Effects of predators on the behaviour and morphology of a habitat-forming sea urchin

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A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy in Marine Science.

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Frontispiece

A sea urchin, Evechinus chloroticus, *sheltering within the Cape Rodney to Okakari Point Marine Reserve.*

Abstract

Predators have well documented density-mediated effects on sea urchin populations, which can indirectly influence sea urchin resources (predominantly macroalgae) via a trophic cascade. Less is known about how predators may affect sea urchin behaviour and morphology and the ecological implications of these interactions. Predators may directly affect sea urchin behaviour and morphology through trait-mediated interactions, or they may indirectly affect these characteristics via cascading trophic effects that increase sea urchin food availability, resulting in behaviours or morphologies similar to those expressed in direct response to predators. Using a range of field and laboratory experiments I aimed to determine the direct and indirect effects of predators on the behaviour and morphology of the habitat-forming sea urchin *Evechinus chloroticus*.

In two well-established north-eastern New Zealand marine reserves, where large snapper (*Pagrus auratus*) and rock lobster (*Jasus edwardsii*) have suppressed grazing by *E. chloroticus* with a resultant increase in kelp densities, *E. chloroticus* remained cryptic in crevices to significantly larger sizes than individuals on the adjacent overfished reefs. Crevice occupancy in sea urchins has previously been attributed to either predator avoidance or a response to plentiful food in the form of kelp detritus. *E. chloroticus* in the marine reserves had much greater access to kelp and other macroalgae than those in the barrens habitat on fished reefs, meaning predators could be responsible for cryptic behaviour via direct (predator avoidance) and/or indirect (trophic cascade) mechanisms. A mesocosm experiment, using adult sea urchins, found that the addition of predation cues (injured conspecifics) strongly increased cryptic behaviour, but food availability had no effect.

Sea urchins within marine reserves were found to have thicker, more crush-resistant tests than those on the adjacent overfished reefs. This putative structural defence could be directly induced by predation cues, or indirectly induced in response to the greater food supply arising from the cascading effect that predation on sea urchins has on kelp abundance. In a six month-long mesocosm experiment, well-fed juvenile sea urchins developed less porous, more crush-resistant tests than those that were poorly fed. Predation cues alone had a relatively minor effect on crush-resistance.

A number of field experiments were carried out to further examine the behavioural response of sea urchins to predation cues from injured conspecifics. Exposed *E. chloroticus* fled from cues released by injured conspecifics, but not those from an extraneous pilchard cue, alarm cues from an injured heterospecific, or the disturbance caused by fish attracted to the cues, indicating that *E. chloroticus* can distinguish between different cues. The response to injured conspecific cues was limited to within one meter of the cue. Exposed sea urchins avoided re-entering an area containing cues throughout the night while in areas where sea urchins were predominantly cryptic an injured conspecific above the crevices restricted the number of sea urchins leaving during the night in order to find food on the reef. On barren reefs sea urchins densities recovered within several days following a ‘predation event’.

Overall, the results show that predators directly affect the behaviour of *E. chloroticus* by causing them to flee or increasing their use of crevices and indirectly affect their morphology by increasing their supply of food. Predator induced changes in behaviour and morphology are likely to enable sea urchin populations to persist in areas where predation pressure is high. Where sea urchins are able to shelter from their predators, predation cues are also likely to play an important role in facilitating behaviourally-mediated trophic cascades or maintaining areas of existing kelp forest.

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Chapter Two

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CO-AUTHORS

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The undersigned hereby certify that:

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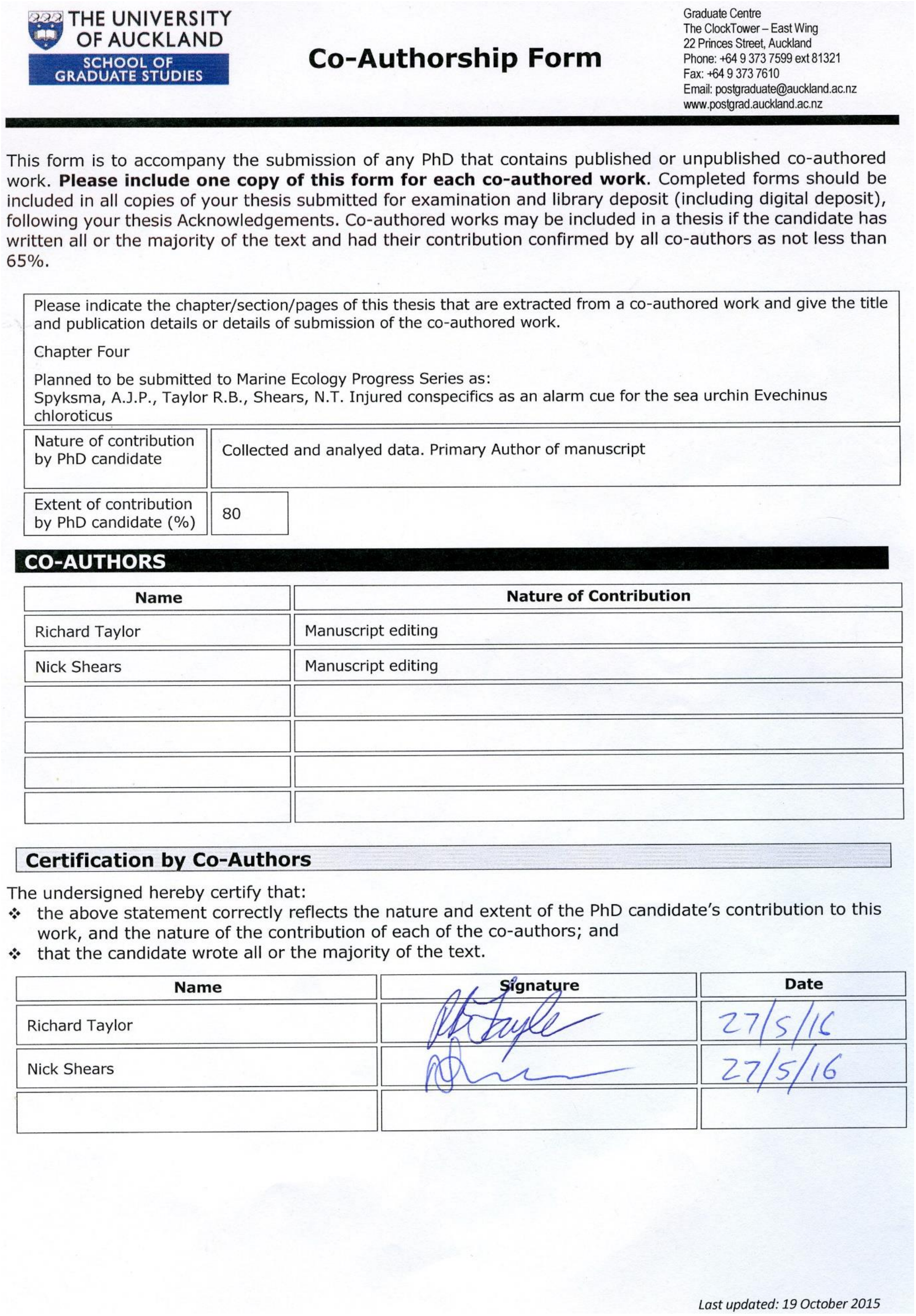

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Contents

Chapter One: General Introduction

The importance of predators

Predators are an important part of almost every known ecosystem and play a pivotal role in structuring food-webs (Terborgh & Estes, 2013). Many predators exert top down influence on food-webs and can facilitate trophic cascades where predators lower the abundance of intermediate prey, which increases the abundance of organisms at the next lowest trophic level (Pace et al., 1999). The importance of predators to ecosystems has been highlighted through studying the effects of anthropogenic overharvesting on many top level terrestrial and aquatic predators. The rapid removal of top predators can alter food-web interactions causing a catastrophic regime shift where an ecosystem suffers from "trophic downgrading", switching to an alternative stable state dominated by intermediate level organisms. These intermediate level organisms overconsume lower level organisms or resources, altering the overall structure and function of their ecosystem (Myers et al., 2007; Carpenter et al., 2011; Estes et al., 2011). For example, on Venezuelan Islands where top predators were removed, herbivorous prey species were 10 – 100 times more abundant than in mainland forests where predators were abundant. On these islands, the density of seedlings and sapling canopy plants was significantly reduced, with likely long term consequences for the structure of the forest ecosystem (Terborgh et al., 2001).

The classical theory of how predators are important to an ecosystem has focused on density mediated indirect interactions (DMII, Fig. 1.1). When consumptive predator effects reduce the abundance of prey, this may indirectly benefit prey resources by releasing them from the pressures of predation or herbivory (Schmitz et al., 2004). While many studies show the importance of direct predation to ecosystems (Estes & Duggins, 1995; Croll et al., 2005; Altieriet al., 2012) this classic approach to trophic ecology assumes that prey simply submit to predators, yet from a life-history or evolutionary viewpoint this makes no sense. In reality, many prey species adopt strategies that help them avoid or resist predators and enable them to persist even in the face of intense predator pressure (Schmitz et al., 2004). Using various predation related cues from their environment prey species can alter their behaviour, morphology or chemistry in order to reduce their vulnerability to predation (Fig 1.1).

Prey characteristics that reduce vulnerability to predators

Behavioural adaptations

Many prey species will alter their behaviour in response to increased predation risk in order to reduce the chances that they will come into contact with predators (Lima & Dill, 1990). The most common behavioural reaction when prey detects a predator is to flee or avoid areas where predation risk is high (Kats & Dill, 1998). Zooplankton undergo a diel vertical migration and head into deeper water at dawn, in order to avoid visual predators found in light surface waters during the day, before heading back to the surface around dusk (Loose & Dawidowicz, 1994). Elk in Yellowstone National Park avoid grazing or moving through areas where wolf densities are highest (Ripple et al., 2001). Prey species may also increase their use of safe refuge habitats (Martín & López, 1999; Grabowski & Kimbro, 2005), reduce their activity rates (Skelly & Werner, 1990), aggregate (Cresswell, 1994) or perform defensive displays (Greene, 1973) in order to lower the risk of being eaten.

Chemical and morphological adaptations

Many prey species also possess highly plastic morphological features that can display multiple phenotypic variations to suit the given environmental conditions (Miner et al., 2005). Induced defences are one form of plasticity where prey species induce chemical or morphological changes that reduce their vulnerability to consumers (Zangerl, 1990; Cronin & Hay, 1996; Steiner & Auld, 2012). Crucian carp develop deeper bodies in ponds containing predatory pike compared to those in predator free ponds, decreasing their vulnerability to predation by pike which are a gape limited predator (Brönmark & Miner, 1992). In the presence of chemical cues from predatory crab and injured conspecifics, the intertidal gastropod *Thais lamellosa* improves its defensive effectiveness by producing larger apertural teeth (Appleton & Palmer, 1988). Many plant species will emit volatile compounds in response to herbivory that help to repel further attacks (Unsicker et al., 2009).

How features that reduce prey vulnerability come about

Induced defences are typically described as a direct response to non-lethal predator effects, where the threat of being eaten causes prey to stimulate costly defensive strategies. (Preisser et al., 2005). These interactions are known as trait- or behaviourally-mediated interactions (TMI/BMI, Fig. 1.1) and have been well documented (Werner & Peacor, 2003; Preisser & Bolnick, 2008). However, an alternative and lesser studied pathway also exists where predators may indirectly affect prey via cascading trophic effects and an increase in prey resources (Fig. 1.1). An increase in prey resources may stimulate behavioural or morphological responses similar to those produced by TMI's. For example, juvenile salmon, *Salmo salar,* shelter for longer periods of time when well nourished. Both pathways should help prey species to persist where predation pressure is high (Fig. 1.1), however direct predator effects have the potential to facilitate trophic cascades (Werner and Peacor, 2003, Fig. 1.1), shifting ecosystems from one state to another, while indirect predator effects are more likely to provide feedback mechanisms that help to maintain the current ecosystem state.

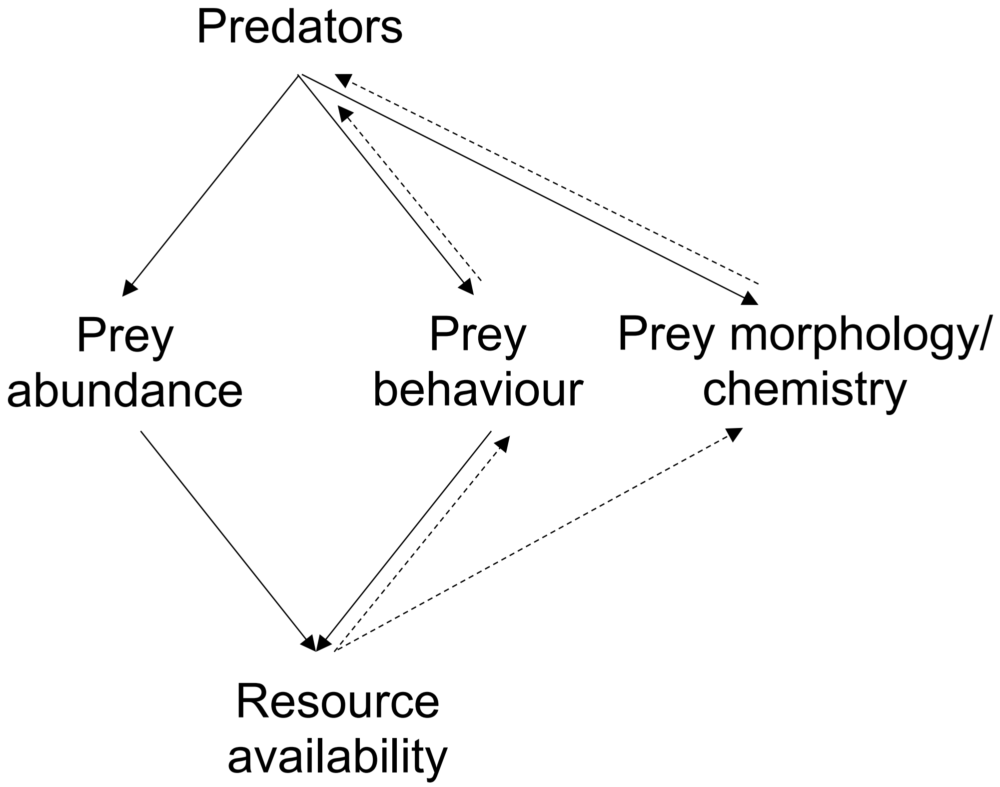

Fig. 1.1: Direct and indirect pathways in which predators may affect prey. Lethal effects may result in changes in prey abundance (density-mediated effects) while non-lethal effects may lead to changes in prey behaviour, morphology or chemistry (trait-mediated effects). Changes in prey abundance and behaviour may facilitate trophic cascades, increasing prey resource availability. Predators may also indirectly alter prey behaviour and morphology via cascading trophic effects culminating in an increase in food supply. Solid lines represent direct predator effects on prey abundance, behaviour, morphology and chemistry, as well as the cascading trophic effects of these interactions on resource availability. Dashed lines represent indirect predator effects on prey behaviour and morphology, as well as the implications of changes in prey behaviour and morphology for predator-prey interactions.

Direct predator effects

Direct effects arise when prey species detect the presence or cues from predators and initiate defensive response in order to increase their chances of survival. In general, defensive strategies designed to increase persistence are costly and represent a trade-off between safety and other fitness related activities (Zhu et al., 2016). Costs can include; lost feeding opportunities, decreased growth rates, lower fecundity and reproductive success (Lima & Dill, 1990; Van Buskirk, 2000; Hoverman et al., 2005). Changes in habitat selection, vigilance and foraging behaviour by elk (*Cervus elephus)* in response to wolves (*Canus lupis*) reduces predation risk but also decreases reproductive physiology and in time the demography of elk populations (Creel et al., 2007). Induced morphological defences in grey tree frog tadpoles, *Hyla chrysoscelis,* improve survival against predatory dragonfly, *Anax junius*, but increase mortality rates from non-predation factors, suggesting there is a significant cost to inducing defences (McCollum & Van Buskirk, 1996).

Fear may facilitate behaviourally-mediated indirect interactions (BMII, Schmitz et al., 2004) as any reduction in foraging rate or increase in time spent in poor resource habitats can effect prey resource levels in a similar fashion to prey density reductions via lethal predations (Werner & Peacor, 2003). Predation risk caused by spiders leads to lower grasshopper damage to plants even though this predation risk does not lower grasshopper densities, facilitating a trophic cascade without necessarily lowering the prey populations (Beckerman et al., 1997).

Indirect predator effects

Predators may also play a less direct role in altering prey behaviour, morphology and general body condition by increasing prey food availability. Density mediated predation can lower intraspecific resource competition (Cornell et al., 1998), leading to increased prey resource abundance (Pace et al., 1999). This may lead to improved food availability for remaining prey. Well-fed prey are likely to have better general body conditions (Murray, 2002), more robust morphological features (Ling & Johnson, 2009), are likely to take fewer foraging risks and may spend more time sheltering (Orpwood et al., 2006). Therefore, if predators improve prey resource levels via cascading trophic effects, then it is possible that this can lead to changes in the behaviours and morphologies of prey species that may be similar to those induced directly by predators.

The predator-sea urchin-kelp forest trophic cascade

On shallow temperate reefs throughout the world an unwanted regime shift has repeatedly occurred where highly productive kelp forests have been converted into unproductive urchin barrens, areas of reef that are grazed by sea urchins and dominated by crustose and coralline algae (Ling et al., 2015). Herbivorous sea urchins are largely responsible for these ecosystem shifts and, at high densities, sea urchin populations are entirely capable of converting kelp forests into ‘urchin barrens’ (Tegner & Dayton, 2000). Predators such as sea otter (Estes & Duggins, 1995), multiple fish species (Cowen, 1983; Sala, 1997; Shears & Babcock, 2002) and lobster (Tegner & Levin, 1983; Andrew & MacDiarmid, 1991; Pederson & Johnson, 2006; Blamey & Branch, 2012) are capable of controlling sea urchin populations but overharvesting of these species has been demonstrated as a key mechanism releasing sea urchin populations from predation and allowing overgrazing to occur (Estes & Duggins, 1995; Shears & Babcock, 2002; Blamey & Branch, 2012). Studies comparing reefs where predators are present, such as marine reserves, and reefs where intense harvesting has reduced predator populations have revealed that trophic cascades exist between predators, sea urchins and kelps. When predators are abundant predation rates on sea urchins are higher, sea urchin densities are lower and kelp forests dominate the reefs while on overfished reefs predation is low, sea urchin numbers are high and ‘urchin barrens’ dominate (Estes & Duggins, 1995; Shears & Babcock, 2002; Ling et al., 2015). These cascades, or lack of, can have important flow on effects to the ecosystem by altering reef habitat structure (Shears & Babcock, 2002, 2003; Dulvy et al., 2004), creating changes in the carbon flow (Salomon et al., 2008) and altering recruitment levels (Mumby et al., 2007).

Predator-sea urchin-kelp forest trophic cascades have generally been described as DMII due to the direct lethal role predators play in controlling sea urchin populations (Fig. 1.1), but predators can also have non-lethal effects on sea urchin behaviour and morphology. The sea urchin *Tetrapygus niger* will flee from chemical cues released directly from the predator starfish *Heliaster helianthus.* Predation risk may therefore facilitate BMIIs in kelp forest systems by promoting sea urchin behaviours that increase their survival chances but decrease their impact on primary resources (Fig. 1.1). For example, chemical cues from a more diverse range of predators decreases sea urchin grazing rates, which has a positive effect on kelp biomass (Byrnes et al., 2006). Predation risk may also induce morphological defences that help individuals resist or deter predators when they come into contact. *Strongylocentrotus droebachiensis* induces a thicker test in response to cues from the predatory Jonas crab

Cancer borealis (Selden et al., 2009). The potential role of predators in changing sea urchin behaviour and morphology is still poorly understood and similar behavioural and morphological changes may also be indirectly related to predators via trophic cascades, which increase the availability of food. Sea urchins will shelter more when food is readily available and they do not need to actively forage (Harrold & Reed, 1985), while well fed sea urchins inside kelp forests have thicker tests than those on barren reefs (Ling & Johnson, 2009). If a predator facilitated increase in kelp supplies the remaining sea urchin population with more resources this may allow them to take fewer behavioural risks or inadvertently invest energy into morphological defences (Fig. 1.1). This thesis aims to look at the relative importance of the direct and indirect effects of predators on sea urchins and for what the ecosystem implications of these might be.

Marine reserves in north-eastern New Zealand

Marine reserves or no-take marine protected areas (MPAs) provide an excellent natural experimental setting for investigating top down predator effects. MPAs have been widely used as large scale experimental tools that control for the effects of fishing pressure and allow for comparisons between ‘natural’ ecosystems with and without higher trophic level predators (Edgar & Barrett, 1999). In north-eastern New Zealand the Cape Rodney to Okakari Point Marine Reserve (549 ha, established in 1975 but opened in 1977) and nearby Tawharanui Marine Reserve (350 ha, established 1982) have frequently been used to examine the effects of the overharvesting of top predators on the predator-sea urchin-kelp forest system. All marine life is fully protected within both reserves, while on the surrounding coast the sea urchin predators *Pagrus auratus* (“snapper”) and *Jasus edwardsii* (“red rock lobster”) are heavily targeted by commercial and recreational fishers. The sea urchin *Evechinus chloroticus* is lightly harvested at sites outside of the marine reserves that are readily accessible from shore. Both marine reserves and their surrounding coasts are exposed to similar environmental conditions (Shears, Babcock, & Salomon, 2008) and have large areas of subtidal rocky reef containing communities typical of moderately exposed north-eastern New Zealand coasts (Choat & Schiel, 1982). Past research has generally focused on predator abundances inside the reserve (Kelly et al., 2000; Willis et al., 2003; Pande et al., 2008) and the lethal effects of predators (Andrew & MacDiarmid, 1991), concluding that trophic cascades involving predators (snapper *Pagrus auratus* and lobster *Jasus edwardsii*), sea urchins (*Evechinus chloroticus*) and kelp (the laminarian kelp *Ecklonia radiata*) are facilitated by a DMII (Babcock et al., 1999; Shears & Babcock, 2002). However, sea urchins are still relatively abundant within the reserves alongside both predators and kelp (Shears and Ross 2010) and are often found hiding in cracks and crevices (Cole & Keuskamp, 1998; Shears & Babcock, 2003). This would suggest that lethal predation is not the only effect that predators have on sea urchin populations and that within these areas sea urchins are able to successfully persist even though predation pressure is strong.

Aims and objectives

The aim of this thesis is to examine the potential direct and indirect effects of predators on sea urchin behaviour and morphology on shallow reefs in north-eastern New Zealand. These interactions could play an important role in allowing sea urchins to persist in areas where predators are abundant, as well as affecting the relationship between sea urchins and kelp, which has implications for how trophic cascades are manifested and the reef system as a whole.

The objectives of this thesis are to:

Determine whether sea urchin sheltering behaviour is induced via predation cues or through increased food availability.

Increased sheltering behaviour (within refugia) has been postulated as an anti-predator behaviour (Tegner & Levin, 1983) as well as a response to an increased food supply (predominantly drift algae, Harrold & Reed, 1985). Field surveys were used to investigate sea urchin sheltering patterns inside and outside of marine reserves where predator abundances and food availability differ. A mesocosm experiment was used to distinguish between the relative effects of predation cues and drift algae on sheltering behaviour.

Determine whether morphological resistance to predation is induced directly by predators or indirectly by predators through cascading trophic effects.

Changes in sea urchin morphology are known to be caused by differences in food availability (Levitan, 1991) as well as predation pressure (Selden et al., 2009). An assessment of sea urchin morphology inside and outside of marine reserves was conducted. A six month long mesocosm experiment containing juvenile sea urchins was used to investigate the relative effect of predation pressure and food on putative defensive morphological features of sea urchins.

Determine if conspecific alarm cues induce behavioural reactions on subtidal rocky reefs.

While mesocosm experiments provide excellent insights into species behaviour, additional experimentation in the field is required to confirm that observed mesocosm outcomes are likely to occur in nature. Using time-lapse photography and diver surveys an investigation was carried out into whether alarm cues invoked behavioural responses in the field, how specific the cue had to be to stimulate a response, over what spatial scale and temporal scale alarms cues acted and how exposed and cryptic sea urchins behaved at night in response to these cues.

Chapter Two: Cryptic behaviour in a habitat-forming sea urchin is a response to predation risk, not resource availability

Introduction

Trophic cascades have traditionally been viewed as density-mediated interactions (DMII), in which predators reduce the abundance of prey, and the prey's primary resource increases in response (Fig. 2.1; Carpenter et al., 1985; Pace et al., 1999). However, predators can also cause trophic cascades by altering the behaviour of prey (Fig. 2.1; Werner & Peacor, 2003; Schmitz et al., 2004; Preisser et al., 2005). These behaviourally-mediated indirect interactions (BMIIs) occur when the impact of prey on their resource is reduced by the direct threat of predation (Werner & Peacor, 2003; Preisser et al. 2005). For example, in Yellowstone National Park the mere presence of wolves deters elk from entering certain areas and facilitates plant regrowth (Ripple et al., 2001). However, prey behaviour can also be influenced by resource availability, with individuals taking fewer risks and spending more time in shelter when food is plentiful (Orpwood et al., 2006). Consequently, changes in prey behaviour may also occur as an indirect response to predators (Fig. 2.1), such as when predators indirectly increase food availability by reducing the effect of prey on their resources either through the effects of predation risk or DMII.

The predator-sea urchin-kelp interaction is perhaps the best known example of a marine trophic cascade (Estes & Duggins, 1995; Shears & Babcock, 2002; Blamey & Branch, 2012; Byrnes et al., 2006). In many regions, the destruction of kelp forests by sea urchins has been attributed to the overharvesting of sea urchin predators such as sea otters, fishes or lobsters (Steneck et al., 2002). Predators are generally thought to increase kelp biomass by removing sea urchins, i.e. a DMII (Estes & Duggins, 1995; Blamey & Branch, 2012). However, little attention has been given to the potential role that predators play in altering sea urchin behaviour and driving changes in kelp biomass through BMIIs. It has been shown that the mere presence of predators can initiate predator avoidance, escape responses or defensive behaviours in sea urchins (Hagen et al., 2002; Vadas & Elner, 2003; Manzur & Navarrete, 2011), which can create sea urchin-free patches of reef (Watson & Estes, 2011). Furthermore, predation-related cues can reduce sea urchin grazing rates (Byrnes et al., 2006; Matassa, 2010). Consequently, the presence of predators could lead to shifts in sea urchin behaviour and contribute to the maintenance and persistence of kelp forests.

The microhabitat occupied by sea urchins is often categorised as either “exposed”, where the sea urchin is on an open reef surface, or “cryptic”, where it occupies a refuge such as a crevice (Sala & Zabala, 1996). Refuge occupancy has often been considered an anti-predator behaviour (Bernstein et al., 1981; Tegner & Levin, 1983). However, cryptic behaviour in sea urchins could also be a response to plentiful food, particularly in the form of detrital kelp (Harrold & Reed, 1985; Vanderklift & Wernberg, 2008). Detritus is steadily produced by kelp forests and subsidises consumers within the forest and in adjacent habitats (Krumhansl & Scheibling, 2012), so when drift is readily available sea urchins can adopt a cryptic ‘sit and wait’ feeding strategy, whereas when food is scarce they leave refugia and forage in the open (Harrold & Reed, 1985). This suggests that predators may lead to a more cryptic population of sea urchins through two mechanisms: (1) as a direct response to predation risk, or (2) indirectly via a trophic cascade that increases food availability for sea urchins.

In north-eastern New Zealand the recovery of kelp forests within well-established marine reserves has been attributed to the recovery of previously harvested predators and subsequent declines in sea urchin densities (Babcock et al., 1999; Shears & Babcock, 2002). While this trophic cascade has largely been assumed to be density-driven, sea urchins within marine reserves are typically more cryptic (Cole & Keuskamp, 1998; Shears et al., 2008) and it has been suggested that predator-induced changes in sea urchin behaviour may facilitate the recovery of kelp (Shears & Ross, 2010). However, it remains unknown whether the increased crypticity at reserve sites is due to the higher abundance of predators or a greater availability of the sea urchins’ preferred food (kelp). In the present study, I examine whether the cascading effects of predators on kelp is augmented by a BMII, whereby sea urchins increase their occupancy of crevices due to increased predation risk, or whether increased crypticity is an indirect response to predators (i.e., through increased food availability). Sea urchin densities, size-specific rates of crevice occupancy of sea urchins, and kelp densities were compared between two well-established marine reserves and adjacent fished areas. A mesocosm experiment was then used to determine the relative effects of predation cues and food supply on sea urchin behaviour.

Methods

Field survey

Two well-established marine reserves located on moderately exposed rocky coasts and adjacent fished areas in north-eastern New Zealand were used as a natural experiment (Figure S2.1, see Chapter One for a detailed description of the area).

Sea urchins and kelp were surveyed at four sites within each marine reserve and at four sites within each of two adjacent fished areas (Figure S1). Sites were based on previous work done by Babcock et al. 1999 and were chosen to represent an even spread of sites across each area. Field surveys were carried out in August 2013 for the Leigh area and October-November 2013 for the Tawharanui area. Sea urchin densities, sea urchin crevice occupancy, and kelp densities were quantified at each site within five 1-m^2 quadrats haphazardly-placed within the 4-6 m depth zone. This depth range is within the depth zone where *Evechinus* is most abundant on moderately exposed reefs in north-eastern New Zealand (Shears et al. 2008). The test diameter of each sea urchin was measured using calipers (± 5 mm), and its position recorded as either "cryptic" (at least partially hidden or wedged under/between rocks below the surface of the reef) or "exposed" (on open surfaces of reef). All *Ecklonia radiata* plants, including new recruits, were measured (stipe and primary lamina length ± 5 mm) and recorded. No other macroalgae were present in significant numbers.

To check whether habitat complexity influenced spatial patterns of crevice occupancy by sea urchins, I quantified rugosity and crevice volume within five 1-m^2 quadrats. Three measurements of rugosity were made along straight lines crossing each quadrat (along two edges and through the middle). A 1-m length of chain (28-mm link length) was moulded to the rock surface, and rugosity calculated as the inverse of the linear distance spanned by the chain (Risk 1972). Crevice availability was estimated by counting and measuring all crevices $\geq$125 cm^3 (i.e. 5 × 5 × 5 cm). It was not practical to measure smaller crevices and this minimum size was used as it would accommodate an urchin of approximately 40 mm test diameter, which is the size where urchins typically emerge from a cryptic to exposed lifestyle at fished sites (Shears and Babcock 2002). This approach therefore provides a measure of crevice availability for urchins $\geq$40 mm. Based on these measurements total volume of available crevices was calculated in each quadrat as well as the number of crevices inside each quadrat that fitted into two broad size classes: "Small" < 1 L and "Large" >1 L. Small crevices were considered large enough to house urchins up to ~100 mm test diameter, whereas larger crevices could house multiple urchins.

Surveys of sea urchin predators were carried out in 2014 around the Leigh and Tawharanui coastlines. Relative abundances of *Pagrus auratus* were estimated in autumn, between March and May, using 30 minute baited underwater video (BUV; Willis & Babcock 2000), following the survey design of Willis et al. (2003). Video drops were conducted in autumn (March – May) between 5 – 15 m, water depth, on sandy substrate within 50 m of the reef edge. Eighteen replicate deployments were made inside LMR with a further eighteen carried out along the adjacent fished coast. Both areas were spilt into 6 sampling areas with 3 replicate samples haphazardly taken within each. Twelve replicate deployments were made inside TMR, with a further twelve along the adjacent fished coast. Both areas were spilt into 3 sampling areas with 4 replicate samples haphazardly taken within each. Footage was analysed to obtain the maximum number of legal-sized individuals (>270 mm for length) in the field of view within a single frame during each recording (Willis & Babcock, 2000). *Jasus edwardsii* densities, sampled between May and June, were quantified using 50 m x 10 m (500 m^{-2}) visual transect surveys. Five replicate transects were carried out at six sites within each marine reserve (three shallow and three deep) and a combined total of six sites across the two fished areas (three shallow and three deep). Marine reserve sites were randomly selected out of five possible locations per depth and fished sites were randomly selected out of a number of possible sites. Shallow sites were rocky reef habitats between 0 - 10 m water depth, while deep sites were rocky reef habitats between 10 – 20 m water depth. The size of each observed individual was estimated visually (following Kelly et al., 2000) and the number of legal-sized lobster (≥100 mm carapace length), which are generally more successful predators (Andrew & MacDiarmid, 1991), per transect was analysed.

Experiment

To determine how predation cues and/or food availability influenced behaviour in the sea urchin *Evechinus chloroticus* a mesocosm experiment was run at the Leigh Marine Laboratory between September and October 2013. Eight 1500-L outdoor tanks were set up. Tanks were 1.8 m diameter and contained a 1-m^2 rock covered area in the centre, allowing sea urchins access to exposed and cryptic microhabitats. Rocks were collected from a nearby reef, and were between 15-30 cm diameter, free of macroalgae and predominantly covered in crustose coralline algae. The 1 m^2 area was surrounded by a 15-mm mesh cage to prevent sea urchins moving off the reef. To mimic the natural subtidal environment each tank was fitted with a 60 L dump bucket to provide turbulence, fed with flow-through seawater from the adjacent coast at a rate of 1500L h^{-1}, and was covered by shade cloth that excluded 80% of the natural light. *Evechinus chloroticus* between 50-79 mm test diameter were collected from a nearby fished reef (36˚ 18’ 12.54”S, 174˚ 48’ 02.58”E) and transferred into a 1500-L seawater tank to settle for three days. On the morning the experiment began these were transferred (fully submerged) to the tanks (n=10 per tank).

Urchins were subjected to two treatments in a fully-crossed design. For the predation cue treatment one large sea urchin was cracked open and placed inside the tank between ~5-6 pm three times per week (with the old sea urchin being removed each time) to simulate a nearby conspecific being eaten (“+predation cue”). Control tanks were not subjected to this simulated predation (“-predation cue”). In the food availability treatment 10 *Ecklonia radiata* blades were added to the reef three times per week at ~5-6 pm (“+food”) while control tanks received no additional food (“-food”). Uneaten *Ecklonia radiata* blades were not removed.

Observations were made at 12 am, 8 am, 12 pm and 8 pm in four day blocks, over a three week period. At each time the position of each sea urchin was recorded as either “exposed” (visible on the outside of the reef) or “cryptic” (at least partially hidden under rocks or wedged between rocks and the cage). Due to the limited number of tanks available (two per treatment/level combination), the experiment was run twice using a new set of sea urchins on the second occasion to give a total of four replicates for each treatment/level combination.

Data analysis

Field data on predators, sea urchins, kelp and habitat complexity were analysed using PERMANOVA in PRIMER v6 to account for the non-normality associated with count data. The PERMANOVA design consisted of two fixed factors; Area (Leigh or Tawharanui) and Status (Reserve or fished) and a random factor; Site nested within Area*Status. Count data were log-transformed prior to analysis to correct for heterogeneity of variance and analyses were based on Euclidian distance matrices. Chi squared tests were used to compare the differences in the proportion of cryptic sea urchins in each size class between reserve and fished populations.

To examine how sheltering behaviour (cryptic or exposed) changed in relation to predation cues and food availability in the mesocosm experiment a generalized linear model (family = binomial) was conducted in R v.3.0.2. The model had three fixed factors: Predation cue (+ or -), Food (+ or -) and Week (1, 2 and 3).

Results

Field survey

The abundance of legal-size *Pagrus auratus* and *Jasus edwardsii* was significantly higher within both marine reserves compared to adjacent fished coasts (Fig. 2.2A, B, Table 2.1). The maximum number of legal-size *Pagrus auratus* averaged 6.6 ± 1.9 individuals BUV drop^{-1} inside LMR, 4.3 ± 1.6 inside TMR, and only 0.1 ± 0.1 and 0.7 ± 0.7 in the respective fished areas. The average density of legal-size *J. edwardsii* was 5.5 ± 1.6 individuals 500 m^{-2} inside LMR and 6.7 ± 2.1 within TMR, and only 0.3 ± 0.1 within both fished areas.

Sea urchin densities were lower within the marine reserves than on adjacent fished reefs (Fig. 2.2C, Table 2.1). This pattern was consistent across both areas, but total average density was lower in TMR (1.2 ± 0.7 m^{-2}) than in LMR (3.8 ± 1.7 m^{-2}). There was no overall difference in the density of cryptic sea urchins between reserve and fished areas, but the density of exposed sea urchins was much lower at reserve sites than fished sites (Table 2.1).

The kelp *Ecklonia radiata* was abundant in the marine reserves and rare in both fished areas (Fig. 2.2D, Table 2.1). Monospecific stands of *Ecklonia radiata* formed canopies at all reserve sites and other brown macroalgae were rare. The density of individuals averaged 12.6 ± 1.0 m^{-2} inside LMR and 17.4 ± 2.0 m^{-2} inside TMR. On adjacent fished reefs densities were significantly lower at 0.6 ± 0.4 m^{-2}.

Rugosity and the number of large crevices did not differ significantly between reserve and fished sites (Fig. S2.2, Table 2.1). All reefs were moderately complex with average rugosity values ranging from 1.35 ± 0.14 to 1.60 ± 0.18 (Fig. S2.2A) and 2-3 large crevices m^{-2} at both fished and protected areas (Fig. S2.2C). In most cases large crevices were capable of fitting multiple sea urchins of any size. There were significantly more small crevices on fished reefs compared to the reserve, however small crevices were still relatively abundant at all sites (Fig. S2.2B).

Crevice occupancy varied with sea urchin size and site (Fig. 2.3, Table 2.2). All sea urchins <40 mm test diameter were cryptic and in general the proportion of individuals that were cryptic declined with increasing size, with larger urchins predominantly found out in the open. At reserve sites urchins generally remained in crevices at larger sizes, with almost all urchins in the 40-59 and 60-79 mm size classes being cryptic, compared to fished areas where the majority of urchins were not cryptic. At Leigh there was a significantly higher proportion of cryptic urchins in reserve for the 60 – 79 mm and 80 – 100 mm size class, but no difference for 40 -59 mm sea urchins, which were still relatively cryptic at fished sites. Most sea urchins within the largest size class were not cryptic, regardless of whether they were found inside or outside of the reserves. Statistical comparisons were limited by low numbers of urchins in some size classes at Tawharanui, but there was a significantly higher proportion of cryptic individuals for the 60 – 79 mm size class, but not the 80-100 mm size class, inside the marine reserve.

Sea urchin size-frequency distributions (Fig. S2.3) within both fished areas were unimodal and left-skewed, with a relatively high proportion of juvenile sea urchins present. Sea urchins inside LMR had a bimodal size distribution with a small trough at 45-55 mm, while TMR sea urchins had a unimodal distribution dominated by large sea urchins (only 23 sea urchins were recorded within this reserve and 90% were larger than 75 mm). Very few small individuals were recorded from either marine reserve.

Experiment

In the mesocosm experiment, sea urchins responded to the presence of crushed conspecifics by becoming increasingly cryptic through time, regardless of food availability (Fig. 2.4, Table 2.3). When predation cues were not present sea urchins became less cryptic over time, again regardless of food availability. In “+predation cue” tanks, an average of 38 - 48% of sea urchins were cryptic during the final week (day 15-17), while in “–predation cue” tanks only 3-3.5% of sea urchins were cryptic. Food availability did not have a significant effect on sheltering behaviour. There was also a clear diurnal pattern in crevice occupancy across all four of the treatment combinations, with a higher proportion of sea urchins being cryptic during daytime hours (Fig. S2.4).

Discussion

Sea urchin densities were lower and kelp densities considerably higher in marine reserves, where predators are abundant, than on the adjacent coast where predators are fished. These findings are consistent with the previously documented predator-sea urchin-kelp trophic cascade for these reserves (Babcock et al., 1999; Shears & Babcock, 2002). It was also found that sea urchins within marine reserves were more cryptic, with only the largest individuals (>80 mm TD) in both reserves regularly found out in the open (“exposed”). While these patterns may be a direct behavioural response to predators, an alternative explanation is that cryptic behaviour is indirectly induced by predators via cascading trophic interactions that increase the availability of kelp within marine reserves (Fig. 1.1). A mesocosm experiment was run to distinguish between these contrasting mechanisms and clearly demonstrated that cryptic behaviour in sea urchins was induced by predation cues, and not greater food availability. This result indicates that not only do predators reduce sea urchin densities through direct consumption, they also alter the behaviour of sea urchins. This predator-induced cryptic behaviour is likely to strengthen the existing predator-sea urchin-kelp trophic cascade, while also allowing sea urchins to persist, albeit at lower densities, within marine reserves where predators are abundant.

It has been suggested that crevice occupancy in sea urchins is a predator avoidance response (Bernstein et al., 1981; Tegner & Levin, 1983; Cole & Keuskamp, 1998), yet sea urchins may also occupy crevices when drift kelp is readily available (Harrold & Reed, 1985; Vanderklift & Wernberg, 2008). This mesocosm experiment is the first to simultaneously assess the relative effects of predation risk and food availability on sea urchin crevice occupancy. I found that crevice occupancy was induced by cues from an injured conspecific, but not by the addition of drift kelp. This active microhabitat choice made by sea urchins in response to predation cues also indicates that another explanation for greater crevice occupancy in the presence of predators, which is that exposed sea urchins are more likely to be removed by predators, leaving only those that happen to occupy crevices can be dismissed.

Lethal predation on sea urchins clearly reduces the impact of sea urchin populations on kelp (Blamey & Branch, 2012), and in my study total sea urchin densities were lower in marine reserves where predators are relatively abundant. While previous studies have shown higher predation rates on exposed sea urchins at reserve compared to fished sites (Shears & Babcock, 2002), my findings suggest that the effect of predators extends beyond direct predation to influencing the sheltering behaviour of sea urchins. If a reef has adequate structural complexity then sea urchins will seek out this shelter in response to predator cues, dampening the effects of direct predation on overall abundance (Hereu et al., 2005; Alexander et al., 2009). At all sites examined in this study there was at least moderate levels of reef complexity, and there were comparable amounts of available shelter at reserve and fished reefs. However, inside marine reserves a larger proportion of sea urchins were cryptic compared to the surrounding fished areas. Sea urchins in crevices are less accessible to a wide range of predators (Andrew & MacDiarmid, 1991), and are assumed to have reduced grazing impact (Carpenter, 1984; Hereu, 2005). Kelp densities were considerably higher inside both marine reserves than on fished reefs. While this is consistent with the generally lower densities of sea urchins, it is also likely facilitated by the greater crypticity of urchins in marine reserves. It was not uncommon to sample 1 m^{-2} quadrats containing 5-10 cryptic sea urchins within mature kelp forest at marine reserve sites.

The mesocosm experiment demonstrated that predation-related cues promoted sheltering behaviour, which is consistent with size-related patterns of crypticity in the field. *Evechinus chloroticus* <40 mm test diameter were exclusively cryptic at all sites in the field, which is typical for small individuals of many sea urchin species due to their susceptibility to a variety of predators (Scheibling, 1996; Sala et al., 1998). Inside both marine reserves, where predator densities are higher, most sea urchins were cryptic until they reached about 80mm, consistent with other studies in north-eastern New Zealand (Cole & Keuskamp, 1998) and elsewhere (Bernstein et al., 1981; Sala & Zabala, 1996). Predation rates on *E. chloroticus* decline with size (Shears and Babcock 2002), but large lobster have been demonstrated to consume individuals as large as 89 mm (Andrew & MacDiarmid, 1991), that individuals may only reach an escape in size once they are very large. The sea urchin population inside TMR contained a relatively low proportion of cryptic individuals compared to the population within LMR. However, this was due to low numbers of juvenile sea urchins, coupled with the majority of urchins recorded being larger than 80mm. The particularly low number of juvenile sea urchins in TMR contrasts patterns from the LMR, and also previous data from TMR where juveniles are common (Shears and Babcock 2002; Shears et al 2008). Consequently, the current low densities likely reflect low recruitment in recent years rather than possible indirect effects of predators or marine protection. All sea urchins smaller than 80mm in TMR were cryptic, which is consistent with previous studies and the pattern of crypticity in the LMR (this study).

The provision of additional resources did not affect the shelter-occupancy of sea urchins in this study. Food availability was hypothesised as a likely driver of cryptic behaviour (Fig. 1.1) as sea urchins are often found occupying crevices in kelp forests (Bernstein et al., 1981; Harrold & Reed, 1985; Filbee-Dexter & Scheibling, 2014). The lack of response to food addition may be associated with the artificial conditions in the tanks, where random placement of kelp meant that there was a more uniform distribution as opposed to drift accumulating in depressions, as it does in the wild (Krumhansl & Scheibling, 2012) Furthermore, other mechanisms such as the physical action of kelp (whiplash effect) may cause urchins to be cryptic (Konar & Estes, 2003). Although not detected in this experiment, suppression of urchin grazing by living or detrital kelp help kelp forests elsewhere persist in the presence of sea urchins. Similar indirect mechanisms may occur in other plant-dominated systems where prey-behavioural decisions, such as risk taking or habitat selections are affected by resource availability (Lima, 1998).

This study provides the first evidence that sea urchin sheltering behaviour strengthens a kelp forest trophic cascade. This is a similar finding to other temperate systems, where sheltering behaviour can impact the strength of trait mediated indirect interactions (Grabowski & Kimbro, 2005, Trussell et al., 2006). Furthermore, the response of sea urchins to predation cues also has broader implications for prey populations. Refuge use can allow prey populations to persist in the face of intense predation pressure (Magalhaes et al., 2007), albeit generally at lower densities (Hines & Pearse, 1982; Micheli et al., 2008). Clumping of individuals in refugia may aid fertilization success, reducing predator-driven Allee effects and lowering the risk of localised extinction (Gascoigne & Lipcius, 2004). A potential indirect mechanism was also identified whereby predator-driven trophic cascades may lead to changes in prey behaviour, due to increased resources. While there was no evidence for this mechanism in my study, further research on BMIIs should consider the potential role of increased resources in altering prey behaviour and also the ecological implications if such mechanisms exist.

Recent studies and reviews have shown the importance of predator avoidance and behavioural modification in structuring different ecosystems (McIntosh & Townsend, 1996; Ripple & Beschta, 2004; Berger, 2010; Madin et al., 2010) and suggest that behaviourally-mediated effects should be considered potentially as important as density modifications (Beckerman et al., 1997; Schmitz et al., 2004; Trussell et al., 2006). Furthermore, these mechanisms do not act in isolation as predators can simultaneously have density- and behaviourally-mediated effects on herbivores (Preisser et al., 2005). My findings are consistent with this and suggest that the previously reported recovery of kelp forests in north-eastern New Zealand marine reserves is due to both direct predation on sea urchins and predator-induced changes in behaviour of sea urchins. These results highlight the need for research that simultaneously investigates the relative strength of density- and behaviourally-mediated effects so we can gain a clearer understanding of the effects of predators on ecosystem structure.

Table 2.1: Results from PERMANOVA assessing the effects of Area, Status, Area x Status and Site (Area x Status) on A) densities of legal-sized snapper (*Pagrus auratus*), legal-sized lobster (*Jasus edwardsii*), sea urchins (*Evechinus chloroticus*) and the kelp *Ecklonia radiata*, and B) crevice availability metrics including rugosity, and the number of small and large crevices. *: 0.05 > p > 0.01; ** 0.01 > p > 0.001; *** p < 0.001

Variable	**Area**		**Status**		**Area x Status**		**Site (Area x Status)**		**Residuals**
	MS	***F***	**MS**	***F***	**MS**	***F***	**MS**	***F***	**MS**
A) Densities									
Legal sized *Pagrus auratus*	0.21	0.40	120.20	**232.94*****	0.45	0.88	0.51	**3.13****	0.16
Legal sized *Jasus edwardsii*	0.24	0.22	44.44	**40.95*****	0.30	0.28	1.09	**3.60*****	0.30
All *Evechinus chloroticus*	1.94	1.70	1.94	**1.70****	1.37	1.20	1.14	**1.94***	0.59
Exposed *E. chloroticus*	0.18	0.19	26.79	**28.72*****	0.46	0.49	0.93	1.75	0.53
Cryptic *E. chloroticus*	0.31	0.29	2.92	2.75	4.55	4.29	1.06	**2.13***	0.50
Ecklonia radiata	0.12	0.34	16.54	**48.01*****	0.59	1.71	0.34	1.11	0.31
B) Crevice availability									
Rugosity	5.66	3.40	0.00	0.00	1.45	0.87	1.67	**2.05***	0.81
Number of small crevices	2.52	1.86	6.70	**4.94***	1.99	1.47	1.36	1.69	0.80
Number of large crevices	0.21	0.11	1.24	0.64	0.52	0.27	1.94	**2.31***	0.84

Table 2.2: Results from Chi-squared tests assessing for differences in the proportions of cryptic sea urchins between fished and reserve sites at A) Leigh and B) Tawharanui. Chi-squared tests were run on 2x2 contingency tables. Significant p values are bold

Size classes (test diameter)	***df***	**x-squared**	***p***
A) Leigh			
<40 mm		*N/A*[1]	
40-59 mm	1	2.11	0.15
60-79 mm	1	18.52	**<0.001**
80 - 100 mm	1	17.86	**<0.001**
>100 mm	1	2.55	0.11
B) Tawharanui			
<40 mm		N/A[1]	
40-59 mm		*N/A*[2]	
60-79 mm	1	13.37	**<0.001**
80 - 100 mm	1	1.09	0.30
>100 mm		*N/A*[2]	

[1] 100% of observed sea urchins were cryptic

[2] Chi-squared test could not be performed due to lack of data

Table 2.3: Results from generalised linear model (family = binomial) assessing the effects of Food (+ or -), Predation cue (+ or -) and Week on the proportion of sea urchins sheltering in the mesocosm experiment. Significant p values are bold.

Source of variation	Coefficient	SE	Z value	p value	odds ratio
Intercept	-0.928	0.590	-1.574	0.116	NA
Food	-0.424	0.239	-1.772	0.076	0.65
Predation cue	-0.183	0.691	-0.265	0.791	0.83
Week	-0.740	0.328	-2.260	**0.024**	0.48
Predation cue x Week	1.101	0.368	2.989	**0.003**	2.51

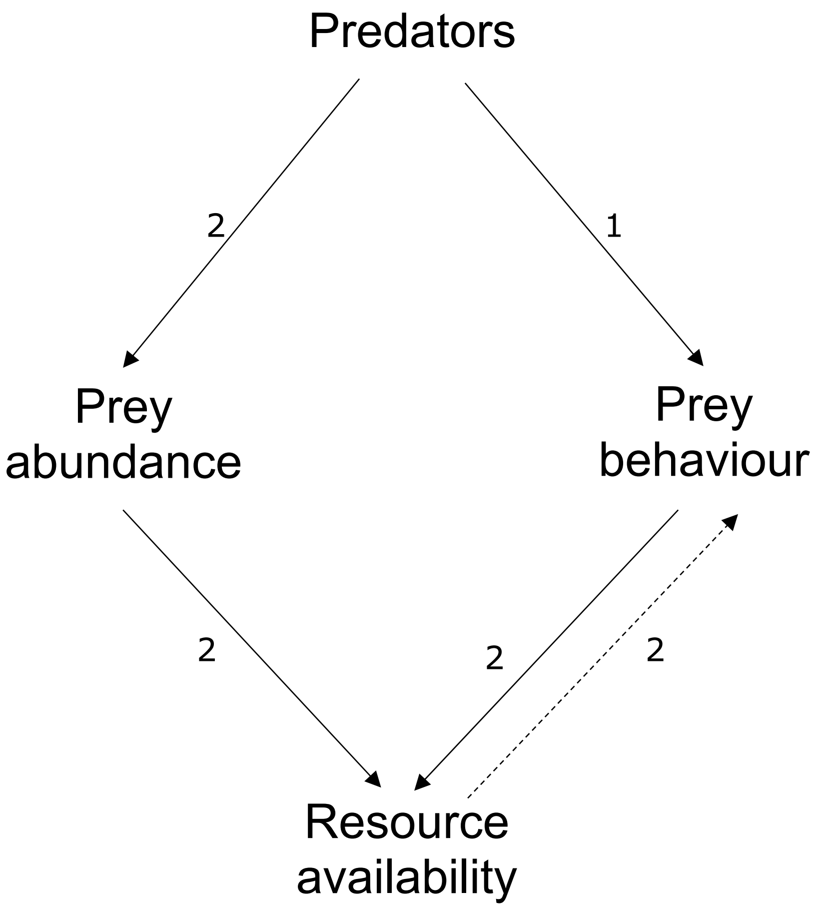

Fig. 2.1: Alternative pathways by which predators may influence prey behaviour. (1) represents a direct pathway where predation risk cause prey to alter their behaviour, while (2) represents an indirect pathway where predators alter prey resource availability through DMIIs or BMIIs and prey change their behaviour in response to these changes in resource availability. Solid lines represent direct predator effects and the DMII/BMII associated with each effect while the dashed line represents the hypothesised indirect predator effect.

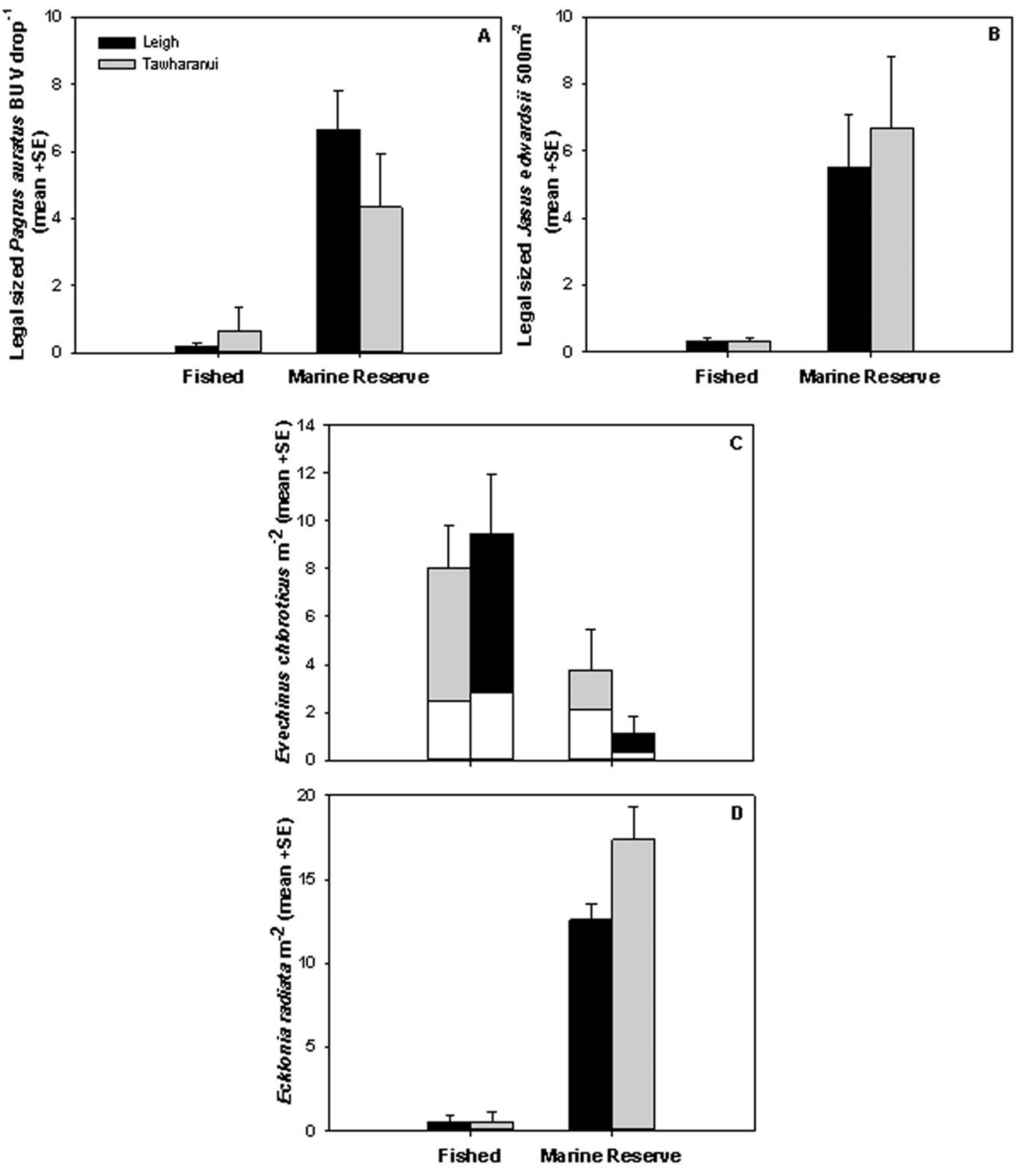

Fig. 2.2: Relative densities of sea urchin predators, (A) *Pagrus auratus* (legal sized snapper BUV drop^{-1} ± SE) and (B) *Jasus edwardsii* (legal sized lobster 500m^{-2} ± SE), (C) sea urchins *Evechinus chloroticus* (m^{-2} ± SE) and (D) kelp *Ecklonia radiata* (m^{-2} ± SE) on fished versus protected reefs at Leigh and Tawharanui, north-eastern New Zealand. In panel (C) the white areas of each bar represent cryptic *E. chloroticus* and shaded areas represent exposed individuals.

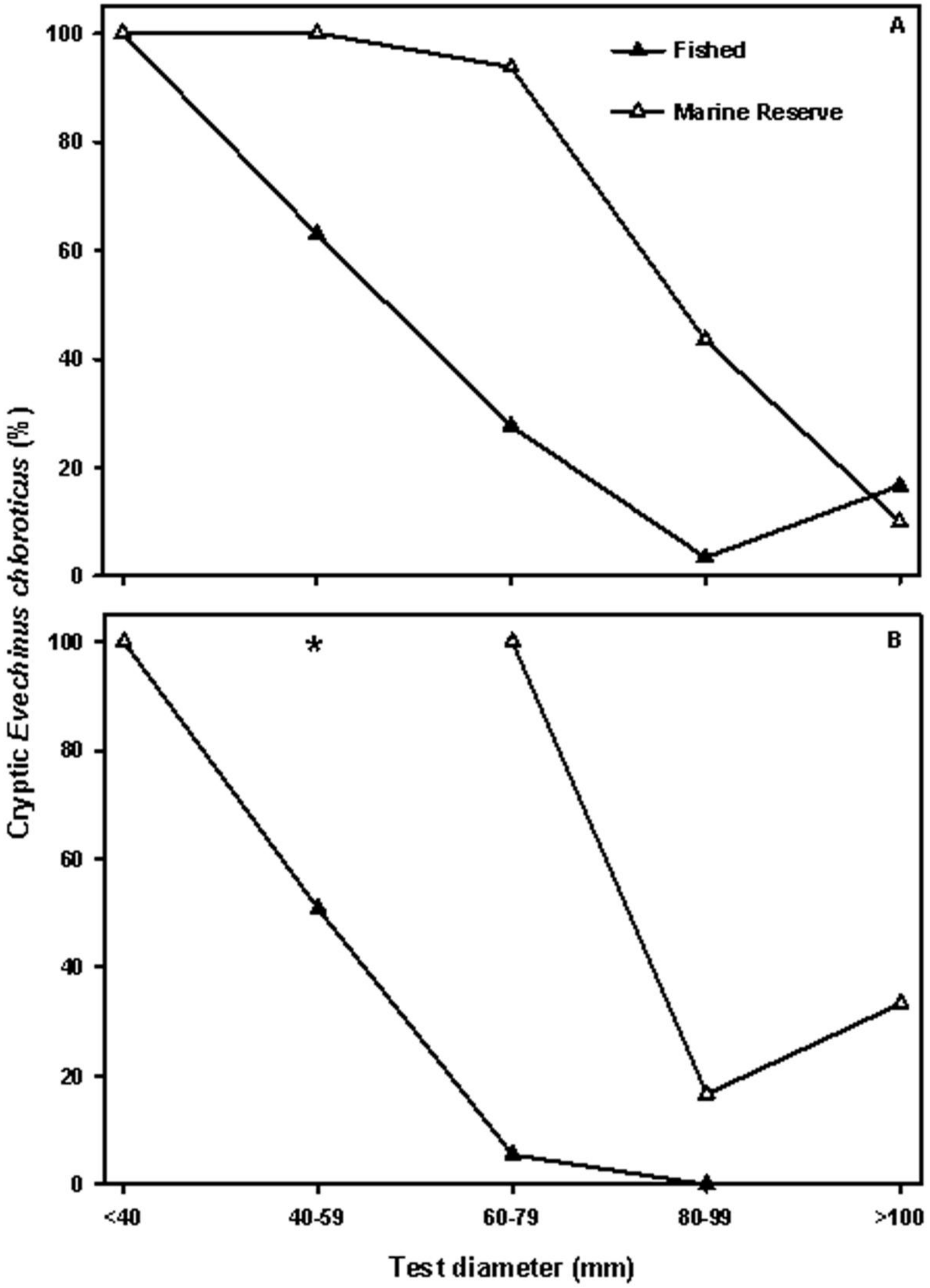

Fig. 2.3: Proportion of sea urchin *Evechinus chloroticus* occupying crevices or under rocks ("cryptic") on fished versus protected rocky reefs at (A) Leigh and (B) Tawharanui, north-eastern New Zealand. *No 40-59 mm sea urchins were recorded inside TMR.

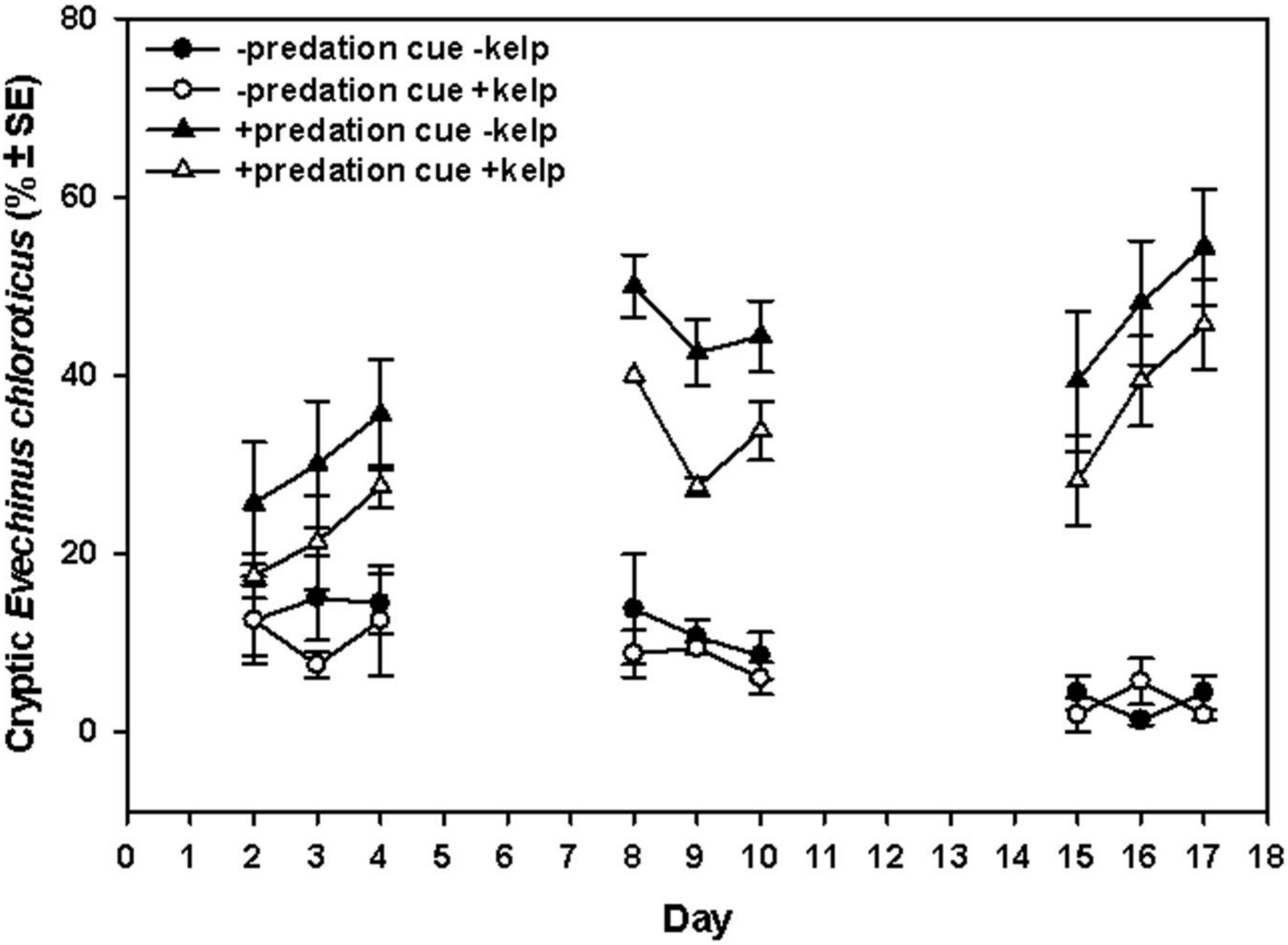

Fig. 2.4: Proportion of sea urchin *Evechinus chloroticus* occupying crevices or under rocks ("cryptic") in a mesocosm experiment in which predation cues and food availability were manipulated

Chapter Three: Predators induce morphological defences in herbivores indirectly through a trophic cascade

Introduction

Individuals of many prey species respond directly to the potential threat of nearby consumers by manufacturing structural or chemical defences that reduce their vulnerability to attack (Tollrian & Harvell, 1999; Schoeppner & Relyea, 2005). Such induction of defences usually occurs following the prey's detection of mechanical, tactile, visual or chemical cues from consumers, and have been reported for a wide range of prey taxa (Brönmark & Miner, 1992; Tollrian, 1995; Dahl & Peckarsky, 2002; Bourdeau, 2009; Rasmann & Agrawal, 2011). Induction of defences in plants have also been demonstrated to occur via indirect means (Wäckers & Bezemer, 2003; Heil & Kost, 2006). Indirect induction of defences has not been demonstrated at higher trophic levels, e.g. herbivores, but it is possible that prey defences could be induced in herbivores via indirect or "unintentional" mechanisms. For example, predators can have cascading effects on lower trophic levels that ultimately result in more food for herbivores. Additional food resources allows for greater investment in defences (Chivers et al., 2008) that in turn decrease a prey's susceptibility to predation. While this alternative pathway may be an incidental response to predators, it will have a similar long-term effect as the direct induction of defences in that it reduces the vulnerability of prey populations to predation.

Sea urchins are important grazers on many temperate rocky reefs. They are encased in a test (skeleton) made of magnesium-enriched calcite ossicles (Stock, 2014). The test is porous but remarkably strong (Weber et al., 1969), and confers at least some protection against predators that crush their prey (Sala, 1997). Calcite spines project from the test surface, helping to repel predators (Tegner & Levin, 1983), spread impact loads (Strathmann, 1981) and capture food (Contreras & Castilla, 1987). These features are highly plastic and can differ morphologically depending on variations in abiotic factors such as water motion (Lewis & Storey, 1984), or biotic factors such as food availability (Ebert, 1980; Edwards & Ebert, 1991) and predation cues (Selden et al., 2009). Predators can induce structural defences in sea urchins via unsuccessful attacks or chemical cues released by predators or injured prey. For example, waterborne cues from predatory crabs induce thicker tests in *Strongylocentrotus droebachiensis* (Selden et al., 2009).

Predators also have the potential to induce these defensive features in sea urchins indirectly through their cascading impacts on the availability of kelp, a major food for many sea urchins. When predators are rare (often due to overfishing), sea urchins can attain high densities and create "urchin barrens", where kelp and other food is scarce (Filbee-Dexter & Scheibling, 2014). Starving sea urchins invest in their feeding apparatus at the expense of other body parts including the test (Black et al., 1984; Ebert et al., 2014). Some sea urchins even shrink when food-limited, as they reallocate calcite from the test to their jaws (Levitan, 1991). When predators are sufficiently large and abundant they initiate a trophic cascade, whereby sea urchins are either eaten or restricted to crevices where they eat little living kelp, allowing the kelp forests to recover (Shears and Babcock, 2002). In food-rich habitats sea urchins tend to have thicker tests (Rogers-Bennett et al., 1995; Ling & Johnson, 2009), which potentially help the urchins persist in the face of high predator pressure.

In this chapter I examine the influence of predators on putative morphological defences of the sea urchin *Evechinus chloroticus* on rocky reefs in north-eastern New Zealand. First, morphological attributes of sea urchins inside two well-established marine reserves, where sea urchin predators and kelp are abundant, and in adjacent fished areas where sea urchin predators and kelp are rare were examined. A six-month long mesocosm experiment was then run, subjecting sea urchins to different levels of predation cues and food availability, to determine whether the patterns observed in the field were a direct response to the presence/absence of predation cues or an indirect response to food availability.

Methods

Morphological variation in sea urchins

Morphological attributes of the endemic sea urchin *Evechinus chloroticus* were quantified in two marine reserves in north-eastern New Zealand, and in adjacent fished areas; see Fig. S2.1 for locations and Chapter One for a detailed description of the area). Dense forests of kelp *Ecklonia radiata* occur inside both marine reserves at depths of 4-6 m, while similar depths on overfished reefs are virtually devoid of *Ecklonia radiata* and are characterised by urchin barrens (Chapter Two).

During June and July 2013 *Evechinus chloroticus* of a range of sizes were collected (n=20) from 4-6 m depth at four sites within each of the following four areas: LMR, the Leigh fished coastline (LFC), TMR and the Tawharanui fished coastline (TFC; see Figure S1 in Supporting Information). All *Evechinus chloroticus* were held in flow-through sea water tanks at the University of Auckland's Leigh Marine Laboratory for up to 18 hours until processing. Test diameter was measured using calipers (± 1 mm). Four primary spines were removed from the equator of the test and their lengths measured (± 0.1 mm). Each sea urchin was placed on a device designed to test crushing resistance, a measure of strength considered relevant to predation by snapper, which take an entire sea urchin in their mouth and bite down until the test is crushed (N. Shears, pers. obs.). The device consisted of an analogue set of scales, calibrated using a known weight, sitting underneath a bracket with a metal shaft and foot (maximum surface contact area 30 cm^{-2}). The shaft was wound down onto the aboral surface of a sea urchin at a constant speed until the test cracked, evident by a loud pop and sudden release in pressure. A slider indicated the load (± 1.0 kg) required to crack the test. Spines absorb the impact of static loading (Strathmann, 1981) and also caused the foot to slip from the centre of the aboral surface, resulting in pressure being applied heavily to one side of the sea urchin only. To counter this, all spines on the aboral surface were trimmed back to the test using scissors before crushing. The thickness of the cracked test was taken as the average of four measurements made at randomly chosen points using calipers (± 0.1 mm).

Induction of defences

To determine whether food availability and/or predation cues were responsible for the morphological variation observed in the field survey, a mesocosm experiment was run using juvenile *Evechinus chloroticus* over a 6 month period, , from June to December 2013. In May 2013 sea urchins of 10-40mm test diameter were collected from a fished reef (Nordic Reef Fig. S3.1, 36°17'35.19"S, 174°48'35.54"E) and transported back to the Leigh Marine Laboratory fully submerged. Sea urchins were held in a flow-through 1500-L tank for 4 weeks, without feeding, so that they all started the experiment at a similar level of hunger.

The sea urchins used for the experiment (n=256) had initial test diameters between 16 and 29 mm (±1 mm). Individuals were ordered by size, and starting with the smallest, a single individual was added to each of the 32 replicate tanks, then another individual to each of the 32 tanks, until each tank contained eight individuals. The individual tanks were 10L buckets, each containing a small coralline algae-covered rock to provide habitat for the juvenile urchins. To allow addition of predation cues (a crushed conspecific) tanks were fitted with a clear plastic lid with holes drilled in it that was positioned 9.5 cm from the bottom on the tank. The lid also had a 10 mm hose running through it to allow seawater into the bucket. A small venturi was fitted to the hose, on the upper side of the lid, to allow the water containing the predation cue to circulate down into the bucket. The experiment was run in outdoor tanks in a continuous flow seawater system and under 80% shade cloth to mimic natural light levels in the field.

Sea urchins were subjected to two treatments (food and predation cue) each with two levels (+ and -) in a fully-crossed design. Each group had eight replicate buckets of eight sea urchins. For the food treatment sea urchins received one blade of fresh *Ecklonia radiata* weekly (“+food”). Control buckets (“-food”) were given one blade of *E. radiata* per month. For the predation cue treatment, a large *E. chloroticus* was cracked in half, and one half was placed on the lid of a bucket (“+predation cue”). This was done twice a week with the cracked half remaining until being replaced by a new one. Control buckets were not subjected to crushed conspecifics (“-predation cue”).

At the completion of the experiment sea urchins were processed to obtain size, test thickness, resistance to crushing and spine length, using the same methods described above except that a finer-scale crushing device was employed due to the small size of the sea urchins. This was a hollow piston (weighing 2.2 kg) that could be filled with water. Water was slowly added until the sea urchin, placed directly underneath the piston foot, was crushed. The water was weighed to gain the total (including the piston weight) crushing resistance (±0.1 kg). The largest individuals required one or two 1kg lead weights to be added to the piston prior to crushing, as not enough water could be held inside the piston.

An environmental scanning electron microscope (eSEM) was used to examine differences in the microstructure of the sea urchin test between treatments. The five largest sea urchins (~30 mm) were selected from each of the four treatment groups. These were dried for 48 hours at a constant temperature of 60°C, then soaked for ~ 48 hours in NaOH to remove any organic material (Hughes, Brunner, Cook, Kelly, & Wilson, 2012). Sea urchins were soaked in a 3M NaOH solution for 18 hours, removed then re-soaked in weaker 2M NaOH solution for a further 24 hours. An interambulacral plate was then removed from each sea urchin. A small section from this plate's equator was broken off and mounted on a slide then platinum-coated prior to examination under a Quanta eSEM.

A series of images were taken across the face of the interambulacral plate and analysed using the particle analysis tool in ImageJ v1.44. Plate structure varied between the edge and centre of the plate, therefore any images containing edges were excluded from the analysis. 100 non-overlapping quadrats (100µm x 100µm) were equally divided between the remaining images. Within each, the number of pores, the average pore size (± 0.1µm diameter) and the total pore space were measured using the particle analysis tool.

Data analysis

All statistical analyses were carried out using R v.3.0.2. To analyse sea urchin morphological attributes linear mixed models were fitted with random slopes and intercepts using REML. Test diameter nested within site was a random factor, and reserve (yes or no), area (Leigh or Tawharanui) and test diameter were fixed factors. Homogeneity of variance and normal distribution of each variable were visually assessed prior to analysis by plotting residuals against fitted values. To analyse morphological attributes of juvenile sea urchins, linear mixed models were fitted with random slopes using REML. Bucket was treated as a random factor and food (+ or -), predator (+ or -) and test diameter were fixed factors. For both sets of analyses optimal models were fitted using backwards elimination of fixed factors or interactions that explained little variation. Differences in growth and test microstructure of juvenile sea urchins were analysed using two-way ANOVA. The factors for this were food (+ or -) and predation cue (+ or -).

Results

Morphological variation in sea urchins

An interaction between area and status existed for test thickness. (Fig. 3.1A & B, Table 3.1). Inside LMR sea urchins had thicker tests than similar sized individuals on the surrounding fished reefs. There was no clear difference in test thickness between sea urchins inside and outside of TMR.

Crushing resistance increased significantly with test diameter (Fig. 3.1C & D, Table 3.1). The crushing resistance of sea urchins inside marine reserves was significantly higher than on fished reefs, with 11.7 ± 3.0 kg more force required to crush sea urchins at reserve sites compared with fished sites. There was a marginally significant area effect, with sea urchins from the Leigh coastline requiring 6.6 ± 3.0 kg more force to crush than individuals from the Tawharanui coastline.

Spine length increased significantly with test diameter (Fig. 3.1E & F, Table 3.1). Spine length did not vary significantly with reserve status, but sea urchins around the Tawharanui coastline had spines averaging 1.6 ± 0.6 mm longer than those on individuals around the Leigh coastline.

Induction of defences

Growth in test diameter was marginally higher in the + food than – food treatments (0.67 ± 0.05mm/month versus 0.52 ± 0.05 mm/month; $F_{1,28} = 4.123$, p= 0.052) but there was no effect of predators ($F_{1,28} = 1.849$, p= 0.185) or any food-predator interaction ($F_{1,28} = 0.198$, p= 0.660) (Fig. S3.1).

For test thickness there was a significant interaction between predation cue and test diameter (Fig 3.2A, Table 3.2). When predator cues were present large urchins tended to have thinner tests than when there was no predation cue. Food did not have a significant effect on test thickness.

For crushing resistance both food and predation cues interacted significantly with test diameter (Fig. 3.2B, Table 3.2). At large sizes urchins with food and with predator cues had higher crushing resistance, although food had a much greater effect than predation cues on overall crushing resistance.

Spine length showed a significant food effect and a significant interaction between predation cues and test diameter (Fig. 3.2C, Table 3.2). A sea urchin fed weekly possessed 1.7 ± 0.3 mm longer spines than the same sized sea urchin fed only monthly. Larger sea urchins in predation cue treatments tended to have longer spines than when predation cues were not present.

The average number of pores per 100 μm^2 (6.5-7.0) did not differ significantly between the four treatment groups (Fig. 3.3A), regardless of food ($F_{1,19} = 0.862$ $p = 0.376$) or predation cues ($F_{1,19} = 0.188$, $p = 0.680$). Sea urchins fed weekly did, however, have significantly smaller pores (Fig. 3.3B & 3.4, 13.18 ± 0.32 μm^2 versus 14.91 ± 0.38 μm^2, $F_{1,19} = 9.681$, $p = 0.007$) and less total pore space (Fig. 3.3C & 3.4, 11.80 ± 0.44 % versus 14.11 ± 0.36 %, $F_{1,19} = 14.004$, $p < 0.002$) than those fed monthly. Predation cues did not influence either feature ($F_{1,19} = 0.000$, $p = 0.992$ and $F_{1,19} = 0.240$, $p < 0.631$, respectively).

Discussion

Induced defences, whether structural or chemical, are generally considered to be a direct response to predation cues (Tollrian & Harvell, 1999) and have been demonstrated for many organisms (Appleton & Palmer, 1988; Brönmark & Miner, 1992; Schoeppner & Relyea, 2005), including sea urchins (Selden et al., 2009). This provides the first example of a putative structural defence in herbivores being induced indirectly by predators through a trophic pathway involving increased food availability. Sea urchins inside marine reserves where predators are abundant had more crush-resistant tests than similar-sized individuals from adjacent fished coastlines where predators are rare. The difference could potentially be explained by direct induction of crush resistance due to the presence of predation cues, more food in the marine reserves due to a trophic cascade in which predator suppression of sea urchin grazing releases kelp, or a combination of both of these mechanisms. A mesocosm experiment showed the main effect was primarily due to greater food availability increasing crush-resistance, with predation cues having a weaker effect.

Investing energy into defensive features should reduce predator-driven mortality in a prey population (Van Buskirk & Schmidt, 2000). Predatory fishes typically attack sea urchins by biting down on the test until it cracks open (Shears & Babcock, 2002), so greater resistance to crushing should make sea urchins less vulnerable to predators. Studies investigating predation on freshwater snails showed that individuals with thicker shells were less vulnerable to the chipping and crushing actions of predatory crayfish than thinner shelled conspecifics (Hoverman & Relyea, 2009). I found that sea urchins inside marine reserves had more crush-resistant tests than individuals on fished reefs, at all sizes. Crush-resistance may be particularly important for small sea urchins, which are generally more susceptible to predation than large individuals as they are easier to break open (Clemente et al., 2013). It is important to note that some sea urchin predators such as larger lobster penetrate the sea urchin through the peristomial membrane (Tegner & Levin, 1983), so increased crush-resistance alone would not reduce vulnerability to such predators.

To provide effective protection the test must be able to absorb and resist static loads applied (Strathmann, 1981), and its strength is related to its thickness and porosity (Lawrence, 1987). While the field results from marine reserve sites concur with previous studies in demonstrating that sea urchins in food-rich habitats had thicker tests than those on urchin barrens (Rogers-Bennett et al., 1995; Ling & Johnson, 2009), juvenile sea urchins fed weekly in the mesocosm experiment did not have thicker tests than those fed monthly. However, they were found to be significantly more crush resistant suggesting that test thickness is only of secondary importance to increasing crush-resistance. It was found that sea urchins fed weekly in-filled more of the test with calcite, making it less porous than those fed monthly, and argue that this is the more important factor leading to increased crush-resistance. The mesocosm experiment also showed some evidence of a directly induced defence where crush resistance increased more substantively with sea urchin size in the presence of predator cues, compared to when predator cues were absent. This finding concludes with Seldon et al., (2009) that sea urchins can directly induce morphological defences. However, I suggest that when food is available it is the more important factor in inducing increased crush-resistance as the addition of food had a greater effect on crushing resistance than predation cues.

In the mesocosm experiment greater food availability resulted in longer spined individuals, a similar finding to Rogers-Bennett et al. (1995). Longer spines are beneficial for food acquisition (Contreras & Castilla, 1987), which is particularly important for cryptic sea urchins that rely on their spines to collect drift algae (Lawrence, 1987). Longer guard spines may also help with protection against predators (Tegner & Levin, 1983). Sea urchins that lost their guard spines in response to exposure to the harmful dinoflagellate *Ostreopsis siamensis* were more susceptible to predation than healthy sea urchins with a full armament of guard spines (Shears & Ross, 2010), demonstrating their importance in predator repulsion. The significant interaction between sea urchin size and predation cues, in the mesocosm experiment, also shows that there is some investment into developing longer spine when faced with heightened predation risk, but again this is not as great as the effect of additional food.

The availability of resources can have serious consequences for an organism’s fitness and vulnerability to predation (Rice et al.,1987). Induced defences which reduce prey vulnerability, occur independently of an organisms resource levels (Brönmark & Miner, 1992), but should be expressed at reduced levels when resources are limited (Van Buskirk, 2000; Zhu et al., 2016). High resource availability can therefore benefit the induction of defences (Chivers., et al., 2008) and may become the more important factor in determining overall state of the defence, such is the case in the north-eastern New Zealand system. Trophic cascades are an important and widely demonstrated mechanism by which predators may inadvertently increase the availability of food for surviving prey (Silliman & Bertness, 2002; Shears & Babcock, 2002; Ripple & Beschta, 2012). This is the first study to demonstrate that such predator-driven ecosystem changes can indirectly lead to increases in structural defences in herbivores. While not specifically tested in this study it has widely been demonstrated that increased structural defences will ultimately reduce the vulnerability of herbivores to predation (Dahl & Peckarsky, 2002; Domenici et al., 2008)

The term indirect induction has previously been described in plants (Arimura et al., 2000; Kessler & Baldwin, 2001) but it is not analogous to the indirect induction of defences described in this study. In response to herbivory plants can produce volatiles that indirectly reduce herbivory by attracting herbivore enemies to the plant (Heil & Kost, 2006). While this is a deliberate action aimed at reducing predator effects the indirect induction of prey defences observed occurred ‘unintentionally’, where greater food uptake consequently strengthened morphological aspects involved in defence.

Induced defences can allow species to co-exist (Miner et al., 2005) by promoting population stability in a food chain (Verschoor et al., 2004). Increased primary production, a result of cascading trophic effects, may create a potentially important feedback mechanism allowing herbivore populations to stabilise and persist, albeit at comparatively low densities, in the presence of predators.

Table 3.1: Linear mixed model results for the effects of Status (reserve or fished), Area (Leigh or Tawharanui) and test diameter on test thickness, crush-resistance and spine length, morphological features related to defence, from the sea urchin *Evechinus chloroticus* along the north-eastern coastline of New Zealand.

	Coefficient	**SE**	**DF**	***t***	***p***
(a) Test thickness					
Intercept	0.31	0.06	285	5.61	**<0.001**
Reserve	0.23	0.06	12	3.90	**0.002**
Area	-0.14	0.06	12	-2.36	**0.039**
Size	0.02	0.00	285	26.04	**<0.001**
Reserve x Area	-0.18	0.08	12	-2.17	0.051
(b) Crush-resistance					
Intercept	-20.08	3.12	271	-6.44	**0.001**
Reserve	11.73	3.00	12	3.91	**0.002**
Area	-6.63	3.00	13	-2.21	**0.046**
Size	0.97	0.03	271	32.83	**<0.001**
(c) Spine length					
Intercept	8.87	0.65	284	13.69	**<0.001**
Reserve	0.00	0.61	13	-0.01	0.995
Area	1.56	0.61	13	2.57	**0.023**
Size	0.14	0.01	284	17.27	**<0.001**

Table 3.2: Linear mixed model results for the effects of food (yes or no), predation cue (yes or no) and test diameter on test thickness, crush-resistance and spine length of juvenile sea urchins, *Evechinus chloroticus*¸ grown in the induction experiment.

	Coefficient	**SE**	**DF**	***t***	***p***
(a) Test thickness					
Intercept	0.18	0.04	143	4.39	**<0.001**
Food	0.02	0.01	29	1.45	0.159
Predator	0.10	0.01	29	1.63	0.113
Test diameter	0.02	0.00	143	14.50	**<0.001**
Predator x Test diameter	-0.01	0.00	143	-2.37	**0.019**
(b) Crush-resistance					
Intercept	-0.79	1.18	156	-0.68	0.501
Food	-5.87	1.32	29	-4.45	**<0.001**
Predator	-3.02	1.30	29	-2.32	**0.028**
Test diameter	0.18	0.05	156	3.84	**<0.001**
Food x Test diameter	0.35	0.05	156	6.63	**<0.001**
Predator x Test diameter	0.14	0.05	156	2.71	**0.008**
(c) Spine length					
Intercept	-1.45	0.78	163	1.85	0.066
Food	1.70	0.30	28	5.63	**<0.001**
Predator	-3.21	1.13	28	-2.84	**0.008**
Test diameter	0.38	0.03	163	12.13	**<0.001**
Predator x Test diameter	0.13	0.04	163	3.00	**0.003**

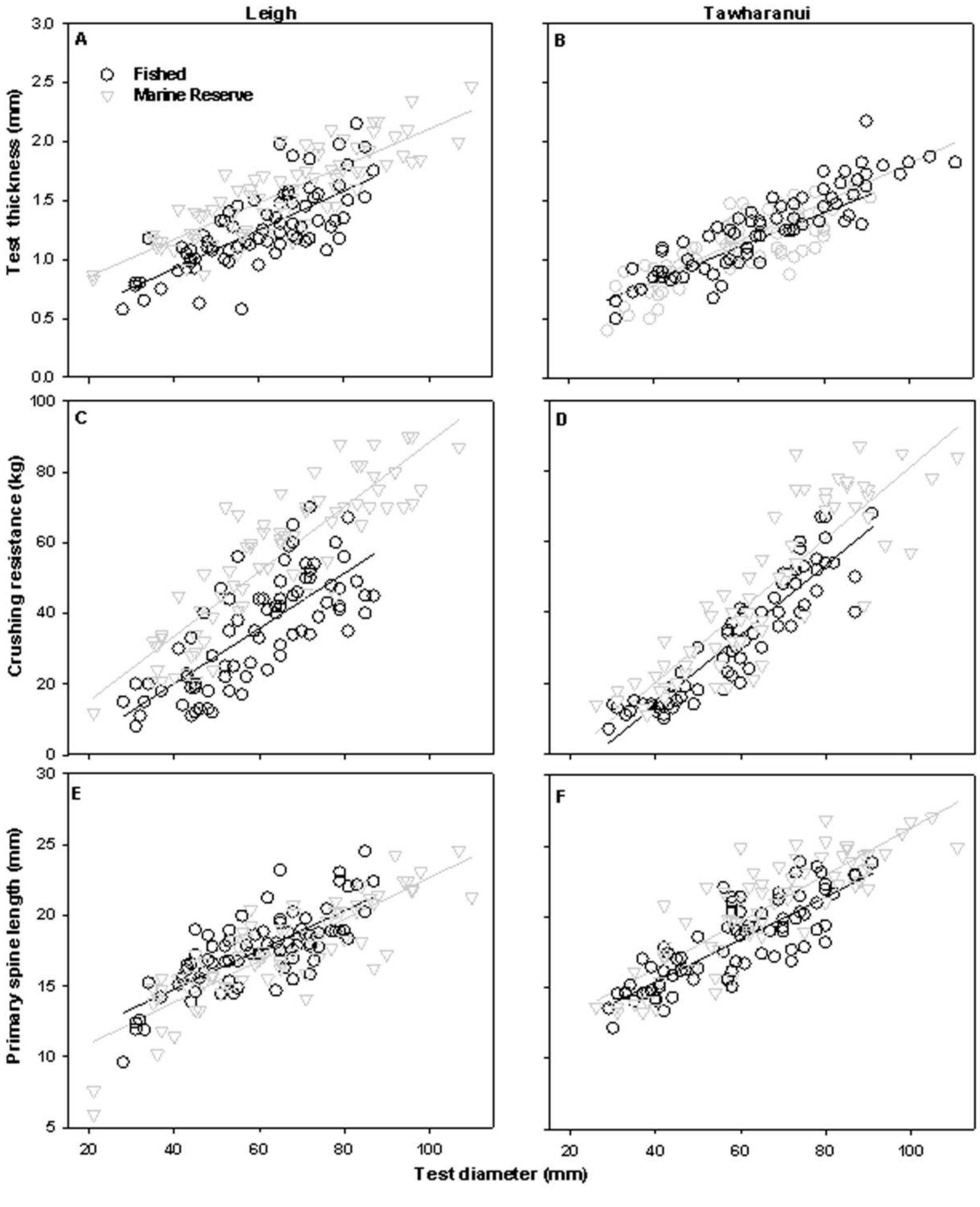

Fig. 3.1: Crush-resistance (A,B), test thickness (C,D) and primary spine length (E,F) for the sea urchin *Evechinus chloroticus* along the Leigh and Tawharanui coasts in north-eastern New Zealand.

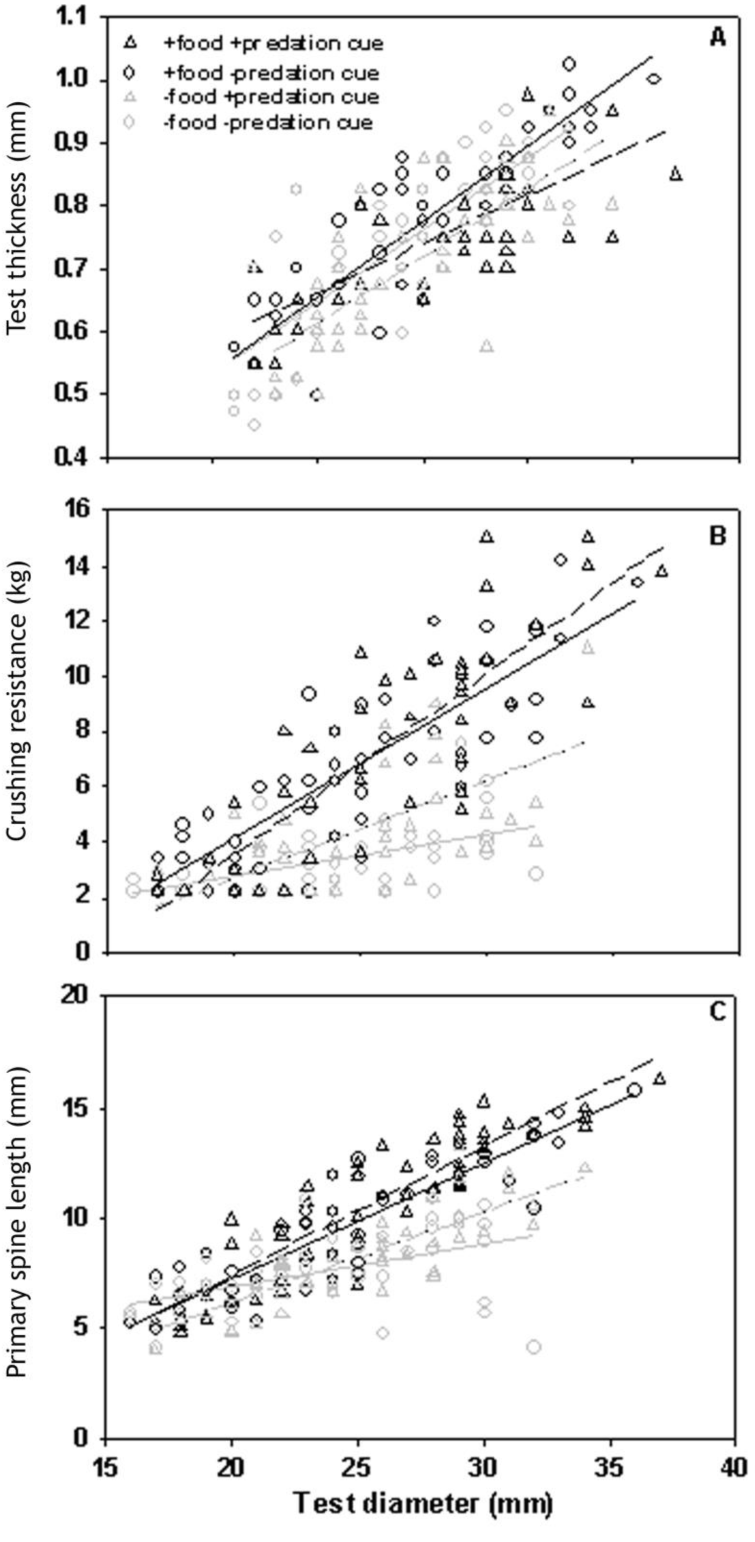

Fig. 3.2: Test thickness (A), crush-resistance (B) and primary spine length (C) of juvenile *Evechinus chloroticus* grown under different food and predation cue conditions in a mesocosm experiment. Solid regression lines indicate -predation cue treatments, dashed regression lines indicate +predation cue treatments.

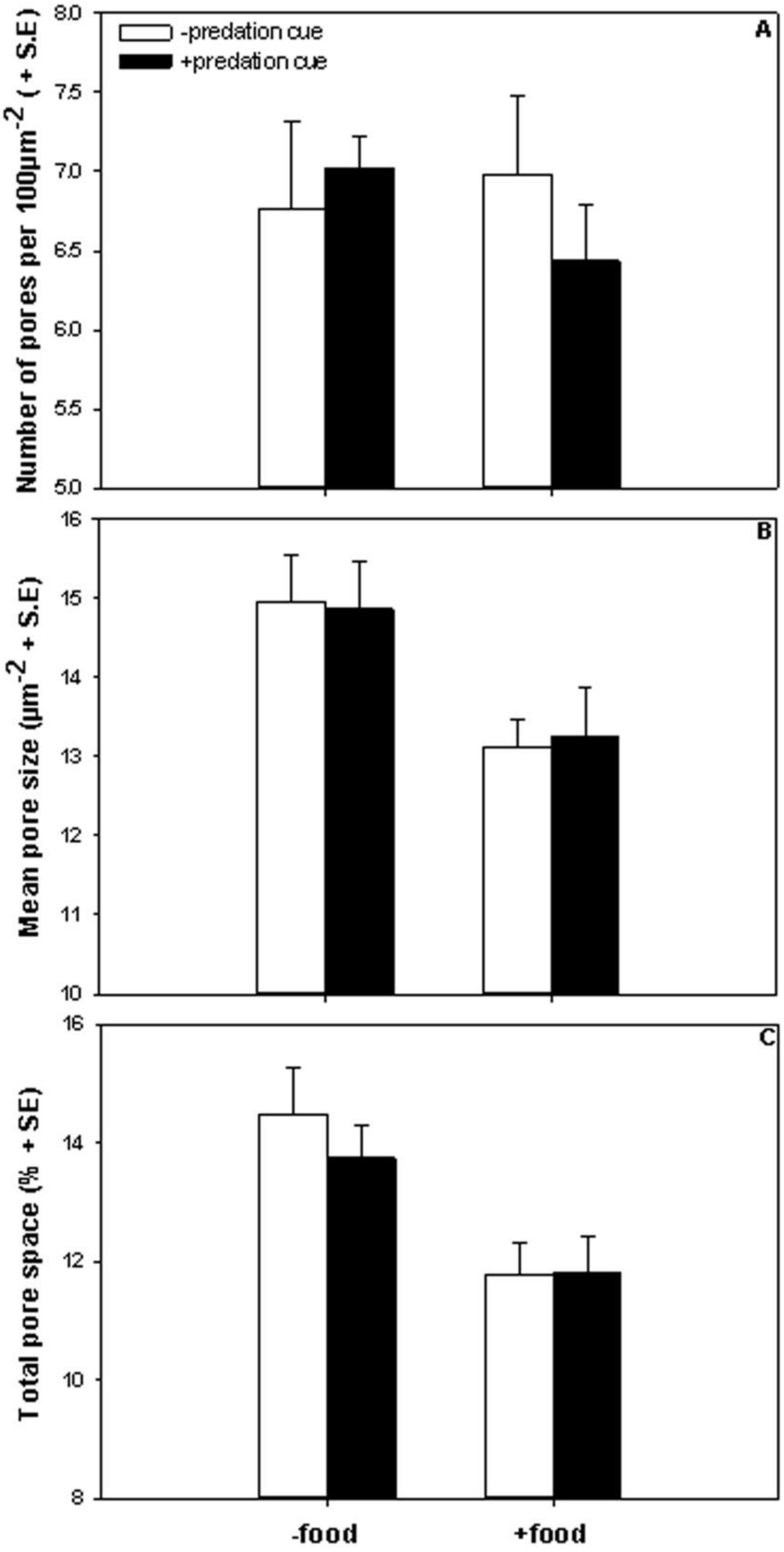

Fig. 3.3: Number of pores (A), average pores size (B) and total pore space (C) in the interambulacral plate of *Evechinus chloroticus* grown under different food and predation cue conditions in the mesocosm experiment.

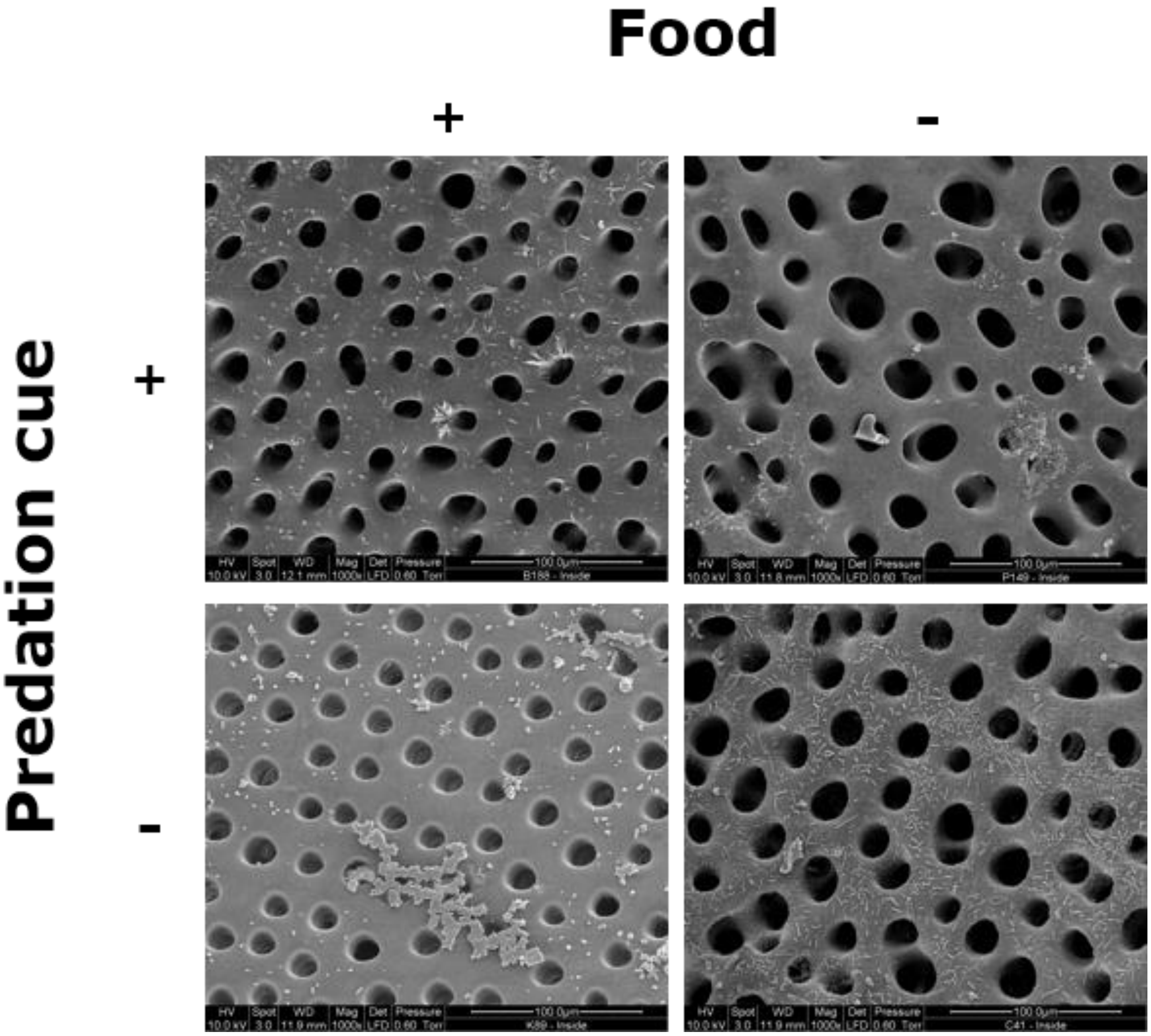

Fig. 3.4: eSEM images of the porous surface of an interambulacral plate from a sea urchin grown under different food and predation cue conditions in the mesocsom experiment. Sea urchins fed on a weekly basis (+) food have smaller pores and more infilled calcite space between each pore.

Chapter Four: Injured conspecifics as an alarm cue for the sea urchin *Evechinus chloroticus*

Introduction

While predators can exert strong lethal control on prey populations, prey individuals do not simply submit to predation and many use anti-predator behaviours in order to increase their chances of survival (Lima & Dill, 1990; Kats & Dill, 1998; Schoeppner & Relyea, 2005). Prey rely on visual, mechanical or chemical cues to provide information about their predators (Dicke & Grostal, 2001). In the sea, many prey species possess well-developed chemosensory receptors so use chemical cues as their main source of predator information (Buskirk et al 2014). Chemical cues have the advantage of being able to be detected from distance, even in low visibility or areas of high habitat complexity (Dodson et al., 1994; Brönmark & Hansson, 2000).

Anit-predator behavioural responses reflects an apparent trade-off between safety and the benefits gained from other activities (Lima & Dill, 1990). Foraging is commonly foregone when prey initiate anti-predator behaviours and prey will spend less time in risky, food-rich habitats and more time in safer, food-poor habitats (Beckerman, Uriarte, & Schmitz, 1997; Cowlishaw, 1997). Non-consumptive predator effects (NCEs) such as altering prey behaviour may indirectly influence the abundance and biomass of lower trophic levels, thus facilitating trophic cascades via a behaviourally-mediated pathway (Werner & Peacor, 2003; Schmitz, Krivan, & Ovadia, 2004). The strength of NCEs are likely to depend on the perceived level of risk from a predation cue (Turner, 2008; Schoeppner & Relyea, 2009a) as well as the spatial and temporal scale that the cue acts over (Turner & Montgomery, 2003; Van Buskirk et al., 2014). Therefore understanding what cues prey respond to as well as the spatial and temporal scale they act over is necessary for understanding the ecological importance of NCEs.

Sea urchins are an important rocky reef herbivore capable of completely removing dense stands of macroalgae when their grazing behaviour is unrestricted (Ling et al., 2015). Unrestricted grazing is often seen as a result of overharvesting sea urchin predators, which removes top-down pressure on sea urchin populations (Tegner & Dayton, 2000). When abundant, predators can have density-mediating effects on sea urchin populations, lowering the grazing pressure exerted by sea urchins on their resources. Therefore, predators of sea urchins can indirectly influence primary producers by reducing the abundance of sea urchins, through a density-mediated indirect interaction (DMII). DMIIs are well documented in systems containing sea urchins (Estes & Duggins, 1995; Shears & Babcock, 2002; Blamey & Branch, 2012), however, like many other prey species sea urchins use anti-predator behaviours where possible to increase their chances of survival (Duggins, 1983; Hagen, Andersen, & Stabell, 2002). Predator-induced changes in behaviour can strengthen the predator-sea urchin-kelp forest trophic cascade by reducing sea urchin grazing rates (Byrnes et al., 2006), therefore investigating sea urchin behaviour should be considered as important as investigating sea urchin densities in these systems.

Changes in sea urchin behaviour have been demonstrated in response to kairomones that are released directly from predators (Manzur & Navarrete, 2011; Urriago et al., 2011), as well as alarm cues released when other prey, including conspecifics, are injured or killed (Hagen et al., 2002; Watson & Estes, 2011; Chapter Two.). Fleeing from the immediate area (Mann et al., 1984; Parker & Shulman, 1986; Rodriguez & Ojeda, 1998; Vadas & Elner, 2003; Hagen et al., 2002; Manzur & Navarrete, 2011; Urriago et al., 2011; Watson & Estes, 2011), or sheltering in refuge habitats (Bernstein et al., 1981; Scheibling & Hamm, 1991; Chapter Two) are the most commonly observed behavioural responses to predation cues. That sea urchins respond to predation cues has been well-established, however many studies have only investigated the initial reaction to the cue and not compared the response to alternative extraneous cues. This leaves several important questions regarding the importance of conspecific alarm cues for sea urchins unanswered. These include (1) Are behavioural responses specific to conspecific alarm cues? Prey may be responding specifically to alarm cues released by a conspecific or the response could just be a generic response observed whenever chemical cues are detected (2) Over what distance do sea urchins respond to predation cues? The spatial extent of a cue will help determine a predator's sphere of influence. (3) How do sea urchins respond to predation cues during the night? Many sea urchin species are nocturnally active (Nelson & Vance, 1979; Tuya et al., 2004; Young & Bellwood, 2011), so understanding if predation cues will affect their behaviour at night when they would normally do the majority of their grazing is important. (4) How long does it take before sea urchins relax their behaviour following exposure to a predation cue? The length of time taken for sea urchins to re-enter an area will have important implications for macroalgal recruits settling on the reef.

In north-eastern New Zealand, the endemic sea urchin *Evechinus chloroticus* (family: Echinometridae) is the most important reef herbivore. This sea urchin forms part of a well-documented density-mediated trophic cascade (Babcock et al., 1999; Shears & Babcock, 2003; Shears et al., 2008) between predators (snapper, *Pagrus auratus* and lobster, *Jasus edwardsii*), sea urchins and kelp (*Ecklonia radiata*). While the lethal effects of predators on *E. chloroticus* are well understood (Andrew & MacDiarmid, 1991; Shears & Babcock, 2002), very little is known about how predators affect their behaviour. In Chapter Two (a mesocosm experiment) I found that cues from injured conspecifics increased crevice occupancy by *E. chloroticus*, showing that this species does respond behaviourally to indirect predation cues. While this provided good information about anti-predator behaviours, further field studies are required to assess whether these cues are also important in a natural setting.

In this chapter I investigated whether cues from injured conspecifics were important in the wild for altering behaviour of *E. chloroticus*. In addition, I aimed to gather important information about the spatial and temporal scale over which potential predation cues acted. Utilising time-lapse photography and field surveys I asked (1) Did *E. chloroticus* respond specifically to conspecific alarm cues or did other extraneous ones also evoke behavioural reactions? (2) What was the spatial extent over which sea urchins responded to conspecific alarm cues? (3) How did exposed and cryptic sea urchins respond throughout the night to conspecific alarm cues? (4) What was the relaxation time before sea urchins re-entered areas containing conspecific alarm cues?

Methods

Camera and experimental set up

All field experiments using time-lapse photography were set up using the same method. GoPro cameras were mounted, facing directly down onto the rocky substrate, on custom built quadpods (Fig. 4.1). Quadpods consisted of a metal frame containing four adjustable legs allowing the camera to be positioned 1.12 m to 2.04 m above the reef. GoPro cameras were set to record one photo every minute. For night time filming a flash was required so a Panasonic Lumix TS4 camera was used. These had limited time-lapse capabilities (a maximum of 60 photos) so were set to turn on just before dusk and take a photo every 15-20 minutes with the internal flash set to Auto. Cues were applied to the experiments by placing the cue (or empty pot for controls), within a 1.5 L container (“bait pot”), on the rocky substrate below the camera.

Bait pots had 30 holes drilled throughout to allow the chemical cues to permeate out into the water column. To avoid disturbing the sea urchins prior to or during the experiment reference measurements were made at the end of the recording so that accurate movement distances could be calculated using ImageJ.

Field sites

All experiments using the quadpods were carried out on a large area of reef on the fished coastline near Leigh in north-eastern New Zealand (36°18'9.52"S, 174°48'1.65"E). This site consisted of large expanses of urchin barrens, with low topographical complexity, interspersed with deep vertical crevices. *E. chloroticus* was abundant on the reef and also within some of the crevices.

Cue specificity and spatial extent

Behavioural response to injured conspecifics and an extraneous cue

In December 2014 a number of one-hour trials were carried out to compare the response of sea urchins to a crushed conspecific (one medium-large injured *E. chloroticus* ~70-80 mm test diameter) and an extraneous cue (one large crushed pilchard ~120-150 mm length). A pilchard (*Sardinops neopilchardus*) was chosen as the extraneous cue because it is a common prey species in north-eastern New Zealand, but does not occur in the same habitat, or have the same guild of predators as *E. chloroticus* (Paul & Parkinson, 2001). Pilchards are often used as bait by fishermen because they release a strong odour plume into the water, making them a reliable extraneous cue to use. Two controls were also used including (1) an empty bait pot to replicate the physical disturbance of placing the cue, and (2) no bait pot to assess if the bait pot itself was causing any disturbance.

Quadpods were set up over patches of sea urchins ($\geq$ 5 ind.m^{-2}) on ‘barren’ sections of reef, and filmed for one hour. Two quadpods were used for this experiment so the four treatments were randomly applied in two consecutive one hour trials. Quadpods were at least 5 m apart and then moved 10 m between trials. The first 20 minutes of the filming was the ‘pre-cue’ period, and was used to establish normal movement patterns and ensure that the quadpod was not causing any disturbance. The ‘post-cue’ period (the 40 minutes following the addition of a cue at minute 20) was used to investigate the behavioural response of individuals to the cues. In total five replicates were carried out for each treatment.

The response to the cues was measured as the total distance moved by live *E. chloroticus* during the 'post cue period'. Distance measurements were made by tracking the distance moved by each individual within a 0.5 m radius of the bait pot, every two minutes (a sequence of 30 photos) using the ImageJ plugin Manual Track. An individual's total movement was calculated as the sum of all distances moved between corresponding photos until the end of the sequence or the sea urchin was no longer visible in the field of view. Total movement 'pre cue' and 'post cue' was analysed using one-way ANOVA, with treatment (control, empty bait pot, pilchard and conspecific) as the fixed factor. Post hoc testing was carried out using the Tukey HSD test. Movement 'post-cue' was also broken down into 10 minutes intervals and analysed using two-way repeated measures ANOVA, with treatment (control, empty bait pot, pilchard and conspecific) as the fixed factor and time as the repeated measure. Post hoc testing was carried out using pairwise t-tests with the Bonferroni correction**.**

Spatial extent of behavioural response to injured conspecific cues

Footage from the injured conspecific treatment was then used to investigate the spatial scale over which sea urchins responded to conspecific alarm cues. Control footage from the empty bait pot was analysed for comparison. In ImageJ, concentric rings were placed around the bait pot corresponding to a 0.5 m radius, a 1.0 m radius and a 1.5 m radius. The position of each visible sea urchin within each ring was marked at three time points; minute 0 (P1), minute 20 (P2) and minute 60 (P3) and straight line distances between each point were measured.

The response variable was the proportion of sea urchins moving 'post cue' within each of the three rings. Sea urchins were deemed to have moved if the straight line distance was >10cm 'post cue' (P2-P3). A generalised linear model (family = binomial) with two fixed factors, treatment (control, one crushed conspecific, two crushed conspecifics) and starting ring (0.5 m, 1 m, 1.5 m) was used to analyse whether the proportions of sea urchins moving (moving = yes or no) differed between treatments and/or starting ring.

Response to cues from injured heterospecifics

Due to the limited response of *E. chloroticus* to extraneous pilchard cues, investigations were carried out to see if more closely related prey species, i.e. other sea urchin species, would induce a behavioural response. A quadpod experiment was set up in February 2015 to investigate how *E. chloroticus* responded to an injured *Centrostephanus rodgersii* (family: Diademetidae). This species represents the only other sea urchin commonly found on shallow reefs in northern New Zealand that performs a similar functional role to *E. chloroticus*

(Pecorino et al., 2012). A trial comprising four replicates of two treatments, one crushed *C. rodgersii* (~110-120 mm test diameter) and one crushed *E. chloroticus* (~70-80 mm test diameter) was set up in the exact manner of the above experiments. Due to the similar movement patterns ‘pre’ and ‘post’ cue in all treatments from the previous experiment a specific control was not used in this experiment. Instead the movement ‘pre cue’ was used as the control.

The response variable measured was total distance moved by live *E. chloroticus* during the ‘post cue’ period. Movement distances were measured in ImageJ and a two-tailed t-test were used to analyse movement ‘pre’ and ‘post’ cue.

Response to fish activity

Fish were attracted to bait pots containing chemical cues, therefore could be a confounding factor, causing disturbance or releasing cues that altered sea urchin behaviour. In March 2015 a quadpod experiment was set up to investigate the response of *E. chloroticus* to injured conspecifics when fish had access to, or were excluded from the baitpot. Quadpods were set up using the same methods as above but fish were excluded from one of the quadpods using a 10mm mesh net, weighed down at one end with chain and held up with net floats at the other end. Prior to recording all fish were removed from within the net.

The response variable measured was total movement ‘post cue’, however as the net may have confounded movement and prevented sea urchins from moving beyond the confines of the net, the proportion of sea urchins moving within the 0.5 m radius of the bait pot was also investigated. A two-tailed t-test was used to analyse total movement ‘post cue’, while the proportion of sea urchins moving was analysed using a chi-squared test.

Night time behaviour of exposed and cryptic sea urchins

Many species of sea urchins, including *E. chloroticus,* are nocturnally active (Tuya et al., 2004; Dumont, Himmelman, & Russell, 2006; Young & Bellwood, 2011) with feeding activity intensifying around dusk and dawn (Radford et al., 2008), therefore it was necessary to incorporate night time observations into this study to assess how predation cues affected sea urchin behaviour throughout the night. Overnight experiments were run using the quadpods between July and September 2015.

Exposed sea urchins

Recordings were carried out on patches of barren reef to see how exposed sea urchins behaved at night and whether the addition of predation cues altered this behaviour. Quadpods were set up over patches of sea urchins, however only two treatments were used: an injured conspecific and an empty bait pot as the control. Recordings started around 1100 with bait pots being placed under the camera at 1120. At 1200 GoPro cameras were replaced with the Panasonic cameras and the contents within the bait-pots were scattered onto the reefs. Recordings continued for the following 20 hours with one photo taken every 20 minutes. In total four spatially and temporally independent replicates were carried out.

The response variable analysed was sea urchin density within a 0.5 m radius of the initial bait pot position (and where the majority of the discarded sea urchin remained). Differences in density between the cue and control treatments were analysed every hour using two-tailed T tests or Mann-Whitney U tests where log transformed data failed the assumptions of normally or homogeneity of variance.

Cryptic sea urchins

Recordings were carried out over crevices containing sea urchins during the day to investigate whether individuals would leave these crevices at night to feed and if the addition of a predation cues just outside of the crevice altered their behaviour. Quadpods were set up over the open crevices (open crevices = vertical crevices with opening width >10 cm, average opening width = 19.95 ± 1.23 cm), containing ≥5 individuals, that intersected the study site. Using the Panasonic cameras, a photo was taken every 15 minutes from 1600 to 0700 the following morning. Two treatments, an injured conspecific and an empty bait pot as the control were used, with a total of five spatially and temporally independent replicates. To ensure that the cue remained above the crevice and did not fall down into it, bait-pots were left in place for the entire recording, as opposed to the contents being scattered on the reef.

The response variable analysed was the proportion of observed sea urchins that were cryptic at any given time. This metric was used instead of density because it gave a better representation of cryptic vs exposed sea urchins. Urchins were considered cryptic if they remained below the lip of the crevice. Sea urchins that left the field of view continued to be recorded with their last observed position (cryptic or exposed) being used for the remainder of the observation. Hourly comparisons between the proportion of observed sea urchins that were cryptic in control and cue crevices were made using Chi-squared tests.

Relaxation time for sea urchins exposed to injured conspecific cues

Over a two week period field observations were carried out at a number of plots containing injured conspecific alarm cues to investigate what the relaxation time was between when sea urchins fled from the cue and re-entered the area. In December 2015 fifteen plots were set up at 6m water depth (low tide) on an area of low topography barren reef near Leigh, north-eastern New Zealand (36°17'56.73"S, 174°48'21.12"E). On day 0 plots were set up at least 3 m apart, in a randomised order, and marked with a 1kg weight in the centre, plus two smaller weights as references for photo calibrations. Each plot was assigned to one of three treatments; one injured conspecific (injured on day 1 to represent a single predation event) two injured conspecifics (one injured at day 1 and the other at day 7 to represent a predator returning to the same area to hunt) and a control containing no injured conspecific cue. Treatments were applied by crushing a conspecific (collected on the same reef but well away from the plots) and placing it into the centre of the plot inside a bait pot. Bait pots were also used in the control plots but these remained empty. After 40 minutes the bait pot contents were scattered on to the reef and the bait pots removed.

All plots were surveyed at day 0, 1, 2, 3, 5, 7, 9 and 13 by taking a photo directly above the centre of the plot from a height of 2-3m. The density of sea urchins within a 1m radius of the central weight was calculated and then the differences between treatments was analysed using a two-way ANOVA with treatment (control, cue at day 1, cue at day 1 and 7) and day as the fixed factors.

Results

Cue specificity and spatial extent

Behavioural response to injured conspecifics and an extraneous cue

Total movement did not vary between treatments or controls ‘pre cue’ but varied significantly ‘post cue’ (Fig. 4.2A, Table 4.1). *E. chloroticus* exposed to injured conspecifics responded strongly by moving away (fleeing) from the cue source. Movement was significantly higher in response to the injured conspecific cue (Fig 4.2A, 48.13 ± 14.86 cm, average ± SE) than the extraneous pilchard cue (17.61 ± 6.18) or either control treatments (5.73 ± 1.78 empty pot & 7.42 ± 2.09 control).

‘Post cue’ there was a significant effect of treatment on the distance moved, however there was also a significant interaction between treatment and time (Fig 4.2B, Table 4.2). Sea urchins moved significantly further than in both controls, except for in the final time period (31 - 40 minutes) and only moved significantly more than individuals in the pilchard treatment during the first half of the post cue period (1 – 20 minutes).

Spatial extent of behavioural response to injured conspecific cues

Sea urchins responded to conspecific cues over a relatively small spatial scale in the field (Fig. 4.3, Table 4.3). The proportion of sea urchins moving in response to alarm cues from an injured conspecific fell steadily as distance from the cue increased and beyond 1 m the proportion of moving sea urchins was indistinguishable from the proportion in the control. Sea urchins exposed to an injured conspecific were 4.2 times more likely to be moving if they were within 0.5 m of the cue than if they were beyond 1m.

Behavioural response to heterospecific cues

E. chloroticus did not respond to alarm cues released from injured *Centrostephanus rodgersii*, a heterospecific sea urchin. ‘Pre cue’ sea urchins in both the conspecific and heterospecific treatments displayed similarly low levels of movement (Fig. 4.4, $t_8 = -0.421$, $p = 0.685$), however movement differed significantly between the two treatments ‘post cue’ ($t_8 = -3.857$, $p = 0.004$). Movement was high ‘post cue’ in response to an injured conspecific (23.38 ± 3.94 cm), while individuals in the heterospecific treatment continued slowly moving (4.32 ± 1.79 cm), as they had ‘pre cue’.

Behavioural response to fish activity

Fish activity around the bait pot did not affect sea urchin behaviour. Both the distance moved ‘post cue’ ($t_6 = 1.921$, $p = 0.103$) and the proportion of sea urchins moving (Fig. 4.5, $\chi^2_1 = 0.488$, $p = 0.485$) were similar (~60 % of sea urchins moving) regardless of whether fish were present around the bait pot or not.

Night time response of exposed and cryptic sea urchins

Exposed sea urchins

Sea urchins initially fled from alarm cues released by an injured conspecific, resulting in a decline in density. Densities remained significantly lower in treatment plots than in control plots for the remainder of the observation as sea urchins largely avoided re-entering the area (Fig. 4.6). Densities within 0.5m of the cue fell from 7.75 ± 0.63 individuals to 2.5 ± 1.32 immediately after the cue was released. Densities fell further during the early evening (5pm –

10pm) to 0.25 ± 0.25, remaining low for the remainder of the night and into the following morning. In the control plots sea urchin densities were high throughout the recording but there was a similar decline in density during the early evening, falling from 8.00 ± 1.08 to 5.5 ± 0.29. Densities remained stable at around 5.5 from 10pm onwards

Cryptic sea urchins

Cryptic sea urchins emerged from their crevices and moved onto the reef during the early evening but a significantly higher proportion of the crevice population remained in crevices throughout the night when injured conspecific cues were present above the crevice (Fig. 4.7). The control observations showed that sea urchins vacated their crevices from 6pm onwards and by 10pm less than half (43.33 ± 8.55 %) of the observed sea urchins remained in crevices. In contrast, when conspecific cues were present 79.83 ± 7.98 % of sea urchins were cryptic at 10pm. Homing behaviour was observed in the control treatments with many of the observed sea urchins re-entering the same crevices from approximately 1 am onwards to the point where 70 % of the observed sea urchins were once again cryptic the following morning.

Relaxation time for sea urchins exposed to injured conspecific cues

Initially densities fell in all treatments between day 0 and 2 (Fig. 4.8). Sea urchin densities were generally lower in treatment plots than control plots during days 3 – 7 (Fig. 4.8), but overall there was no significant differences in densities between treatments or days (Table 4.4). Densities within a 1m radius increased at day 3 in the control treatment and remained around 6 for the remained of the experiment. Densities were lower in both treatment groups until the day 9 observation. While sea urchin densities did appear to drop again after the release of an injured conspecific at day 7, the fact that the drop occurred from day 9, not day 7, suggests that it was unrelated.

Discussion

This study has demonstrated that under natural field conditions the sea urchin *E. chloroticus* responds specifically to the cues released from injured conspecifics. Observations showed that sea urchins would flee from cues released from an injured conspecific but not extraneous extracts released from a crushed pilchard, alarm cues released from injured heterospecifics or the high levels of fish activity around the bait pots containing the chemical cues. Flight behaviour was only observed within 1 m of the cue, beyond which behaviour was indistinguishable between cue and control trials. During the night exposed sea urchins avoided re-entering areas they had been in, while in areas where sea urchins were predominantly cryptic conspecific cues strongly reduced the number of sea urchins leaving their crevices through the night in order to feed. On urchin barrens conspecific alarm cues did not cause any long term avoidance and sea urchin densities recovering quickly near where an injured conspecific had been placed.

This is the first study to investigate the behavioural response of *E. chloroticus* to any form of predation cue in the wild. It showed that exposed sea urchins fled the immediate area following the release of a cue. Fleeing from predation cues is a common response employed by prey to improve the chances of survival (Kats & Dill, 1998; Domenici et al., 2011) and my findings are consistent with Vadas & Elner (2003) who found that the sea urchins, *Lytechinus variegatus* and *Tripneustes ventricosus* fled from conspecific alarm cues in the field. Prey also often respond to alarm cues released by heterospecific species, particularly if they share common predators (Chivers & Smith, 1998). This has been demonstrated in sea urchins, however the behavioural response to such cues is often reduced compared to the response to conspecifics (Vadas & Elner, 2003). Interestingly *E. chloroticus* did not flee from injured heterospecifics, despite the fact that both species share a common predator, the lobster *Jasus edwardsii* (Andrew & MacDiarmid, 1991; Ling et al., 2009). The ecological-coexistence hypothesis suggests that a species will respond weakly to signals from non-coexisting heterospecifics (Schoeppner & Relyea, 2009b) which may explain the lack of response shown by *E. chloroticus*. While the two species co-exist in northern New Zealand and on offshore islands (Shears and Babcock, 2004), *C. rodgersii* was rare at the study site.

Due to the logistical difficulties of manipulating adult snapper and lobster I was not able to investigate whether *E. chloroticus* responds to cues emitted from their main predators. Predator kairomones provide important information about predators (Schoeppner & Relyea, 2005, 2009a) and it is likely that *E. chloroticus* would respond to these cues considering that responding to cues released directly from predators is common amongst other sea urchin species (Hagen et al., 2002; Manzur & Navarrete, 2011) and *E. chloroticus* is known to flee directly from the predatory starfish *Coscinasterias muricata* (Pers. obs.).

E. chloroticus responded to cues from injured conspecifics over a relatively small spatial scale and beyond 1 m from the cue source (bait pot) the proportion of sea urchins that were moving was indistinguishable between control and treatment observations. This is consistent with the sea urchin *Tetrapygus niger*, which only fled from predatory starfish that were closer than 0.5m (Manzur & Navarrete, 2011; Urriago et al., 2011) and also other prey species such as the gastropod *Physa acuta*, which has a characteristic response range to predatory fish cues of 1 m (Turner & Montgomery, 2003). Dilution is likely to limit the spatial extent to which cues can be detected. Increased water motion and rougher substrate surfaces dilute chemical concentrations, particularly if they occur close to the substrate surface (Weissburg & Zimmer-Faust, 1993; Webster & Weissburg, 2009; Large et al., 2011). As this study site was shallow and relatively exposed to open ocean swell it was constantly affected by wave action. This is likely to quickly disperse chemical cues from injured conspecifics.

While not specifically measured it was obvious from the recordings that both exposed and cryptic sea urchins were more mobile at night than day, which is consistent with other studies on *E. chloroticus* (Andrew & MacDiarmid, 1991; Chapter Two), and other sea urchin species such as *Paracentrotus lividus* in the Mediterranean Sea (Hereu, 2005). In control treatments exposed sea urchins grazed close to where they had been located during the day, while cryptic sea urchins left their shelter around dusk to feed on the exposed reef before returning to the same crevice before dusk. This homing behaviour is also consistent with other species of sea urchins that shelter during the day (Nelson & Vance, 1979; Andrew, 1993; Tuya et al., 2004). The presence of conspecific alarm cues affected sea urchin behaviour in both experiments, with *E. chloroticus* avoiding areas containing alarm cues. Exposed sea urchins fled and did not return to the area containing the cue for the duration of the recording (20hrs) while most cryptic individuals remained within their crevices for the duration of the recording when a cue was above the crevice opening. This is significant because it shows that predation cues restrict the spatial distribution of sea urchins and create areas where very little sea urchin grazing activity occurs, even during peak feeding times around dusk (Radford et al., 2008). It was clear that sea urchins restricted to crevices were only exerting grazing pressure on resources within the crevice, which is beneficial for resources outside of the crevices. This suggests that in the presence of predators and predation cues sea urchins will be more likely to stay in crevices, which was also a finding in Chapter Two. It remains unclear what the spatial extent of avoidance behaviour in exposed sea urchins would be as I could not observe them once they left the field of view. It is possible that these sea urchins flee to available shelter, in which case their grazing pressure would be reduced. However, if shelter is not available then sea urchins may simply move to other areas of the reef where they resume feeding activities, lowering the grazing pressure in one area but increasing it in another.

In the cue relaxation time experiment sea urchin densities declined in all plots before the addition of injured conspecific cues. It is unclear what caused this decline, however it is possible that setting up the experiment caused some sort of disturbance, leading to individuals moving away from the plots. Densities recovered quickly in the control plots (by day 3) and while sea urchin densities were generally lower in treatment plots than control plots over the next 5 days, overall there was no significant difference in densities between the different treatments or days. Within urchin barrens the cues released from an injured conspecific did not appear to lead to any long term avoidance of an area. This result contrasts those from Watson & Estes (2011), who found that densities of the red sea urchin, *Mesocentrotus franciscanus,* were significantly reduced within a 25m^2 area containing 10-12 injured conspecifics for at least 10 days. This was long enough to allow macroalgae recruits to start growing on the reef, however it is unclear from their study whether starfish affected recolonization. Large sunflower stars, *Pycnopdia helianthoides* were attracted into the plots by the dead urchins and this species is known to cause a flight response in sea urchins (Duggins, 1983). The strongest response to predators is often seen when chemical cues directly from predators and cues from injured conspecifics are detected (Schoeppner and Relyea, 2009a), therefore is possible that to affect behaviour long term, prey must be exposed to predation cues from both sources.

The limited spatial extent and short-term effect of injured conspecific cues on the sea urchins in this study suggest that conspecific cues would have a limited effect in habitats where populations are dominated by exposed sea urchins, such as where predators are generally rare. In these areas behaviourally-mediated interactions are unlikely to be important initially in facilitating the recovery of kelp. However, the finding that sea urchins were less likely to emerge from crevices in the presence of conspecific alarm cues could have important ecological implications. Sea urchins have been shown to increase shelter use when predators are abundant (Chapter Two), and theory predicts that prey should remain within refuge habitats long after predators have left the area (Sih, 1992). If conspecific alarm cues are important for maintaining sheltering behaviour this may represent an important feedback that helps to maintain or enhance kelp forests by restricting the amount of time individuals spend actively foraging. Further study is needed to determine if increased conspecific cues can directly promote cryptic behaviour in the field, which could ultimately lead to increased macroalgal biomass, as well as how sea urchins respond to combinations of injured conspecific and predator cues.

Table 4.1: One-way ANOVA results investigating the effects of treatment (injured conspecific, crushed pilchard, empty bait pot and control) on the total movement distance of *E. chloroticus* ‘pre’ and ‘post cue’.

Variable	***df***	**SS**	**MS**	**F**	***P***
'Pre cue'					
Treatment	3	11.84	3.95	0.29	0.834
‘Post cue'					
Treatment	3	6420.00	2139.90	8.06	**0.002**

Table 4.2: Two-way repeated measures ANOVA results investigating the effects of treatment (injured conspecific, crushed pilchard, empty bait pot and control) and time (21-30, 31-40, 41-50 and 51-60) on the total movement distance of *E. chloroticus* ‘post cue’.

Variable	***df***	**SS**	**MS**	**F**	***P***
Treatment	3	1351.10	450.40	26.96	**<0.001**
Time	3	30.90	10.30	0.61	0.606
Treatment x Time	3	380.20	42.20	2.53	**0.016**
Residuals	60	1002.20	16.70		

Table 4.3: Generalised linear regression (family = binomial) results investigating the effects of treatment (empty bait-pot (control) and injured conspecific) and distance from cue (0.0 to 0.5m, 0.5 to1.0m, 1.0 to 1.5m) on the response level of sea urchins. Baseline values are empty bait-pot and 0.0 to 0 0.5m from the cue except for comparisons made between 0.5 to 1m and 1 to 1.5m.

Variables	**Coefficient**	**SE**	**Z value**	**p value**	**odds ratio**
Intercept	-2.128	0.473	-4.499	**<0.001**	NA
Distance from source (0.5m to 1.0m)	0.182	0.644	0.283	0.777	1.200
Distance form source (1.0 to 1.5m)	0.379	0.719	0.527	0.598	1.461
One crushed sea urchin	2.591	0.564	4.583	**<0.001**	13.342
0.5 to 1.0m x One crushed sea urchin	-1.063	0.756	-1.406	0.116	0.415
1.0 to 1.5m x One crushed sea urchin	-2.318	0.876	-2.647	**0.008**	0.240
Comparison between 0.5 to 1m and 1.0 to 1.5m					
1.0 to 1.5m x One crushed sea urchin	-1.2549	0.836	-1.5091	0.333	0.347

Table 4.4: Two way ANOVA results assessing the effects of treatment (control, cue at day 1, cue at day 1 and 7) and day on the density of *E. chloroticus* within a 1m radius of the plot centre.

Variable	***df***	**SS**	**MS**	**F**	***P***
Treatment	2	59.5	29.73	2.39	0.10
Day	1	4.8	4.83	0.38	0.53
Treatment x Day	2	8.2	4.11	0.33	0.72
Residuals	114	1417.1	12.43		

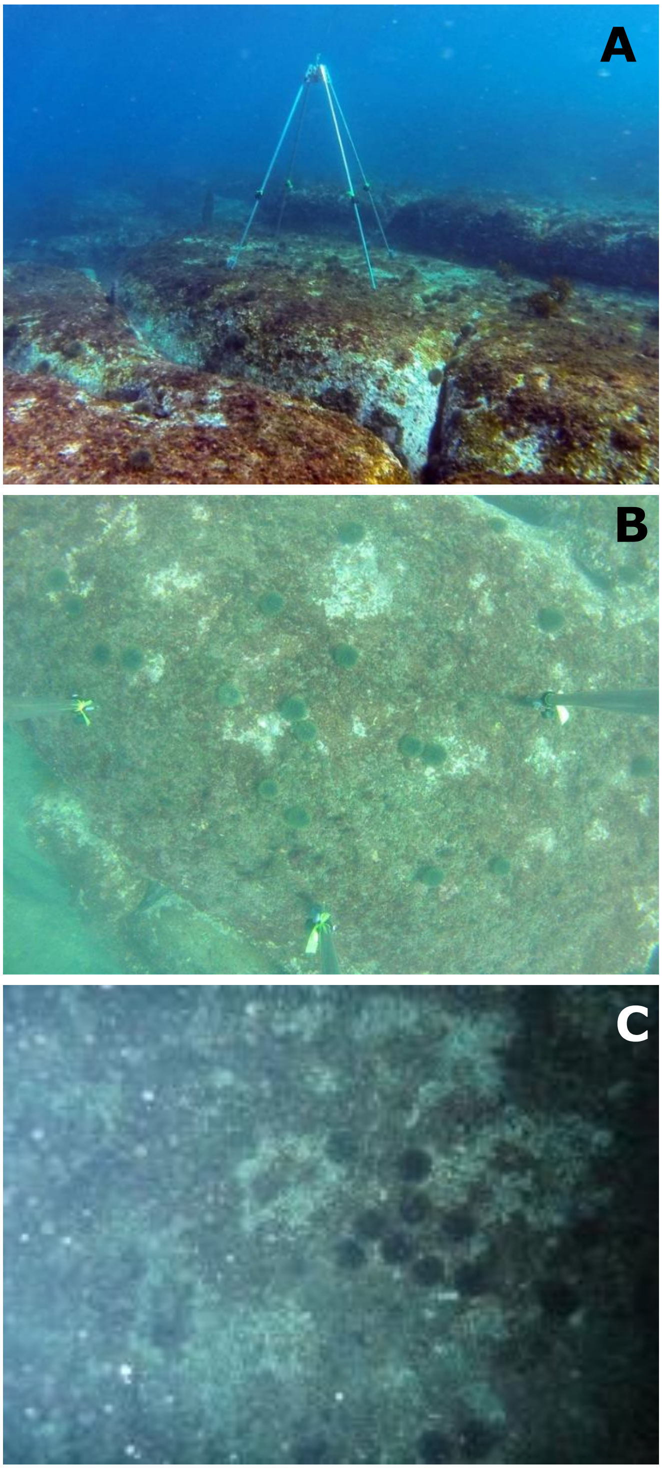

Fig. 4.1: The quadpods used to photograph sea urchin behaviour in the field. A) the quadpod set up over a patch of sea urchins, B) GoPro photo taken during the day and C) a Panasonic Lumix camera taken at night.

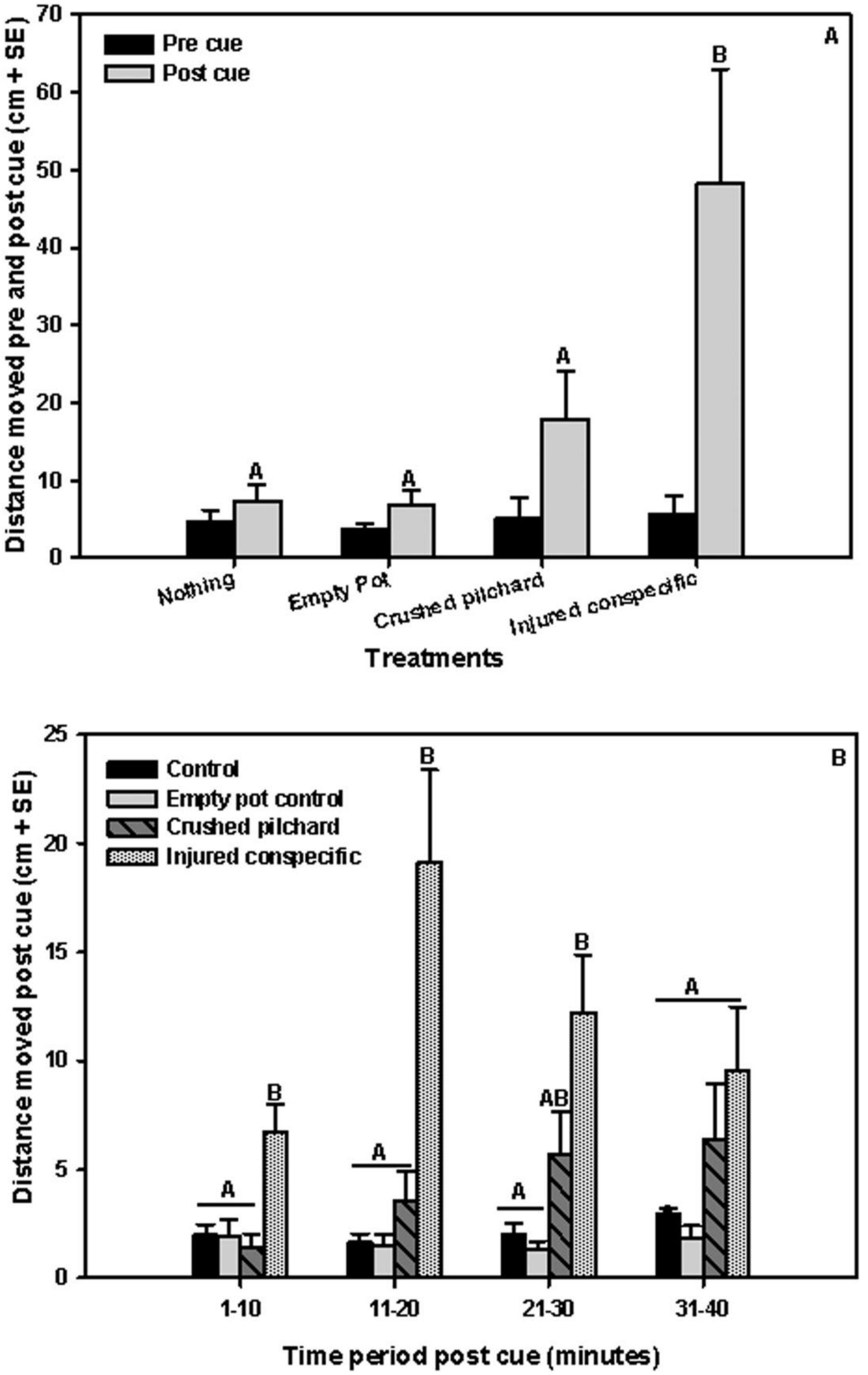

Fig. 4.2: Total distance moved (cm) by the sea urchin *E. chloroticus* A) 'pre' and 'post' the introduction of various cue and B) every 10 minutes 'post cue'. Bars not sharing the same letter (A or B) are significantly different ($p<0.05$) and in A) letters are only corresponding to the movement distances 'post cue'.

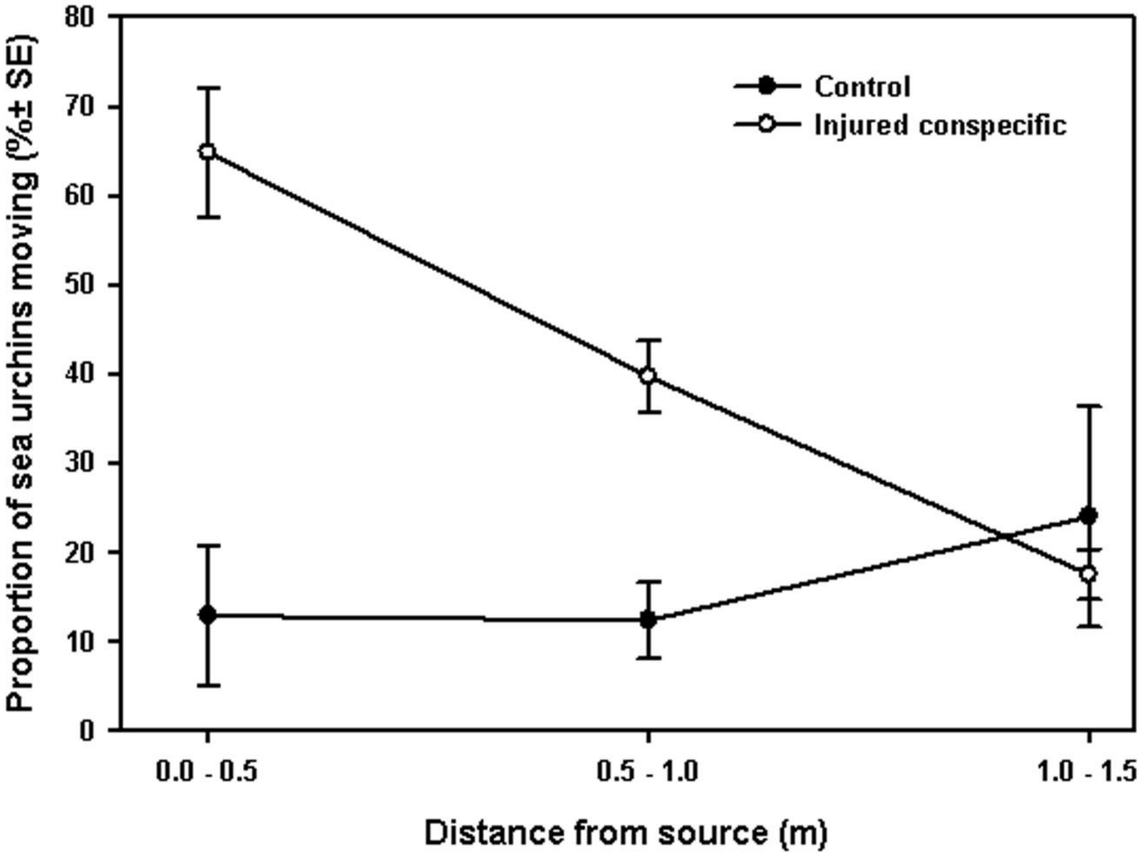

Fig. 4.3: Spatial extent of the behavioural response to cues from an injured conspecific by *E. chloroticus*. Response expressed as the proportion of sea urchins within certain starting distances (0.0 to 0.5m, 0.5 to 1.0m, 1.0 to 1.5m) from the cue source that were moving.

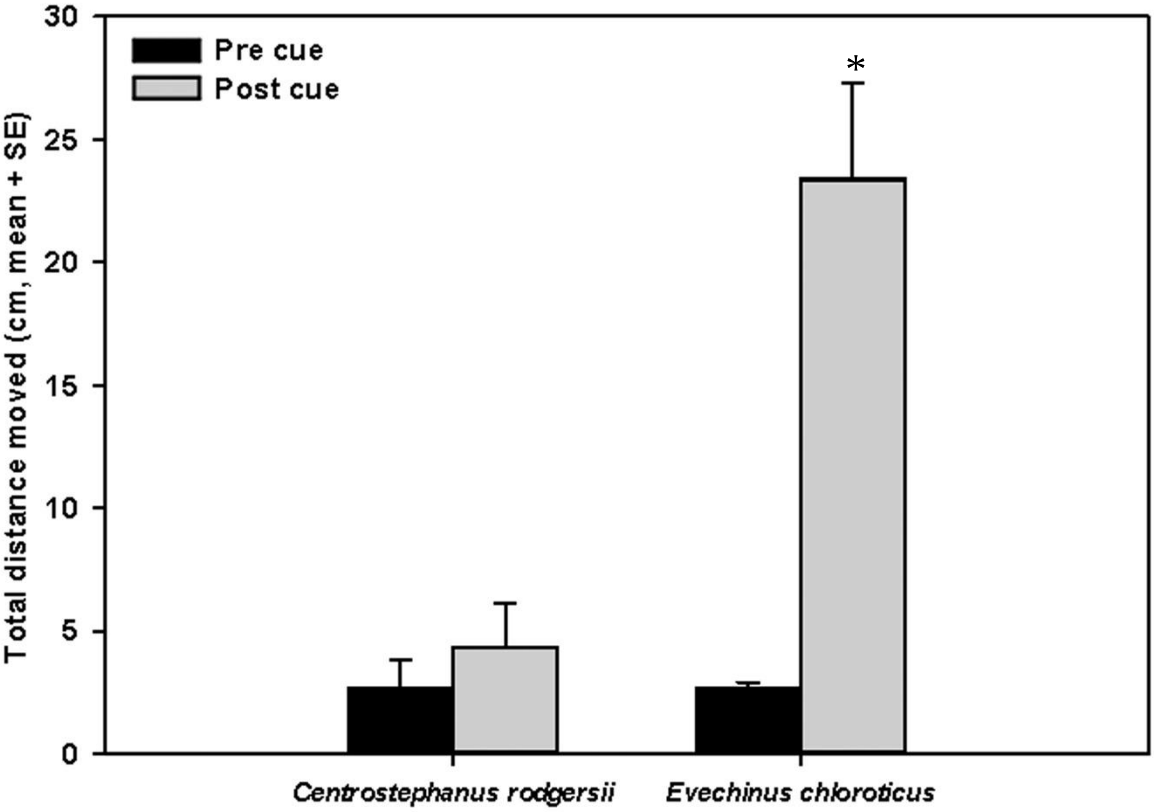

Fig. 4.4: Total distance moved (cm) by *E. chloroticus* ‘pre’ and ‘post’ cue in response to an injured conspecific or an injured heterospecific, *C. rodgersii*. * denotes significant differences ($p<0.5$)

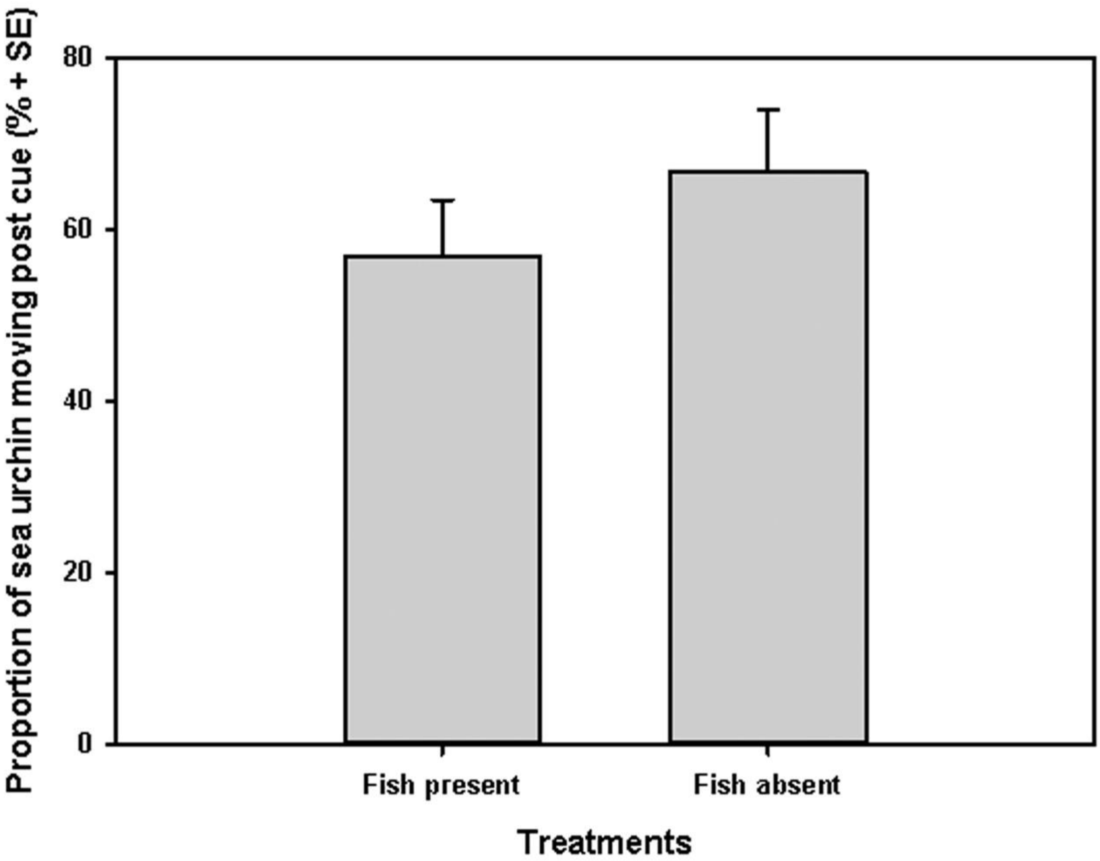

Figure 4.5: Behavioural response of *E. chloroticus*, ‘post cue’ to the cues of an injured conspecific when fish were allowed access to, or were excluded from the bait pot. Response is expressed as the proportion of sea urchins within a 0.5m radius of the bait pot that were moving.

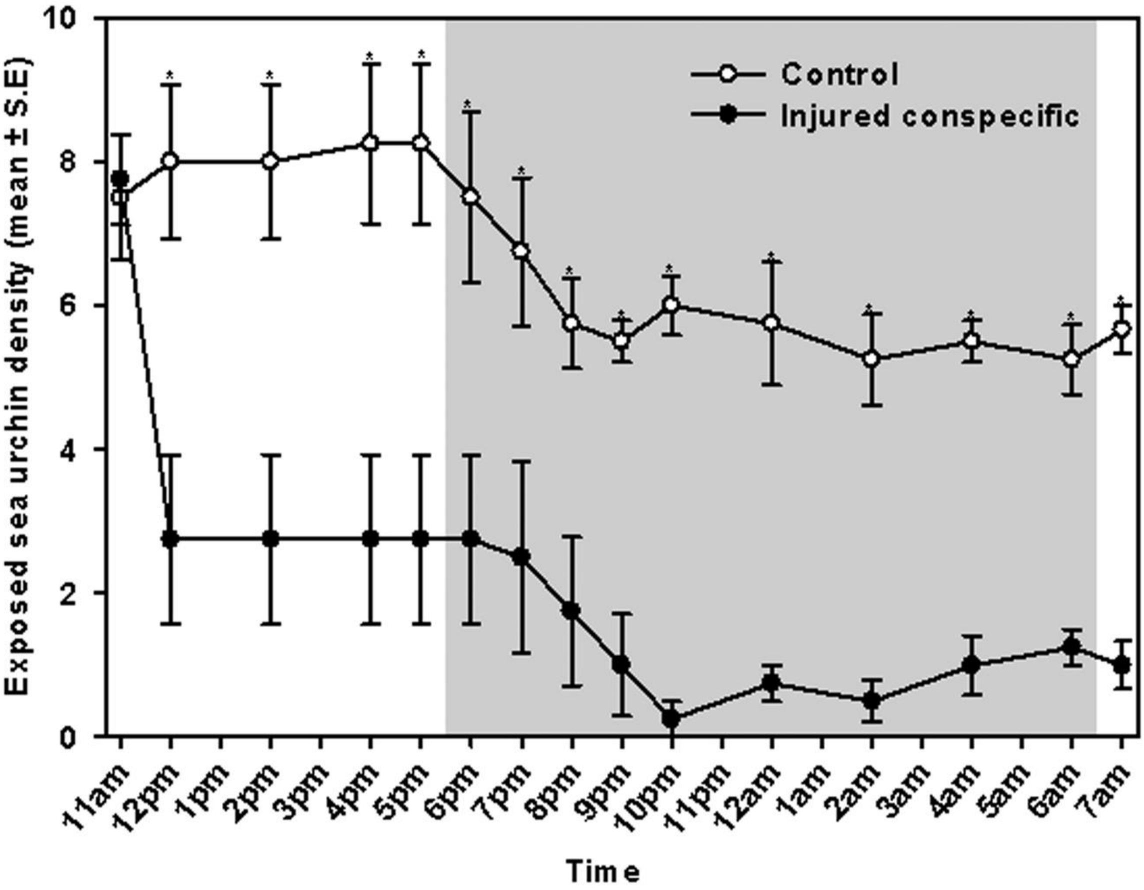

Fig. 4.6: Density of exposed *E. chloroticus* throughout the night within a 0.5m radius of an injured conspecific. Grey area represents night time observations. * denote significant differences ($p < 0.05$) between densities in the control and treatment observations ($p < 0.05$).

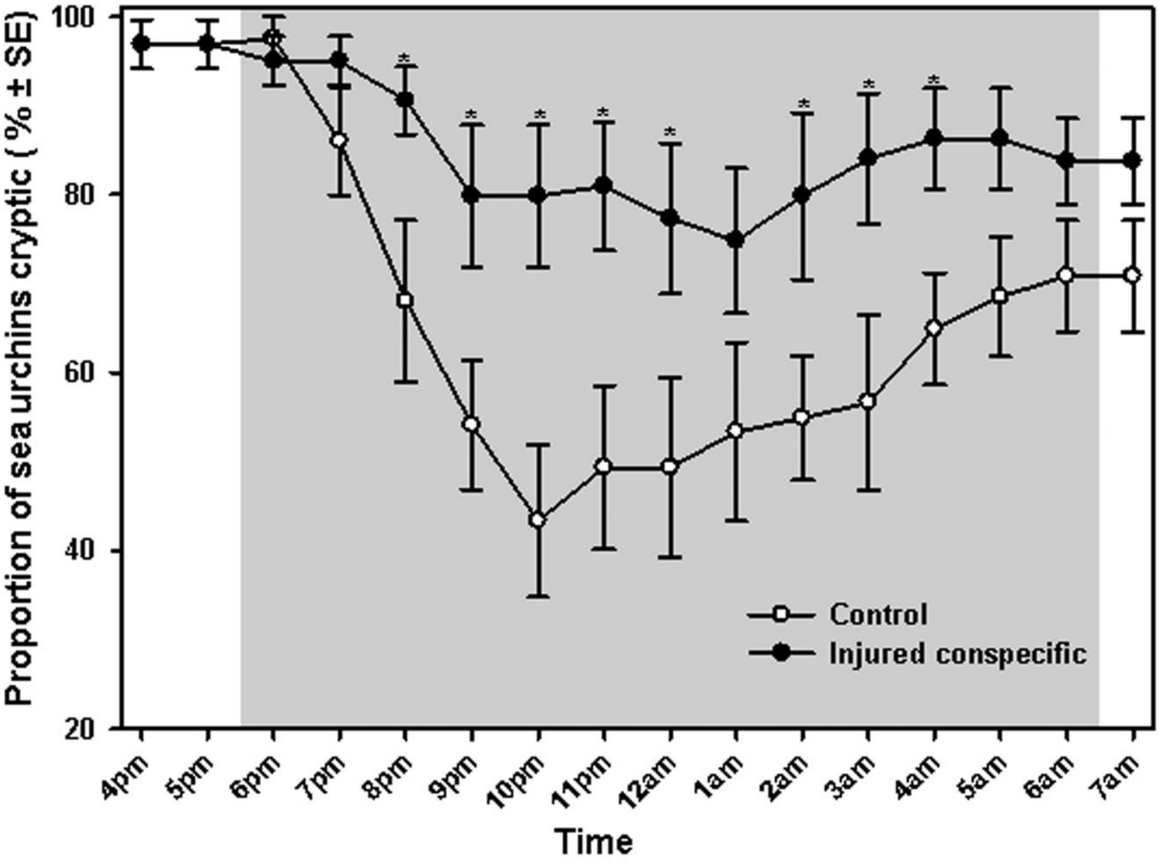

Fig. 4.7: The proportion of *E. chloroticus* remaining crevice bound throughout the night in response to an injured conspecific located above the crevice. Grey area represents night time observations. * denote significant differences (p <0.05) between control and treatment observations (p <0.05).

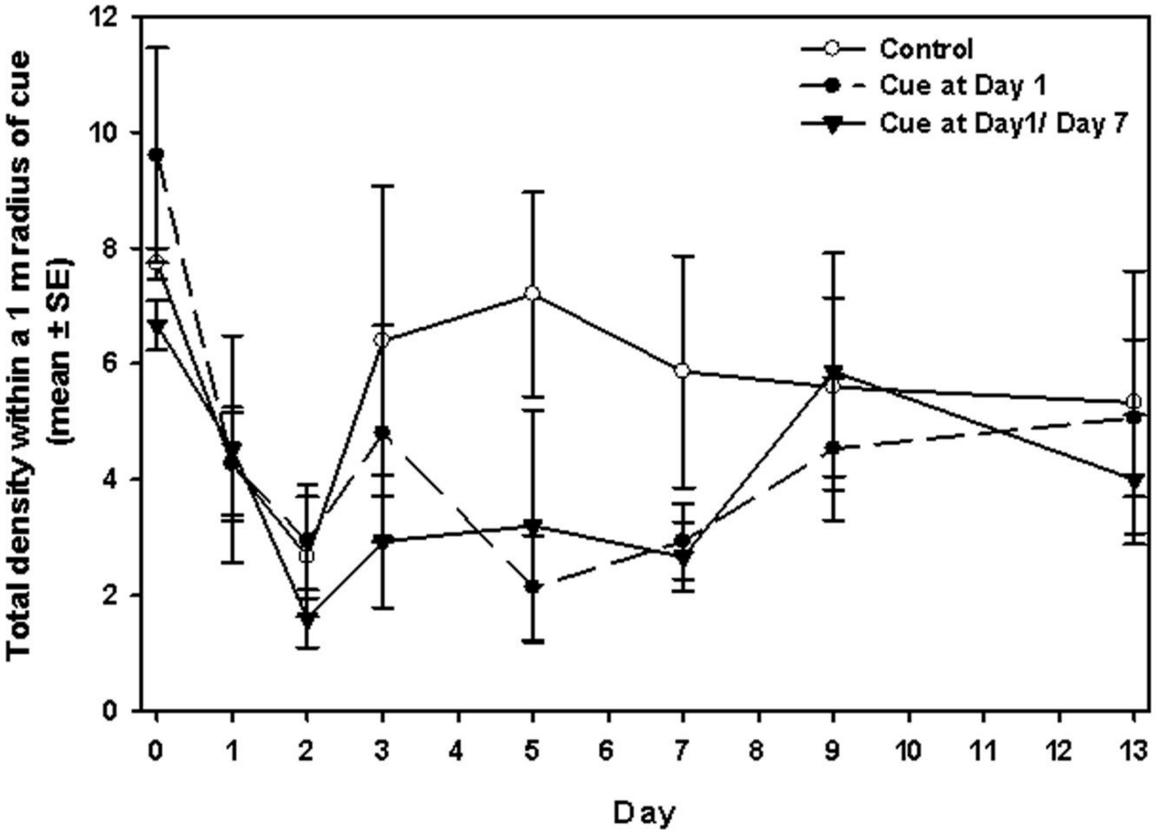

Fig. 4.8: Density of *E. chloroticus* within a 1 m radius of the centre of each plot in response to different treatments (control, injured conspecific day 1, injured conspecific day 1 and day 7), over a two week period.

Chapter Five: General Discussion

While the lethal effects of predator are well understood, the effects that predators can have on prey behaviour and morphology often receive little attention or are overlooked, yet these effects can also have important implications for predator-prey interactions and the ecosystem. This thesis provided insight into the effects of predators on the behaviour and morphology of the habitat-forming sea urchin *E. chloroticus*. Predators play a direct role in influencing the behaviour of this species (Chapter Two and Four, Fig 5.1), while indirectly influencing their morphology via cascading trophic effects that increase the sea urchins' food supply (Chapter Three, Fig 5.1). Changes in behaviour and morphology should increase sea urchin persistence in areas such as marine reserves, where predator pressure is high (Fig 5.1), while behavioural changes, such as increased crevice occupancy, likely strengthens the density-mediated trophic cascade already demonstrated in this system (Shears & Babcock, 2002; Shears et al., 2008) via a behaviourally-mediated pathway (Fig 5.1).

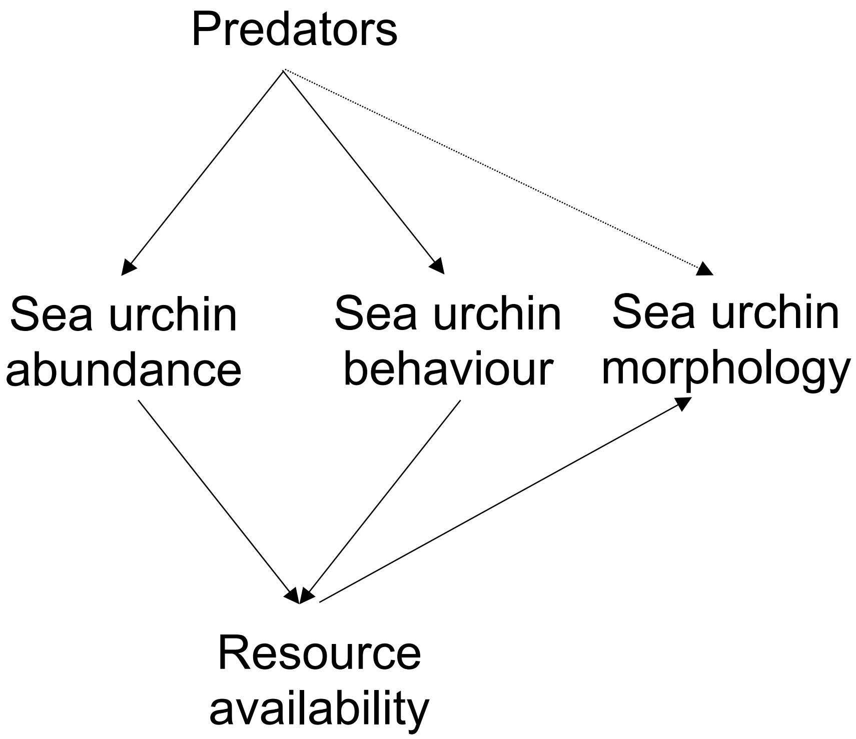

Fig. 5.1: The direct and indirect pathways in which predators affect *E. chloroticus*. Predators have direct lethal effects on abundances and direct non-lethal effects on behaviour. These effects can alter the interactions between sea urchins and their resources, facilitating trophic cascades that increase resource abundance. This creates a feedback mechanism whereby predators indirectly influence sea urchin morphology by increasing the food supply to the remaining population. Predators also have a weak non-lethal effect on sea urchin morphology.

Population persistence

Predators may inadvertently aid prey persistence through direct and indirect interactions. Even though predation pressure on sea urchins is generally higher inside marine reserves (McClanahan & Muthiga, 1989; Sala & Zabala, 1996; Shears & Babcock, 2002), populations are still able to persist. Within north-eastern New Zealand marine reserves most sea urchins resided within cracks and crevices on the reef, which was a direct result of increased predation pressure, as shown in Chapter Two. Occupying refuge habitats is a particularly good form of avoidance behaviour because predator access is generally restricted in these areas, increasing prey survival (Burks et al., 2001; Hereu et al., 2005; Alexander et al., 2012; Clemente et al., 2013). This also allows individuals to live within closer proximity to one another, which may be particularly important for broadcast spawners such as sea urchins because fertilisation success declines exponentially with distance between individuals (Gascoigne & Lipcius, 2004). This behavioural response to predation may represent an important mechanism for stabilising prey populations and preventing localised extinction in the presence of predators (Sih, 1987; Berryman & Hawkins, 2006).

Predators may further aid prey persistence via the induction of morphological defences. While most investigations show that changes in prey morphology are predominantly induced in direct response to predation (or herbivory) cues (Brönmark & Miner, 1992; Cronin & Hay, 1996; Dahl & Peckarsky, 2002) I found evidence that predators may also indirectly or ‘inadvertently’ cause prey to induce defences through cascading trophic effects that alter their resource levels (Chapter Three). As the abundance and biomass of prey resources increases, due to cascading lethal and non-lethal trophic effects a feedback mechanism is likely to occur where food becomes more available to the remaining prey population. Being well-resourced has been shown to enhance the induction of prey defences (Chivers et al., 2008), therefore if more resources are available to prey species due to their predators then in these systems predators are likely to be indirectly important in lowering prey vulnerability and improving their population persistence.

Behaviourally-mediated trophic cascades

Predation risk may cause prey species to avoid profitable feeding grounds in order to improve their chances of survival (Lima & Dill, 1990). Inside north-eastern New Zealand marine reserves sea urchins sheltered in crevices to larger sizes than those on the adjacent fished reefs (Chapter 2). This is significant because larger sea urchins tend to consume more resources than smaller individuals (Contreras & Castilla, 1987; Barker et al., 1998) and are therefore likely to have a disproportionately large effect on the abundance and biomass of their resources. Predator induced reductions in sea urchin grazing pressure can increase kelp biomass (Byrnes et al., 2006) and sheltering behaviour is likely to strengthen the already demonstrated density-mediated trophic cascade occurring inside north-eastern New Zealand marine reserves (Babcock et al., 1999; Shears et al., 2008) by reducing the amount of time sea urchins spend on the reef actively foraging (Chapter Four). This suggests that density- and behaviourally-mediated indirect interactions can occur simultaneously in kelp forest ecosystems, which is consistent with many other ecosystems (Křivan & Schmitz, 2004; Schmitz et al., 2004).

Injured conspecifics as a predation risk cue

While sea urchins in the mesocosm experiment (Chapter Two) showed a strong behavioural response to cues from injured conspecifics it was important to test whether these cues also altered prey behaviour in natural field settings. As revealed in Chapter Four sea urchins also responded strongly to cues from injured conspecifics in field experiments, making them a valid tool for investigating predator effects on prey behaviour and morphology. Predation cues increased sea urchin sheltering behaviour in the mesocosm (Chapter Two) and restricted sea urchins to crevices throughout the night when they would normally move out onto the reef to graze (Chapter Four). Thus in environments where prey are able to shelter from their predators, conspecific alarm cues alone may play an important role in altering the interaction between prey and their resources. While alarm cues also elicited a strong response in exposed sea urchins that could not flee to shelter, within a week the density of sea urchins close to where the cue had been released had recovered. Experiments investigating predations cues in the wild were carried out on barren reefs where sea urchins are highly mobile (Hereu, 2005; Dumont et al., 2006) and always searching for food. The information gained from a single conspecific was also likely to degrade quickly. When food resources fluctuate slowly, i.e. on stable barrens, prey should spend more time foraging and less avoiding predators (Higginson et al., 2012). Therefore it is possible that on barren reefs the cues from a single predation event are not considered risky enough to prevent hungry, mobile sea urchins from avoiding an area for more than a few days.

Conclusion

This study has clearly demonstrated that predators can affect prey in a broader variety of ways than the simple “predator eats prey” scenario, with effects extending to their behaviour and morphology. These non-lethal effects can have important implications for predator-prey interactions, as well as for the structure of the ecosystem, and therefore should be considered equally important as lethal predator effects. Predator effects on density, behaviour and morphology can occur simultaneously and may occur through direct and indirect pathways, therefore it is important that future research projects aim to incorporate the potential for lethal and non-lethal predator effects as well as being aware of the multiple pathways in which they can occur.

Future directions

Based on the experiments and results from this study, there are several further questions worthy of investigation:

(1) What are the relative contributions of density-mediated and behaviourally-mediated indirect interactions to the overall strength of the kelp forest trophic cascade?

Research is required to investigate the relative effects of density and trait-mediated interactions on the kelp forest trophic cascade. Mesocosm experiments that quantify the grazing pressure of sea urchins exposed to live predators (density-mediated interactions) and predator cues (trait-mediated interactions) may provide an excellent first step for this type of investigation. A similar method to that of Trussell et al (2006), who investigated the relative strengths of density-mediated and behaviourally-mediated indirect interactions on a crab-whelk-barnacle food chain, could be used.

(2) Does* E. chloroticus *respond behaviourally or morphologically to cues released directly from predators?

As alarm cues from injured conspecifics enter the water column as a direct result of predation encounters, the cue environment is likely to contain both alarm cues and predator kairomones (Schoeppner & Relyea, 2005). Using quadpods, sea urchin behaviour could be investigated in response to chemical cues emanating directly from predators as well as situations involving both predator and alarm cues.

(3) Do indirectly induced defences reduce the vulnerability of sea urchins to predation?

More crush-resistant shells have been shown to lower gastropod vulnerability to predators (Boulding, 1984; Palmer, 1985). A tethering experiment, such as in McClanahan & Muthiga, (1989) or Shears & Babcock, (2002), but using a mixture of similar sized individuals from reserve and non-reserve sites would be useful for revealing if the marine reserve sea urchins with stronger test are less vulnerable to predation.

(4) Does fleeing from predation cues lower the grazing impact of exposed sea urchins?

Understanding the behaviour of exposed sea urchins after they have fled from predation cues could provide insight into whether or not these trait-mediated interactions cause a reduction in grazing rate on ‘urchin barrens’ or if sea urchins simply move to another patch of reef and continue to graze.

(5) Do sea urchins inside marine reserves rely solely on drift kelp as a food source?

Sea urchins, which were predominantly cryptic inside the marine reserves, were morphologically more robust than those on overfished reefs. While Chapter Three suggested that this was due to a greater availability of food inside the marine reserves it remains unclear what the main food source was for these sea urchins. Isotope analysis on the gut contents of cryptic individuals could be useful for whether food was derived from live kelp, drift kelp or a completely different source.

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Appendices

Appendix One: Supplementary material for Chapter Two

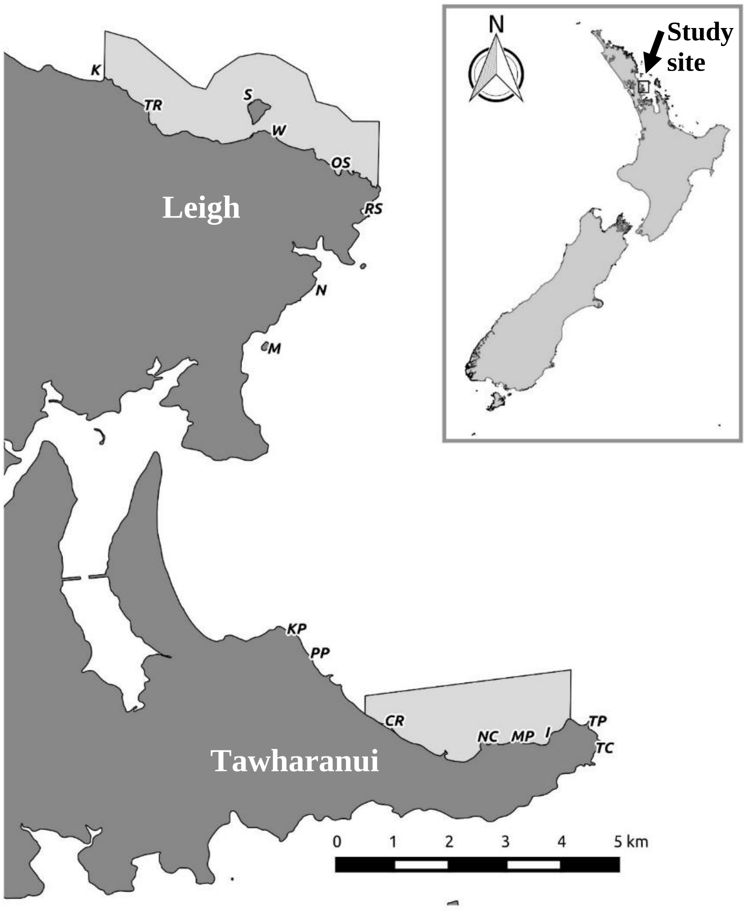

Fig. S2.1: Location showing general areas (Leigh and Tawharanui) and specific sites surveyed for predator, sea urchins and kelp in north-eastern New Zealand. Shaded areas indicate marine reserves. Labels denote sampling sites. From north to south; Kemps Bay (K), Te Rere Point (TR), Schiel's Pool (S), Waterfall Reef (W), One Spot (OS), Rodney South (RS), Nordic Reef (N), Matheson Bay (M), Karamuroa Point (KP), Pukenihinihi Point (PP), Comet Rocks (CR), North Cove (NC), Midpoint (M), Iguana (I), Twin Peaks (TP) and Takatu Cave (TC). Shaded areas represent marine reserves. *Inset*: Map of New Zealand showing study site in north-eastern New Zealand

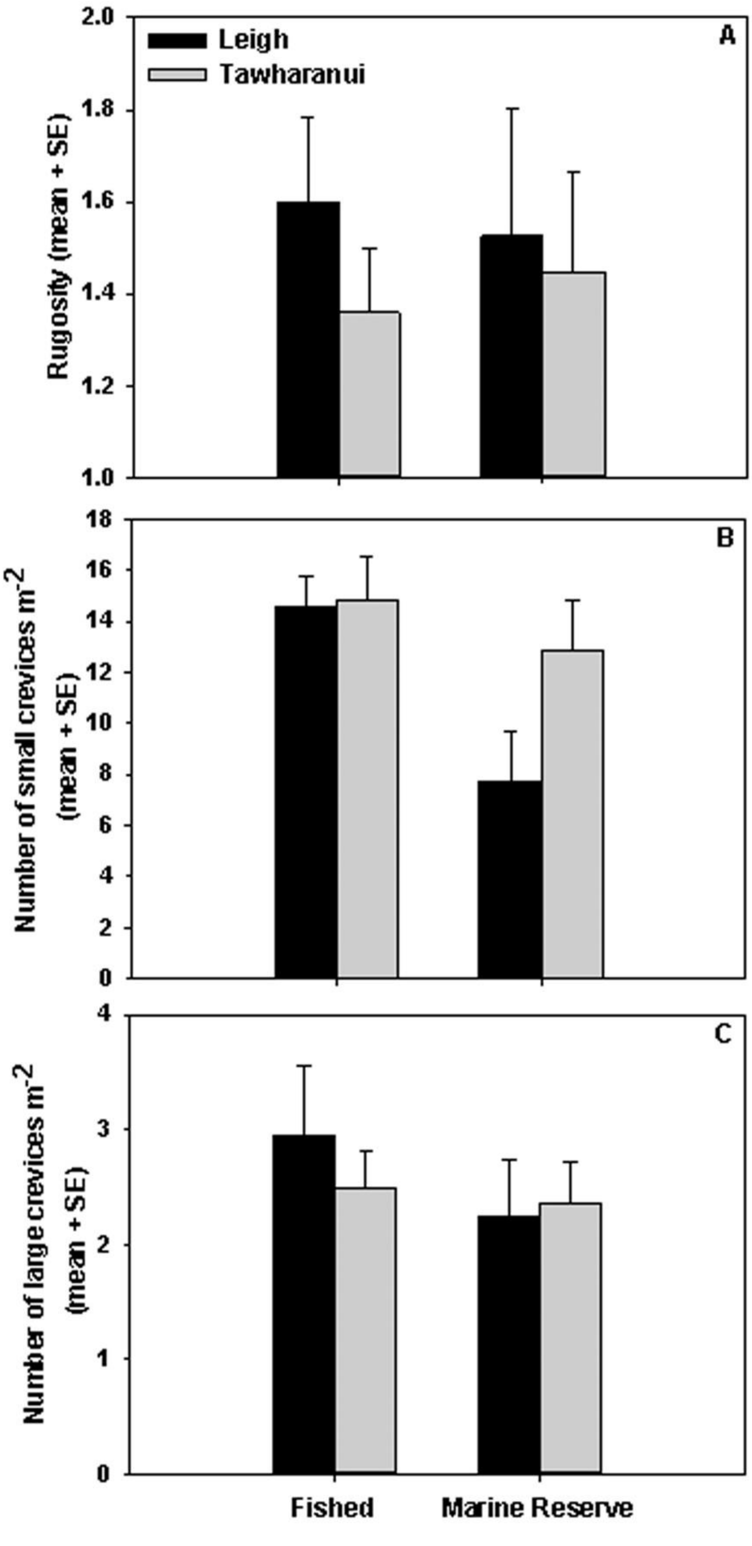

Fig. S2.2: Crevice availability measurements (A) rugosity, (B) number of small crevices (<125cm^{-3}) and (C) number of large crevices (>125cm^{-3}) on fished versus protected reefs at Leigh and Tawharanui, north-eastern New Zealand.

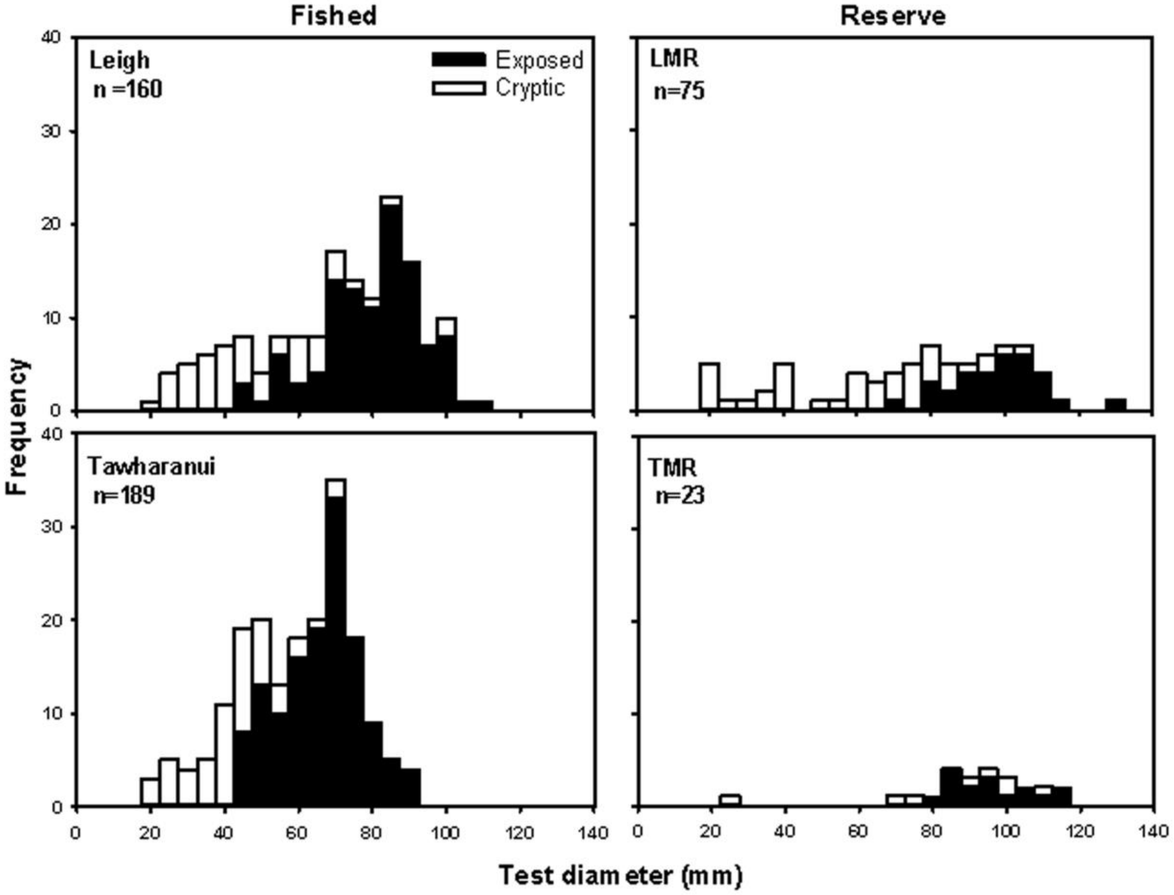

Fig. S2.3: Size-frequency distributions of the sea urchin *Evechinus chloroticus* sampled on fished and protected rocky reefs at Leigh and Tawharanui, north-eastern New Zealand. The white area of each bar represents cryptic individuals and the black area represents exposed individuals.

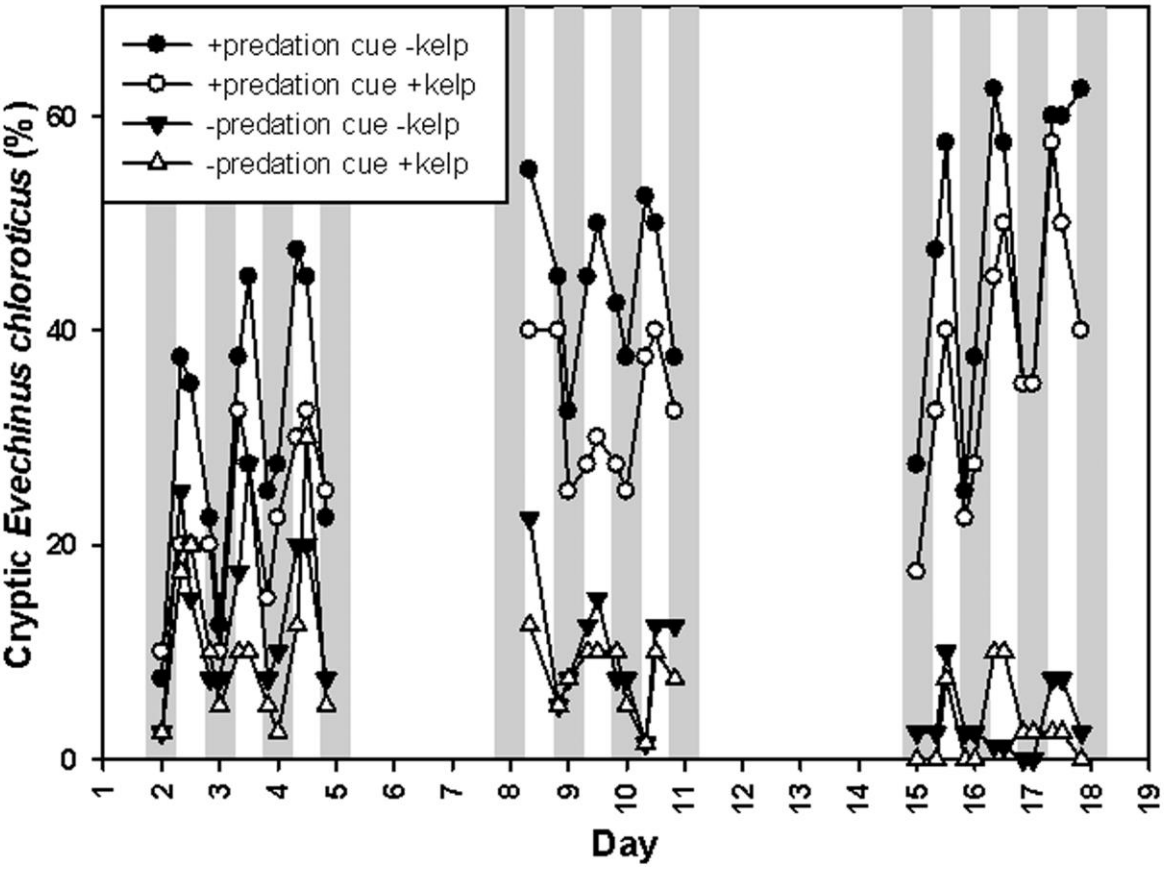

Fig. S2.4: Diurnal pattern of sea urchin *Evechinus chloroticus* crevice occupancy in a mesocosm experiment in which food supply and predation cues were manipulated. Grey bars represent night time hours. Standard error bars have been omitted for clarity but the average error as a percentage of the mean, for each treatment group was as follows: “+predation cue, -food” 25%, “+predation cue, +food” 29%, “-predation cue, -food” 72% and “-predation cue, +food” 75%.

Appendix Two: Supplementary material for Chapter Three

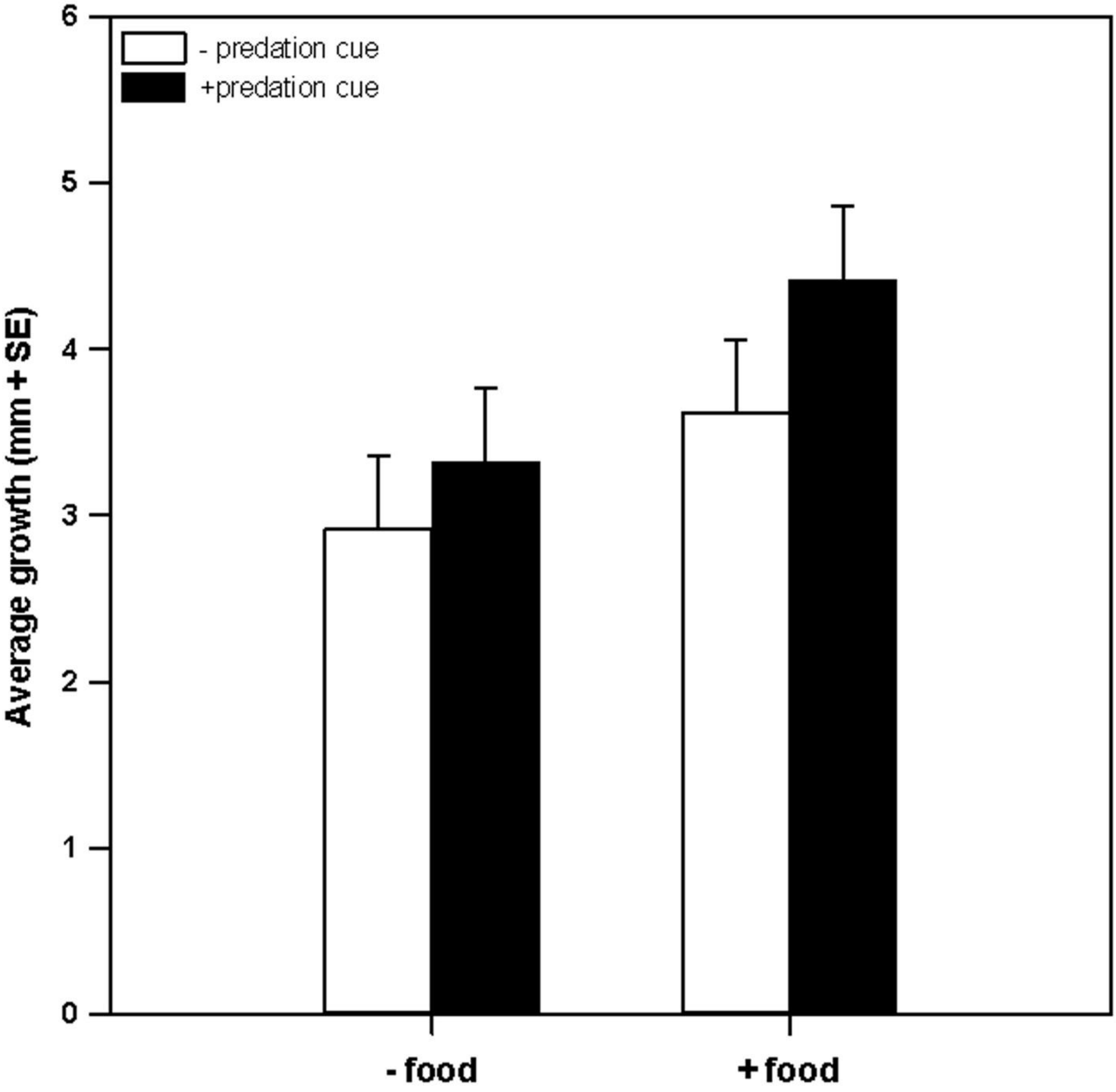

Fig. S3.1: Average *Evechinus chloroticus* growth over six months when grown under different food and predation cue conditions in the mesocosm experiment