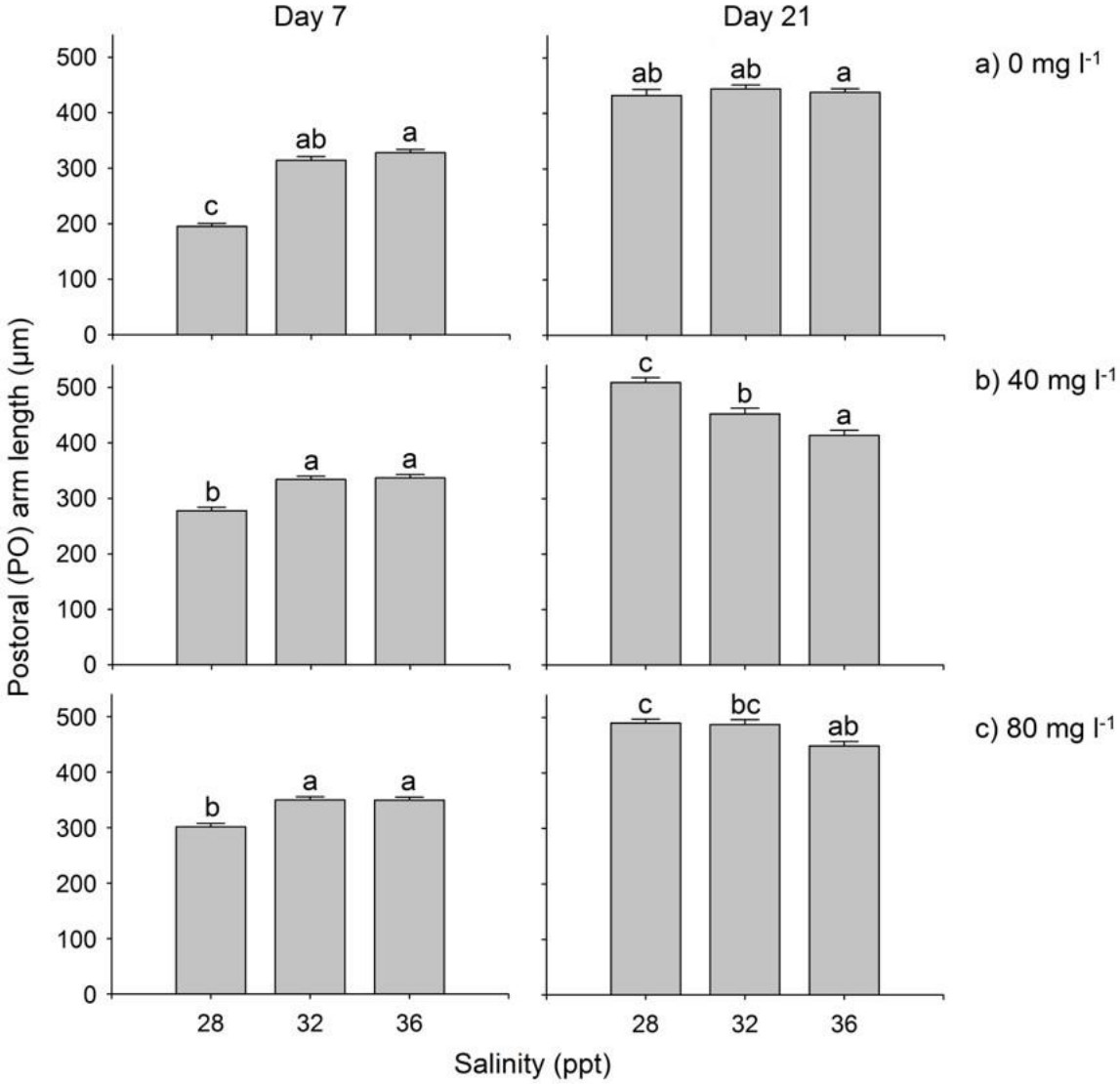


Fig. 4.2. Effect of reduced salinity and suspended sediments after the 4 d treatment (Day 7 post-fertilisation), and near the end of larval development (Day 21 post-fertilisation) on *Evechinus chloroticus* larval size. Bars represent means ± SE. Letters above bars indicate significant differences in means based on post-hoc Tukey tests on the interactive effect of treatments at each age.

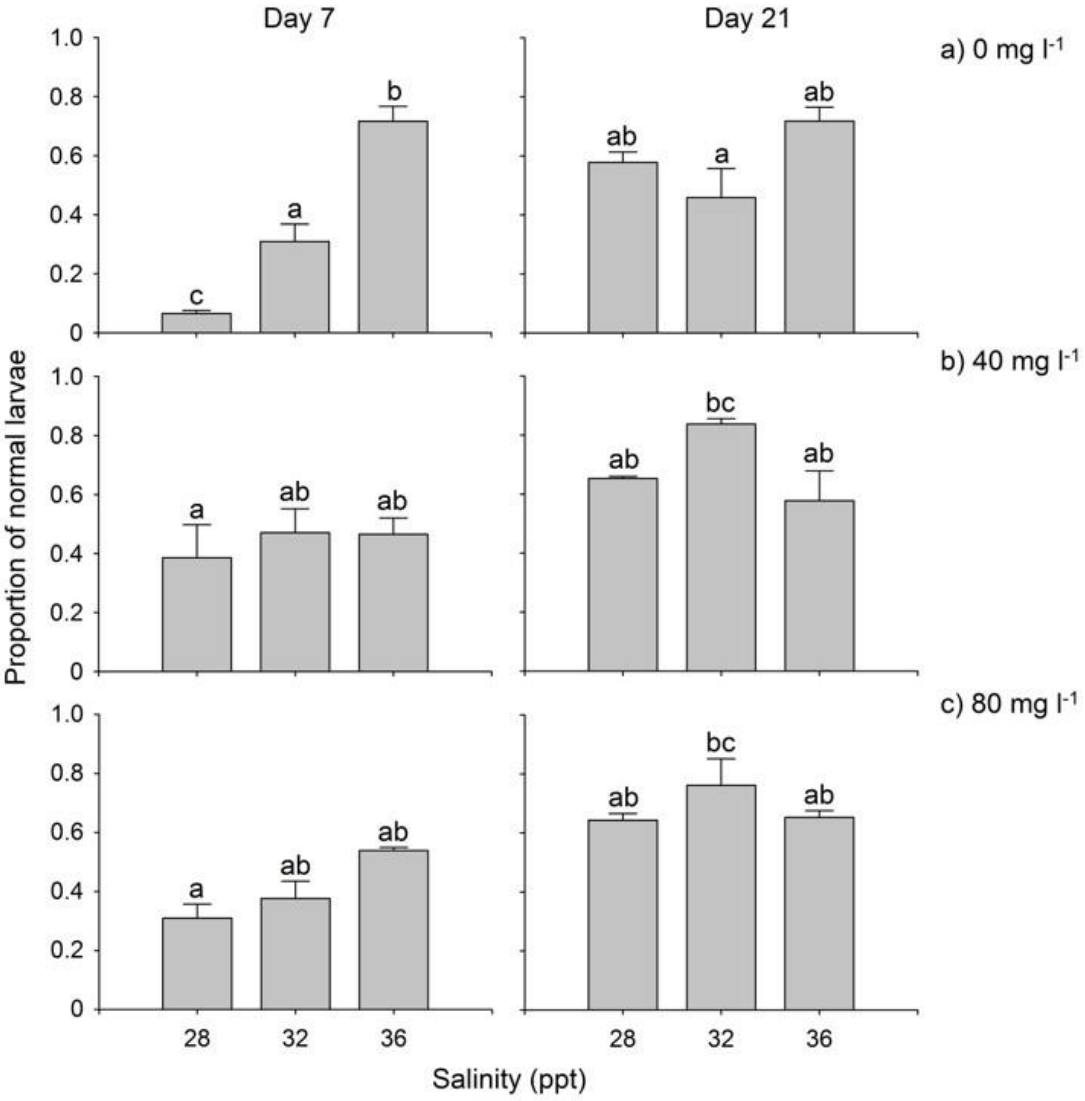


Fig. 4.3. Effect of reduced salinity and suspended sediments after the 4 d treatment (Day 7 post-fertilisation), and near the end of larval development (Day 21 post-fertilisation) on *Evechinus chloroticus* larvae. Bars represent means ± SE. Letters above bars indicate significant differences in means based on post-hoc Tukey tests on the interactive effects of treatments at each age.

Table 4.1. Results of ANOVA on the effect of low salinity (28, 32, control: 36 ppt) and suspended sediments (control: 0, 40, 80 mg l^{-1}) on *Evechinus chloroticus* larval size (PO: post-oral arm length), proportion of normal larvae, body length (BL), PO:BL ratio and larval survival, after the 4 d treatment (Day 7) and near the end of larval development (Day 21). Variables were log and arcsine square root-transformed, respectively. Significant effects ($p < 0.05$) are highlighted in **bold**. Jar identity (n = 3) was a random effect nested within the main effects in each model.

Source	Day 7				Day 21			
	df	MS	F	p	df	MS	F	p
Larval size (PO)								
Salinity	2	0.39	19.9	**<0.001**	2	0.033	1.8	0.185
Susp. sed. (SS)	2	0.198	9.75	**<0.001**	2	0.031	1.7	0.208
Salinity × SS	22	0.02	4.86	**<0.001**	22	0.018	5.7	**<0.001**
Error	243	0.004			243	0.003		
Proportion of normal larvae								
Salinity	2	0.29	23.188	**<0.001**	2	0.015	1.114	0.349
SS	2	0.025	2.057	0.156	2	0.038	2.797	0.087
Salinity × SS	4	0.095	7.658	**<0.001**	4	0.064	4.716	**<0.001**
Error	18	0.012			18	0.013		
Body length								
Salinity	2	0.201	13.9	**<0.001**	2	0.016	2	0.164
SS	2	0.117	8	**<0.001**	2	0.005	0.6	0.557
Salinity × SS	22	0.015	8.4	**<0.001**	22	0.008	3.5	**<0.001**
Error	243	0.002			243	0.002		
PO:BL ratio								
Salinity	2	0.006	84.3	**<0.001**	2	0.001	0.9	0.416
SS	2	0.002	22.5	**<0.001**	2	0.002	4.3	**0.026**
Salinity × SS	22	0.002	3.2	0.137	22	0.001	2.8	**<0.001**
Error	243	0.002			243	0.001		
Larval survival								
Salinity	2	0.06	1.574	0.234	2	0.003	0.095	0.91
SS	2	0.048	1.262	0.307	2	0.023	0.773	0.476
Salinity × SS	4	0.049	1.282	0.314	4	0.012	0.413	0.797
Error	18	0.038			18	0.03		

4.3.2 Effect of larval experiences and deposited sediments on juvenile performance

Settlement success was reduced by the interaction of larval exposure to low salinity and deposited sediments added during settlement ($F_{(2,48)} = 3.21$, $p = 0.049$), but not larval exposure to suspended sediments. Larvae from the 28 ppt treatments had the lowest settlement success (~11%), and were not affected by the addition of sediments during settlement (Fig. 4.4). However, when deposited sediments were added, settlement success for larvae from the 32 and 36 ppt treatments declined to almost half of that compared to bowls with no added deposited sediments. Conversely, size at settlement was only affected by larval exposure to reduced salinity ($F_{(2,48)} = 3.29$, $p = 0.045$). The mean size of the juveniles obtained from larvae that had been reared for 4 d at the lowest salinity (28 ppt) was significantly smaller (mean diameter ± SE: 226 ± 63 µm) compared to 32 ppt (288 ± 21 µm) and 36 ppt (292 ± 14 µm).

The proportion of normal juveniles at 3 d post-settlement was affected by the individual effects of larval exposure to low salinity and suspended sediments, as well as the interaction between them. However, even though the individual effect of deposited sediments was significant, the interaction among the three factors was not (Table 4.2). All juveniles from larval treatments of 28 ppt and no suspended sediments were abnormal at 3 d post-settlement, regardless of whether deposited sediments were added. The number of normal juveniles was significantly lower when exposed as larvae to 28 ppt in low and high suspended sediments, as well as both 32 and 36 ppt in high suspended sediments, whether or not deposited sediments were added.

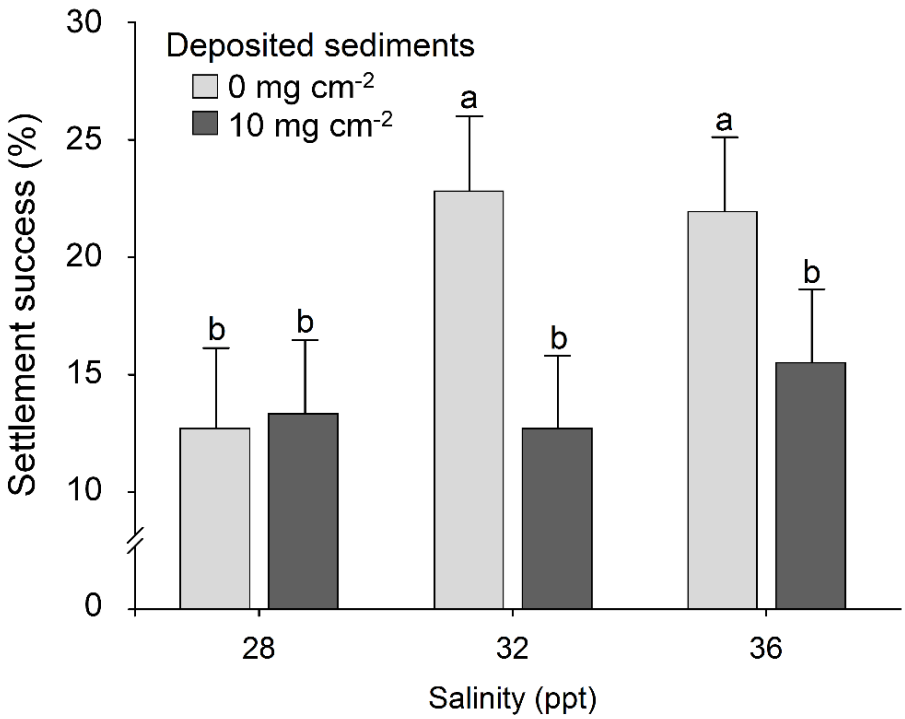


Fig. 4.4. Effect of larval experiences and deposited sediments on settlement success of *Evechinus chloroticus*. Bars represent mean settlement success (± SE). Letters above bars indicate significant differences in means based on post-hoc Tukey tests on the interactive effects of treatments.

Survival of juveniles at 28 d post-settlement was affected by the interaction of larval exposure to salinity and suspended sediments, as well as deposited sediments during settlement (Table 4.2). Although larvae were only exposed to deposited sediments for 48 h, while metamorphosis occurred, there was a negative effect on subsequent juvenile survival (Fig. 4.5). Survival was highest among larvae that were in control conditions and not exposed to deposited sediment during the settlement process. At 28 d post-settlement, all juveniles that as larvae experienced a 4 d exposure to 28 ppt, as well as juveniles from high suspended sediment larval treatments had died. The only survivors were juveniles from 32 and 36 ppt and either no or low suspended sediments during larval development.

Control juveniles increased in size by approximately 20% at 28 d compared to their size at 3 d post-settlement, regardless of whether deposited sediments were added (Fig. 4.5). However, growth of juveniles that had been exposed as larvae to low

suspended sediments, in 32 and 36 ppt salinity, was significantly lower when deposited sediments were added during settlement. The interactive effects among the three factors were significant for growth of juveniles (Table 4.2).

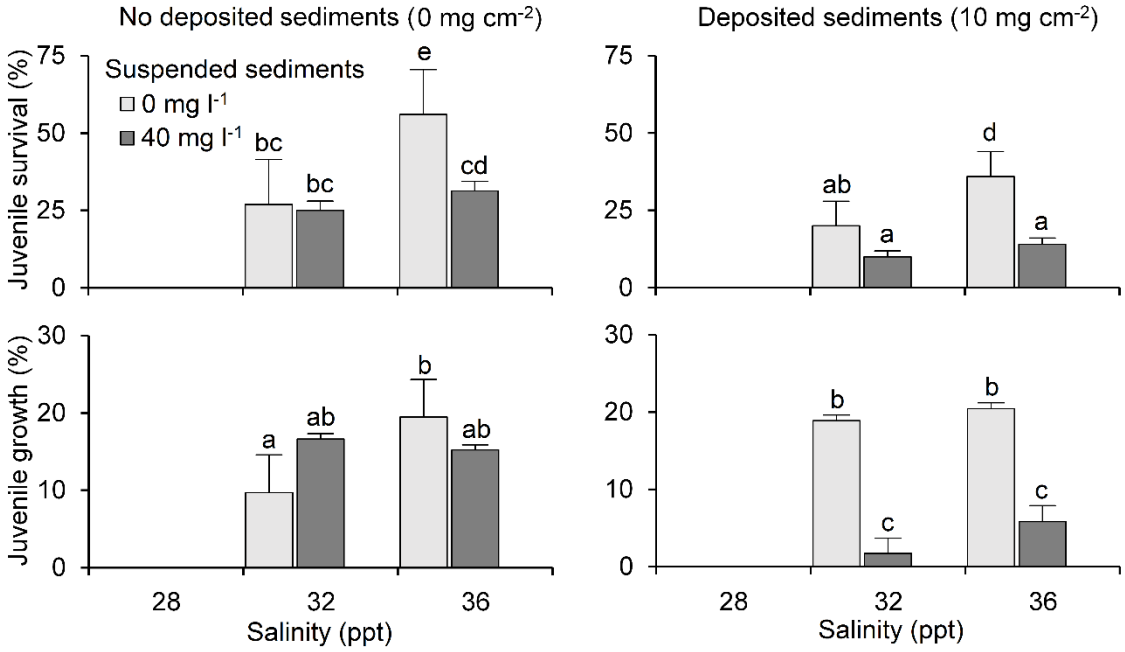


Fig. 4.5. Juvenile survival and growth of *Evechinus chloroticus* at 28 d post-settlement from different larval treatments and deposited sediments. Growth is relative to juvenile size at 3 d post-settlement. There were no surviving juveniles from all 28 ppt and high suspended sediments (28 ppt and 80 mg l^{-1}, not shown) larval treatments. Bars represent mean survival and growth (± SE), and letters above bars indicate significant differences in means based on post-hoc Tukey tests on the interactive effects of treatments.

Table 4.2. Results of ANOVA on the effect of low salinity (28, 32, control: 36 ppt), suspended sediments (control: 0, 40, 80 mg l^{-1}) and deposited sediments (control: 0, 10 mg cm^{-2}) on the proportion of normal *Evechinus chloroticus* juveniles at 3 d post-settlement, juvenile survival at 28 d post-settlement and juvenile growth at 28 d post-settlement, relative to size at 3 d post-settlement. Variables were arcsin square root-transformed. Significant effects ($p < 0.05$) are highlighted in **bold**.

Source	df	MS	F	p
Proportion of normal juveniles				
Salinity	2	1.431	153.323	**<0.001**
Suspended sediment (SS)	2	0.478	51.182	**<0.001**
Salinity × SS	4	0.558	59.822	**<0.001**
Deposited sediment (DS)	1	0.105	11.220	**0.002**
Salinity × DS	2	0.017	1.769	0.185
SS × DS	2	0.009	0.961	0.392
Salinity × SS × DS	4	0.011	1.192	0.331
Error	36	0.009		
Juvenile survival				
Salinity	1	1040.17	163.16	**<0.001**
Suspended sediment (SS)	1	988.17	155.01	**<0.001**
Salinity × SS	1	504.17	79.08	**<0.001**
Deposited sediment (DS)	1	988.17	155.01	**<0.001**
Salinity × DS	1	104.17	16.33	**<0.001**
SS × DS	1	1.50	0.23	0.634
Salinity × SS × DS	1	37.50	5.88	0.027
Error	16	102.00		
Juvenile growth				
Salinity	1	73.15	1581.6	**<0.001**
Suspended sediment (SS)	1	316.10	68.34	**<0.001**
Salinity × SS	1	28.38	613.70	**<0.001**
Deposited sediment (DS)	1	75.26	1627.25	**<0.001**
Salinity × DS	1	2.6	56.22	**<0.001**
SS × DS	1	444.62	9613.41	**<0.001**
Salinity × SS × DS	1	71.07	1533.66	**<0.001**
Error	16			

4.4 Discussion

We examined the immediate and latent effects of short-term exposure to multiple stressors, similar to a runoff after a major rain event, on the sea urchin *Evechinus chloroticus*. Our results suggest that a 4 d exposure to reduced salinity and high

concentrations of suspended sediments in early larval stages, can have significant latent effects on juvenile performance long after settlement. Growth and survival of juveniles were reduced by the combination of these two stressors as well as the addition of deposited sediments during the settlement process. These detrimental effects on juveniles may have consequences for recruitment and impact the dynamics of the adult population.

Short exposure to low salinity can have strong consequences on early life stages of echinoderms (reviewed by(Stickle & Diehl 1987, Russell 2013). Developmental success of the sea urchins *Arbacia lixula* and *Paracentrotus lividus* was significantly lower than controls at <29 ppt, where only ~60% of the embryos reached the pluteus stage after exposure to reduced salinity for 2 – 3 days (Carballeira et al. 2011). Exposure to salinities ≤31 ppt during the first 24 h of development also had a negative effect on gastrulation and development rates of *E. chloroticus* (Delorme & Sewell 2014), and embryos failed to complete development at 27.5 ppt (Antonie 2003). However, these studies focussed on a single life stage, and none followed up the effects of salinity after metamorphosis.

Here, reduced salinity had a strong sub-lethal effect on larvae immediately after the 4 d treatment. Interestingly, larvae seemed to have recovered from stress at the end of development, but the effects of low salinity were observed again after metamorphosis. Larvae from all 28 ppt treatments showed low settlement success and juveniles did not survive past 28 d post-settlement. Similar results were found for the sand dollar *Dendraster excentricus*, where larvae exposed to low salinity for a week recovered from stress and developed significantly longer arms than controls (George & Walker 2007). However, contrary to what we found, the sand dollars that had been exposed to reduced salinity for a week produced more juveniles than controls, while those at constant low salinity produced fewer or no juveniles (George & Walker 2007).

The present study is the first to show the latent effects of low salinity on settlement success and juvenile performance of sea urchins. Our results are similar to those for a few other invertebrates where it has been examined. For example, Pechenik et al. (2001) demonstrated that exposing polychaete larvae (*Capitella* sp.) to a short pulse of reduced salinity for 48 h can have strong sub-lethal effects. Salinities of 10 and 12 ppt did not kill the larvae but resulted in reduced post-settlement survival and juvenile

growth rates (Pechenik et al. 2001). Similarly, Montory et al. (2014) found that size at metamorphosis and growth rate of juveniles of the gastropod *Crepipatella fecunda*, decreased when larvae were briefly exposed to low salinities (15 and 20 ppt), while the effects on larvae were a delay in time from hatching to metamorphosis and high mortality rates. More recently, Lambert et al. (2018) observed that metamorphosis of the ascidian *Botrylloides violaceus* was reduced when larvae were exposed to salinities <16 ppt, and the colonies had fewer zooids when exposed to <25 ppt, compared to larvae in 30 ppt treatments.

Other latent effects of early larvae exposure to short durations of stress have previously been observed for *E. chloroticus*. Rouchon and Phillips (2017) demonstrated that a 2-d exposure to copper during larval development did not have visible consequences for the larvae, but latent effects appeared from 8 d post-settlement. By 25 d post-settlement, juveniles exposed to copper as larvae had impaired growth and were smaller than controls (Rouchon & Phillips 2017). Here, not only did brief larval exposure to low salinity and high sediment affect juvenile growth, but survival as well. Collectively these studies demonstrate that brief exposure to ecologically realistic levels of a variety of stressors associated with runoff can have cryptic downstream effects on juveniles that can impact recruitment, regardless of whether they have an immediate effect on larvae.

In general, reduced salinity had a greater immediate effect on larval development than suspended sediments, although the effects were interactive because the effect of the lowest salinity treatment was more pronounced without suspended sediments, compared to when suspended sediments were present. Interactions between salinity and suspended sediments have not been well studied. However, contrary to what we observed, Humphrey et al. (2008) found a synergistic effect of sediment loads and hyposaline conditions on the coral *Acropora millepora*. Fertilisation was reduced by >50% with increasing concentrations of suspended sediments (100 mg l^{-1}) and low salinity of 30 ppt (Humphrey et al. 2008). The mechanism by which low salinity could be interacting with suspended sediments in the present study is still unknown, although negative impacts of low salinity can be reduced by other factors, such as temperature (Delorme & Sewell 2014, Mak & Chan 2018). Phillips and Shima (2006) found that *E. chloroticus* larvae in high suspended sediment treatments had longer arms than larvae

where no sediments were added, suggesting that sediments might increase the ability of larvae to feed.

Even though it has been demonstrated that suspended sediment can cause negative effects on fertilisation success of *E. chloroticus* (Miller et al. 2014), and impact larval survival of other invertebrate species (Gilmour 1999, Humphrey et al. 2008), in the present study it was not a significant factor determining settlement success. These results are in accordance with Phillips and Shima (2006), who found that suspended sediment caused high larval mortality rates, but were not an impediment to successful metamorphosis. However, we observed that larvae exposed to high suspended sediments for a short period had poor performance as juveniles, in all salinity treatments, and none of them survived by 28 d post-settlement. Similarly, Humanes et al. (2017) found that high suspended sediments reduced survivorship of the coral *A. millepora*, and growth of *A. tenuis* and *Pocillopora acuta* juveniles. Moreover, Gilmour (1999) observed that even though embryonic development of *A. digitifera* was not affected by suspended sediments, larval settlement was significantly reduced by them.

In the present study, a fine coating of deposited sediments not only reduced settlement success but was also deleterious for juvenile growth and survival. Deposited sediments directly inhibited settlement success on the abalone *Haliotis diversicolor* (Onitsuka et al. 2008), and can also modify behaviour of *H. iris*, which can indirectly cause mortality by predation (Chew et al. 2013). Our results are in accordance with those of Walker (2007), who found that deposited sediment can inhibit settlement success of *E. chloroticus*, and also reduced survival of juveniles, even at low levels of sediments.

Coastal habitats are dynamic environments, and organisms are particularly at risk because they are subjected to both broad-scale climate stressors, as well as local sources such as terrestrial runoff (Halpern et al. 2007). Low salinity and increased suspended sediment are likely to often co-occur as a result of runoff after rain events (e.g. see Appendix 7 for data from Wellington Harbour). Our findings suggest that environmentally realistic exposure to reduced salinity and sediment can have previously unrecognised, significant latent effects on sea urchin early life stages. These effects manifest after metamorphosis and last long after settlement, causing juvenile mortality that can impact recruitment to populations. Terrestrial runoff is likely

to increase in the next few decades, which will likely have important consequences not only for this important herbivore species, but for other benthic organisms developing in coastal areas.

Chapter 5

Predation on *Evechinus chloroticus* new settlers and juveniles

Two-month old juvenile *Evechinus chloroticus* from larval cultures

Chapter 5

5.1 Introduction

The early life stages of marine invertebrates has been recognised as the most vulnerable to biotic and abiotic stress (Caselle 1999, Cole et al. 2000). Post-settlement mortality can be extremely high during the first days of benthic life (Hunt & Scheibling 1997, Osman & Whitlatch 2004, Phillips 2017). Many processes can cause mortality to new settlers, including biological and physical factors, such as disease, bulldozing (i.e. dislodgement of settlers while herbivores are grazing), predation, temperature, salinity and hydrodynamics (Dayton 1971, Gosselin & Qian 1997, Hunt & Scheibling 1997, Jennings & Hunt 2011). Of all of those, predation might be one of the most important causes of settler mortality (Osman & Whitlatch 1984, Carrasco & Phillips 2012, Lord & Barry 2017). However, predator-prey interactions at those early life stages remain largely unknown (Hunt & Scheibling 1997, Jones & Grutter 2008, Clemente et al. 2013), with only a few studies on mobile species.

For sea urchins, post-settlement events are considered a bottleneck (Harrold et al. 1991, Jennings & Hunt 2011), and it is increasingly recognised that micropredation likely has a major role in shaping population structure (McNaught 1999, Bonaviri et al. 2012, Coleman & Kennelly 2019). Sea urchin settlers have a wide range of predators, including small crustaceans, such as crabs and shrimps, gastropods, sea stars and polychaetes (Scheibling & Robinson 2008, Fagerli et al. 2014). However, refuges, like algal turf and cobble, can allow settlers to successfully avoid predation (Jennings & Hunt 2011, Yiu & Feehan 2017).

Once sea urchins have survived the first year of life, they are usually considered recruits to the adult population (Ebert 1983, Balch & Scheibling 2001). However, juveniles are still susceptible to bigger predators, such as lobsters and fish (Guidetti 2006, Ling & Johnson 2012). In fact, field experiments have demonstrated that there is a higher predation pressure in smaller sea urchins compared to larger sizes (Clemente et al. 2007, Seytre et al. 2013, Selden et al. 2017). Juveniles usually occupy cryptic habitats inside crevices or take shelter under cobble or conspecifics to avoid predation (Pederson & Johnson 2006, Eklöf et al. 2009, Zhao et al. 2014). However,

they tend to be more vulnerable once they outgrow the spatial refuge provided by crevices, but are not yet large enough to escape predation by virtue of their size alone (Tegner & Levin 1983, Clemente et al. 2013).

Predation is also a major process controlling the abundance and population structure of sea urchins (Bonaviri et al. 2009, Dee et al. 2012, Fagerli et al. 2014), and can have cascading effects on the benthic community (McClanahan et al. 2011, Vergés et al. 2012, Azzarello et al. 2014). It has been observed that predation on sea urchins is higher inside marine reserves, where predators, such as fish and lobster, are more abundant (Ling & Johnson 2012, Vergés et al. 2012). Control of echinoid abundance can avoid overgrazing and contribute to the maintenance of the macroalgal community (Flukes et al. 2012, Kriegisch et al. 2016).

New Zealand's marine reserves are good example of where top-down control of predators structure shallow reef communities (Taylor et al. 2011, Spyksma et al. 2017a). Several studies have identified the importance of predation by the rock spiny lobster (*Jasus edwardsii*) and snapper (*Chrysophrys auratus*) on the sea urchin (*Evechinus chloroticus*), also known as kina (Babcock et al. 1999, Shears & Babcock 2002). With the establishment of the Leigh Marine Reserve, densities of predators considerably increased over time, reducing the abundance of sea urchins, to the point where the growth of macroalgae was no longer controlled by kina (Shears & Babcock 2003, Babcock et al. 2010). Barren habitats began to be less common inside the marine reserve, compared to unprotected areas nearby (Babcock et al. 1999).

Besides the main predators, *J. edwardsii* and *C. auratus*, other species like the blue cod (*Parapercis colias*), banded wrasse (*Notolabrus fucicola*) and scarlet wrasse (*Notolabrus miles*) are also likely predators of kina, especially of juveniles (Ayling & Cox 1982, Andrew & MacDiarmid 1991, Shears & Babcock 2002). Andrew and Choat (1982) also found goatfish (*Upeneichthys lineatus*), spotty (*Notolabrus celiodotus*), leatherjacket (*Meuschenia scaber*) and red moki (*Cheilodactylus spectabilis*) were predatory fish of *E. chloroticus* juveniles based on gut content analysis (noting that some taxonomic names have changed from the original publication). Invertebrates, such as the eleven-armed (*Coscinasterias muricata*) and seven-armed sea stars (*Astrostole scabra*), and the triton shell (*Charonia capax*) have also been reported to

prey on kina from field observations (Andrew & Choat 1982, Andrew 1988, Shears & Babcock 2002).

Most of the studies on the predation of *E. chloroticus* have involved experiments in the field. Andrew and Choat (1982) found that small individuals escape predation despite the high abundance of predatory fish. Predation on both juveniles and adults was mainly attributed to fish, but no direct observations were made (Andrew & Choat 1982). Later, Andrew and MacDiarmid (1991) observed that predation by lobsters was higher on small sea urchins (10 mm) compared to adults, but the presence of shelters increased survivorship. Similarly, Shears and Babcock (2002) estimated mortality of tethered sea urchins, and observed that predation by lobster and snapper was higher on smaller individuals (25 mm). However, there is no information on potential predators of new settlers or the effect of refuges on the survival of settlers and juveniles through direct observations on predation.

The main objective of this study was to assess the predation of sea urchin *Evechinus chloroticus* settlers (<1 mm) and juveniles (10 – 40 mm), as well as the role of size and refuge on their survival. Specific aims were to: 1) identify micropredators and bulldozers of new settlers, 2) test the effect of refuge availability on new settler mortality, 3) assess how vulnerable new settlers are to predation compared to two-month old settlers, 4) identify predators of juveniles and 5) test the effect of refuge availability on juvenile mortality.

5.2 Materials and methods

Laboratory experiments were conducted to examine predation dynamics of two life stages of *Evechinus chloroticus*: settlers (<1 mm test diameter) and juveniles (10 – 40 mm). Three micropredation experiments were conducted to identify potential predators of new settlers (Experiment 1), the effect of refuges on new settler mortality (Experiment 2); and the effect of settler size on their mortality (Experiment 3). Furthermore, two juvenile predation experiments were carried out to examine potential juvenile predators (Experiment 4) and the effect of refuge on juvenile mortality (Experiment 5).

Sea urchin settlers were obtained from larval cultures (for details of the methods see Chapter 4). Competent larvae were left undisturbed in 1.5 l jars with filtered seawater (FSW, 0.2 µm) until settlement occurred. Prior to the introduction of competent larvae, jars were inoculated with cultured diatoms (mixed species), that were allowed to form a biofilm for seven days, to provide food and substrate for the settlers. Jars were submerged in a water bath at near constant ambient temperature (18 ± 1ºC). Water changes in the jars were completed three times per week by inverse siphoning. New settlers (0.40 ± 0.04 mm test diameter) were used within a week of settlement for Experiments 1 and 2, while two-month old settlers (0.85 ± 0.11 mm) were used for Experiment 3 (see below for details). Sea urchin juveniles and small adults (13 – 52 mm) were collected from the subtidal zone in Wellington Harbour. The sea urchins were kept in a sea table with flowing raw seawater (RSW), and fed ad libitum with macroalgae (*Macrocystis pyrifera* and *Ulva* sp). Prior to trials, the test diameter was measured, and sea urchins were divided in four size categories: 13 – 22, 23 – 32, 33 – 42 and 43 – 52 mm (see below for details).

Experiment 1: Potential predators of new settlers

Eight species of macroinvertebrates from four phyla (four crustaceans, two molluscs, one polychaete and one sea star), and one species of fish were selected as potential predators and bulldozers of *E. chloroticus* new settlers (Table 5.1). All invertebrates were <3 mm and considered juveniles except for polychaetes, while fishes were <36 mm long, and considered young adults. Predators were collected from around the Wellington area and kept separately in small plastic containers with mesh sides in a water bath with flowing RSW for up to a week before the experiments began. They were fed with small pieces of mussels to ensure they were able to eat, and then starved for 72 h. Six replicate glass bowls with 150 ml of FSW (n = 54) were arranged per predator species. Ten new settlers were placed in each bowl and left undisturbed for an hour before adding a single predator. Controls consisted of three bowls with ten settlers in each, but no predators. Observations on the number of settlers eaten or dead were conducted 24 h after the addition of the predator. Surviving settlers were carefully searched for in the bowls and counted. If needed, more settlers were added to total ten. The experiments ran for another 24 h and were terminated 48 h after the

addition of the potential predators. No mortality of sea urchins was observed in the controls, and none of the predators died during the experiment.

Table 5.1. Species used as potential predators of *Evechinus chloroticus* new settlers and their mean size (± SD). Size is carapace length for crabs, total length for polychaetes, limpets, snails and triplefins, and tip of arm to opposite tip of arm length for sea stars.

Species	Common name	Size (mm)	Min	Max
Notomithrax sp	Decorator crab	1.67 ± 0.11	1.52	1.86
Halicarcinus sp	Pillbox crab	1.61 ± 0.18	1.48	1.95
Petrolisthes elongatus	Blue half-crab	0.41 ± 0.03	0.37	0.45
Pagurus sp	Hermit crab	1.53 ± 0.36	1.09	1.96
Eulalia sp	Polychaete	2.63 ± 0.73	1.49	3.73
Notoacmea elongata	Limpet	0.80 ± 0.04	0.75	0.85
Diloma aethiops	Snail	0.56 ± 0.05	0.50	0.61
Patiriella regularis	Cushion sea star	0.99 ± 0.18	0.81	1.26
Forsterygion lapillum	Triplefin	32.35 ± 4.46	25.40	35.50

Experiment 2: Effect of refuges on new settler mortality

Two crustaceans were selected as amongst the most voracious predators from the previous experiment, hermit crabs (*Pagurus* sp) and decorator crabs (*Notomithrax* sp), to test for the effect of refuges on the mortality of new settlers. The same bowls were used as above, however two different substrates were added to them as refuges. These included articulated coralline algae and small pebbles (~5 mm long) set up in discrete patches covering up to a third of the bottoms of the bowls. Coralline algae were selected as refuge because settlers are usually attracted to them (Huggett et al. 2006, Yiu & Feehan 2017) and provide a more complex spatial structure than bare rocks (Lamare & Barker 2001).

Six replicate bowls were used per predator species and per refuge type (n = 24). Ten settlers were placed in each bowl and were given two hours to move and seek refuge

in the substrate. After this period, a single predator was added to each bowl. Controls consisted of three replicate bowls per predator with no substrates added, 10 settlers and a single predator (n = 6). Different individual predators were used for this experiment. Observations on sea urchin mortality were conducted as described above. The number of settlers taking shelter under algae and pebbles was noted.

Experiment 3: Effect of settler size on their mortality

To test for the vulnerability to predation of new settlers (0.40 ± 0.04 mm) compared to two-month old settlers (0.85 ± 0.11 mm), six replicate bowls were arranged per predator species and per settler age group (n = 24). Ten sea urchins from each age group were placed in each bowl and left undisturbed for 2 h, and then a single predator (*Pagurus* sp and *Notomithrax* sp) was added to each bowl. Controls consisted of three bowls with ten new settlers and three with ten two-month old settlers, but no predators were added. Observations on sea urchin mortality were conducted as described above. No mortality was observed in the controls during the experiment.

Experiment 4: Potential predators on juveniles

Potential predators were identified from the literature (Andrew & Choat 1982, Andrew 1988, Shears & Babcock 2002) and personal observations in the field. Adult specimens included two species of crustaceans, the decorator crab (*Notomithrax minor*) and the spiny rock lobster (*Jasus edwardsii*), and two species of sea stars, the seven-armed (*Astrostole scabra*) and the eleven-armed sea stars (*Coscinasterias muricata*). Predators were collected from the Wellington Harbour and the South coast a few days before the experiments, and kept in 2,000 l tanks with flowing RSW. Measurements were taken prior to the trials and included carapace length for crabs, total length for lobsters, and arm to arm length for sea stars (Table 5.2).

Table 5.2. Species used in the experiments as predators of *Evechinus chloroticus* juveniles and the mean size (± SD) of individuals. Size is carapace length for crabs, total length for lobsters, and tip of arm to opposite tip of arm length for sea stars.

Species	Common name	Size (cm)	Min	Max
Notomithrax minor	Decorator crab	4.76 ± 0.45	4.11	5.45
Jasus edwardsii	Spiny rock lobster	34.85 ± 4.80	30.5	45.0
Coscinasterias muricata	Eleven-armed sea star	20.57 ± 8.26	12.80	36.5
Astrostole scabra	Seven-armed sea star	34.75 ± 2.66	31.0	37.5

Due to the differences in predator sizes, the experiments were conducted in two different set ups. For decorator crabs, six replicate 5 l buckets with flowing RSW were used, while for the larger lobsters and sea stars, six replicate 2,000 l tanks were set up. In all cases, predators were fed with pieces of mussel before the trials to ensure they were capable of eating and then, starved for 72 h. Three sea urchin juveniles, starting with the lowest size class (13 – 22 mm), were placed in the middle of each replicate tank or bucket, before a single predator was added. The number of sea urchins eaten was quantified at 24 h; eaten juveniles were replaced with new juveniles of the same size class, and the experiment ran for another 24 h. After this period, the predators were offered progressively larger juveniles, three at a time (23 – 32, 33 – 42, 43 – 52 mm) for 48 h intervals. A possible escape size for the sea urchins was detected when bigger individuals were not eaten. Controls consisted of a bucket with three juveniles, but no predators were added. No juvenile mortality was observed in control buckets, nor did any predators die over the course of the experiments.

Experiment 5: Effect of refuge on juvenile mortality

The most voracious predator, the decorator crab, was selected based on findings from the previous experiment, to test for the effect of refuge on the survival of juveniles. Replicate buckets (n = 6) were arranged with the bottoms completely covered with small cobbles (5 – 10 mm) up to 5 cm deep. Cobbles were selected as refuge based on observations in the field of juveniles covered with small rocks, when no other structural refuge (i.e. crevices) was available. Three sea urchin juveniles (13 – 22 mm)

were added and given two hours to move and use the cobbles to hide, before a single predator was added. Controls consisted of three buckets with three juveniles and a single predator, but no refuge was available. The number of sea urchins eaten was recorded at 24 h, new individuals were added to replace juveniles eaten, if necessary. Again, surviving sea urchins were counted at 48 h and the experiment was terminated. The number of juveniles covered with cobbles was noted. Different predator individuals were used for this experiment.

Statistical analyses

Mortality of settlers and juveniles was analysed separately using general linear models, estimated by least squares. Mortality of settlers was not significantly different between the two predators tested in Experiments 2 and 3 ($F_{2,22} = 0.64$, $p = 0.43$), so this factor was removed from the analysis. The fixed factors for each experiment were: Settler predators (Experiment 1), Settler refuge (Experiment 2), Settler size (Experiment 3), Juvenile predators and size (Experiment 4) and Juvenile refuge (Experiment 5). In all cases, post-hoc Tukey tests were used to compare means across treatments when factors were significant ($p < 0.05$). All statistical analyses were conducted with the software R v3.2.4 using the packages 'lmtest' (Zeileis & Hothorn 2002), 'lsmeans' (Lenth 2016) and 'MASS' (Ripley et al. 2018).

5.3 Results

Experiment 1: Potential predators of new settlers

Hermit crabs and decorator crabs were the most effective predators of new settlers, from the nine species tested (Fig. 5.1). Mean mortality of newly settled sea urchins by predation from hermit and decorator crabs were 65.8% and 45.0%, respectively. Triplefins and pillbox crabs also consumed sea urchin settlers but caused lower mortalities (Table 5.3). Other species caused mortality by bulldozing/crushing, mainly the cushion stars (31.7%), and in lower amount snails (7.5%) and limpets (6.7 %). In

this case, settlers were found dead and their test crushed in bits. Mortality of settlers by blue half-crabs (3.3%) and polychaetes (1.7%) might have been caused by reasons other than predation or bulldozing. The settlers were found dead but tests were intact.

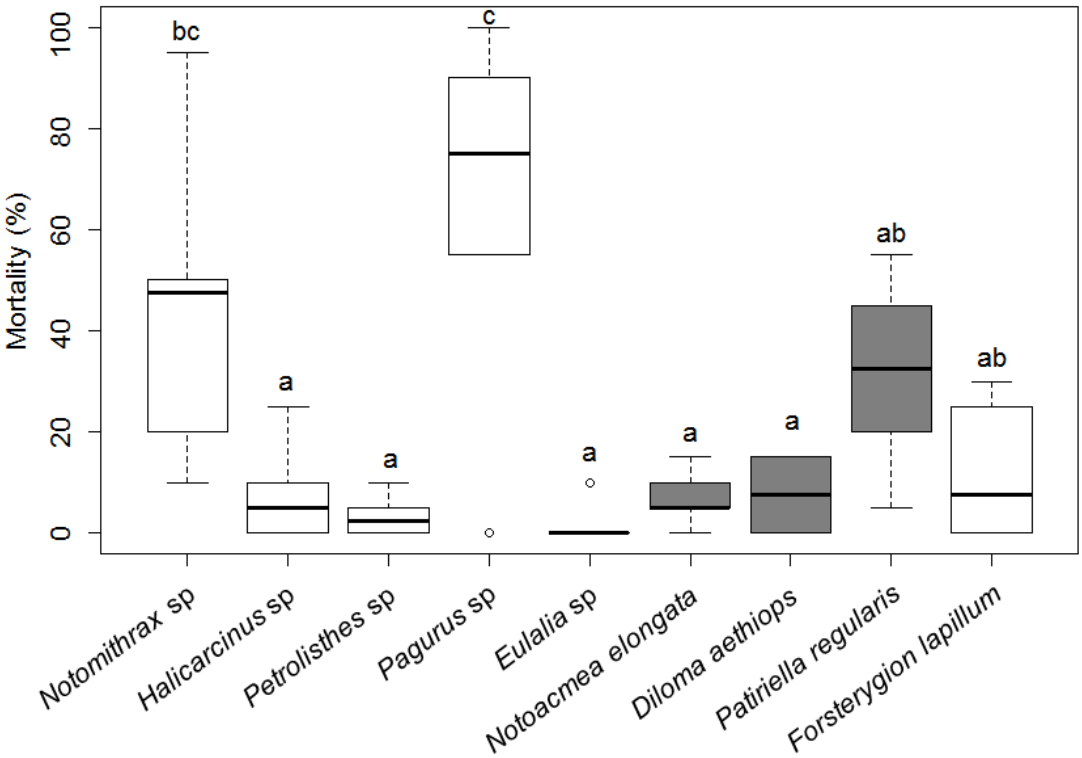


Fig. 5.1. Mortality of *Evechinus chloroticus* new settlers by predation (clear boxes) or bulldozing (shaded boxes) from different species of macroinvertebrates and fish. Boxes represent the mean and quartiles, and bars the standard error; letters above boxes indicate significant differences based on post-hoc Tukey tests.

Experiment 2: Effect of refuges on new settler mortality

The presence of articulated coralline algae as a refuge significantly reduced mortality of new settlers by half (Fig. 5.2). Settlers were attracted to the coralline algae. On average, 72% of the settlers were observed to be on top or underneath the algae. Mortality in bowls with pebbles was intermediate, but not significantly different from the control where no refuge was added. Settlers were not particularly attracted to pebbles, only 48% of them were observed nearby. Predation by the two species of crabs was

not significantly different (Table 5.3), although the number of sea urchins eaten by hermit crabs was slightly higher in the controls.

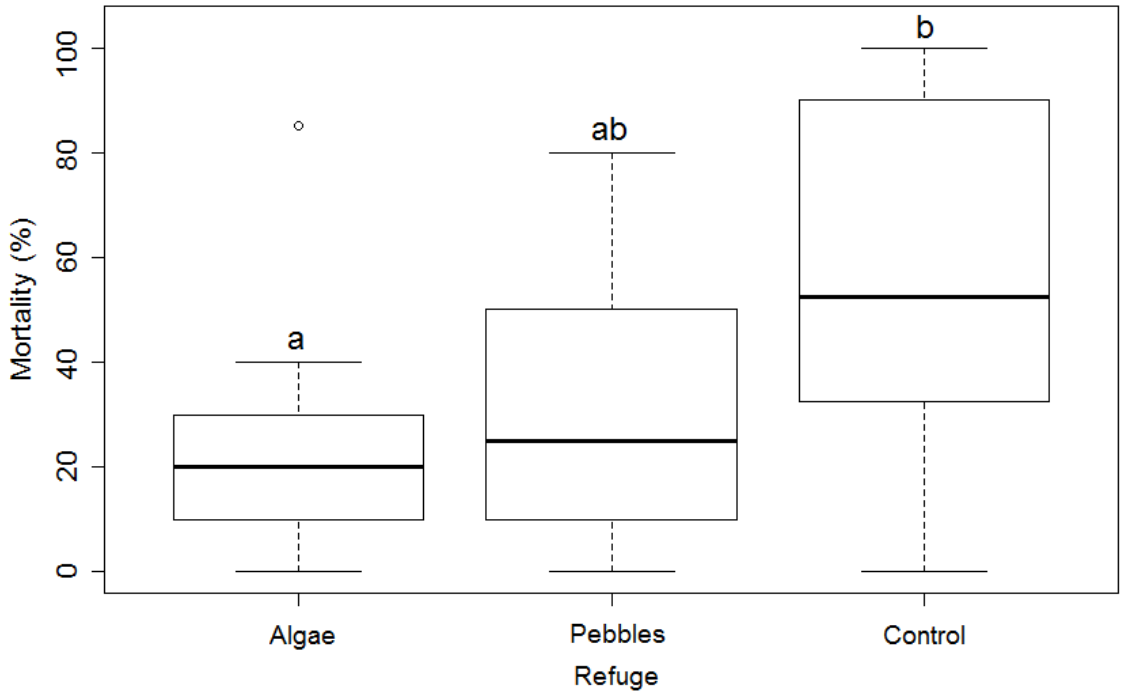


Fig. 5.2. Effect of refuges on mortality of *Evechinus chloroticus* new settlers. Results were pooled across the two predators (*Notomithrax* sp and *Pagurus* sp). Boxes represent the mean and quartiles, and bars the standard error; letters above boxes indicate significant differences based on post-hoc Tukey tests.

Experiment 3: Effect of settler size on their mortality

New settlers were more vulnerable to mortality by crab predators than two-month old settlers (Table 5.3). Mean mortality of new settlers was almost double than that of those that were two months old (Fig. 5.3). Older settlers had almost doubled their size and developed stronger spines after two months, compared to recent settlers. Both decorator and hermit crabs consumed settlers at the same rate (Fig. 5.4).

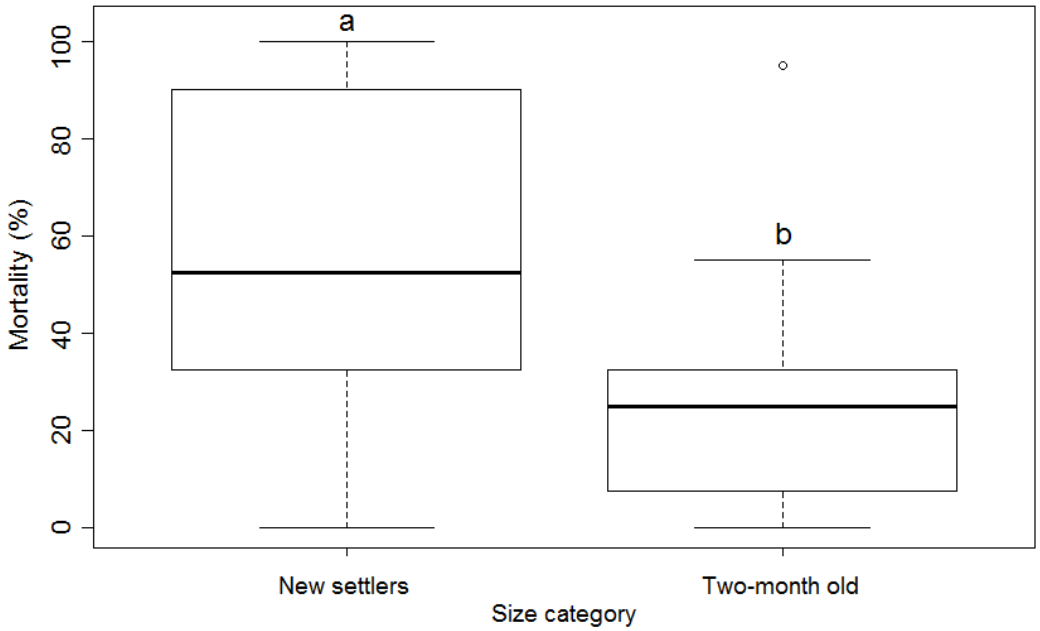


Fig. 5.3. Effect of *Evechinus chloroticus* settler size on their mortality. New settlers were 0.40 ± 0.04 mm and two-month old settlers 0.85 ± 0.11 mm. Results were pooled across the two predators (*Notomithrax* sp and *Pagurus* sp). Boxes represent the mean and quartiles, and bars the standard error; letters above boxes indicate significant differences based on post-hoc Tukey tests.

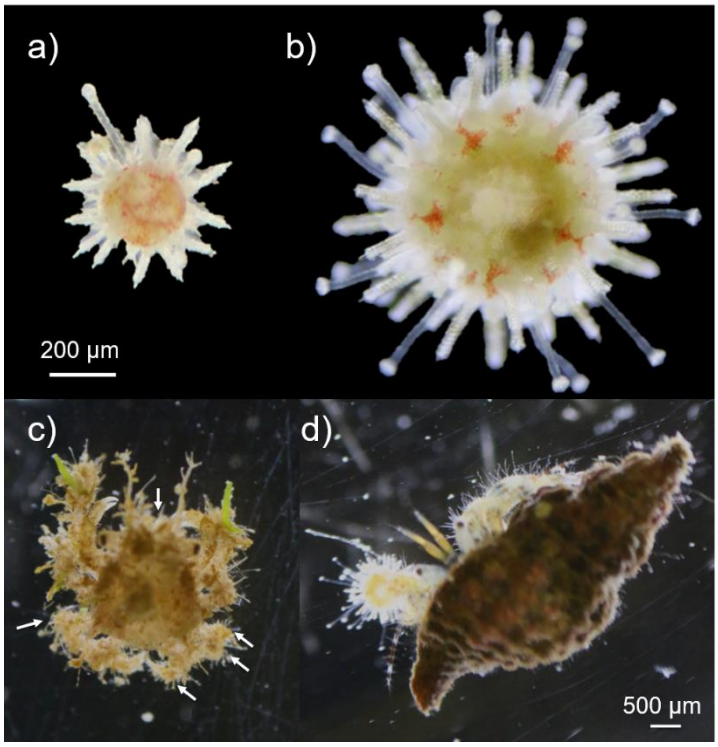


Fig. 5.4. a) New settler, b) two-month old settler, c) decorator crab feeding on recent settlers (pointed with arrows), and d) hermit crab eating a two-month old settler.

Table 5.3. ANOVA results of *Evechinus chloroticus* settler mortality. Experiment 1: potential predators, Experiment 2: effect of settler refuge, and Experiment 3: effect of settler size. Sum of squares (SS), degrees of freedom (df), ANOVA statistic (F), and p value (p) are given. Significant effects ($p < 0.05$) are highlighted in **bold**.

Source	SS	df	F	p
Experiment 1				
Settler predators	24212	8	9.32	**< 0.001**
Error	14612	45		
Experiment 2				
Settler refuge	6923.4	2	4.6096	**0.0167**
Error	26284.5	35		
Experiment 3				
Settler size	4537.5	1	4.9064	**0.0374**
Error	20345.8	22		

Experiment 4: Potential predators on juveniles

Decorator crabs were active predators that consumed most of the juvenile sea urchin's body parts and caused damage to their test and spines (Fig. 5.5). Lobsters also consumed most of the sea urchin test or crushed it in half and ate the internal parts of the juveniles. The seven-armed sea stars were slower predators due to their feeding mechanism (extending their stomachs out of their mouths, to externally digest the prey). The remains of the sea urchin juveniles were always smooth tests with no tissue left and loose spines were found in the bottoms of the tanks. Surprisingly, no predation was observed by the eleven-armed sea stars.

Smaller size classes were significantly more vulnerable to predation by crabs (Table 5.4). Mortality of 13 – 22 mm and 23 – 32 mm juveniles was significantly higher (69.4% and 55.5%, respectively), than 33 – 42 mm juveniles (13.8%). In contrast, there were no significant effects of sea urchin size class for lobsters or seven-armed sea stars,

for which predation was overall lower and similar across urchin sizes (Fig. 5.6). Only lobsters consumed the largest size class (43 – 52 mm), but the mortality was very low (<1%).

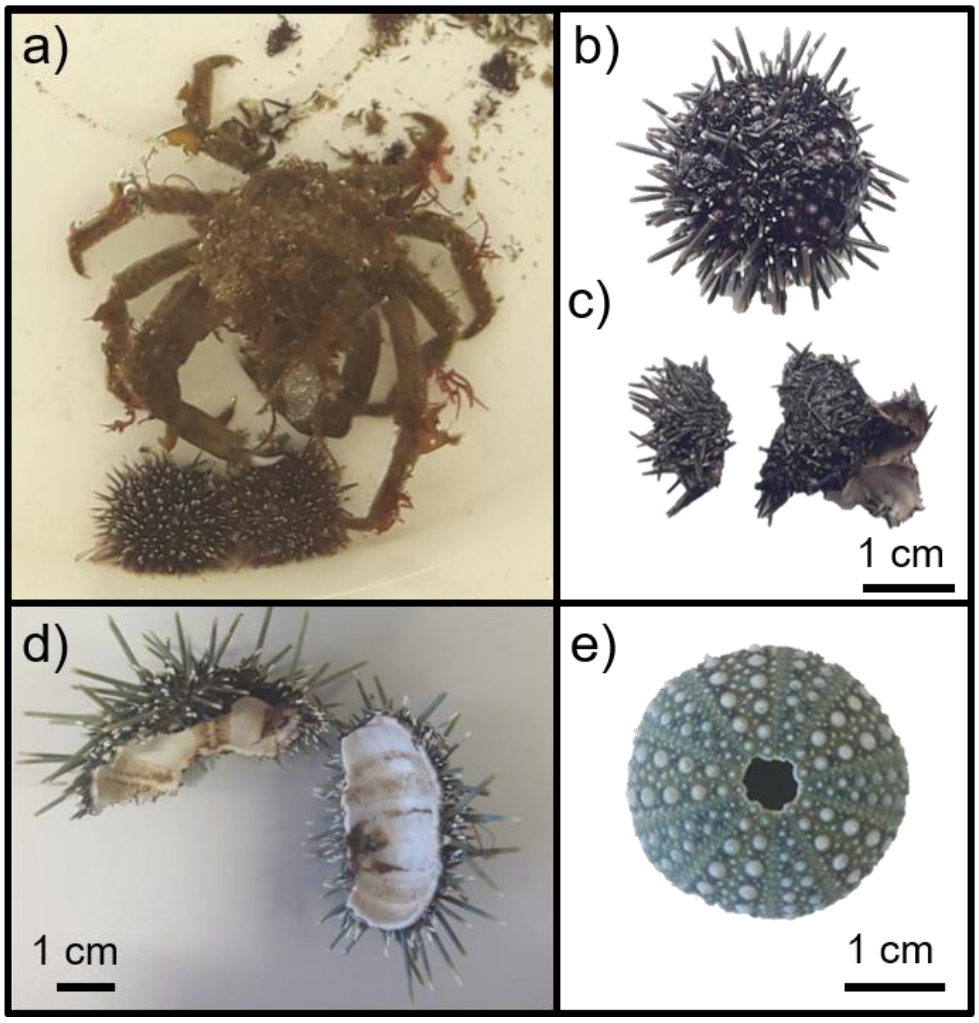


Fig. 5.5. a) Decorator crab (*Notomithrax minor*) feeding on *Evechinus chloroticus* juveniles. b) Juvenile's test and spines damaged by the crab's chelae. Remains of juveniles' tests after predation by c) Decorator crab, d) spiny rock lobster (*Jasus edwardsii*), and e) seven-armed sea star (*Astrostole scabra*).

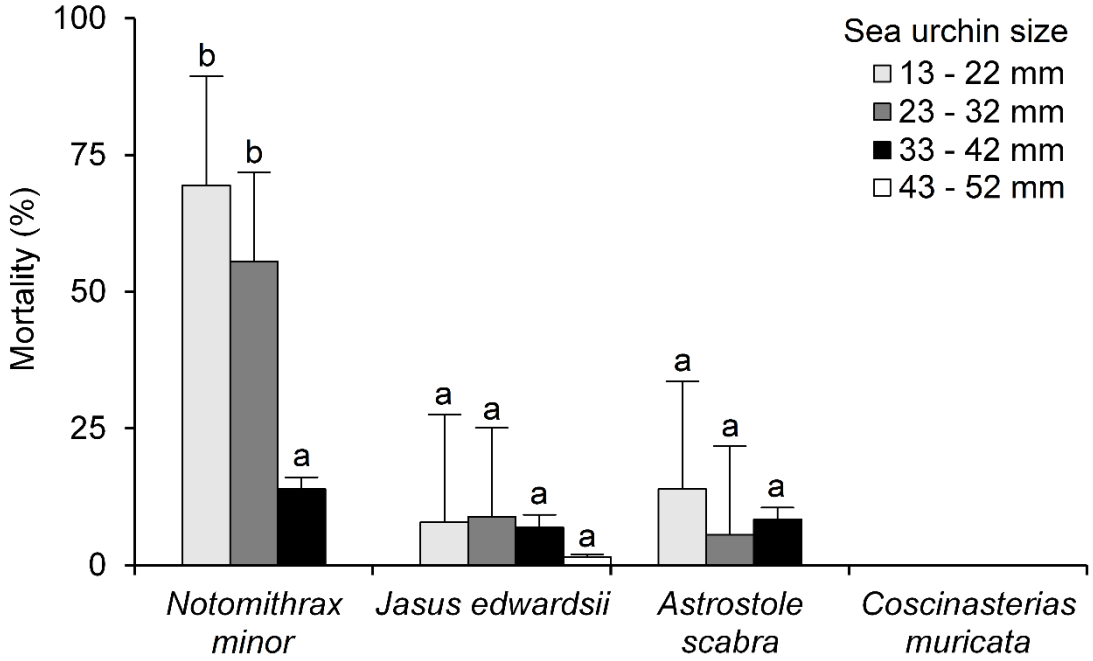


Fig. 5.6. Mortality of *Evechinus chloroticus* juveniles and small adults due to predation of four species of macroinvertebrates. Bars indicate means (± SE), and letters above bars indicate the significant differences in means based on post-hoc Tukey tests.

Experiment 5: Effect of refuge on juvenile mortality

The effect of refuge on the survival of sea urchin juveniles (13 – 22 mm) from decorator crab predation was tested (Fig. 5.7). All juveniles from the refuge treatment took shelter under the cobbles, and because the cobbles covered up to 5 cm deep of the buckets, juveniles disappeared from the surface. Mortality by predation was 3.75 times higher in the absence of cobbles, compared to when cobbles were present and sea urchins were able to cover themselves (Table 5.4).

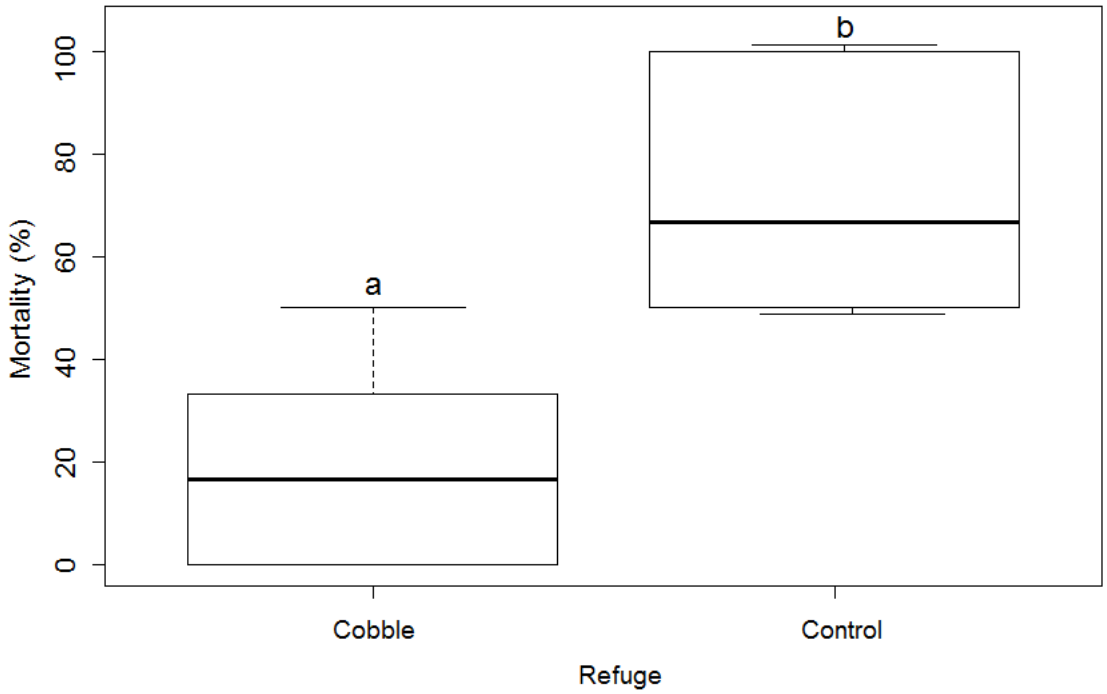


Fig. 5.7. Effect of refuge on *Evechinus chloroticus* juvenile mortality due to predation by decorator crabs (*Notomithrax minor*). Boxes represent the mean and quartiles, and bars the standard error; letters above boxes indicate significant differences based on post-hoc Tukey tests.

Table 5.4. ANOVA results of *Evechinus chloroticus* juvenile mortality. Experiment 4: juvenile predators and size, and Experiment 5: effect of refuge. Sum of squares (SS), degrees of freedom (df), ANOVA statistic (F), and p value (p) are given. Significant effects ($p < 0.05$) are highlighted in **bold**.

Source	SS	df	F	p
Experiment 4				
Juvenile predators	15344.5	2	37.69	**<0.001**
Juvenile size	7899.9	3	12.94	**<0.001**
Predator * Size	13011.0	6	10.65	**<0.001**
Error	21165.6	104		
Experiment 5				
Juvenile refuge	8356.1	1	16.56	**0.002**
Error	5046.1	10		

5.4 Discussion

The present study identified two new predators of the early life stages of the sea urchin *Evechinus chloroticus*, hermit crabs and decorator crabs. It also demonstrated that seven-armed sea stars feed on sea urchin juveniles. This species and eleven-armed sea stars are described in the literature as potential predators of *E. chloroticus* (Andrew & Choat 1982, Andrew 1988, Shears & Babcock 2002), but have not been tested through laboratory experiments until now. This is also the first study to have assessed mortality caused by predation on newly settled *E. chloroticus*.

Only a few studies have experimentally assessed predation on newly settled sea urchins (Scheibling & Robinson 2008, Jennings & Hunt 2011, Bonaviri et al. 2012, Yiu & Feehan 2017). In California, Scheibling and Robinson (2008) found that *Strongylocentrotus droebachiensis* new settlers had 75% to 100% predation rates by hermit crabs and shrimps, and bulldozers like gastropods also caused high mortalities. Moreover, in the Mediterranean, Bonaviri et al. (2012) observed >80% mortality of *Paracentrotus lividus* new settlers by hermit and brachyuran crabs. Similarly, in the present study, hermit and decorator crabs were the most effective predators, causing mortalities of 66% and 45% respectively. However, other invertebrates, like cushion stars, also caused mortality by bulldozing/crushing.

The first few days of benthic life are crucial for the successful recruitment to the adult population. However, it is well known that mortality of new settled invertebrates is extremely high (Gosselin & Qian 1997, Bohn et al. 2013, Phillips 2017), and predation is one of the major causes (Osman et al. 1992, Hunt & Scheibling 1997). For sea urchins, it has been estimated that less than 1% of the settlers survive long enough to reach 2 mm (Tomas et al. 2004). In the present study, older settlers had significantly lower mortality rates than recent settlers. After two months, settlers had doubled their size and developed stronger and longer spines compared to new settlers, and to some degree, this deterred predation.

The availability of refuges is critical to reduce predation pressure on sea urchin settlers and juveniles (Scheibling & Hamm 1991, Dee et al. 2012). It has been demonstrated that settlers of different species are chemically attracted to coralline algae (Lamare & Barker 2001, Scheibling & Robinson 2008). This can significantly reduce predation,

compared to when no refuges are available (Yiu & Feehan 2017). Kelp and the availability of crevices and cobble also reduced mortality of juveniles <14 mm by 30% (Clemente et al. 2013, Feehan et al. 2014). In the present study, a higher percentage of settlers were attracted to coralline algae, which reduced their mortality by 32% compared to when no refuges were available. Interestingly, the covering behaviour of sea urchin juveniles observed in the present study, also reduced their mortality by 53%. It has been suggested that predation cues, rather than food availability, induce *E. chloroticus* to remain hidden inside crevices (Spyksma et al. 2017b). In fact, sea urchins usually leave crevices when they reach 40 mm, which is thought to be the predation escape size for some species, including *E. chloroticus* (Andrew 1988, Clemente et al. 2013, Spyksma et al. 2017b).

The findings of 34 studies that involved laboratory or field experiments on predation of echinoids are summarised in Table 5.5. The analysis of all studies revealed that nine out of ten times, refuges increased sea urchin survival (e.g.(Andrew & MacDiarmid 1991, Hereu et al. 2005, Dee et al. 2012, Zhao et al. 2014, Nichols et al. 2015). Moreover, half of these studies involved predation on juveniles or settlers, most of them acknowledging that those are the most vulnerable life stages compared to adults (e.g.(Sala 1997, Shears & Babcock 2002, Pederson & Johnson 2006, Boada et al. 2015). Most of the studies involved predation by fish (21 out of 34), while 24 studies involved lobsters, crabs and/or sea stars, and only five studies tested predation by gastropods or other invertebrates.

Like the current study, crabs have been identified as the most effective predators mainly of sea urchin juveniles (Scheibling & Robinson 2008, Young & Bellwood 2011, Bonaviri et al. 2012, Clemente et al. 2013). Furthermore, there is an effect of sea urchin size over predation rates, where smaller individuals are generally the most vulnerable. Fagerli et al. (2014) found that predation in the laboratory on *S. droebachiensis* juveniles (2 – 3 mm) by crabs and hermit crabs (63 and 30%, respectively) was higher than that of tethered 10 mm juveniles in the field (15%). In addition, Clemente et al. (2013) found that the smallest size classes (5 – 10 and 10 – 14 mm) of *S. purpuratus* had higher mortality than larger juveniles. However, most studies have focussed on relatively large juveniles. In the present study, new settlers and the smallest juvenile class exhibited significantly higher predation rates (65.8 and 69.4%, respectively) than

juveniles >33 mm, by hermit and decorator crabs. This confirms that predation is an important source of mortality from very early on.

Effect of predator size, mainly of crabs, has also been tested in the laboratory (Scheibling & Robinson 2008, Bonaviri et al. 2012, Clemente et al. 2013, Boada et al. 2015). Scheibling and Robinson (2008) and Clemente et al. (2013) did not find a significant interaction between predator and sea urchin size. However, smaller predators did not consume larger sea urchins as effectively as bigger predators. Bonaviri et al. (2012), on the other hand, found that larger hermit crabs showed significantly higher predation rates on *P. lividus* new settlers (1 – 2 mm) than smaller predators. Here, sea urchin settlers were smaller than in any other previous study (<1 mm) and the hermit and decorator crabs used for these experiments were very small too (<3 mm). However, larger predators might not have been able to detect such a small size of sea urchins, which emphasises the role of micropredators on the post-settlement mortality of sea urchins. In contrast, larger predators in the juvenile predation experiments might have been able to consume larger sea urchins. For example, lobsters, which were considerably bigger than decorator crabs, were to only predators that consumed juveniles >42 mm.

Lobsters have been identified as efficient predators of adult sea urchins, and sometimes the only ones that can eat large individuals (Tegner & Dayton 1981, Tegner & Levin 1983, Andrew & MacDiarmid 1991, Scheibling & Hamm 1991). For example, Ling et al. (2009a) showed that only large individuals of the rock lobster *Jasus edwardsii* were successful predators of the sea urchin *Centrostephanus rodgersii* in eastern Tasmania. Sea urchin juveniles, on the other hand, are usually more vulnerable, but some can escape predation due to their cryptic behaviour, i.e. remaining inside crevices or covering with rubble (Pederson & Johnson 2006, Ling & Johnson 2012). In the present study, there was no effect of sea urchin size on predation by lobsters, but mortality was generally low (6% pooled across all juvenile size classes). Similarly, Andrew and MacDiarmid (1991) found that large lobsters ate all *E. chloroticus* sizes, including large individuals. In contrast, Shears and Babcock (2002) observed that predation on *E. chloroticus* was higher for 30 – 40 mm individuals, compared to larger size classes. Mortality in both studies was significantly higher than the values observed here (67% and 42% pooled across sea urchin size classes, respectively). Furthermore, Ling and Johnson (2012) showed that survival rates of

tethered *C. rodgersii* were 10 times lower for small individuals on protected reefs where abundance of large predators, like the rock lobster, was higher. However, those observations were obtained from tethering experiments, inside and outside marine reserves; therefore, comparisons must be made with caution.

Fewer studies have considered predation on echinoids by sea stars (Dee et al. 2012, Urriago et al. 2012). However, asteroids are active predators that represent a large source of mortality in some habitats (Bonaviri et al. 2009, Eklöf et al. 2009). In the present study, only one of the two sea star species tested consumed *E. chloroticus*. Assumptions on predation by *C. muricata* have been based on the remains of sea urchin tests (Andrew & Choat 1982, Andrew 1988, Shears & Babcock 2002) or direct observations in the field (Lamare pers. comm.), but no predation experiments been made in laboratory. Studies on prey composition of *A. scabra* do not mention kina as preferred prey (Town 1981), and only a few experiments have tested the escape behaviour of *E. chloroticus* in the presence of *A. scabra* (Dix 1969, Town 1979). Interestingly, during the survey dives for Chapters 2 and 3, seven-armed sea stars were observed to prey on large kina (~80 mm) in two occasions at Breaker Bay. In contrast, no eleven-armed sea stars were observed to feed on sea urchins in the Harbour, where both species were abundant (Glockner-Fagetti pers. obs.).

Fish are probably the most effective sea urchin predators, although sometimes echinoids escape predation when they reach larger sizes (Sala 1997, Shears & Babcock 2002, Clemente et al. 2007, Young & Bellwood 2012, Johansson et al. 2013). Higher abundance and biomass of predatory fish, usually related to a protection status, largely contribute to control sea urchin populations and maintaining a balance between urchin density and macroalgal cover (Guidetti 2006, Pederson & Johnson 2006, Eklöf et al. 2009, Cook & Vanderklift 2011, McClanahan et al. 2011, Vergés et al. 2012, Seytre et al. 2013, Selden et al. 2017). At the Leigh Marine Reserve in northeastern New Zealand, Andrew and Choat (1982) observed that fish do not completely remove *E. chloroticus* juveniles from shallow rocky reefs, casting doubt on the role of predators structuring sea urchin populations. In contrast, Cole and Keuskamp (1998) attributed the low densities and bimodal size structure of urchins to the higher abundance of predatory fish in this area. Moreover, Leleu et al. (2012) observed that sea urchin densities declined after the abundance of lobsters and fish increased in the same no-take marine reserve. No predation experiments have been carried out on *E. chloroticus*

in the marine reserves of the Wellington region. It would be worth experimentally assessing the role of predatory fish in the field inside and outside the marine reserve. In the present study, only triplefins were tested as potential predators of new settlers. However, they are abundant and common in all Wellington sites and unlikely affected by marine reserve protection status.

Even though predator abundances were not estimated in the present study, there are notable differences in fish and invertebrate assemblages between the Harbour and the South coast. Lobster and snapper are virtually absent from the Harbour sites, the predominant fish observed at Kau Bay were blue cod (*Parapercis colias*) juveniles (<15 cm), and spotties (*Notolabrus celiodotus*), while in Shelly Bay only spotties were observed (Glockner-Fagetti pers. obs.). In contrast, the fish composition on the South coast is more diverse, including the banded wrasse (*Notolabrus fucicola*), blue cod and red moki (*Cheilodactylus spectabilis*) amongst others (Pande & Gardner 2009). Moreover, the presence of lobsters and seven-armed sea stars has been recorded at Breaker Bay and Princess Bay (Pande & Gardner 2009, Byfield 2013). The extent of predation pressure by lobsters and sea stars in shaping population structure of *E. chloroticus* in the Wellington region is still unclear, however, this study suggests that micropredation (especially by crabs) should be recognised as a potentially important factor controlling survival of new settlers and determining recruitment to adult populations.

Table 5.5. Summary of studies examining predation on sea urchins through laboratory (L) and field (F) experiments.

Species	Predator	Treatment	Findings	Reference
Strongylocentrotus purpuratus and *S. franciscanus* (Adults)	Sea star (*Pycnopodia helianthoides*), lobster	(F) (L) Observations on predation and feeding behaviour	Sea stars, lobsters, horn sharks and sheephead are mayor predators of *S. purpuratus*	Tegner and Dayton (1981)
Evechinus chloroticus (<30 mm)	Fish and gastropods	(F) Adult canopy and exclusion cages	Adults did not affect juvenile densities. Juveniles escaped predation despite the high densities of fish	Andrew and Choat (1982)
S. purpuratus and *S. franciscanus* (<30 and >60 mm)	Spiny lobster (*Panulirus interruptus*)	(L) Species preference and size	Preference of *S. purpuratus* over *S. franciscanus*. Small *S. franciscanus* were protected under canopy of adults	Tegner and Levin (1983)
E. chloroticus (10 to 90 in 10 mm intervals)	Rock lobster (*Jasus edwardsii*)	(L) Combinations of predator and sea urchin sizes, and presence of shelter	Higher predation on small sea urchins (<50 mm). Presence of shelter increased survivorship	Andrew and MacDiarmid (1991)
S. droebachiensis (3 - 6 and 25 - 30 mm)	Sculpins, whelks, crabs (*Cancer* spp, *Carcinus* sp), lobster	(F) Cage experiments with cobble as refuge and predator	Predation by *Cancer* spp was highest without refuge for both juveniles and adults. Predation may influence population structure	Scheibling and Hamm (1991)
Paracentrotus lividus (<10 and <60 mm)	Fish (*Diplodus sargus, D. vulgaris, Coris julis*)	(F) Direct observation on predation	Predation was size dependent. *C. julis* mayor predator of juveniles	Sala (1997)
E. chloroticus (25 - 75 mm)	Lobster (*J. edwardsii*), snapper (*Pagrus auratus*)	(F) Tethered sea urchins	Most intense predation on smallest sea urchins and by lobster and snapper	Shears and Babcock (2002)

Table 5.5. Continued.

P. lividus (2 - 10 mm)	Fish (*C. julis*, *D. sargus*)	(F) Cage experiment, increasing structural complexity	Predation increased at higher predator abundance and decreased at greater structural complexity	Hereu et al. (2005)
P. lividus and *Arbacia lixula* (20 - 35 and >35 mm)	Fish (*Diplodus* spp)	(F) Tethered sea urchins at different protection levels	Predation was higher at protected locations and for smaller *P. lividus* than *A. lixula*. Fishing bans may restore predator-prey interactions	Guidetti (2006)
Heliocidaris erythrogramma (Juveniles and adults)	Fish, lobster (*J. edwardsii*)	(F) Tethered and tagged sea urchins inside and outside marine reserve, and caging experiment	Higher mortality inside marine reserve where predators were more abundant. Significant predation by lobsters on adults compared to cryptic juveniles	Pederson and Johnson (2006)
Diadema aff. *antillarum* (<20 and >30 mm)	Fish (*D. cervinus* and *D. sargus*), sea star (*Coscinasterias tenuispina*)	(F) Tethered sea urchins	Most intense predation was on juveniles. Adults >40 escaped predation. Predation does not control population structure in barrens	Clemente et al. (2007)
S. droebachiensis (New settlers <1.3 mm and 11 - 15 mm)	Crustaceans, gastropods, polychaetes, asteroid, fish	(L) Potential predators and predator and prey size	Settlers were consumed by crabs and bulldozed by periwinkles. Juveniles attained size refuge at 10 mm	Scheibling and Robinson (2008)
P. lividus, A. lixula (30 - 35 mm)	Fish (*D. sargus*, *D. vulgaris*), sea star (*Marthasterias glacialis*)	(F) Tethered sea urchins at different depths and sites	Higher predation in sites where fish were more abundant. *M. glacialis* mayor source of mortality, might control population structure	Bonaviri et al. (2009)
Tripneustes gratilla (23 - 89 mm)	Fish, snail, sea star	(F) Tethered sea urchins at different protection levels	Strong protection effect on predation pressure in seagrass beds. Potential buffered effect of canopy on predation	Eklöf et al. (2009)

Table 5.5. Continued.

H. erythrogramma and *C. tenuispinus* (12 - 92 mm and 41 -129 mm)	Fish, lobster	(F) Tethered sea urchins. (L) Lobster did not eat tethered individuals	Fish abundance and predation on *H. erythrogramma* were higher inside marine reserve. Sea urchin size was not a significant factor	Cook and Vanderklift (2011)
S. droebachiensis (New settlers 1 - 3 mm)	Benthic invertebrates including molluscs, polychaetes, tunicates	(F) Cage experiments with cobble and possible competitors	Growth of sea urchins was higher in cages without other organisms	Jennings and Hunt (2011)
Echinometra viridis (NS)	Fish	(F) Tethered sea urchins inside marine reserve	Predation was low (<35%) but higher in deeper sites	McClanahan et al. (2011)
Echinometra mathaei (40 - 50 mm)	Fish	(F) Tethered sea urchins during day and night	Higher predation during the day. The biomass of potential fish predators was poor predictor of sea urchin abundance at local scales	Young and Bellwood (2011)
P. lividus (New settlers 1 - 2 mm)	Crabs (*Pagurus* sp, *Calcinus* sp, *Pilumnus* sp), shrimp	(L) Predator size	Most voracious predators were large hermit crabs. Micro-predators were more abundant in forest than barren. Micro-predation may contribute to shape population structure	Bonaviri et al. (2012)
Eucidaris galapagensis (20 - 30 and 50 - 60 mm)	Fish (*Bodianotus* sp, triggerfish), sea star (*Pentaceraster comingi*)	(F) Tethered experiment using rubble habitat as refuge	Predation was higher in exposed than rubble habitats for smaller individuals. Sea urchins displayed nocturnal activity to avoid predators	Dee et al. (2012)
C. rodgersii (40 - 70 and 80 - 120 mm)	Lobster (*J. edwardsii*), fish (*Notolabrus tetricus*)	(F) Tethered and tagged sea urchins, different size and shelter, inside and outside marine reserve	Survival was ten times lower (small) and 6 times (large) lower in exposed substrates in marine reserve. Higher survival of juveniles in crevices.	Ling and Johnson (2012)

Table 5.5. Continued.

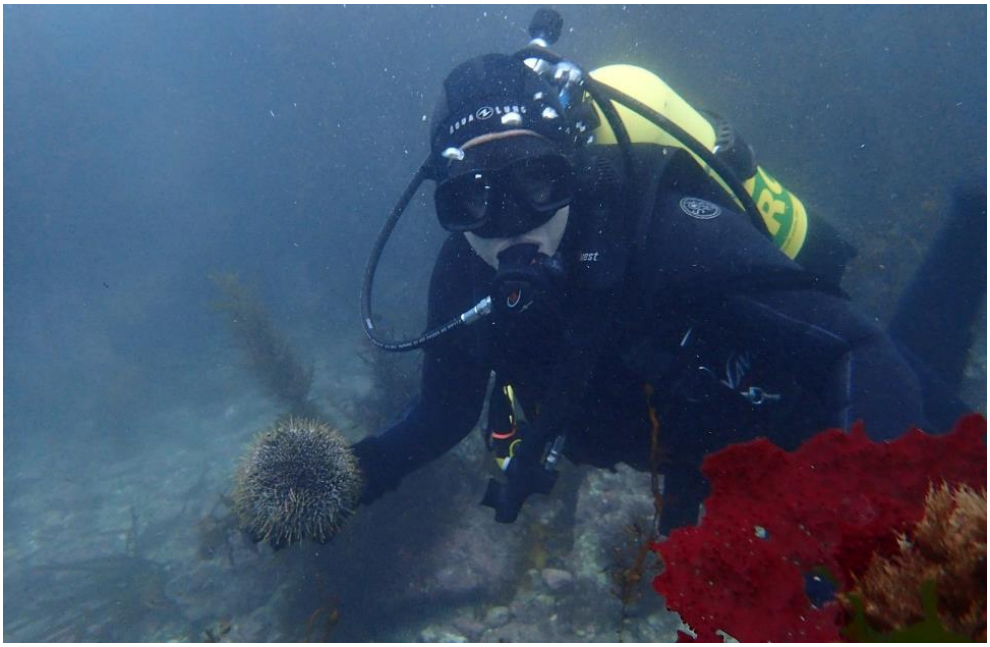
Tetrapygus niger (15 - 20 and 50 - 60 mm)	Sea stars (*Heliaster helianthus* and *Meyenaster gelatinosus*)	(F) Tethered sea urchins on elevated surfaces	Predators were more abundant in low surfaces and urchins had higher survival rate in elevated surfaces. *M. gelatinosus* greater threat than *H. helianthus*	Urriago et al. (2012)
P. lividus (40 - 100 mm)	Fish	(F) Direct observation on predation at different protection levels	Predation was higher in shallow protected sites, compared to deeper sites. Sea urchins more abundant in shallows can have impact algal community	Vergés et al. (2012)
E. mathaei, Diadema setosum, Echinothrix calamaris (40 - 50 mm)	Fish (*Balistoides* sp, *Balistapus* sp, *Lethrinus* sp and *Choerodon* sp)	(F) Predation on tethered sea urchins recorded by remote video cameras	*Balistapus* and *Balistoides* are mayor predators, and *E. mathaei* the most vulnerable species	Young and Bellwood (2012)
S. purpuratus (5 - 30 mm)	Crabs (*Pachygrapsus* sp, *Cancer* sp), sea star (*Pisaster*), fish	(L) Juvenile and predator size, habitat complexity, adult canopy	*Pachygrapsus* most efficient predator. Most susceptible individuals <14 mm. Refuges significantly reduced mortality	Clemente et al. (2013)
E. mathaei (30 - 60 mm)	Fish (*Coris aygula*, *Choerodon rubescens*, etc)	(F) Tethered sea urchins among different habitats	Two fish species responsible of 65% of predation events. Different sea urchin density among habitats due to other mechanisms than predation	Johansson et al. (2013)
P. lividus and *A. lixula* (20 - 30 and >45 mm)	Fish (*D. sargus, D. vulgaris*)	(F) Tethered sea urchins in rocky reef and barren, inside and outside marine reserve	Mortality depended on protection level and season. Smaller individuals were more vulnerable to predation	Seytre et al. (2013)

Table 5.5. Continued.

S. droebachiensis (2 - 3 and 10-20 mm)	Crabs (*Pagurus* sp, *Hyas* sp, *Carcinus* sp, *Cancer* sp), *Nereis pelagica*	(F) Predator abundance and tethering. (L) Alternate prey *Mitilus*	*Carcinus* and *Cancer* preyed on tethered juveniles. *Cancer* was the most efficient predator in lab experiments and more abundant in kelp forest than barrens	Fagerli et al. (2014)
S. droebachiensis (5-9, 10-14, 15-19 mm)	Crabs (*Cancer* spp)	(L) Kelp as refuge. (F) Cages with kelp as refuge	Kelp provide refuge for juveniles reducing mortality by 30%. Kelp facilitates recruitment of sea urchins	Feehan et al. (2014)
S. intermedius (10 - 20 mm)	Crab (*C. japonica*)	(L) Covering material like shells	Mortality of sea urchins without covering material was higher but not significant	Zhao et al. (2014)
S. purpuratus and *S. franciscanus* (60 - 80 mm)	Fish (*Semicossyphus pulcher*), lobster (*Panulirus interruptus*)	(F) Tethered sea urchins on rocky substrate and macroalgal habitat during day and night	Macroalgal provided refuge for sea urchins reducing mortality during day but not at night, when lobsters are active	Nichols et al. (2015)
P. lividus (10 - 30, 30 - 50 and >50 mm)	Fish (*D. sargus*)	(F) Tethered sea urchins using different prey size	Small sea urchins were more vulnerable to predation by fish	Boada et al. (2015)
S. purpuratus and *M. franciscanus* (20 - 35, 35 - 50 and 50 - 70 mm)	Fish (*Semicossyphus pulcher*)	(F) Direct observation on predation at different protection levels	Predation was higher inside reserves and decreased with increasing sea urchin size. Recovery of predator size may restore resilience	Selden et al. (2017)
S. droebachiensis (1 - 3 mm)	Crabs (*Pagurus* spp and *Cancer oregonensis)*	(L) Coralline algae as refuge	Chemical attraction to algae. Refuge significantly reduced predation, which may facilitate recruitment	Yiu and Feehan (2017)

Chapter 6

General Discussion



Diving on the South coast

Chapter 6

6.1 Summary of main findings

My thesis examines the distribution and recruitment patterns of echinoderms and contributes to the knowledge of some of the major biotic and abiotic factors affecting early life stages of the sea urchin *Evechinus chloroticus*. This research attempts to elucidate the role of pre- and post-settlement events shaping adult populations, using kina as a model species. Echinoderms play significant ecological roles in benthic marine communities and some species are culturally and commercially important. However, the ecological processes that regulate community structure are still poorly understood and their recruitment patterns have been rarely studied in New Zealand.

The main findings of this thesis were as follows. Recruitment of *E. chloroticus* (Chapter 2) is infrequent and spatially variable, likely contributing to the different adult population structure in two adjacent locations in the Wellington region of central New Zealand: the Harbour (high density, smaller size) and the South coast (low density, larger size). Large episodes of recruitment might not be seen in up to four years on the South coast. Echinoderm assemblages (Chapter 3) more generally are highly correlated with habitat composition and recruitment has a moderate positive relationship with temperature, with interannual and species-specific variation. In Chapter 4, I highlight that environmentally realistic exposure to low salinity and sediments, similar to runoff after major rain events that commonly occur in New Zealand, can have previously unrecognised latent effects on sea urchin early life stages. Finally, in Chapter 5, I emphasise the role of micropredation as a significant source of post-settlement mortality of *E. chloroticus*, and identified new predators of settlers and juveniles. In the present chapter, I focus on the implications of my findings for a better understanding of the processes that shape population structure in shallow rocky reefs.

6.2 Echinoderm community in the shallow rocky reefs

The rocky reef communities in New Zealand are typical of temperate marine ecosystems. They are usually dominated by large brown algae and the echinoderm fauna is an important component of the invertebrate assemblage (Schiel & Foster 1986, Shears & Babcock 2007, Edgar et al. 2013). Echinoderms have distinctive roles in the different trophic levels. Sea urchins, like *Evechinus chloroticus*, have an important top-down control over macroalgae (Andrew & Choat 1982, Villouta et al. 2001), while asteroids, such as *Patiriella regularis* or *Coscinasterias muricata*, are a highly abundant and can be key scavengers or predators controlling the abundance of prey species (Crump 1971, Day et al. 1995). However, the processes that shape their populations are not well understood and the limited studies conducted have focussed predominantly in just a few locations in the north (e.g. Maori Bay) and the south (e.g. Fiordland).

The two adjacent locations in the Wellington region, with distinctive oceanographic conditions, are ideal to investigate the processes driving differences in community structure. In the present study, seawater temperature was significantly higher in the Harbour compared to the South coast, which could be attributed to a better mixing of subantartic waters in the Cook Strait (Walters et al. 2010) and retention of water in the shallower Harbour (Heath 1977). Both locations were also characterised by different habitat composition. Shells and cobble mainly composed the substrate in the Harbour sites, where macroalgal cover was very low. The South coast sites, on the other hand, had more macroalgal cover, like Princess Bay, while Breaker Bay, in the mouth of the Harbour, was the most heterogeneous site, composed by cobble, large boulders and patches of macroalgae.

Abundance and distribution of echinoderms have been attributed to habitat structure and complexity (Entrambasaguas et al. 2008, Hermosillo-Nuñez et al. 2015). Setyastuti et al. (2018) observed that the habitat composition, especially seagrass, rock and dead coral, was significantly correlated with increasing diversity and abundance of echinoderms from a tropical island in Indonesia. In the present study (Chapters 2 and 3), habitat composition was largely responsible for the observed echinoderm assemblage. With the exception of *P. regularis*, that was abundant everywhere, the abundance of other echinoderm species was specific to sites with

certain characteristics. *E. chloroticus* and *C. muricata* were dominant in the Harbour, while the sea cucumber *Australostichopus mollis* and the brittle star *Ophiopsammus maculata* had a strong correlation with macroalgae and sand, and were more abundant in Princess Bay and Moa Point, respectively. Similarly, Anderson et al. (2005) observed that holothurians and ophiuroids were abundant in kelp beds of northeastern New Zealand, while in the temperate coast of Chile, Villegas et al. (2008) observed that the sea urchin *Tetrapygus niger* was significantly more abundant in barren grounds compared to kelp beds.

Additional characteristics of the population, such as size structure, were analysed for *E. chloroticus* (Chapter 2). Populations in the Harbour had smaller mean size, due to the presence of a juvenile cohort, while sea urchins on the South coast reached significantly larger sizes and no juveniles were found. It has been observed that *E. chloroticus* can reach larger sizes with abundant kelp (Choat & Schiel 1982, Wing & Wing 2015), but when food resources are limited, sea urchins can slow down their growth to maintain their reproductive effort (Andrew 1989, Levitan 1989). Here, *E. chloroticus* density was negatively correlated with mean size. This indicates that sea urchins in the Harbour, which may be food resource-limited, might be maintaining their reproductive effort at the expense of not increasing their size, whereas other processes like recruitment limitation and higher predation pressure likely maintain the low densities observed on the South coast.

Differences in other sessile invertebrate assemblages have long been documented between these two locations (Morton & Miller 1973). For example, intertidal mussels and barnacles are significantly more abundant in the Harbour compared to the South coast (Helson & Gardner 2004, Demello & Phillips 2011). This has been attributed not only to differential oceanographic conditions, such as currents and availability of food, but also to a higher larval supply and settlement success in the Harbour compared to the South coast, and higher post-settlement mortality in the latter (Helson & Gardner 2004, Helson et al. 2007, Demello & Phillips 2011). Moreover, the nutrient-enriched waters in the Harbour might favour larval quality of the reef fish *Forsterygion lapillum* and propitiate higher retention and recruitment in this location, compared to the less productive open coast (Shima & Swearer 2009a, Shima & Swearer 2009b). Here, I presented evidence that contrasting recruitment patterns also occur for echinoderms, which is likely due to environmental factors, but also to pre- and post-settlement events

affecting recruitment (Chapters 4 and 5). Collectively, these studies suggest that differential oceanographic conditions, such as productivity, temperature and currents, have significant effects on patterns of recruitment of invertebrates, as well as for some intertidal fish species, which have strong implications for the population dynamics and benthic community composition. Together, recruitment studies can help define areas of protection and identify vulnerability to anthropogenic disturbance.

6.3 Importance of recruitment shaping populations

Probably one of the biggest questions that has remained unanswered in marine ecology is to what extent do natural processes that affect recruitment regulate adult populations (Caley et al. 1996, Hunt & Scheibling 1997). It has been a difficult question to answer for different reasons. Our understanding of spatial and temporal variation in recruitment is still limited, mainly due to the difficulties in measuring all its components, like larval supply and settlement success. The number of competent larvae ready to settle at particularly optimal conditions can be highly variable. In addition, the quantification of small and cryptic settlers can be very challenging and hard to estimate. Settlers may overcome a wide range of sources of mortality, like physical stress, bulldozing, predation, competition, etc. before recruiting to the adult population. However, different approaches have been undertaken to better understand the recruitment process.

Amongst them, the use of artificial collectors has been a useful technique to monitor settler supply of sessile and mobile species at frequent intervals (Keough 1983, Menge 1991, McShane & Naylor 1996), allowing the researcher to isolate settlement from other components of recruitment (Connell 1985, Harrold et al. 1991). In the present study, settlement pulses of echinoderms were monitored during summer and over three years, using artificial collectors. Abundance of juveniles (individuals <40 mm) was also surveyed to estimate rates of recruitment (Chapters 2 and 3). Only one major settlement event occurred during the three-year study for *C. muricata*, in the Harbour and Breaker Bay. *E. chloroticus* settlement was observed in the same sites, but it did not occur the first sampled year and the magnitude was significantly lower. In contrast,

settlement of ophiuroids occurred mainly at Princess Bay and Breaker Bay, and continuously throughout the sampled years.

Spatial differences in settlement between the Harbour and the South coast are likely due to large-scale oceanographic patterns affecting larval supply between the two locations. Differential rates of settlement have been observed between neighbouring but contrasting habitats (Chiantore et al. 2008, Prado et al. 2012, Ouréns et al. 2014). Balch (1999) found that ophiuroids tended to have higher settlement rates in barrens, while sea star settlers were more abundant on kelp fronds. Lamare and Barker (2001) observed that settlement rates of *E. chloroticus* were higher in Doubtful Sound (Fiordland), compared to Tory Channel (Marlborough Sounds). Lamare (1997) suggested that Tory Channel is an example of an open marine population, where the high variation in larval supply results in low settlement rates. The input of new individuals is lower than mortality, causing it to be a recruitment-limited population (Lamare 1997). The present study contributes to the growing evidence that the low water flow in bays and harbours might contribute to retention of larvae and higher settlement rates, compared to more hydrodynamic regime of an open coast, which might disperse larvae away from suitable substrate for settlement. In this case, the South coast could be a recruitment limited population similar to Tory Channel, while the Harbour could be self-recruiting, similar to Doubtful Sound.

The interannual variation in settlement observed in the present study was moderately correlated with environmental variables, such as seawater temperature. The highest *C. muricata* and *E. chloroticus* settlement pulses coincided with the warmest months (January and February) and the warmest year (2019). Previous studies have identified increasing water temperature with higher settlement rates of the sea urchins *Strongylocentrotus droebachiensis* and *Diadema africanum* (Hart & Scheibling 1988, Hernández et al. 2010). In contrast, Lamare (1997) found that greater settlement of *E. chloroticus* in the southern fiords was correlated with cooler and more productive El Niño years, resulting in higher recruitment rates. However, oceanographic and physical conditions of fiords likely differ from the dynamics of harbours and open coasts, like the ones studied here and from other habitats in New Zealand. Fiords have a characteristic estuarine circulation pattern, where high levels of larval retention have been observed (Lamare 1998, Wing et al. 2003), while a highly dynamic system such

as the South coast would likely disperse the larvae away from the coast (Walters et al. 2010).

Long-term studies have demonstrated that interannual variation in echinoderm recruitment is very common and large episodes of settlement are highly sporadic. Loosanoff (1964) did not find a clear pattern between years of good and poor recruitment in the temperate sea star *Asterias forbesi*, and only a single major settlement event was observed in 25 years. Ebert (1983) and Pearse and Hines (1987) observed a single large recruitment event of the sea urchins *S. purpuratus* and *S. franciscanus*, in 16 and nine years of sampling, respectively. Similarly, Zann et al. (1987) and Fisk (1992) observed a single mass recruitment episode of the sea star *Acanthaster planci* in nine and five years of sampling. Collectively, these and the present study show that echinoderm recruitment is very infrequent and it might not happen for long periods.

Recruitment studies have also shown that settlement pulses are not always directly correlated with the presence of a juvenile cohort. For example, in seagrass habitats of the Mediterranean, Tomas et al. (2004) did not observed successful recruitment despite the arrival of *Paracentrotus lividus* settlers in four years of sampling, while Prado et al. (2012) found a bottleneck in the population, where most settlers failed to recruit. However, adult abundance exceeded that of recruits, to which the authors attributed to migration of individuals from nearby areas (Prado et al. 2012). In the present study, no *E. chloroticus* <60 mm were found in the South coast sites, while in Breaker Bay, individuals 40 – 50 mm were present only in 2019. One-year-old juveniles (<20 mm) were only observed in Shelly Bay in 2017. Size structure and settlement data presented here, demonstrates that there has not been a large episode of recruitment in 2 to 3 years in the Harbour and in up to 4 years on the South coast. Breaker Bay, on the other hand, might be an area where sea urchins are recruiting and migrating to adjacent areas on the South coast.

Decoupling between settlement pulses and recruitment rates have been attributed to high mortality of settlers. Sala and Zabala (1996) observed that 75% of *P. lividus* settlers died within 6 months after settlement. Similarly, López et al. (1998) estimated that only 0.5 to 0.7% of sea urchin settlers attained <2 mm in size and only 0.04% survive the first year of life. Rowley (1990) showed that mortality of newly settled *S.*

purpuratus in the field was higher in kelp beds compared to barrens, which was consistent with the hypothesis that adult densities are lower in the kelp beds because of the higher mortality in this habitat. Causes of settler and juvenile mortality have been enumerated, but the events occurring during those early life stages remain largely unknown. In the present study, the role of some events causing high post-settlement mortality are examined and their implications for recruitment success and shaping adult populations are analysed (Chapters 4 and 5).

6.4 The role of pre- and post- settlement events

Larval supply can be affected by a series of environmental and biological factors that ultimately affect settlement rates. A number of studies have investigated the effects of stressors during larval development of marine invertebrates, but fewer have addressed the consequences in the following life stage. Latent effects on larvae can have visible effects only after metamorphosis (Chiu et al. 2007, O'Connor et al. 2014, Pechenik 2018). The present study provides evidence that factors affecting larval stages can have latent effects on sea urchin juveniles (Chapter 4). In this case, environmentally realistic exposure to low salinity and sediments had previously unrecognised effects on juvenile performance that could compromise recruitment success to the adult population.

Coastal areas are highly dynamic systems, but also the most vulnerable to human land-based activities, such as runoff (Halpern et al. 2008, Fredston-Hermann et al. 2016). In addition, with the change of rainfall patterns by the turn of the century, storms will be more frequent and stronger (Harley et al. 2006), increasing the input of freshwater into coastal areas. This is of significant relevance especially for regions like New Zealand, where the number of rainfall events is projected to increase by 32% in the next few decades (Renwick 2013). In the present study, the highest rainfall values during summer were recorded in February 2018 (6 mm), which also coincided with low values of salinity recorded in the Harbour (28 ppt). The Wellington Harbour has input of freshwater runoff that can reduce salinity after heavy rain to a depth of about 5 m (Booth 1975). Additionally, there was a strong negative correlation between salinity and turbidity in this location (see Appendix 7 for more details). These patterns might

coincide with the spawning period of echinoderms and probably other invertebrate species, likely compromising the abundance and distribution of competent larvae (Sköld et al. 2002, Georgiades et al. 2006).

Sediments in runoff, identified as one of the biggest threats to coastal areas in New Zealand (Morrison et al. 2009, MacDiarmid et al. 2012), can disrupt reproductive cycles and have deleterious effects on early life stages of fish and invertebrates (Wilber & Clarke 2001, Phillips & Shima 2006, Onitsuka et al. 2008, Humanes et al. 2017). Phillips and Shima (2006) observed that exposure to suspended sediments caused high mortality on *E. chloroticus* and abalone (*Haliotis iris*) larvae, concluding that runoff could compromise recruitment of these two important herbivore species by reducing larval supply. In Chapter 4 I showed that larval survival was not affected by the suspended sediment treatments, but exposure to the highest concentrations caused poor performance in juveniles. Similarly, Gilmour (1999) and Humanes et al. (2017) observed that larval exposure to suspended sediments reduced larval settlement and growth of juveniles on the corals *Acropora digitifera* and *A. tenuis*, respectively. Collectively, these and the present study highlight the vulnerability of a surviving cohort after being exposed to short-pulse of stressors during larval stages.

Negative effects of reduced salinity have long been identified in early life stages of marine organisms (Metaxas 1998, Humphrey et al. 2008, Carballeira et al. 2011, Diederich et al. 2011). However, very few studies have recognised sub-lethal effects on larvae that become visible only after metamorphosis. Pechenik et al. (2001) and Montory et al. (2014) observed that short larval exposure to low salinity reduced juvenile growth of the polychaete *Capitella* sp and the gastropod *Crepipatella fecunda*, respectively. The present study is the first to show that a brief larval exposure to low salinity and high concentrations of suspended sediments can have latent effects on settlement success and juvenile performance of sea urchins. However, the mechanism by which these stressors cause latent effects on juveniles is still not well understood. Salinity could be physiologically interfering at a critical stage, preventing larvae to develop important structures, such as the rudiment, which later can have consequences for metamorphosis and juvenile performance (Hodin per. comm.). A detailed investigation of the developmental stages before and after exposure to stress would be helpful to determine any disruption in the growth of crucial larval structures (Heyland & Hodin 2014).

Carry-over effects have been previously identified in *E. chloroticus* and other invertebrate species. Rouchon and Phillips (2017) demonstrated that *E. chloroticus* larval exposure to copper did not have visible consequences for development, but latent effects appeared after settlement, where juveniles had impaired growth and were generally smaller than controls. Dupont et al. (2012) demonstrated a trans-life-cycle effect of ocean acidification: when adults were pre-exposed for four months to elevated pCO_2 conditions, their offspring had significantly lower rates of settlement. Fischer and Phillips (2014), on the other hand, showed that high temperature reduced larval survival of the intertidal gastropod *Siphonaria australis*, when they were previously exposed to periodic stress (e.g. elevated UVB, salinity and temperature). Furthermore, Hettinger et al. (2012) showed that larvae of the oyster *Ostrea lurida* reared in low pH conditions had a decreased shell growth as juveniles. The present study contributes to the knowledge on the wide range of stressors that can cause carry-over effects on invertebrate juveniles, with possibly stronger and far-reaching consequences for recruitment, since adverse larval experiences can produce weakened and more vulnerable juvenile cohorts.

Behavioural responses could allow larvae to escape from freshwater plumes or sharp haloclines in the field. From laboratory experiments, some studies have shown that sea urchin larvae can control their vertical position to avoid low salinity gradients (Metaxas & Young 1998, Arellano et al. 2012, Bashevkin et al. 2016). Sameoto and Metaxas (2008) suggested that larvae that avoid low salinity layers might have more chances to survive and this could indirectly influence larval distribution in the water column. Lamare (1998) and Antonie (2003) investigated the vertical distribution of *E. chloroticus* larvae at Doubtful Sound, characterised by a low salinity layer from 0 to 2 m depth. Larvae were clearly absent from this surface waters of the fiord, suggesting a behavioural avoidance of reduced salinity (Lamare 1998, Antonie 2003). However, even if larvae can respond to haloclines, drastic changes in the water column in a few days, such as freshwater runoff, still represent a threat to invertebrate larvae developing in the water column.

Other post-settlement events are important sources of mortality for young invertebrates. It has been suggested that micropredation is an important mechanism structuring sea urchin populations (Jennings & Hunt 2010, Bonaviri et al. 2012). The present study (Chapter 5) demonstrated that both hermit crabs (*Pagurus* sp) and

decorator crabs (*Notomithrax* sp) are effective predators of new settlers. This is also the first time that predation on *E. chloroticus* has been examined through laboratory experiments at this early life stage. Only a few studies have identified predators of sea urchin settlers (<3 mm). Scheibling and Robinson (2008) observed that *S. droebachiensis* new settlers were consumed by crabs and bulldozed by periwinkles, while Jennings and Hunt (2011) demonstrated that settler growth and survival was higher when other invertebrates (potential predators and competitors) were absent. Finally, Bonaviri et al. (2012) identified hermit crabs as the most efficient micropredators of *P. lividus* new settlers and Yiu and Feehan (2017) demonstrated that refuges significantly reduced mortality of *S. droebachiensis* settlers from predatory crabs. Collectively, these and the present study demonstrate that predation is a significant cause of sea urchin mortality from early on.

Distinctive predation pressure has been observed between different habitats, like barrens and kelp forest, due to the high abundance of predators (Rowley 1990, Jennings & Hunt 2011). In the present study, a considerable number of hermit and decorator crabs (approximately the same size as the predators used for the experiment) were found in the artificial collectors, and their abundance was significantly higher in the Harbour sites, compared to the South coast (see Appendix 3). Even though the number of crabs in the collectors might not reflect their true abundance in the field, it is an indicator that they share habitat with sea urchin settlers. Predation pressure might be higher in the Harbour compared to the open coast. However, there is likely more larval supply and retention in the Harbour, based on the number of settlers found in Kau Bay and Shelly Bay.

In the present study, juvenile and adult *Notomithrax* spp efficiently preyed on *E. chloroticus* settlers and juveniles, respectively. *Notomithrax minor* is common in harbours and in sand and shell bottoms (Wilkens & Ahyong 2015). It has been identified as a common prey of fish and elasmobranchs (King & Clark 1984, Denny & Schiel 2001). However, this is the first time that decorator crabs are recognised as predators of *E. chloroticus* (Woods 1993). In contrast, *C. muricata*, despite being mentioned as a potential predator of kina, did not prey on sea urchin juveniles. These two species are highly abundant in the Harbour, but it does not appear that there is a strong predator-prey interaction between them. Eleven-armed sea stars might not be a threat to sea urchins in the Wellington region, as they might preferentially feed on

mussels or other bivalves. *E. chloroticus* usually flee from this predatory sea star (Spyksma 2016), but some individuals have been observed to feed on the remains of tethered sea urchins from field experiments in northern New Zealand (Shears & Babcock 2002).

The differences in *E. chloroticus* population structure between the Harbour and the South coast might be driven, in part, by the differential abundances in predators and subsequent predation pressure between the two locations. Abundance of lobsters and predatory fish have been recorded in Breaker Bay and Princess Bay and included the banded wrasse, blue cod and red moki (Pande & Gardner 2009, Byfield 2013). In contrast, lobsters are virtually absent from the Harbour sites, and the most abundant fish are blue cod (mainly juveniles) and spotties (Glockner-Fagetti pers. obs.). As it has been previously observed, higher abundances of predatory fish are thought to be the cause of lower densities of *E. chloroticus* in protected areas (Cole & Keuskamp 1998, Shears & Babcock 2002). The low sea urchin densities observed on the South coast might not represent an important pressure on macroalgal community growth, which in turn provides refuge to other species and maintains a balance in the ecosystem. In contrast, the low macroalgal cover and high sea urchin density observed in the Harbour suggest that *E. chloroticus* could be exerting top-down control over macroalgal growth in this location. However, further investigations in this matter are needed to support further conclusions.

6.5 Species identification through DNA barcoding

DNA techniques have been previously used to characterise genetic diversity of *P. regularis* populations in New Zealand and Tasmania (O'Loughlin et al. 2002, Waters & Roy 2004), while phylogenetic analysis have been carried out for *C. muricata* (Waters & Roy 2003, Perrin et al. 2004). However, fewer studies have focussed on early life stages of echinoderms (Ward et al. 2008) or other invertebrate species (Pradillon et al. 2007, Phillips et al. 2008). Genetic identification through DNA sequencing has been attempted for asteroid larvae (Evans et al. 1998, Knott et al. 2003). Evans et al. (1998) successfully identified brachiolaria from zooplankton tows in Tasmania, which included *C. muricata* and *P. regularis*. DNA techniques have also been used to monitor

outbreaks of the crown-of-thorns sea stars *Acanthaster* spp (Uthicke et al. 2015, Uthicke et al. 2018b). *A. cf. solaris* larvae have been identified from plankton samples using PCR-based test and monitor the dispersal of larvae (Uthicke et al. 2018a, Uthicke et al. 2019). Similarly, identification of *Asterias amurensis* larvae from plankton samples using PCR-based tests has been useful to monitor the dispersal of this invasive species in Tasmania (Evans et al. 1998, Deagle et al. 2003).

The present study demonstrates that DNA barcoding (amplification of approximately 650-bp from the mitochondrial cytochrome oxidase I (COI) gene) is an effective technique to identify echinoderm species at their early life stages. It also provides morphological evidence through photographs (see Fig. 3.7) and 100% bootstrap support, placing sea star spp1 within *C. muricata* samples obtained from GenBank (see Appendix 5). Future studies could consider using the methods described here to identify echinoderm settlers. However, appropriate preservation of the samples is crucial to obtain positive results.

6.6 Limitations and future directions

The present research contributed to the knowledge on the distribution and recruitment patterns of echinoderms, and identified key biotic and abiotic factors affecting early life stages, using the sea urchin *Evechinus chloroticus* as a model species. The role of pre- and post-settlement events, including latent effects and micropredation, was highlighted as significant factors shaping adult populations. However, there are still gaps in our knowledge about the events that control recruitment and ultimately determine size and distribution of marine populations, especially during larval stages. Future research should attempt to determine sources and sinks of echinoderm larvae and use DNA techniques to identify the species. Larval abundance and distribution could be coupled with settlement pulses observed in the field and to environmental variables. In addition, as the population structure of species like *E. chloroticus* and *C. muricata* appears to be so distinctive between two adjacent habitats, it would be worth studying larval dispersal and connectivity in the Wellington region and other parts of New Zealand (Nagel et al. 2015).

The differences in the magnitude of settlement of the different echinoderm species are likely due to species-specific processes, such as reproductive cycles. Future research should focus on reproductive patterns and analysis of gonad condition of the different echinoderm species, such as the cushion star, eleven-armed and sea urchin, whose reproductive characteristics are known for some areas in New Zealand, but not particularly in this region (Barker 1977b, 1979, Byrne & Barker 1991, Lamare et al. 2002, Sköld et al. 2002). It is of specific interest that even though *P. regularis* adults were very abundant in all sites and juveniles were found in the Harbour and Breaker Bay, no settlers were found in the collectors (although there is a possibility that sea star spp2 is *P. regularis*). The possible explanations to this is that cushion stars might be recruiting at a different depth, such as the intertidal, or that spawning in the Wellington region does not occur in summer.

The depths used in the present study were based on findings that higher settlement and sea urchin densities occur at 5 to 8 m deep (Witman & Grange 1998, Lamare & Barker 2001). However, future studies on echinoderm recruitment should aim to cover other depths, as this might be an important factor. The use of bio-balls as artificial collectors was appropriate to study echinoderm settlement. As further experiments proved, sea stars in the field settled in larger numbers in the collectors made of bio-balls, compared to plastic turfs and settlement plates, and laboratory experiments proved that settlement success of sea urchins was higher in buckets when these collectors were provided (see Appendix 4 for details). However, due to overall low settlement, detection might be improved with greater replication or sampling effort.

Predation experiments in the field were not carried out in the present study, but future work should attempt to test predation by fish and lobster and compare predation pressure inside and outside a marine reserve (e.g. Taputeranga Marine Reserve). In addition, it would be relevant to study to what extent *E. chloroticus* control macroalgal cover on the South coast. Studying the trophic cascade interactions could help elucidate the role of predators controlling sea urchin populations and maintaining a healthy macroalgal cover. However, environmental conditions in the Wellington region are not always optimal for continuous field studies, since oceanographic conditions can change drastically in a short period. Additionally, any experimental setup in the field should be designed to resist strong wave action and currents.

6.7 Conclusions

Coastal areas are highly susceptible to human impact. Understanding the structure of invertebrate community can help identify changes in the population dynamic and the relationship with the constantly changing environmental conditions. This research provides insights on the distribution of echinoderms and the correlation with habitat composition, as well as the processes that shape population structure. Recruitment patterns of *Coscinasterias muricata* and *Evechinus chloroticus* coincide with the body of literature showing that echinoderm recruitment can be highly sporadic and spatially variable, and emphasise the need of long-term studies to understand the large-scale processes that regulate recruitment.

The present study provides further knowledge on the role of key pre- and post-settlement events, using *E. chloroticus* as a model species. Latent effects of runoff can have important and previously unrecognised consequences for sea urchin juveniles, which might compromise recruitment to the adult population. This research highlights the vulnerability of a surviving cohort after being exposed to short-pulse of stressors during larval stages. In addition, it demonstrates that micropredation is an important source of mortality from early on. Pre- and post-settlement processes might be affecting other invertebrate species the same way as *E. chloroticus* and the patterns observed here can help understand the early life events of invertebrates that have remained largely unknown.

Linking environmental variables, species assemblage and recruitment patterns can help identify hotspots for conservation and protection from anthropogenic stressors. The low recruitment patterns of kina observed here could be similar to other parts of New Zealand, where sea urchin barrens are not very common. For relatively long-lived species, even if recruitment is sporadic populations can be sustained if adult mortality is low. However, *E. chloroticus* is subject to exploitation, not only in the Wellington region, but also across the country, which might disrupt the trophic balance between predators, urchins and macroalgae.

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Appendices

Appendix 1. Environmental variables

Table A1. Mean values (SE) of seawater temperature (ºC), salinity (ppt), chlorophyll (RFU) and turbidity (NFU) recorded by the CTD at Island Bay from December 2016 – April 2017 and November 2017 – April 2018, and at Kau Bay from November 2017 – April 2018.

		Temperature		Salinity		Chlorophyll		Turbidity	
Year	Month	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Island Bay									
2016	Dec	14.28	0.06	34.74	0.03	0.85	1.78	8.03	4.02
2017	Jan	15.21	0.04	34.75	0.02	2.14	0.98	16.75	2.21
2017	Feb	15.50	0.04	34.87	0.02	50.20	1.04	0.41	2.33
2017	Mar	14.97	0.04	34.67	0.02	1.04	1.02	11.32	2.30
2017	Apr	14.45	0.05	34.53	0.02	19.68	1.27	0.13	2.86
2017	Nov	14.20	0.07	34.84	0.03	11.36	1.97	3.77	4.43
2017	Dec	15.60	0.04	34.64	0.02	19.40	0.98	135.86	2.21
2018	Jan	16.15	0.04	34.57	0.02	12.56	0.98	38.23	2.21
2018	Feb	17.36	0.04	34.16	0.02	17.60	1.03	172.71	2.33
2018	Mar	16.41	0.04	33.83	0.02	25.05	1.07	28.57	2.41
2018	Apr	15.18	0.04	34.54	0.02	0.00	1.00	15.54	2.25
Kau Bay									
2017	Nov	17.26	0.06	34.48	0.11	0.39	0.06	36.71	2.60
2017	Dec	17.99	0.03	32.39	0.05	1.52	0.03	59.60	1.18
2018	Jan	17.97	0.03	29.62	0.06	1.23	0.04	98.47	1.45
2018	Feb	19.13	0.03	34.24	0.06	0.62	0.04	24.21	1.45
2018	Mar	17.52	0.03	33.00	0.05	1.21	0.03	43.15	1.18
2018	Apr	15.69	0.03	31.32	0.05	0.96	0.03	47.31	1.28

Appendix 2. Sea urchin density and size structure

Table A2. Size structure of *Evechinus chloroticus* at each site and sampled year. Mean test diameter (mm), standard deviation (SD), mode, minimum (MIN) and maximum (MAX) sizes are given.

	Mean	SD	Mode	MIN	MAX
2017					
Princess Bay	73.2	19.7	53	50	110
Moa Point	74.1	12.0	82	55	91
Breaker Bay	90.0	13.8	95	65	125
Kau Bay	63.6	10.3	64	40	82
Shelly Bay	53.5	29.5	16	11	96
2018					
Princess Bay	72.1	13.1	65	52	105
Moa Point	71.6	7.9	72	59	85
Breaker Bay	88.8	16.3	95	28	112
Kau Bay	67.9	8.9	77	45	90
Shelly Bay	54.5	14.3	60	18	90
2019					
Princess Bay	78.2	15.4	85	60	124
Moa Point	79.3	16.4	N/A	52	95
Breaker Bay	87.9	18.5	93	40	127
Kau Bay	64.7	8.1	70	40	88
Shelly Bay	54.9	13.1	60	26	81

Appendix 3. Abundance of potential predators in artificial collectors

The abundance of micropredators and bulldozers (<5 mm) of newly settled sea urchins was estimated in artificial collectors from November 2017 to April 2018 at each of the sampled sites. Individuals were identified to genera. Crabs were the most abundant group, with at least two *Halicarcinus* species, two *Pagurus*, one *Notomithrax*, and one *Petrolisthes*. The snail *Diloma aethiops* was easily identified for its conspicuous shell colour patterns. Abundance of predators and bulldozers was significantly higher at Shelly Bay and Kau Bay, compared to the South coast sites and Breaker Bay ($chi^2 = 228.7$, $p < 0.01$). Hermit and decorator crabs were significantly more abundant in Shelly Bay with a mean of 3.6 and 4.4 ind $collector^{-1}$, respectively (Fig. A3).

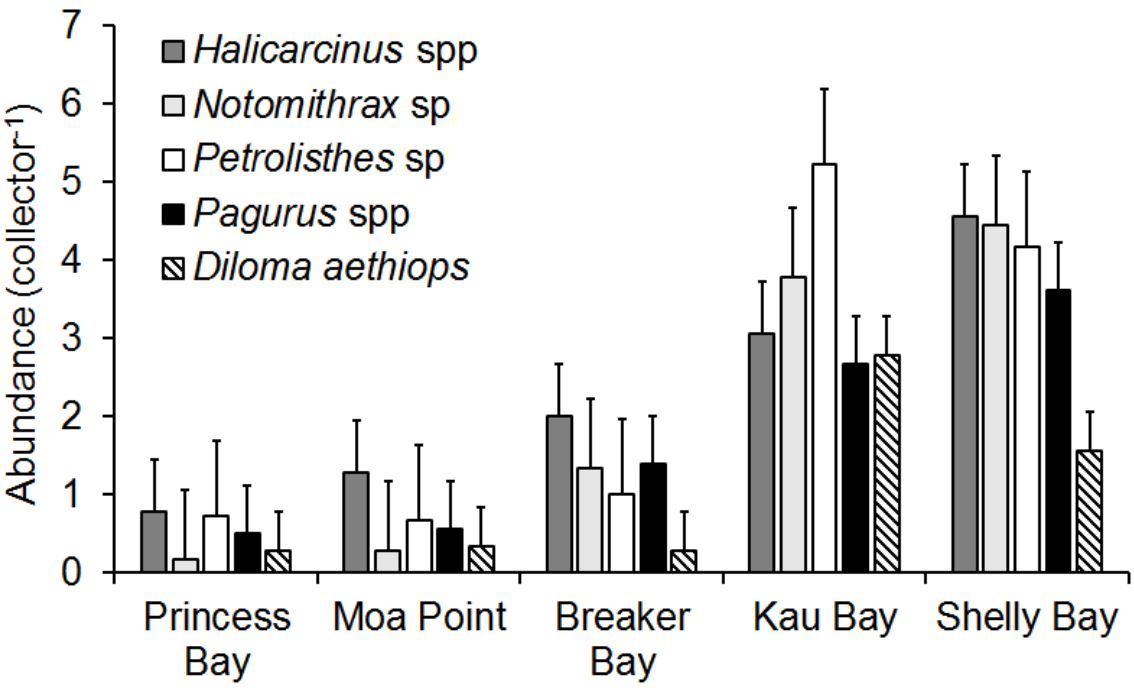

Fig. A3. Abundance of predators and bulldozers (<5 mm) per collector. Bars indicate means (± SE), and letters above bars indicate the significant differences in means based on post-hoc Tukey tests.

Appendix 4. Sea urchin settlement: field and laboratory experiments

Methods

Due to the low settlement rates of kina observed in the first year, I tested another two artificial collectors in the field that have been previously used in settlement studies. Plastic turf collectors, modified from Harrold et al. (1991), were deployed in March and April 2017 in Shelly Bay. These consisted in PVC pipes (30 cm length, 15 cm diameter), filled with plastic turf, suspended 1 m above the seafloor. The second type of collectors were settlement plates, modified from Rogers (2011), which consisted of two acrylic sheets with 1 × 1 cm plastic grid in both sides (20 × 40 cm). The settlement plates were deployed in February 2019 in Breaker Bay, and were suspended 1 m above the seafloor with a buoy.

In addition to the field trials, larval settlement in the artificial collectors was tested in the laboratory. Larvae were reared under control conditions in 1.5 l glass jars with filtered seawater (FSW, 0.2 µm) at a density of 2 larvae ml^{-1}, for 25 days. Six replicate buckets with 5 l FSW were arranged for larval settlement. One artificial collector made of plastic bio-balls, like the ones used in the field, was added to half of the buckets. Competency of larvae was checked under a dissecting microscope (45x magnification). When approximately 80% of the larvae showed competency, three larval cultures were split in two and each half was poured in the replicate buckets, one containing the collector and one without any settlement surface. Larvae were left undisturbed for four days before estimating settlement success. After this period, the collector from each bucket was retrieved and washed separately, the water from the washing was collected in a bucket and then, strained through a 150 µm sieve. Kina that settled in the buckets with and without an artificial collector was also estimated. The settlers were preserved in 70% ethanol.

Results

I found *Coscinasterias muricata* settlers (sea star spp1) in the collectors during March and April 2017. The mean number of settlers was higher in the artificial collectors made of bio-balls compared to the ones made of plastic turf, and settlement was higher in

March compared to April 2017 (Fig. A4.1). Unfortunately, no sea urchin settlement was recorder for that year at any of the sampled sites.

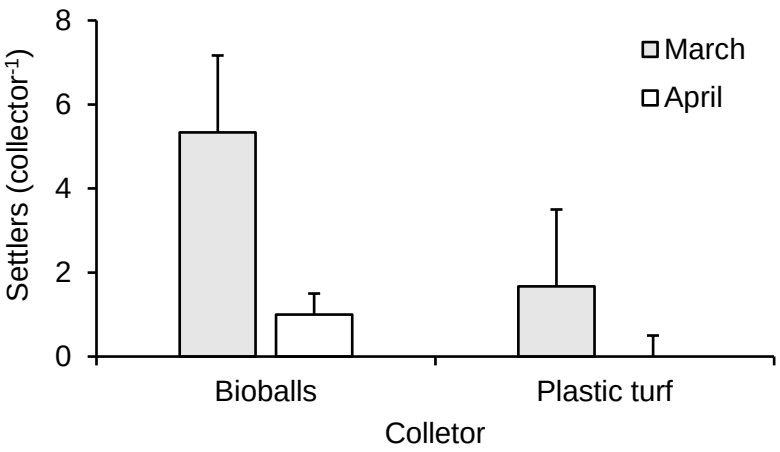

Fig. A4.1. Mean number of settlers (± SE) in two different types of artificial collectors deployed during the first sampled year (March and April 2017).

The settlement plates that were deployed at Breaker Bay in February 2019 were recovered in the first week of March. However, no sea urchin or any echinoderm were observed to settle in the plates or in any other collector, either in Breaker Bay or another site. Sea urchin settlement was recorded the month before in Breaker Bay and Shelly Bay.

In the laboratory experiments, settlement of sea urchin was recorded with and without artificial collectors. Within the replicate buckets that contained a collector, I found more sea urchins that settled in the collector compared to the walls of the bucket (Fig. A4.2). Comparing sea urchin settlement in buckets with and without a collector, the differences were not significant, but slightly more sea urchins settled in the collectors compared to the empty bucket (Fig. A4.3). This experiment demonstrate that collectors provide a suitable substrate for sea urchin settlement.

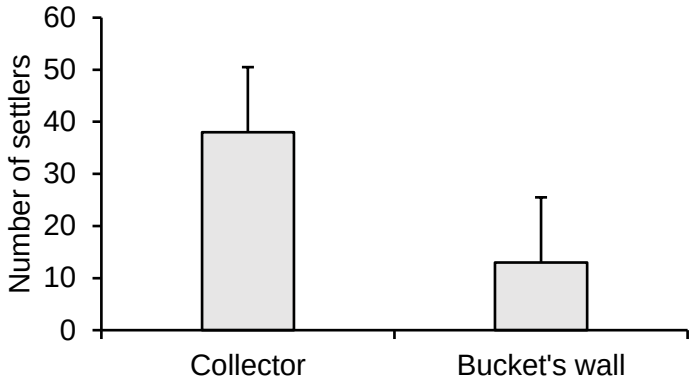

Fig. A4.2. Comparison of the mean number of sea urchins (± SE) settled in the collectors and in the sides of the buckets containing the collector.

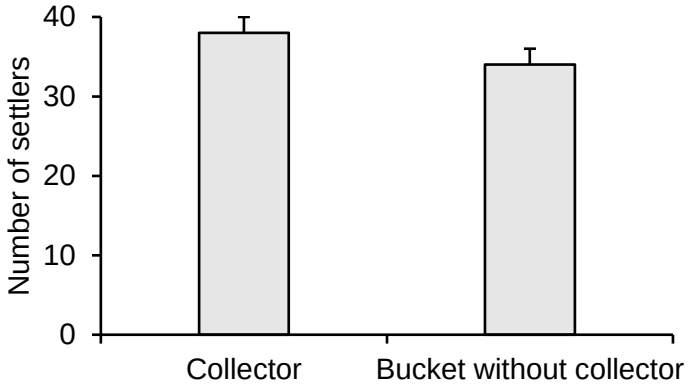

Fig. A4.3. Comparison of the mean number of sea urchins (± SE) settled in the collectors and in the buckets that did not contain a collector.

Appendix 5. DNA sequencing results for sea star spp1

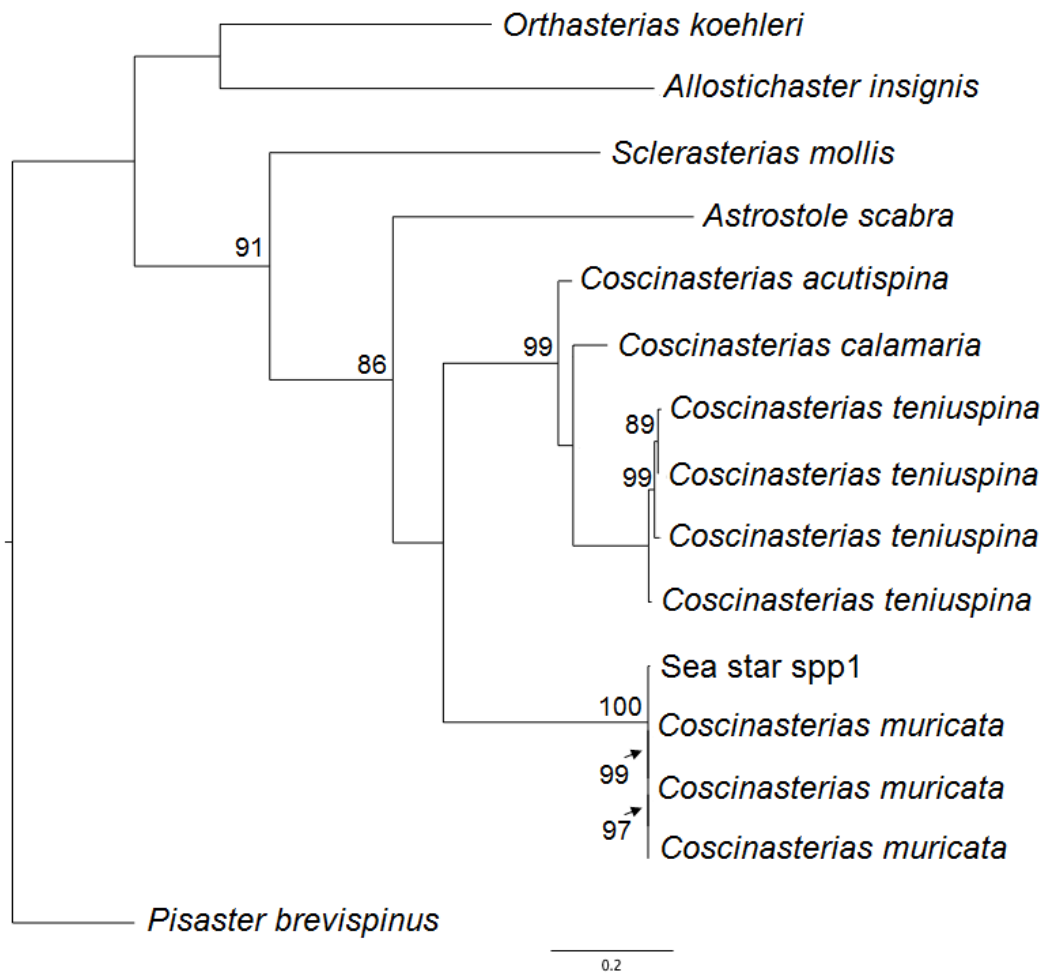

Fig. A5. Maximum-likelihood tree of concatenated COI dataset of spp1, three closest BLAST hits and genera within the family Asteriidae. Values <85% ML bootstrap not shown. Sea star spp1 grouped with high support with *Coscinasterias muricata*. *Pisaster brevispinus* was used as outgroup. GenBank accession numbers top to bottom: AF485003.1, AF545002.1, AF485004.1_1, AF485005.1, AF485025.1, AF485034.1, AF485008.1, AF485015.1, AF485020.1, AF485022.1, AF485036.1_, AF485038.1_, AF485037.1_, HM542328.1.

Appendix 6. Recruitment sampling

Table A6.1. Density and mean size (± SD) of echinoderm juveniles in Shelly Bay.

	2017		2018	
	Density	Size ± SD	Density	Size ± SD
Recent settlers (≤5 mm)				
Evechinus chloroticus	0	-	0	-
Patiriella regularis	6.4	3.9 ± 0.5	0	-
Coscinasterias muricata	0	-	0	-
Ophiopsammus maculata	0	-	0	-
Ophiuroids (≤2 mm)	15.2	1.7 ± 0.2	8.8	1.5 ± 0.2
One-year-old recruits (<20 mm)				
Evechinus chloroticus	0.46	15.8 ± 2.0	0	-
Patiriella regularis	0.3	12.0 ± 5.2	0.02	9.9 ± 0.1
Coscinasterias muricata	0.06	18.9 ± 0.8	0.02	5.6 ± 0.1
Ophiopsammus maculata	0	-	0	-
Ophiuroids (≤2 mm)	30.4	3.5 ± 2.7	11.2	2.7 ± 0.8
Juveniles (>20 mm)				
Evechinus chloroticus	0.70	28.5 ± 8.1	0.54	40.2 ± 8.5
Patiriella regularis	0	-	0.08	19.0 ± 3.3
Coscinasterias muricata	0.22	29.7 ± 14.7	0.16	26.1 ± 10.4
Ophiopsammus maculata	0	-	0	-
Ophiuroids (≤2 mm)	0	-	0	-

Table A6.2. Density and mean size (± SD) of echinoderm juveniles in Kau Bay.

	2017		2018	
	Density	Size ± SD	Density	Size ± SD
Recent settlers (≤5 mm)				
Evechinus chloroticus	0	-	0	-
Patiriella regularis	1.6	4.7 ± 0.3	0	-
Coscinasterias muricata	0	-	0	-
Ophiopsammus maculata	0	-	0	-
Ophiuroids (≤2 mm)	2.4	1.73 ± 0.6	0	-
One-year-old recruits (<20 mm)				
Evechinus chloroticus	0	-	0	-
Patiriella regularis	4.3	1.4 ± 4.1	0.12	14.8 ± 5.1
Coscinasterias muricata	0	-	0	-
Ophiopsammus maculata	0	-	0	-
Ophiuroids (≤2 mm)	0	-	1.6	3.2 ± 0.3
Juveniles (>20 mm)				
Evechinus chloroticus	0	-	0	-
Patiriella regularis	0.08	22.5 ± 3.3	0	-
Coscinasterias muricata	0	-	0	-
Ophiopsammus maculata	0	-	0	-
Ophiuroids (≤2 mm)	0	-	0	-

Table A6.3. Density and mean size (± SD) of echinoderm juveniles in Breaker Bay.

	2017		2018	
	Density	Size ± SD	Density	Size ± SD
Recent settlers (≤5 mm)				
Evechinus chloroticus	0	-	0	-
Patiriella regularis	0	-	0.04	4.3 ± 0.5
Coscinasterias muricata	0	-	0	-
Ophiopsammus maculata	0	-	0	-
Ophiuroids (≤2 mm)	0	-	0	-
One-year-old recruits (<20 mm)				
Evechinus chloroticus	0	-	0	-
Patiriella regularis	0.06	16.3 ± 3.1	0.06	8.2 ± 0.9
Coscinasterias muricata	0	-	0.02	8.3
Ophiopsammus maculata	0	-	0.02	9.3
Ophiuroids (≤2 mm)	0	-	1.6	8.5 ± 0.7
Juveniles (>20 mm)				
Evechinus chloroticus	0	-	0.02	27.8
Patiriella regularis	0	-	0	-
Coscinasterias muricata	0	-	0	-
Ophiopsammus maculata	0	-	0.06	11.9 ± 1.6
Ophiuroids (≤2 mm)	0	-	0	-

Appendix 7. Salinity, turbidity and rainfall data for the Wellington Harbour

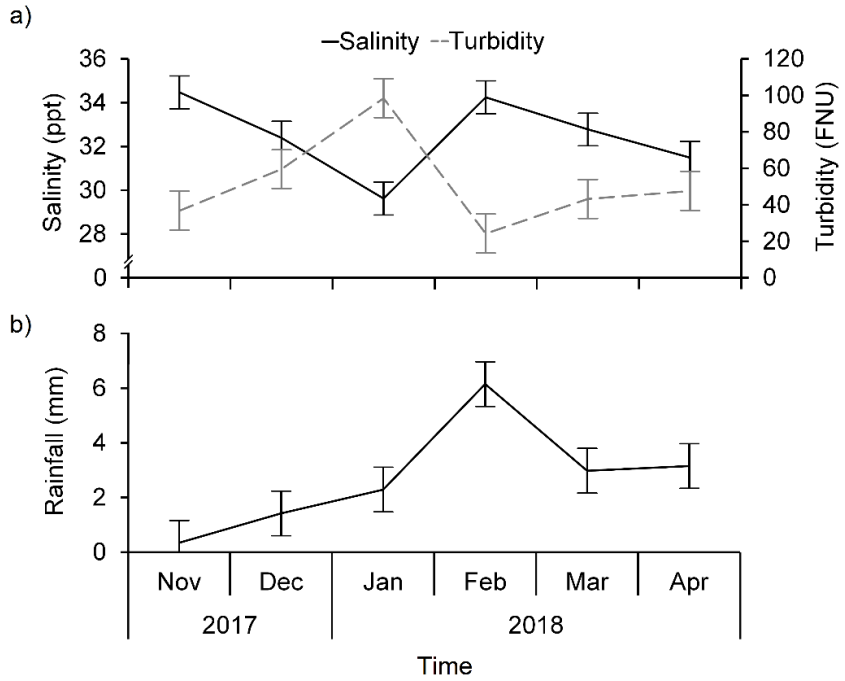

Fig. A7.1. Monthly values (± SE) of a) Salinity (ppt) and turbidity (FNU) recorded by the CTD in the Wellington Harbour (Glockner-Fagetti unpubl. data), and b) Rainfall (mm) recorded by Wellington City Council at Queens Wharf station (Greater Wellington 2018).

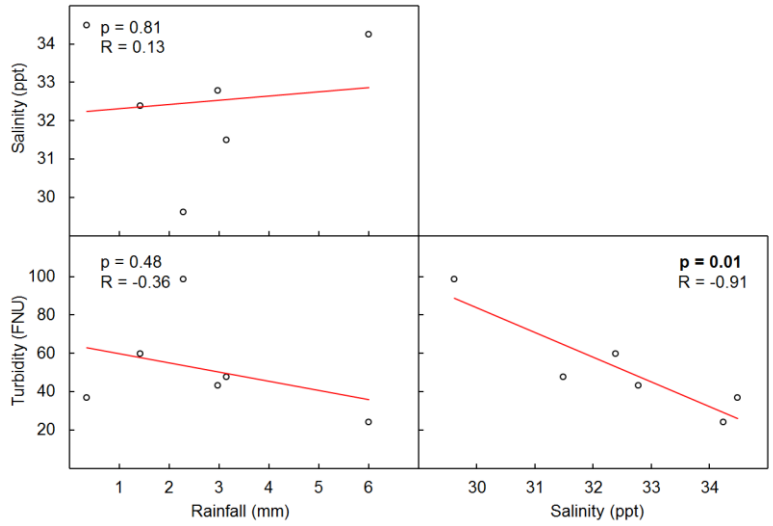

Fig. A7.2. Correlation of monthly values of rainfall recorded by Wellington City Council (Greater Wellington 2018), and salinity (ppt) and turbidity (FNU) recorded by the CTD from November 2017 to April 2018 in the Wellington Harbour (Glockner-Fagetti unpubl. data). Numbers represent R values from Pearson's correlation, and asterisks the degree of significance when $p < 0.05$.