The abundance, diet, and ecology of *Astrostole scabra* within the East Otago Taiāpure

Implications for the management of *Haliotis iris* populations

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Abstract

In communities where commercially important species are regulated by predation, information about basic ecological dynamics is necessary to make the simple recommendations about conservation policies and resource management. The abalone *Haliotis iris* is a commercially important species that is recovering from the effects of over harvesting within the East Otago Taiāpure. The present study examined the ecology of a common *H. iris* predator, the seven armed sea star *Astrostole scabra*. *A. scabra* prey preference, handling times, isotopic turnover and the effect of water motion on predatory capability were investigated experimentally to help explain observations of wild *A. scabra* populations. *A. scabra* demonstrated no prey preference via chemoreceptive detection in turbulent water plumes but did demonstrate a rheotactic feeding strategy, moving against a current to encounter prey. *A. scabra* locomotion and prey capture success was negatively affected by water motion and *H. iris* was more likely to escape *A. scabra* predation in high water motion conditions. *A. scabra* handling time was short when consuming *H. iris* and the mussel *Perna canaliculus* but significantly greater for the Turbinid snail *Cookia sulcata*. Handling time information was useful for adjusting field surveys of diet to account for disproportionately greater observations of prey species with long handling times. Isotopic turnover in *A. scabra* was examined and found to be longer than the six month experimental period. Field surveys identified that *A. scabra* abundance and diet was highly variable among sites and *A. scabra* abundance was significantly lower at wave exposed sites. Adult (100 – 124 mm) *H. iris* were a major dietary component of *A. scabra* and constituted 55% of the observed diet. Several factors were determined to affect the distribution of *A. scabra* including wave exposure, substrate, salinity and prey availability. Results from isotope analysis of *A. scabra* diet were concurrent with field survey results and identified populations with significantly greater diets of *H. iris*. In conclusion, because *H. iris* was a major dietary component of *A. scabra*, if the population size of *A. scabra* were to increase the recovery of *H. iris* populations may be threatened by predation. Furthermore, the fact that adult *H. iris* were consumed by *A. scabra*, may mean that large breeding individuals would be removed and *H. iris* populations would suffer reduced recruitment. *A. scabra* abundance should be monitored in the future to detect any further increase in abundance.
Preface

The completion of this thesis has been a long journey, one I have enjoyed (mostly) and learnt much from. I am incredibly thankful and proud to have known all of those who have helped me along the way and made this experience one I will never forget. Firstly, a huge thanks to my supervisors, Chris Hepburn and Steve Wing for your experience, guidance, encouragement and patience throughout the entire process.

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Chapter 1

General Introduction

Astrostole scabra and Haliotis iris within the East Otago Taiāpure (Courtesy Chris Hepburn)
1.1 The Role of Predators in Marine Ecosystems

Predators play an important role in structuring ecosystems (Duggins 1983, Babcock et al. 1999). By inflicting ‘top down’ control on prey communities they shape the way in which marine ecosystems function (Babcock et al. 1999, Heithaus et al. 2008). Top predators in marine ecosystems are frequently targeted by fisheries and are therefore vulnerable to over-exploitation (Coleman and Williams 2002). The depletion of top predator populations can result in a trophic cascade (Coleman and Williams 2002). Trophic cascades occur when densities of top predators decline, directly reducing mortality of lower level predator species and indirectly increasing predation on lower trophic levels (Coleman and Williams 2002). Failure to predict a trophic cascade can have catastrophic effects on other sectors of the ecosystem and can eventually result in the collapse of other fisheries (Scheffer et al. 2001, Beisner et al. 2003). Such a fishery collapse was experienced in northwest Atlantic coastal ecosystems, where overfishing of large sharks relaxed predation pressure on smaller shark and ray species thereby allowing populations to grow (Myers et al. 2007). Subsequently, increased predation of small sharks and rays raised predation pressure on scallop populations, resulting in the closure of a century-old scallop fishery (Myers et al. 2007). Failure to predict these catastrophic changes in community structure can have costly consequences for other sectors of the ecosystem (Beisner et al. 2003).

Fishery-altered ecosystems, often lack top down control and exhibit reduced productivity when compared with un-fished ecosystems, like those present in marine protected areas (Babcock et al. 1999, Shears and Babcock 2002, 2004). Marine reserves allow the abundance of apex predators to be restored and re-establish top down control in an ecosystem (Babcock et al. 1999, Shears and Babcock 2002, 2004). Studies of New Zealand marine reserves have identified the importance of the New Zealand rock lobster *Jasus edwardsii* (Palinuridae) and the New Zealand snapper *Pagrus auratus* (Sparidae) in controlling populations of the sea urchin *Evechinus chloroticus* (Echinometridae) (Babcock et al. 1999, Shears and Babcock 2002). Within reserve boundaries *J. edwardsii* and *P. auratus* occur in high abundance and exert high mortality on *E. chloroticus*, reducing herbivory and enabling kelp forest biomass to increase (Babcock et al. 1999). Increased kelp biomass raises the primary productivity of an area and provides habitat for many species (Babcock et al. 1999).

Asteroids are common predators in coastal marine ecosystems and can play important roles in structuring prey communities (Menge 1972, Navarrete and Menge 1996, Wing and Leichter 2011). Asteroids can exert strong predation pressure on prey communities and have the
ability to increase in density after the removal of predators (Navarrete and Menge 1996). Several temperate examples exist of predatory Asteroid species which regulate the abundance of prey species exist and include: *Pisaster ochraceus*, North Pacific Ocean (Robles et al. 1995, Navarrete and Menge 1996); *Asterias rubens*, Norwegian Sea (Saier 2001) and *Heliaster helianthus*, South Pacific Ocean (Navarrete and Manzur 2008, Barahona and Navarrete 2010). Within New Zealand, four predatory Asteroid species are common: *Stichaster australis* (Menge et al. 1999), *Sclerasteria mollis* (Talman et al. 2004), *Coscinasterias muricata* (Wing and Leichter 2011) and *Astrostole scabra* (Town 1979, 1980a, 1980b, 1981).

1.2 Astrostole scabra

*Astrostole scabra* (Hutton 1872) (Family: Asteroidea) is a large, generalist predator of coastal marine ecosystems in New Zealand and is known to predate more than 60 mollusc and crustacean species (Town 1980b, 1981). The most comprehensive study on *A. scabra* biology, movement and diet preference focused on small intertidal individuals by Town (1979, 1980a, 1980b, 1981). Town (1980b, 1981) observed that diet changed according to the size of individuals and between different areas. *A. scabra* is a known predator of the abalone *Haliotis iris* and was the main source of mortality in a *H. iris* population monitored for 12 months (McShane and Naylor 1997). Town (1979, 1981) did not record *H. iris* as a common prey species, as his study focused on small individuals and it is therefore likely that only large *A. scabra* are predators of *H. iris*. The present study intends to examine the ecology and diet of large *A. scabra* which are capable of predating *H. iris*. This work attempts to determine whether *A. scabra* is a potential threat to the recovery of depleted *H. iris* populations within the East Otago Taiāpure.

The abundance of *A. scabra* is thought to be increasing in Otago. Local fishermen of *Jasus edwardsii* have reported marked increases in the number of *A. scabra* found in pots (Pers. comm. Chris Hepburn) and high densities were observed during baseline Taiāpure surveys (Richards 2009). The apparent surge in *A. scabra* abundance has sparked interest in the ecology of this predatory Asteroid. This study intends to collect base line data of *A. scabra* populations within the East Otago Taiāpure so that the size of the population can be monitored by Taiāpure management. Furthermore the diet of *A. scabra* will be investigated to determine to what extent increases in the abundance of *A. scabra* may affect the recovery of depleted *H. iris* populations.
Figure 1.1: *Jasus edwardsii* feeding on an *Astrostole scabra* in Doubtful Sound New Zealand, (Courtesy Stephen Wing).

It is possible that the recent growth of *A. scabra* populations is a result of reduced *Jasus edwardsii* abundance. *J. edwardsii* are the only species known to predate *A. scabra* and has been reduced by overfishing, therefore it is likely that a decline in the abundance of *J. edwardsii* may allow growth of *A. scabra* populations (Stephen Wing, pers. comm., Babcock et al. 1999, Shears and Babcock 2002).

### 1.3 *Haliotis iris*

Members of the *Haliotis* genus, commonly known as abalone, are of high commercial value and vulnerable to over-exploitation, due to their sedentary nature, tendency to aggregate and low rate of replenishment (McShane 1996, Campbell 2000). Over harvesting of Haliotidae species has resulted in the collapse of abalone fisheries in North America (*H. Fulgens, H. Cracherodii, H. Sorensi*) (Karpov et al. 2000), Alaska (*H. Kantschatkana*) (Woodby et al. 2000), and South Africa (*H. midae, H. spdicea*) (Hauck and Sweijd 1999).
Studies of the Australian *Haliotis rubra* fishery suggest it is possible to have a sustainable abalone fishery as long as there is a low harvest rate and high minimum no-take length (McShane 1992, McPhee 2008). McPhee (2008) recognises that abalone have relatively short distance larval distribution, resulting in highly localised population structure. Short larval distribution has implications for managing the spatial distribution of fishing effort. If fishing pressure is focused at particular reefs, localised depletion can occur as recruitment from adjacent reefs is low (McPhee 2008).

*Haliotis iris* (Martyn 1784), commonly known as the black foot paua, is endemic to New Zealand, where it occupies shallow, temperate reefs throughout the country (McShane *et al.* 1994). A commercial fishery exists for *H. iris* and is managed via the Individual Transferable Quota (ITQ) system, which enforces a minimum no take size (125mm) for commercial and recreational fisheries, and a maximum bag limit of ten per person for recreational fishers (Breen *et al.* 2003).

![Figure 1.2: Juvenile *Haliotis iris* on top of a rock within the East Otago Taiāpure (Courtesy Chris Hepburn).](image-url)
Abalone are preyed upon by a suite of predators including reef fishes, eels, octopus, crabs, crayfish and Asteroids (Roberts et al. 2007, McShane and Naylor 1997, Schiel 1993). Predation is most intense for juvenile *H. iris* which display a preference for shallow water habitat, living beneath boulders until a size refuge is reached (McShane and Naylor 1995, Roberts et al. 2007, Cornwall et al. 2009). As *H. iris* grow larger they become less vulnerable to predation and move from their highly cryptic habitat to more open habitat in deeper water. (Roberts et al. 2007).

McShane and Naylor (1997) assessed natural mortality by monitoring enclosed populations of adult *H. iris* and identified *A. scabra* as the main source of mortality. However, predation rates were low, only five of 1000 individuals were consumed during a twelve month period. Predation is likely to increase if the abundance of *Astrostole scabra* increases as reported by East Otago Taiapure surveys and commercial fishermen (Richards 2009).

1.4 Abiotic effects on Predator and Prey interactions

The impact of a predator population is greatly influenced by the size of the predator population as too many or too few predators can have large influences on prey populations (Scheffer et al. 2001, Beisner et al. 2003). However, as well as the size of a predator population, the effectiveness of a predator species can also be affected by other abiotic and biotic factors which affect how quickly the ‘predation cycle’ can be executed. The predation cycle refers to the sequence of events in a single predation event, specifically the location, capture and handling time of prey (Harrold 1982, Barbeau and Scheibling 1994). The location of prey depends on several factors including, prey abundance, prey choice and locomotive speed of the predator. Capture rates of prey may be affected by the size of a predator or escape mechanisms prey. Handling time likely depends on the morphology of a prey species and may be prolonged in prey which use shells to conceal themselves from predators. The present thesis tested the importance of such factors on *Astrostole scabra* predator-prey interactions to help explain what factors primarily determine the level of *A. scabra* predation in a particular area. Several primary factors including water motion, depth, temperature, prey choice, prey capture rates, handling times of prey species, predator abundance and prey abundance were expected to affect *A. scabra* predation and will be incorporated into experiments and field surveys in this thesis.
1.5 Study site, The East Otago Taiāpure

This study was conducted within the East Otago Taiāpure (Figure 1.3). Taiāpure marine reserves are local management tools established in areas culturally important to Māori, and possess legislation to protect local populations of culturally important species from overharvest (Hepburn et al. 2010). Tangata whenua (Local Māori, people of the land) and the local community are responsible for the management of fishing within reserves boundaries and can introduce regulations to aid the management of a particular fishery (Bess 2001). Introduced regulations can dictate the species, size, and quantity of fish that can be taken, as well as harvest method(s) used and time of year particular species may be caught (Hepburn et al. 2010). Because Taiāpure reserves are managed by people with a historic knowledge of the area, management issues can be identified and introduce specific, targeted regulations to protect threatened species endangered (McCarthy and Possingham 2006). Taiāpure allow commercial fishing to continue under the conditions there is no expansion of fishing effort (Hepburn et al. 2010). The East Otago Taiāpure was established in 1999 and has since imposed a total ban on the gathering of Haliotis iris from the Huriawa Peninsula, while at other reefs bag limits have been halved from ten to five per person, per day (Satyanand 2010). Studies of Astrostole scabra were useful to East Otago Taiāpure reserve managers, as they determined whether A. scabra is a key predator of H. iris and if A. scabra is likely to impacting the recovery of depleted H. iris populations.

Three study sites were used in the present study, Big Rock, Puketeraki and Huriawa, all of which occurred within the East Otago Taiāpure (Figure 1.3). Astrostole scabra used in laboratory experiments were collected from three sites, Aramoana Mole, Puketeraki and Huriawa, experiments were conducted at Portobello Marine laboratory (Figure 1.3). Prey species used in experiments were collected from Matainuka and Warrington (Figure 1.3). Additional information on A. scabra, prey species and sites used can be found in the appendix (p 126).
1.6 Thesis objectives

The overall objective of the present thesis was to:

Investigate aspects of *A. scabra* biology and ecology to predict the influence of *A. scabra* predation on local prey populations.

In order to address this objective the following two aims were addressed:

Firstly, this study aimed to examine aspects of the *Astrostole scabra* predation cycle, including the location, selection, capture ability and handling times of prey. Each aspect was examined in detail to allow assumptions to be made about the ecology of wild *A. scabra* populations. Furthermore this thesis examined the effect of environmental factors such as water motion and temperature on the locomotion and capture success of *A. scabra*. Water motion in the form of wave action is an important disturbing force in marine ecosystems and spatial differences in wave action are often reflected in the biota of an area.
Secondly, the present thesis aimed to calculate the density, distribution and diet of *Astrostole scabra* populations within the East Otago Taiāpure. Feeding surveys were used to identify diet and distribution of *A. scabra* across three wave sheltered sites and three wave exposed sites. Diet was also examined using stable isotope analysis to test the accuracy of data collected in field surveys. Information collected from field surveys and stable isotope analysis was used to assess whether *A. scabra* presents a threat to the recovery of *H. iris* populations.

1.7 Thesis outline

1.7.1 Chapter 2 – Chemoreception and prey preference in *Astrostole scabra*

Chapter involves a behavioural experiment in which *Astrostole scabra* were exposed to two water plumes, each containing the scent of prey to examine whether *A. scabra* has the ability to distinguish prey odours in moving water. The experiment aimed to identify whether *A. scabra* preferentially selects some species more often than others.

1.7.2 Chapter 3 – Effect of water motion on *Astrostole scabra* and *Haliotis iris* predator-prey interactions

Chapter tested *Astrostole scabra* locomotion speed and ability to capture *Haliotis iris* when subjected to varying levels of water motion. Particular focus was given to the *H. iris* escape response and its effectiveness in evading Asteroid predation.

1.7.3 Chapter 4 – *Astrostole scabra* handling times

Chapter examined *Astrostole scabra* handling time for *Haliotis iris*, *Cookia sulcata* and *Perna canaliculus* to identify how handling time varies between different species and different sized individuals. Results were used to adjust field survey results of *A. scabra* diet to account for differences in handling times between prey species.
1.7.4 Chapter 5 – Field survey of Astrostole scabra distribution and diet

Field surveys were conducted at wave exposed and wave sheltered sites to identify the density, distribution and diet of *Astrostole scabra* populations. Surveys of *Haliotis iris*, *Cookia sulcata* and *Perna canaliculus* conducted at the same sites in 2008 – 2009 were used to examine how prey abundance affects *A. scabra* density.

1.7.5 Chapter 6 – Stable isotope analysis of Astrostole scabra diet

Stable isotope analysis is used to calculate isotope signatures of *Astrostole scabra*, *Haliotis iris*, *Cookia sulcata* and *Perna canaliculus* to calibrate with field survey results of *A. scabra* diet. This chapter also involved a lab experiment which calculated turnover rates and isotopic fractionation in *A. scabra* fed a constant diet for six months.

1.7.6 Chapter 7 – General discussion

Results from lab experiments in chapters 2, 3 and 4 were summarised describe *A. scabra* ecology as a predator. Knowledge about the ecology of *A. scabra* was used explain the observations of *A. scabra* within the East Otago Taiāpure in order to determine which factors have the greatest influence on *A. scabra* distribution and predation potential. The threat of *A. scabra* predation to *H. iris* populations was discussed to provide recommendations for the management of both species.
Chapter 2

Chemoreception and Prey Preference in *Astrostole scabra*

A rock wall forces *Astrostole scabra* to decide which odour plume to move towards.
2.1. Introduction:

2.1.1. Chemoreception in Asteroids


2.1.2. Astrostole scabra prey

Astrostole scabra is a large generalised predator known to consume more than 60 prey species (Town 1980b). Town (1980b) studied A. scabra diet and food preference in small, intertidal individuals from Kaikoura, New Zealand using still water preference tests, where individuals were left overnight to consume a preferred prey species. A preferred prey species is the one which is chosen most often by a predator when given a choice. Optimal foraging theory
predicts that choices should favour species with highest calorific yield per hour of handling time (Menge 1972). Town (1980b) observed preference towards some prey species and discrimination against others. He also observed variation in diet of A. scabra collected from separate sites and between large and small individuals (Town 1980b). Small A. scabra used by Town (1980b) consumed mainly intertidal chitons and gastropod species, while larger A. scabra are observed to consume larger subtidal species including Haliotis iris and green lipped mussels, Perna canaliculus (Town 1980b).

The present study examined prey preference of large A. scabra, collected from Otago reefs, in a moving water choice experiment. Town (1980b) conducted his preference experiments in still water and allowed A. scabra to handle prey overnight before selecting a preferred species to consume. Therefore prey selection allowed direct contact with prey before a preferential choice was made. In this experiment A. scabra was required to move towards and select preferred prey based purely on olfactory cues. Therefore this experiment design tested A. scabra's chemoreceptive ability as well as its dietary preference. Prey species tested in this experiment included H. iris and P. canaliculus, as well as two Trochoid snail species, Cookia sulcata and Turbo smaragdus. T. smaragdus occurs in high abundance along both Kaikoura and Otago coast lines (Town 1980b, pers. obs.). Although T. smaragdus occurs in high abundance, Town (1980b) identified that it was rarely consumed by A. scabra in the field and was therefore selected against as a prey item. Preliminary field surveys identified C. sulcata as a common food item for large A. scabra in Otago (Pers. obs.). Preference for H. iris or P. canaliculus may indicate that these commercially and culturally important species are important dietary components of large A. scabra within the East Otago Taiāpure.

2.1.3. Flow conditions

Fluid dynamics are an essential part of Asteroid chemoreception and therefore a wide range of methods have been used to test chemosensory abilities under different flow conditions. Research has investigated chemoreception using Y-mazes (Castilla and Crisp 1970, Castilla 1972, Sloan and Northway 1982, Brewer and Konar 2005), flumes (Dale 1997, Drolet and Himmelman 2004, Thompson et al. 2005), wave tanks (Gagnon et al. 2003), choice chambers (Campbell et al. 2001), moving water aquaria (Rochette et al. 1994) and still water aquaria (Town 1980b, Valentinčič 1985, Drolet and Himmelman 2004). Different apparatus often produce different results because flow conditions and therefore signal transmission varies greatly between different methods. (Dale 1997, Drolet and Himmelman 2004). This
experiment was concerned with *A. scabra* prey preference, but more importantly it endeavoured to infer about the chemoreceptive ability of *A. scabra* in the wild. Therefore flow conditions were not made to be laminar and represented conditions present in wave washed environments (Zimmer and Butman 2000). A choice chamber required *A. scabra* to select turbulent water plumes that contained the scent of prey.

2.1.4. Hypotheses

Two hypotheses determined *A. scabra*’s overall chemoreceptive ability. Firstly, if *A. scabra* was capable of distance chemoreception it would select and move towards prey odour plumes more often than paired control water plumes of unscented water. Secondly, if *A. scabra* possessed the ability to differentiate between prey species, it would select and move towards odour plumes of *T. smaragdus* less often than other species as it has been previously shown to be neglected by *A. scabra* as a prey item (Town 1980b). Lastly, we expect that movement rate in *A. scabra* will be temperature dependant, with slow responses predicted to occur on cooler days.

**Methods:**

2.2.1. Experimental design

Prey preference was determined using a series of paired choice experiments, in which *Astrostole scabra* were required to select and move towards one of two scented water plumes, and were based on the tank design used by Campbell *et al.* (2001). Experiments tested ten treatments which comprised every pair combination of *Haliotis iris, Cookia sulcata, Perna canaliculus, Turbo smaragdus* and a control treatment with no prey. Water flowed over prey prior to reaching *A. scabra*. *A. scabra* were required to move to within 5 cm of the odour plume source to establish a positive response. *P. canaliculus* were cleaned of epiphytes prior to tests and were required to have shells open and be respiring before tests could began. Similarly, *C. sulcata* and *T. smaragdus* were required to have their foot extruded from their shells. Paired prey treatments were replicated between 9 and 37 times and were alternated between prey tanks as a means of control. The choice tank was emptied of water every time a new *A. scabra* was tested. Twenty-two *A. scabra* were used in the experiment and were
tested systematically so that no individual was tested more than twice on any one day. Four *A. scabra* individuals were tested before prey treatments were swapped for fresh specimens. *A. scabra* were collected from two sites and ranged in diameter from 28.5 to 51.0 cm. All *A. scabra* were starved for three weeks prior to and throughout preference tests to ensure similar starting condition. Water was collected from Otago Harbour and temperature varied between 9.25°C and 11.5°C during experiments. See Appendix for further information on *A. scabra* used in this experiment.

2.2.2. Preference test tank setup

A two stage tank array was used for preference experiments (Figure 2.2). Sea water flowed into each of the elevated ‘prey tanks’ from the same source. Tank connection pipes contained flow control valves so that flow could be switched on or off. Water began in prey tanks and moved through a ‘mixing chamber’ where it flowed over the bodies of prey before entering the ‘choice tank’. The mixing chamber was positioned within the prey tank and consisted of a PVC pipe open at both ends with a plastic mesh floor (Fig 2.2B). Water was taken up from the bottom of the mixing chamber, flowed over the whole body of the prey and exited from above. The mesh floor of the mixing chamber was used to maximise the signal propagation of prey so that water came in contact with their entire body, including the bottom of foot in gastropod species. Water then flowed through pipes from the mixing chambers into the choice tank, where it formed two parallel water plumes 24 cm apart (Figure 2.1). The 24 cm distance of plumes allowed a wide separation of odour plumes while still ensuring that the smallest *A. scabra* (28.5 cm) would receive both signals. Plumes were separated by a rock wall which extended 40 cm into the Choice Tank. The rock wall made sure *A. scabra* made a definite preferential response as it meant that *A. scabra* could only move towards one plume source. The choice tank maintained a shallow depth (< 10 cm) to avoid effects of negative geotaxis (Castilla 1972). Water exited the system through drainage pipe located behind the subject animal (Figure 2.1 and 2.2).

Prey tanks were elevated to the same height and were maintained in continuous overflow, so that the pressure within each tank would be equal and thus generate similar flows. Connection pipes were of equal length and diameter, however, out flows from prey tanks were slightly different (Figure 2.1). Out flows from prey tanks A and B were 100 and 107 ml s⁻¹ respectively. Odour signals remained largely separated so that *A. scabra* encountered
different scents on each half of the body, therefore any minor differences in flows between tanks was not considered important.

Figure 2.1: Odour plumes flowing into the ‘choice tank’ from ‘prey tanks’ A (blue) and B (green). The rock wall separates the two plumes and forces *A. scabra* to make a clear preferential response. Water drained through a mesh covered hole at the rear of the tank.

2.2.4. Experimental process

*Astrostole scabra* were placed in the choice tank oral side down so that the centre of an individual was 80 cm from the inflow pipes. *A. scabra* were left to acclimatise until arm tips curled up and terminal sensory podia were extended (an indicator of chemosensory detection), at which time flow control valves were then turned on and timing began. Individuals were timed until they reached the marked finish line located 5 cm from the water plume source. If *A. scabra’s* trajectory was towards the stimulus and crossed finish line a positive response was recorded. A negative response was recorded if *A. scabra* moved in any direction other than towards the odour plumes, or did not reach the finish line within eight minutes of exposure to odour plumes.
Figure 2.2: A) Schematic drawing of the two stage tank array used in preference experiments. “P” represents where prey would be placed in the mixing chambers. Unfilled arrows show direction of water flow. Thin lines show water level in tanks. B) ‘Prey tanks’ A and B. Source water flows into prey tanks through the top pipes, and migrates through PVC pipe ‘mixing chambers’ and to exit into ‘choice tank’. Overflow pipes draw off excess water to maintain equal tank depths.
2.2.5. Data analysis

Results were analysed using JMP 9 statistical software to carry out $\chi^2$ comparison tests among treatments, predicting 50:50 ratio null hypothesis for odour plume choices. A general linear model was also used to test the effect of prey tank and prey species on preferential responses made by *A. scabra*. The effect of water temperature on time to reach outflow pipes and proportion of positive responses was analysed using a general linear model.

**Results:**

2.3.1. Analysis of prey preference

The majority of *A. scabra* moved towards the inflow pipes, recording positive responses in 82% of trials ($n = 237$). The rock wall regularly helped *A. scabra* make definite preferential responses. *A. scabra* demonstrated a negative response in 16% of experiments and only 2% of *A. scabra* did not move at all when presented with odour plumes ($n = 237$).

Despite the high rate of positive responses, *A. scabra* demonstrated no statistically significant preference for any prey species in any treatment combination (Table 2.1). Choices were random and reflect a 50:50 choice ratio. Even during trials where prey treatments were paired against control treatments *A. scabra* did not show preference towards prey. In fact, the greatest difference in choice belonged to a control pair, in which the control was selected for most often. Due to the lack of preference, comparisons of preferred prey between collection sites and *A. scabra* size groups have not been included.

*A. scabra* selected Tank A significantly more often than Tank B ($P = 0.036$). The outflow of the two prey tanks was measured prior to experimentation and Tank A was found to flow more quickly than Tank B by 7 ml s$^{-1}$ (Table 2.3). Therefore *A. scabra* appear to move upstream against currents regardless of prey odour and are attracted to stronger currents more than weaker ones. Prey species were housed equally in Prey Tanks A and B therefore choices were not affected by differences in tank selection (Table 2.2).
Table 2.1: Results of *Astrostole scabra* preference test, listing each pairing in order of greatest difference in selection. Significance was derived using a Chi-square test.

<table>
<thead>
<tr>
<th>Treatment pairing</th>
<th>n positive responses</th>
<th>Proportion of times selected</th>
<th>DF</th>
<th>$\chi^2$</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control / <em>P. canaliculus</em></td>
<td>17</td>
<td>0.65 / 0.35</td>
<td>1</td>
<td>1.43</td>
<td>0.225</td>
</tr>
<tr>
<td><em>H. iris</em> / <em>P. canaliculus</em></td>
<td>20</td>
<td>0.60 / 0.40</td>
<td>1</td>
<td>0.79</td>
<td>0.371</td>
</tr>
<tr>
<td><em>C. sulcata</em> / <em>T. smaragdus</em></td>
<td>24</td>
<td>0.58 / 0.42</td>
<td>1</td>
<td>0.66</td>
<td>0.416</td>
</tr>
<tr>
<td><em>C. sulcata</em> / Control</td>
<td>14</td>
<td>0.57 / 0.43</td>
<td>1</td>
<td>0.28</td>
<td>0.593</td>
</tr>
<tr>
<td><em>H. iris</em> / <em>C. sulcata</em></td>
<td>20</td>
<td>0.55 / 0.45</td>
<td>1</td>
<td>0.20</td>
<td>0.655</td>
</tr>
<tr>
<td><em>C. sulcata</em> / <em>P. canaliculus</em></td>
<td>24</td>
<td>0.54 / 0.46</td>
<td>1</td>
<td>0.17</td>
<td>0.683</td>
</tr>
<tr>
<td><em>P. canaliculus</em> / <em>T. smaragdus</em></td>
<td>7</td>
<td>0.57 / 0.43</td>
<td>1</td>
<td>0.14</td>
<td>0.705</td>
</tr>
<tr>
<td>Control / <em>T. smaragdus</em></td>
<td>15</td>
<td>0.53 / 0.47</td>
<td>1</td>
<td>0.09</td>
<td>0.796</td>
</tr>
<tr>
<td><em>H. iris</em> / <em>T. smaragdus</em></td>
<td>21</td>
<td>0.52 / 0.48</td>
<td>1</td>
<td>0.05</td>
<td>0.827</td>
</tr>
<tr>
<td>Control / <em>H. iris</em></td>
<td>33</td>
<td>0.51 / 0.49</td>
<td>1</td>
<td>0.03</td>
<td>0.862</td>
</tr>
</tbody>
</table>
Table 2.2: Comparison of flow and *Astrostole scabra* selectivity between prey tanks A and B. Degrees of Freedom, Chi-square value and p values compare the significance of *A. scabra* choices.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prey</td>
<td>4</td>
<td>1.0288</td>
<td>0.3921</td>
</tr>
<tr>
<td>Tank</td>
<td>1</td>
<td>0.0005</td>
<td>0.9823</td>
</tr>
<tr>
<td>Prey*Tank</td>
<td>4</td>
<td>0.0137</td>
<td>0.9996</td>
</tr>
</tbody>
</table>
2.3.2. Temperature effects

Water temperature varied between 9.25°C and 11.5°C throughout experimentation (Figure 2.3). Positively responding *Astrostole scabra* took longer to reach the finish line when tested in cooler water temperatures ($P = 0.0115$, $F = 3.043$ DF = 5) (Figure 2.3). As temperature increased *A. scabra* moved faster, taking less time to reach the finish line. Temperature did not significantly affect *A. scabra*’s motivation to move towards odour signals when tested using a One Way ANOVA ($P = 0.3826$, $F = 1.062$ DF = 5) (Figure 2.3).

![Graph](image)

**Figure 2.3**: Time for *Astrostole scabra* to reach finish line (○) and, percentage of positive responses (●) at varied water temperatures. Times to reach finish line are means ± S.E. ($n = 12 – 45$), letters denote significant differences between means.

y = $-2.6027x + 110.38$

$R^2 = 0.087$

y = $-27.335x + 460.84$

$R^2 = 0.7843$
Discussion:

2.4.1. Astrostole scabra prey preference

Results collected here demonstrate preferential responses made by Astrostole scabra were not dependant on the odour signals of prey. A. scabra did not select control plumes less often than those containing prey nor did they select against Turbo smaragdus as observed in wild A. scabra (Town 1980b). Therefore A. scabra does not appear to be capable of using distance chemoreception to identify prey when foraging in turbulent water conditions. This experiment was carried out in moving water so that results could be compared with the still water experiments conducted by Town (1980b). Town (1980b) investigated the ability of intertidal A. scabra to select their preferred prey when presented with a range of species. The experiment involved leaving an A. scabra in a water filled plastic tray overnight with a variety of prey species, arranged in a random order (Town 1980b). Town (1980b) observed significant preference for the chiton Ischnochitin maorianus and rejection of other species (Town 1980b). Therefore A. scabra does have the ability to discriminate between prey species in calm water or via direct contact with prey. Contact chemoreception is common in Asteroids and is reported to give more accurate preference responses than experiments which require distance chemoreception (Sloan and Northway 1982). Field surveys by Town (1981) and examples of other Asteroid species demonstrate prey attractiveness is often linked to prey size, therefore it is likely that some tactile senses are also used when selecting or rejecting prey (Penny and Griffiths 1984, Tokeshi et al. 1989). Town (1981) mentioned that Micrelencus dilatatus which was selected against may have in fact been rejected because of the small size of the species. Optimal foraging theory states that the most calorific prey should be the most attractive, therefore quantity as well as quality is important when selecting prey to consume (Barbeau and Scheibling 1994).

2.4.2. Moving water vs still water preference experiments

Despite a lack of preference, Astrostole scabra still responded positively to the water plumes and moved up stream in 82% of trials. Furthermore A. scabra selected the plume with a stronger current more often than the plume with weaker flow, which suggests currents are an important factor in A. scabra foraging behaviour. Asterias rubens demonstrates a similar behaviour, when exposed to stronger currents a greater proportion of individuals move upstream (Castilla and Crisp 1973). Asteroids often locate prey more easily in moving water.
than still water (Gagnon et al. 2003, Drolet and Himmelman 2004). Once sensing prey odours, *Asterias vulgaris* will move against a current to accurately locate distant food sources, however, in still water individuals must move within several centimetres before food can be sensed and is captured (Gagnon et al. 2003, Drolet and Himmelman 2004). *A. scabra* did not differentiate between distant prey species, and therefore is probably not capable distance chemoreception in turbulent water conditions.

2.4.3. Foraging behaviour

Asteroid search behaviour relies just as much on currents, as the odours carried by currents (Rochette et al. 1994, Zimmer and Butman 2000, Drolet and Himmelman 2004). Most Asteroids use one of two search behaviours when locating prey, rheotaxis or cross-stream orientation (Rochette et al. 1994, Drolet and Himmelman 2004). Cross-stream orientation describes Asteroid movement perpendicular to a current until a prey scent is recognised, at which time they move upstream to capture prey (Rochette et al. 1994, Drolet and Himmelman 2004). Good chemoreception is required for cross-stream orientation to be effective, as odours must be sensed from a distance (Drolet and Himmelman 2004). Moving cross-stream maximises the probability of encountering prey odour plumes, and has been described for Asteroid species *Asterias vulgaris* and *Leptasterias polaris* (Rochette et al. 1994, Drolet and Himmelman 2004, Thompson et al. 2005). Rheotactic behaviour refers to orientation and movement directly into prevailing currents, as observed here in *Astrostole scabra* (Moore et al. 1991, Drolet and Himmelman 2004). Rheotaxis can be chemically mediated where chemical signals and current are used together, or current can be used alone (Drolet and Himmelman 2004). *Asterias rubens* demonstrates chemically mediated rheotaxis and moves upstream in currents void of odour, but also selects the bait containing arm of a Y-maze when presented with a choice of prey or no prey (Castilla and Crisp 1970). As *A. scabra* moved upstream but did not select plumes containing prey odour, it is likely that this species uses rheotaxis without chemoreception when searching for prey. It is not uncommon for Asteroids to rely on chance encounter, especially for generalised species that do not need to locate specific, sporadic food sources (Barbeau and Scheibling 1994). It is likely that movement upstream is a means of concealment while foraging, as it allows *A. scabra* to approach prey from an inconspicuous position (Rochette et al. 1994).
2.4.4. Temperature effects

It took Astrostole scabra significantly longer to reach the water plume source in cooler temperatures. Town (1980b) postulated that temperature inhibited A. scabra movement during winter which reduced feeding. Here a temperature range of only 2.75°C resulted in a mean difference of 56 seconds to reach the plume source, a distance of roughly 80 cm. Furthermore, temperatures during experiments only fell to as low as 9.25°C, well above those which are experienced by A. scabra during winter (occasionally < 5°C) (Greig et al. 1988). These results support Town’s hypothesis and suggest that movement speed relies greatly on water temperature. Cool temperatures are known to slow physiological processes in ectothermic invertebrates (Schmidt-Nielson 1997). Reduced movement would limit foraging range and consequently lower the frequency of encounters with prey. Asterias vulgaris predation rate increased with increasing temperature, due primarily to greater time spent searching for prey and more frequent encounters (Barbeau and Scheibling 1994). It is also likely that temperature affects other processes important to sea star predation, such as digestion time and capture success.

Despite reduce movement velocity in cooler waters, motivation to feed was not affected by temperature, as the expression of positive responses did not change across the temperature range. Town (1980b) observed greatest A. scabra feeding rates in summer when sea temperatures are highest, a trend shared by Leptasterias hexactis (Menge 1972). However, other species such as Asterias rubens, demonstrate greater motivation to feed in cooler temperatures (Castilla and Crisp 1973). Temperature regulated feeding motivation is likely to coincide with seasonal peaks of prey abundance (Castilla and Crisp 1973). It is possible that temperature does reduce motivation to feed, as the temperature range used here may have been insufficient to influence A. scabra in such a way. The temperature range experienced by A. scabra was minor when compared to the seasonal sea temperature range which occurs off Otago (4.5 – 23°C) (Greig et al. 1988). Therefore motivation to feed may decline when exposed to more extreme temperatures but did not occur within the temperature range used here. Temperature will be controlled in further experiments to negate confounding effects on movement and digestion time.

It should be noted that changes in water temperature in this experiment were a result of changes in the water temperature of Otago Harbour. Therefore they were not controlled in relation to other variables and it is possible that changes are related to different food sources which were tested on days with different temperatures.
2.4.5 Signal propagation

It is possible that *Astromole scabra* did not sense prey odour signals because they were not of sufficient strength. Inadequate signal strength may be linked to the dilution of odour signals, insufficient number of prey or because signals were overpowered by other odours present in the water. Turbulent plumes were used in this experiment and may have diluted the chemical signals of prey.

Signal transmission is better in laminar flows than turbulent plumes as odours are not mixed as quickly (Zimmer and Butman 2000, Weissburg *et al* 2002, Campbell *et al*. 2001). Odours traveling in turbulent water plumes do not occur as a distinct gradient which can be easily followed, rather they comprise of intermittent odour filaments separated by clean water (Moore *et al*. 1991, Zimmer and Butman 2000, Weissburg *et al*. 2002). For small animals such as crabs it is hard to orientate themselves towards these non-directional cues. However, chemically sensitive Asteroids can use tropotaxis to base movement direction on concentration differences between separate chemoreceptors (Dorlet and Himmelman 2004). The radial symmetry and slow movement makes Asteroids well designed for tropotactic foraging, as they have wide distances between chemoreceptors and can make long term sensory responses based partial scents over time (Castilla and Crisp 1970, Dale 1994, Barbeau and Scheibling 1994, Weissburg *et al*. 2002). Therefore even filamentous odours present in turbulent flows should trigger chemoreceptors on one side of the body. Turbulent odour plumes are common features of the marine environment (Zimmer and Butman 2000). Many studies artificially control flow conditions to create perfectly laminar flow conditions (Zimmer and Butman 2000). This experiment was designed to test chemoreceptive ability of *A. scabra* in conditions present in the natural environment and is why flows were not made to be laminar. Chapter 3 tests predatory success in laminar conditions and may give some indication of whether signal transmission of prey is better in more laminar flows.

In the present set of experiment only one prey individual was used as an attractant, is possible that a single prey item did not exude enough odour to be sensed by *A. scabra*. *Asterias rubens* required 60 to 90 mussels to be attract to the bait containing arm of a Y maze to a statistically significant level (Castilla 1972). However *A. rubens* is a specialised predator and feeds on large mussel aggregations (Castilla 1972). Therefore, when searching for prey it is in their best interest to locate mussel beds of several hundred individuals. Comparatively, *A. scabra* is a generalist predator and consumes mainly transient, singular prey (Town 1980b). It should therefore be advantageous to have the ability to sense and locate single individuals.
An alternative to using numerous prey individuals may have been to damage prey to create intense odour signals (Sloan and Northway 1982). Other studies have observed Asteroid preference for damaged prey over live prey (Brewer and Konar 2005). However the present study aimed to test *A. scabra* as a predator, not a scavenger, and is why whole, live animals were chosen as attractants. Here signal strength of live prey was maximised without harming the prey. Prey were required to have fleshy body parts extruded from shells before tests began and the mixing chamber allowed water to flow over the entire body of prey in an attempt to maximise signal propagation.

### 2.4.6. Conclusions

*Astrostole scabra* orientated movement against currents and lacked any sign of prey preference. *A. scabra* does display prey preference when left with prey for an extended period of time, in still water conditions (Town 1980b). Therefore more accurate preference results may have been obtained using still water or laminar flows. Other studies reduce the effects of turbulence in choice experiments by using unrealistic, laminar, low flow conditions and/or damaged prey to provide intense chemical signals (Zimmer and Butman 2000). Such flow and attractant modifications allow researchers to achieve definitive preference results, but make it difficult or impossible to use results to infer about real biological interactions (Zimmer and Butman 2000). The present experiment aimed to simulate natural conditions to determine the foraging behaviour of wild *A. scabra* which live in a wave-washed environment. Consequently, although results lack information about prey preference they have shed light on the search behaviour used by *A. scabra*. It appears that *A. scabra* does not use distance chemoreception in turbulent conditions, rather, rheotactic search behaviour is used to locate prey. Chemoreception is important for predators that are required to locate sporadic or distant food sources (Drolet and Himmelman 2004). Asteroids commonly consume prey which are abundant and can be obtained over short distances (Rochette *et al.* 1994). Therefore distance chemoreception in Asteroids is often poor and may not be used at all in wave washed environments where odour signals are mixed quickly (Sloan and Northway 1982). The generalistic nature of *A. scabra* means that a wide range of effective prey species are available and therefore abundant. It is likely that distance chemoreception is not essential and prey are located via chance encounter and selected based on contact chemoreception together with tactile sensors which can be used to identify the species and size of a prey item subsequent to capture.
Chapter 3

Effect of Water Motion on *Astrostole scabra* and *Haliotis iris*
Predator-Prey Interactions

The tube feet of *Astrostole scabra* reaching out towards a juvenile *Haliotis iris* within a flume.
3.1 Introduction

3.1.1. Effect of water motion on predator-prey interactions

To accurately understand the interactions between predators and prey in an ecosystem the ‘predation cycle’ must be understood (Harrold 1982, Barbeau and Scheibling 1994). The predation cycle refers to the sequential actions that occur in a single predation event, specifically the location, capture and handling time of prey (Harrold 1982, Barbeau and Scheibling 1994). Predator-prey interactions in coastal marine ecosystems are often mediated by disturbance factors such as wave action (Harrold 1982, Gagnon et al. 2003). As water motion forces increase, predators generally become less effective at capturing prey (Duggins 1983, Gagnon et al. 2003, Barahona and Navarrete 2010). Water motion has been shown to reduce Asteroid locomotion, which they depended on to locate food and avoid physical stress (Sheibling 1981, Town 1981, Barahona and Navarrete 2010, Muller et al. 2011). Movement of the predatory Asteroid *Heliaster helianthus* is negatively affected by wave action to the extent that on days of high swell, behavior is sedentary and foraging does not occur (Barahona and Navarrete 2010). Reduced ability to forage at wave exposed shores is expected to limit predation because Asteroids move less and encounter fewer prey. (Gagnon et al. 2003). Asteroids may also suffer mortality when dislodged by waves, the risk of which is influenced by the size and shape of the organism, and the intensity of water motion (Denny 1994, Gagnon et al. 2003). Therefore spatial and temporal variations in water motion are expected to generate ecosystem heterogeneity in coastal marine ecosystems, and create a mosaic consisting of patches of spatially varied predation levels (Duggins 1983, Denny 1994, Weissburg et al. 2003).

3.1.2. Effects of wave action on *Haliotis iris* and *Astrostole scabra*

*Haliotis iris* generally exhibits faster growth rates and reaches a greater maximum size at wave exposed reefs (Donovan and Taylor 2008). Despite this, wave action is also a major source of mortality for juvenile *H. iris* reseeded to exposed reefs, which often experience low survival attributed to factors such as sedimentation, dislodgment and individuals being crushed by moving rocks during storm events (Schiel 1993, McShane and Naylor 1995, Naylor and McShane 2001, Roberts et al. 2007). Wave exposure has therefore been highlighted as an important factor contributing to low recruitment in many New Zealand abalone populations and can negatively affect the quality of *H. iris* nursery habitat (Naylor
and McShane 2001). Predation related mortality is also expected to be high for juvenile *H. iris* which seek refuge in shallow, cryptic habitat until a size refuge from predation is reached (McShane and Naylor 1995, Roberts *et al.* 2007, Cornwall *et al.* 2009).

Asteroid predation is expected to be reduced by wave action (Duggins 1983, Gagnon *et al.* 2003, Barahona and Navarrete 2010). Protective physical properties and behavioral adaptions belonging to prey species can also reduce the ability of predators to capture prey (Town 1981, Harrold 1982, Barbeau and Scheibling 1994). Prey can reach a size refuge, inhabit cryptic habitat, increase locomotive speed, refine sensory abilities and develop escape mechanisms to reduce the likelihood of capture (Feder 1963, Town 1980b, 1981, Phillips 1977, Harrold 1982, Penny and Griffiths 1984, Barbeau and Scheibling 1994, Griffiths and Gosselin 2008, Bancala 2009). Abalone exhibit a well-documented escape response to Asteroid predators which comprises several specific sub-units (Feder 1963, Donovan and Carefoot 1997, Bancala 2009). Once Asteroid tube feet contact abalone tissue, the prey initially respond by extending posterior and frill tentacles and lifting their shell, described as “mushrooming” (Feder 1963, Bancala 2009). Individuals then “run” away from the direction of contact using laterally alternating waves of the foot (Feder 1963, Bancala 2009). If asteroid tube feet grip the abalone shell, *H. iris* will vigorously twist its shell in an effort to break free (Feder 1963, Bancala 2009). A final desperate response is also recognized where individuals release from the substrate completely, in the hope of being carried away from the predator by currents. The Haliotidae escape response is well documented, but its effectiveness when subjected to varying degrees of water motion has not yet been examined. Asteroid movement and predatory success has only been recorded in the presence or absence of water motion (Gagnon *et al.* 2003). It is likely that disturbance from wave action affects predator-prey dynamics, and therefore should be considered when assessing the interactions of species which reside in areas of high water motion. Flow conditions at wave exposed shores vary in relation to depth, currents in shallow water are strong and turbulent due to breaking waves, while subtidal flows caused by wave surge are oscillatory and tend to be more laminar and directional (Vogel 1981, Sloan and Northway 1982, Weissburg *et al.* 2002, Gagnon *et al.* 2003). A wave tank or U-tank is best suited to accurately simulate the bidirectional, oscillatory currents present at subtidal wave exposed shores (Gagnon *et al.* 2003). A hydrodynamic flume (Vogel 1981, Cornelison *et al.* 2007) was used in this study to generate laminar, unidirectional currents of varying strength, suitable to simulate benthic water motion.
3.1.3. Hypotheses

This experiment examined the effect of water motion on *Astrostole scabra* movement, *A. scabra* predatory success and the expression of *Haliotis iris* escape response. It was hypothesised that increased water motion would reduce *A. scabra* movement speed and predatory success. Furthermore it was hypothesised that larger *A. scabra* would move more slowly than small individuals in flowing water due to a greater drag force being applied to larger bodies (Denny 1994, Vogel 1981). Large *A. scabra* are able to capture larger prey, that are unobtainable to small individuals, and therefore large individuals were predicted to be more successful at capturing prey than small individuals (Town 1981). If *A. scabra* speed and predatory success is hindered by water motion then *H. iris* should escape more frequently and fewer escape responses by *H. iris* will be required during escapes.

3.2 Methods

3.2.1. Experimental design

*Astrostole scabra* and *Haliotis iris* predator prey interactions were tested in a 600 L flume, which recycled water through a pipe running below the tank (Figure 3.1) (further described in Cornelison et al. 2007). Flow was generated by a 1 Hp motor and drive shaft with a propeller. Motor speed was controlled via an electronic panel and could generate a maximum current of 0.26 cm s\(^{-1}\). *A. scabra* speed was determined as the time taken to move 15 cm against the current. Predatory success was determined as the proportion of times *A. scabra* managed to successfully capture *H. iris* in each flow treatment. The *H. iris* escape response was determined as the maximum response behaviour observed before the individual was captured or escaped. Five flow treatments ranging from 0.05 to 0.26 cm s\(^{-1}\) were used and each was replicated 25 times. The twenty-two *Astrostole scabra* used ranged in diameter from 28.5 to 51.0 cm and were starved for two weeks prior to experimentation to ensure consistent starting conditions. Refer to Appendix for information on *A. scabra* used in this experiment. As only 22 *A. scabra* were available for experiments, individuals were used randomly without replacement so that each individual was tested once on each day of experimentation. The number of *H. iris* was also limited and individuals were chosen randomly without replacement so that none were tested more than once in a day. *H. iris* were hatchery reared juveniles and ranged in size from 3.1 – 4.8 cm in length. This prevented them
from becoming exhausted, so that individuals could be used in several trials and be treated as independent trials.

Flow velocity was calculated as the average time taken for a neutrally buoyant dye to migrate 3 m. The flume tank was filled to a height of 0.3 m entirely submerging height the inflow pipe to create a more laminar flow. A 2 mm mesh grate was placed at the intake and outlet pipes of the tank to further assist laminar flow and avoid individuals being washed into the recirculation pipe below. Start and finish lines 15 cm apart were marked on the base of the tank to calculate *A. scabra* speed. Water temperature within the flume was maintained at 10°C as temperature appeared to have an important influence on *A. scabra* movement (Ref. Chapter 2).

Figure 3.1: Flume apparatus used to generate water currents at a known velocity. Water is recycled within the pipe below the tank and flows in from the far end. The blue motor powers a propeller submerged in the out flow pipe. A curved plastic plate directs water downwards into the out flow pipe.
3.2.2. Experimental process

*Astrostole scabra* and *Haliotis iris* were placed in the flume simultaneously and acclimatised for five minutes. *H. iris* was placed upstream of *A. scabra* to provide a chemical stimulus for *A. scabra*. Once acclimatised, *A. scabra* were placed in front of the start line and the majority of individuals would begin to move against the current. Individuals not moving against the currents were picked up and rotated so that their leading arm pointed upstream and movement would then generally continue upstream. Time was recorded from the point that *A. scabra’s* leading arm crossed the start line until the point they crossed the finish line. If *A. scabra* altered its course while being timed it was returned to the start line. Once an *A. scabra* reached the finish line the predation phase of the experiment began. *A. scabra* would generally encounter, and attempt to capture *H. iris*. However *A. scabra* occasionally missed *H. iris*, and would continue past the prey if not in its direct path. On such occasions *H. iris* was slid 15 cm upstream of *A. scabra* to ensure an encounter occurred. *H. iris* was slid along the base of the tank as removal from the substrate required *H. iris* to re-establish its grip. *H. iris* was recorded as being successfully captured if *A. scabra* gained a strong grip on *H. iris’s* shell and retained its hold for one minute. An unsuccessful capture was recorded if *H. iris* managed to escape from *A. scabra*, and move out of reach of *A. scabra’s* arms.

The escape response performed by *H. iris* was recorded as one of four identifiable behaviours:

1. No response. *H. iris* would remain still while completely covered by *A. scabra*.
2. Running. Once coming in contact with *A. scabra*, *H. iris* would often react by lifting its shell, exposing its mantle to its attacker, and using laterally alternating waves to move away.
3. Torsion. If *A. scabra* gained hold of a *H. iris* shell, *H. iris* would rotate its shell in a 180° arc (90° in either direction) in an attempt to break free from *A. scabra’s* grip.
4. Detachment. *H. iris* would detach from the tank bottom to be washed downstream, away from *A. scabra*.

Occasionally *H. iris* would excrete mucus from the respiratory pore opening when contacted by tube feet. This response was not recorded as *H. iris* were retested on successive days and literature suggests this is not sufficient time to regenerate mucus stores (Bancla 2009).
3.2.3. Data analysis

JMP 9 was used to test statistical significance of relationships. *Astrostole scabra* were grouped into four size classes (25 – 30 cm, 30.5 - 35 cm, 35.5 - 40 cm, and > 40.5 cm) to test the effect of predator size on movement and capture success. A general linear model was used to examine the effect of water velocity on movement velocity and capture success. The expression of the *Haliotis iris* escape response was examined using contingency tables. A one way ANOVA compared mean movement rates and predatory success across all water velocity treatments for each size class. Data tested using an ANOVA were required to pass a levene’s test to ensure homogeneity of variance. Significant differences between treatments were identified using Tukey tests.

3.3 Results

3.3.1. Effect of current on *Astrostole scabra* locomotion and capture success

Mean *Astrostole scabra* movement velocity (0.26 cm s\(^{-1}\)) was greatest in weak currents (5 cm s\(^{-1}\)), and declined as currents increased in strength (Figure 3.2). Movement speed was reduced by 68% to 0.11 cm s\(^{-1}\) when subjected to a maximum current of 26 cm s\(^{-1}\) (Figure 3.2). Movement velocity was significantly related to and current velocity (p < 0.001, F = 98.6333, DF = 1). In strong currents *A. scabra* appeared to use more tube feet to hold the base of the tank and fewer tube feet moved forward at any one time. *Haliotis iris* seemed comparatively less affected by strong currents, and was capable of moving faster than *A. scabra* in strong currents.

When subjected to weak currents of 5 cm s\(^{-1}\) *Astrostole scabra* was an efficient predator and successfully captured *Haliotis iris* in 72% of encounters. Capture rate declined as current velocity increased (Figure 3.3). When subjected to a maximum velocity of 26 cm s\(^{-1}\) *H. iris* was captured in only 8% of encounters. Capture success was also significantly related to water motion (p < 0.001, F = 22.7349, DF = 1). The decline in *A. scabra* capture success appeared to be a direct effect of reduced movement speed when subjected to strong currents. When moving slowly, *A. scabra* failed to gain a good initial grip on *H. iris*’s shell without being detected, allowing *H. iris* a greater chance of escape.
Figure 3.2: *Astrostole scabra* movement velocity whilst subjected to various current velocities. Plots are averages ± S.E. ($n = 25$). Letters denote significant differences between treatments.

\[
y = -0.0073x + 0.3054 \\
R^2 = 0.9765
\]

Figure 3.3: Proportion of times *Astrostole scabra* successfully captured *Haliotis iris* at varying flow velocities. Plots are averages ± S.E. ($n = 25$). Letters denote significant differences between treatments.

\[
y = -0.0259x + 0.8111 \\
R^2 = 0.8439
\]
3.3.2. Astrostole scabra size classes

The average speed and proportion of successful captures across flow treatments for the four *A. scabra* size classes is shown in Figure 3.4. Individuals in the size class 35.5 – 40 cm achieved the greatest mean movement velocity and probability of successful capture, however *A. scabra* size had no statistically significant effect on movement velocity (p = 0.3455, F = 1.116, DF = 3) or capture success (p = 0.2772, F = 1.301, DF = 3).

![Figure 3.4](image-url)

Figure 3.4: Capture success rate (bars) and mean movement velocity (points) for four size classes of *Astrostole scabra*. Plots are averages ± S.E. for each treatment (n = 27 – 41).

3.3.3. Haliotis iris escape response

*Haliotis iris* exhibited the general abalone escape response comprising four specific sub-units when contacted by *Astrostole scabra*, (Figure 3.5). Tube feet had to contact the mantle or a pore opening to trigger the response. If *A. scabra* gripped the shell away from a pore, contact went unnoticed until *H. iris* was pulled from the substrate. Once tube feet contacted a *H. iris* pore or tissue, *H. iris* would instantly respond by “mushrooming”, extending its posterior and frill tentacles and lifting its shell. *H. iris* would then continue to “run” away from the direction of contact by making laterally alternating waves of the foot. As it ran, *H. iris* tilted its shell away from *A. scabra*, exposing its mantle to the predator. When *A. scabra* did grip *H. iris*’s shell, torsion would begin and *H. iris* would vigorously twist its shell in an arc of
180° to break free. Torsion weakened \textit{H. iris}'s grip on the substrate and eventually they would release from the substrate completely. If \textit{H. iris} became detached from the substrate in high flow (or on a vertical surface as shown in Figure 3.5) its weight was too great for \textit{A. scabra} to maintain its grip and \textit{H. iris} would be swept away by the current (or fall from the vertical surface, away from \textit{A. scabra}).

Figure 3.5: The escape response of \textit{Haliotis iris}. 1) An unalarmed \textit{H. iris} with tentacles withdrawn. 2) \textit{H. iris} after sensing \textit{Astrostole scabra}, tentacles are extended and the individual is “running” away with laterally alternating waves of the foot. 3) \textit{H. iris} undergoing shell torsion after being gripped by \textit{A. scabra}. 4) \textit{H. iris} at the bottom of the tank.
3.3.4. Effect of current on the Haliotis iris escape response

Sub-units of the *Haliotis iris* escape response were observed and recorded during different current velocities (Figure 3.6). Behaviour progressed from ‘no response’ through ‘running’, ‘torsion’ and ‘detachment’, so that if one response was not effective the following response occurred. Contingency tables identified water velocity to have a significant effect on escape response ($P < 0.001$, Chi-square $= 45.42$, DF $= 12$). It was uncommon for *H. iris* not to react to *Astrostle scabra*’s presence, but when this did occur it was typically in weaker currents. In weak currents the most common response was shell torsion, at which time *H. iris* were commonly captured. As current strength increased, torsion occurred less frequently and the running response became more common. Complete release of the substrate occurred at all current velocities as it occurred every time *A. scabra* captured *H. iris*. Therefore it was only recorded when it was successful and resulted in *H. iris* escaping *A. scabra*’s grip. Release of the substrate only became an effective method of escape in strong currents.

![Figure 3.6: Frequency of Haliotis iris escape response sub units when subjected to different current velocities. 1 = no response, 2 = running response, 3 = shell torsion, 4 = release of substrate and drift away ($n = 25$). Letters denote significant differences in the frequency of response across treatments.](image)
3.4 Discussion

3.4.1. Effect of current on:

3.4.1.1. Astrostole scabra locomotion

Results of the present experiment demonstrated that Astrostole scabra movement velocity was reduced in strong current velocities. Visual observations suggest that when A. scabra experienced strong currents more tube feet were required to hold the substrate so that fewer tube feet could be detached to move forward. Similar results were obtained by Gagnon et al. (2003) who used a bidirectional wave tank to test the effect of water motion on the predatory sea star Asterias vulgaris. A. vulgaris moved shorter distances in the presence of simulated waves (Gagnon et al. 2003).

Strong water motion occurs regularly at wave exposed shores and is assumed to negatively affect movement in asteroids (Gagnon et al. 2003). Direct observations of slow moving animals at wave exposed reefs can be difficult (Scheibling 1981, Gagnon et al. 2003, Barahona and Navarrete 2010). Therefore a flume was used to test the effect of current velocity on the movement and predatory success of A. scabra. In low flow conditions (5 cm s$^{-1}$) the mean movement velocity of A. scabra was 0.26 cm s$^{-1}$. The movement velocity of A. scabra recorded here is comparable to other large sea stars, such as Asterias forbesi and Oreaster reticulatus which moved at speeds of 0.26 cm s$^{-1}$ and 0.33 cm s$^{-1}$ respectively in low flow conditions (Scheibling 1981, Dale 1997). Mueller et al. (2011) recorded in-situ movement rates of four tropical asteroids in weak currents (5 - 8 cm s$^{-1}$). These varied in speed from 0.14 - 0.76 cm s$^{-1}$. Because Mueller et al (2011) tested tropical species in warm water (29.7 - 30.0°C) it is likely that higher temperatures enabled faster movement. For a cold water species such as A. scabra, locomotory speed should occur at the lower end of this spectrum, as observed. Water temperature was found to affect results in preference test experiments (Ref. Chapter 2) and Town (1980a) attributed reduced A. scabra movement in winter to temperature inhibited movement. Temperature was therefore controlled during this experiment to mitigate any thermal influence on locomotory performance.

The type of habitat an Asteroid species inhabits is also thought to affect locomotion rates (Mueller et al. 2011). Species that reside in three dimensional reef habitats have tube feet that are primarily designed for fixation as opposed to locomotion. For those living on sand substrates, locomotion is the primary requirement. Consequently, sand dwelling species such as O. reticulatus have evolved to move faster (0.33 cm s$^{-1}$) compared to A. scabra (Scheibling 1981, Mueller et al. 2011). A. scabra commonly exists on rocky reef habitats that are
subjected to strong currents and should exhibit lower locomotion rates than asteroids which inhabit sand substrates (Muller et al. 2011). Water motion is a significant threat to Asteroids and behaviour is modified to mitigate its effects. *Heliaster helianthus* is negatively affected by wave action and shelters in crevices to avoid detachment during periods of high swell (Barahona and Navarrete 2010). *O. reticulatus* migrates to deeper water during winter to escape turbulent shallow habitats (Scheibling 1980). Town (1980b) observed reduced feeding rates of intertidal *A. scabra* in winter when storms were more frequent. However, he attributed this to temperature inhibited movement rather than storm effects as storm events were not observed to affect feeding activity.

3.4.1.2. *Astrostole scabra* capture success

To my knowledge, no other studies have directly examined the effect of water velocity on Asteroid predatory success of mobile prey. *Astrostole scabra* encountered juvenile *Haliotis iris* while subjected to a range of current velocities. *A. scabra* attempted to feed on *H. iris* during every encounter, demonstrated by moving on top of *H. iris* once captured, and changing initial direction to follow *H. iris* escapees. The rate of successful captures by *A. scabra* declined significantly as current velocity increased to the extent that only 8% of encounters resulted in capture success in maximum flow (26 cm s$^{-1}$). Reduced *A. scabra* movement speed in strong currents appeared to be the principle factor contributing to the decline of capture rates. When *A. scabra* moved slowly, *H. iris* had more time to sense the attacker’s tube feet and move away before being successfully gripped. The *H. iris* escape response was only triggered by tube feet coming in direct contact with the mantle or a pore opening. No response occurred when tube feet contacted the shell alone and this allowed some captures to occur in strong currents. *H. iris* appeared comparatively less affected by strong flows than *A. scabra* and maintained its speed of movement in strong currents. Gagnon et al. (2003) recorded *Asterisa vulgaris* to have higher prey capture rates in the absence of wave action. However the prey used in Gagnon’s experiment was the blue mussel *Mytilus edulis* which is of course sessile and therefore exhibited no escape behaviour (Gagnon et al. 2003).
3.4.1.3 Astrostole scabra size classes

Asteroid locomotion is generally expected to depend on the number and length of tube feet and body size (Muller et al. 2011). Therefore larger sea stars of the same species should move faster in the absence of currents (Muller et al. 2011). Here, A. scabra movement was not significantly affected by size. Size-stratified movement rates were displayed as the mean movement rate of each size class across all current treatments. Data were analysed in this way to simulate average movement rates of A. scabra living in habitats which receive variable levels of water motion. It was hypothesised that large individuals with greater surface area would experience greater drag and consequently have reduced movement. Denny (1988, 1994) suggests that water motion affects the evolution of body size on wave exposed shores as large objects experience greater drag force in water. However the increased drag experienced by animals with large surface can be counteracted by greater body volume which may weigh the animal down or, in the instance of Asteroids allow a greater number of tube feet to grip the substrate (Denny 1988) Large individuals of the Asteroid species Marthasterias glacilis were observed to be more affected by water motion than small individuals (Penny and Griffiths 1984). As a result the number of days observed feeding decreased with increasing size (Penny and Griffiths 1984). The same does not appear to be true for A. scabra.

Larger Asteroid individuals have been shown to be generally more effective predators and achieve higher capture rates of species with escape responses (Menge 1972, Ortiz et al. 2003). Menge (1972) suggested the sea star Leptasterias hexactis rapidly increases in size to facilitate capture of prey with escape responses. Larger A. scabra are capable of, and prefer to capture larger prey unobtainable by small individuals (Town 1981). However, in this study large A. scabra were not observed to be more effective predators when capturing juvenile H. iris.

Town (1980a) observed that small A. scabra were generally found in the intertidal zone and large individuals in the subtidal zone. These results suggest that large A. scabra are not forced to reside in deeper water due to greater influence of strong currents that occur in the intertidal caused breaking waves, and are spatially separated for some other reason (Town 1980b, Denny 1994, Bell and Denny 1994). Large A. scabra prefer to capture larger prey species and larger individuals of the same species (Town 1981). Spatial overlap of predators and prey is an important factor contributing to prey species selection (Town 1981). Therefore
large *A. scabra* may migrate to deeper water to search for larger prey rather than as a refuge from water motion.

3.4.2. Chemoreception in *Astrostole scabra*

*A. scabra* regularly moved past an upstream *H. iris*. The decision not to record encounter rates was made because large *A. scabra* almost filled the width of the tank and thus had an increased chance of accidentally encountering *H. iris* than small *A. scabra*. Chapter Two demonstrated that *A. scabra* lacks the ability to distinguish among odours in turbulent conditions. Propagation of odours is better in laminar flows than turbulent plumes (Weissburg and Zimmer-Faust 1993). The fact that *A. scabra* regularly missed *H. iris* in laminar flow but went on to try and capture the prey if was moved into its direct path suggests that chemoreception in this species is poor. The literature suggests two main forms of prey location in Asteroids, rheotaxis and cross current migration (Rochette *et al.* 1994). Movement against the current observed in this experiment supports a rheotactic foraging strategy (Ref. Chapter 2). Once *A. scabra* contacted *H. iris* it would always attempt to capture the prey and change its movement direction to the direction of contact with *H. iris*. Contact chemoreception is common among asteroids and is likely the method of prey detection used by *A. scabra* (Sloan and Northway 1982).

3.4.3. *Haliotis iris* escape response

Escape responses to Asteroid predators are well documented for gastropods (Phillips 1977, Harrold 1982) including abalone (Feder 1963, Schiel and Welden 1987, Donovan and Carefoot 1997, Bancala 2009). Escape responses have been described for several Haliotidae species including *H. tuberculatalamellosa* (Bancala 2009), *H. kamtschatkana* (Donovan and Carefoot 1997), *H. cracherodii* (Feder 1963) and *H. rufescenes* (Feder 1963, Schiel and Welden 1987). An effective escape response in abalone is considered the reason that *H. cracherodii* is not consumed by Asteroids in proportion to abundance (Feder 1963). Haliotidae escape responses (mushrooming, running and torsion) are triggered by contact with Asteroids only and contact with other objects results in clamping down to the substrate (Banala 2009). Reactions are also specific to the Asteroid species, with more predatory species triggering the strongest escape responses (Phillips 1977). Here *Astrostole scabra* triggered a strong escape response in *Haliotis iris* and the mean expression of response
behaviours changed in relation to current. In weak currents the most common response was shell torsion. This was because *A. scabra* maintained fast movement in calm conditions which allowed tube feet to grip *H. iris’s* shell before being noticed. As current velocity increased, the frequency of shell torsion declined. Running became the most common response in strong currents because *A. scabra* speed was slowed, allowing *H. iris* more time to detect *A. scabra’s* presence and move away before being gripped by tube feet. Occasionally *H. iris* did not demonstrate any escape response. This only occurred in low flow conditions when *A. scabra* moved quickly. Detachment of the substrate often occurred when *H. iris* was caught by *A. scabra*. However it only became effective as an escape mechanism in strong currents when the flow was sufficient to wash *H. iris* from *A. scabra’s* grip. Detachment was also seen to be effective on vertical surfaces as *H. iris* would often fall to the base of the tank and away from *A. scabra* (Figure 3.5). Detachment from the substrate may be either a deliberate escape mechanism or the result of reduced grip during movement. Haliotidae species move differently to most gastropods when escaping predators. Two laterally alternating waves move up either side of the foot, hence the descriptions of “running” (Feder 1963, Donovan and Carefoot 1997). During running the centre of the foot and the portion at the top of each pedal wave is lifted completely off the substrate rather than gliding uniformly over a mucus layer, as seen in the majority of gastropods (Donovan and Carefoot 1997). This method of locomotion is thought to allow faster movement and reduce energy expenditure, as less mucus is required (Donovan and Carefoot 1997). However, increased speed may occur at the expense of suction, allowing *H. iris* to be easily plucked from the substrate.

Escape responses are critical to reducing predatory mortality, especially for slow growing species with low recruitment rates (Phillips 1977, Harrold 1982). Harrold (1982) demonstrated their effectiveness by measuring capture success of the Asteroid *Pisaster giganteus* on two narcotised gastropod species that exhibit escape responses (*Tegula pulligo* and *Calliostoma ligatum*). Capture rates of *T. pulligo* and *C. ligatum* were 27% and 60% higher in narcotised individuals respectively (Harrold 1982). Escape responses become more effective as prey increase in size (Harrold 1982). Juvenile gastropod prey *Balanus carosus* lack strong suction and must escape predators by moving away (Menge 1972), much like *H. iris*. As *B. carosus* grow they become difficult to dislodge when suctioned to the substrate and are selected against as prey (Menge 1972). Adult *H. iris* employ suction to the substrate as a defence mechanism and the evolution of large body size in abalone is expected to occur as a means of limiting predation (Feder 1963, Menge 1972, Estes *et al.* 2005). As prey size
increases, escape responses become more efficient and prey are less obtainable (Town 1981). Effective escape responses of large prey are suggested to limit the growth of large sea stars which cannot acquire sufficient energy from small prey to allow growth (Menge 1972, Tokeshi et al. 1989). The highly generalised diet of *A. scabra* may mean it can feed on a wide range of prey and may enable it to reach a large size (Town 1980b).

Changes in the expression of escape response sub-units at different flow speed demonstrate dynamics in the predator-prey interactions of *A. scabra* and *H. iris*, and give a more detailed understanding of why Asteroid predatory success appears to be limited by water motion. Conversely, results demonstrate that juvenile abalone are more effective at escaping Asteroid predators in strong currents, and thus would be expected to experience lower rates of predation related mortality at wave exposed sites.

### 3.4.4. Hydrodynamics

Sloan and Northway (1982) described subtidal currents as unidirectional. More accurately, typical subtidal currents are bidirectional oscillate back and forward, moving towards the shore as the surge passes over, then returning seaward after the wave has broken (Vogel 1981, Gagnon et al. 2003). As mentioned earlier, a wave tank (Gagnon et al. 2003) or a U-tank (Zimmer and Butman 2000) which can generate bidirectional and oscillatory currents would be ideal in refining an experiment refining the effects of flow on predator ability. However, as neither were available, a unidirectional flume was used in this experiment. The three main hydrodynamic forces which govern benthic invertebrates are drag, lift and acceleration (Denny 1994, Gagnon et al. 2003). Because a unidirectional flow was constant, the acceleration that would occur in an oscillatory flow as current direction switches back and forward was not applied to the animals tested here. Denny (1988, pg. 268) describes acceleration as a “minor component of the total force, and therefore is a quantity we [may] neglect”.

Current velocities ranged from 5 cm s\(^{-1}\) to 26 cm s\(^{-1}\) and were within the realm of those that occur at wave exposed shores or in the subtidal by tidally generated flows (Denny 1994, Bell and Denny 1994). Breaking waves have been associated with turbulent water velocities as high as 110 cm s\(^{-1}\) (Bell and Denny 1994) and 140 cm s\(^{-1}\) (Denny 1994). Currents of this speed would inflict substantial forces on benthic invertebrates, and likely cause detachment in Asteroids. The present experiment aimed to test directional flows which occur in the subtidal
where strong currents are expected to reach approximately 30 cm s\(^{-1}\) (Gagnon et al. 2003). Gagnon et al. (2003) observed detachment of several Asterisa vulgaris individuals subjected to currents of 31 cm s\(^{-1}\). Interestingly, the presence of kelp doubled the rate of detachment by creating a whiplash effect (Gagnon et al. 2003). It is worth noting that benthic invertebrates do not risk dislodgement on a day to day basis, rather dislodgement events would occur during storm events (Denny 1994). Therefore, although strong currents are not always present at wave exposed shores, they do occur more frequently.

The topographic complexity of a substrate can have a substantial effect on flow speed, as complex substratum can create a boundary layer of turbulent currents and reduced velocity (Carpenter and Williams 1993). This experiment provided support for the idea that predator-prey interactions may influenced by current velocity; however, a more detailed experiment is required to assess the extent that substrate complexity effects currents and associated predator-prey interactions.

3.4.5. Ecological interpretation and conclusion

According to optimal foraging theory, natural selection optimises the feeding strategy of a predator to optimise calorie intake and minimise energy use (Scheibling 1981). It is optimal to move short distances to locate prey and to move during low flow conditions when foraging is less exhaustive (Scheibling 1981, Weissburg 2003). Time between successful captures relies of prey availability (Scheibling 1981), movement speed and capture success rate (Harrold 1982). Results obtained here suggest that A. scabra moves slowly and is less capable of capturing mobile prey in strong currents. Therefore two events of the predation cycle are affected by water motion. Firstly, because locomotive speed is reduced, the time to locate prey increases so encounters are less frequent. Secondly, the ability to capture mobile prey is also reduced so that when encounters do occur, they are successful less often. This data supports the theory that wave action mediates spatial differences in predation rates and helps produce mosaics of species distribution by creating patches where prey have refuge from predators (Duggins 1983, Denny 1994, Navarrette and Castilla 2003).
Feeding time for *Astrostole scabra*. Tank, water-bath and camera setup used in handling time experiments.
4.1 Introduction

4.1.1. Importance of handling time for field surveys

Optimal foraging theory predicts predators should maximise calorific intake per unit of time (Menge 1972, Barbeau and Scheibling 1994). Therefore as well as considering the calorific quality and quantity of a prey species, handling time is also an important factor for predators to consider when selecting prey (Menge 1972). Studies that calculate the diet of predators from field observations sometimes fail to calculate the handling time of prey species (Town 1981, Fairweather and Underwood 1983). If handling time varies greatly between prey species, consumption rates will be biased towards those that take a greater time to consume (Fairweather and Underwood 1983). Conversely, the prevalence of species with short handling times will be underestimated by feeding surveys (Fairweather and Underwood 1983). Therefore the handling times of different prey species should be calculated prior to feeding surveys and be used to adjust results to account for such biases (Fairweather and Underwood 1983).

An aim of the present thesis is to calculate the major dietary components of Astrostole scabra diet within the East Otago Taiāpure. In order to accurately define the relative consumption rates of A. scabra prey species, handling times must be calculated for individual species (Fairweather and Underwood 1983).

4.1.2. Effect of prey species on handling time

Astrostole scabra is a generalist predator and is known to consume at least 60 different prey species (Town 1981). As the diet of A. scabra contains a wide range of species it was not feasible to calculate handling times for all prey. It is likely that prey with similar morphological characteristics take similar times to consume. Therefore the present study examined A. scabra handling times for three species of varying morphology. The three prey species tested were the abalone Haliotis iris, the mussel Perna canaliculus, and the Turbinid snail Cookia sulcata. H. iris, P. canaliculus and C. sulcata were all previously identified as prey of A. scabra within the East Otago Taiāpure (Pers. obs.) and each utilise different methods for avoiding or deterring predators. H. iris has a singular shell and exhibits a vigorous escape response (Ref. Chapter 3). P. canaliculus possesses two protective shells which can be closed tightly to evade predators (Petraitus 1990). C. sulcata possesses a calcareous operculum for defence which can be closed tightly to seal off fleshy body parts.
from predators (Vermeij and Williams 2007). This study will assess how handling time is affected by the mechanisms these species possess to avoid or deter A. scabra predation.

As handling time directly affects the energetic benefit of a prey, the ‘profitability’ (grams consumed per hour) of each prey species was compared to identify which species A. scabra should preferentially consume in field surveys (Menge 1972, Barbeau and Scheibling 1994).

4.1.3. Effect of Astrostole scabra size on handling time

The diet of Astrostole scabra has been shown to change with increasing body size, presumably because larger A. scabra become more efficient predators and are capable of capturing larger prey (Town 1981). As an Asteroid increases in size, it requires more food for self-maintenance and continued growth (Menge 1972, Town 1981). The present study included different sized A. scabra to test if larger A. scabra consume prey more efficiently to allow for growth to continue in large individuals.

4.1.4. Hypotheses

It was hypothesised that Haliotis iris would record low handling times compared to other species as its primary defence from predators is an escape response prior to capture (Ref. Chapter 3). The single sided shell was expected to offer little protection from Astrostole scabra once captured. Conversely, Perna canaliculus and Cockia sulcata possess shells which protect soft tissue from predators. Therefore it was expected that it would take longer for A. scabra to gain access to P. canaliculus tissue and handling times would be longer than those of H. iris. C. sulcata was expected to have the greatest handling times, as the cardiac stomach of A. scabra does not make direct contact with fleshy tissue until the operculum is removed, A. scabra will instead rely on digestive enzymes to first leak inside the shell.

As A. scabra select for large sized prey (Town 1980b), it was expected that larger prey would be of more benefit per hour of digestion time. Furthermore it is hypothesised that larger A. scabra would digest prey more quickly than small A. scabra as they will have greater stomach surface area.
4.2 Methods

4.2.1. Experimental design

Astrostole scabra handling times were examined by recording feeding activity on the three prey species Haliotis iris, Perna canaliculus and Cookia sulcata. Nineteen A. scabra were used in the experiment and ranged in diameter from 27.5 cm to 51.0 cm. A. scabra were starved for 20 days prior to experimentation and for a minimum of 10 days between each feeding event. Starvation ensured motivation to feed and to consume the entire prey. More information on A. scabra used can be found in the Appendix. The length and weight of prey species were recorded before being fed to A. scabra. Once feeding had finished shells along with any remaining tissue were re-weighed so the total consumed weight could be calculated.

A single prey item was left in a glass tank (25 x 26 x 40 cm) with a single A. scabra (Figure 5.1). A time lapse camera was used to film feeding activity and recorded one second of footage every minute. The time lapse camera was turned on prior to animals entering tanks and ran for the full duration of prey capture and digestion so handling time could be calculated. The beginning of handling time was defined as the point at which A. scabra became stationary with the prey held beneath its oral opening. A. scabra often had trouble capturing medium and large sized H. iris which would often escape and move out of the tank. As this experiment was concerned only with handling time and not escape rates large H. iris were placed upside down with an A. scabra placed on top. Even then, large H. iris typically righted themselves and escaped several times before eventually conceding. For smaller prey, A. scabra frequently gripped the prey and continued to move around the tank, as if searching for more food. This behaviour has been previously observed in A. scabra, with individuals gathering multiple prey to digest at once and is why handling time began only when A. scabra became stationary (Town 1981). A. scabra moved little while feeding except for the occasional rotation against the wall of the tank when feeding on C. sulcata. It was clear when A. scabra had finished feeding as individuals would drop prey remains and move away to compete several laps of the tank before again becoming stationary.
4.2.2. Tank setup

Tanks were housed within a controlled temperature room maintained at 10°C, as physiological processes are known to be affected by temperature (Schmidt-Nielson 1997). Water originated from Otago Harbour and pipes to tanks ran through a water bath so that source water was acclimatised to 10°C before entering tanks. A water temperature of 10°C was chosen as that would be the approximate water temperature during early summer when field surveys were intended to take place. Tanks were maintained with constant aeration and flow through water. *Astrostole scabra* experienced a continuous light regime so feeding activity remained visible at all times.

![Image of tanks](image)

Figure 4.1: *Astrostole scabra* feeding on *Cookia sulcata* in flow through tank system within a controlled temperature room maintained at 10°C.

4.1.3 Data analysis

Results were analysed in the statistical package JMP 9. A general linear model was used to statistically test the effect of prey species, consumed weight, prey shell size on handling time. General linear models were also used to statistically test the effect of prey species, shell length and *Astrostole scabra* length on prey profitability, a measure of feeding efficiency, calculated as the grams of prey tissue consumed per hour of handling time. Tukey tests were used to identify significant differences between handling times and profitability of prey species.
4.3 Results

4.3.1. Overall analysis of handling time

Handling times varied significantly among prey species (Table 4.1). Handling times for *Haliotis iris* and *Perna canaliculus* were not significantly different, but were significantly shorter than *Cookia sulcata* (Figures 4.1 and 4.2). Prey shell length and consumed weight had no significant overall effect on handling time (Table 4.1).

4.3.2. Relation between weight consumed and handling time

It took *Astrostole scabra* significantly longer to consume *Cookia sulcata* tissue than *Haliotis iris* or *Perna canaliculus* tissue (Figure 4.2). *A. scabra* took on average seven days to digest a single *C. sulcata* and up to 12 days on occasions (Figure 4.2). Handling times for *C. sulcata* were not affected by the amount of tissue consumed and were highly variable, resulting in a poor linear fit ($r^2 = 0.0002$) (Table 4.2, Figure 4.2). Small *H. iris* were digested more quickly than similarly weighted *P. canaliculus* individuals when little tissue (< 25 g) was consumed (Figure 4.2). However, larger *H. iris* took longer to digest than similarly weighted *P. canaliculus* when greater amounts of tissue (> 25 g) were consumed (Figure 4.2). Only the handling times of *H. iris* were significantly affected by consumed tissue weight (Table 4.2). Although not significantly related to weight consumed, the handling times of *P. canaliculus* demonstrated a strong linear relationship ($r^2 = 0.6793$) (Table 4.2, Figure 4.2).

4.3.3. Relation between shell length and handling time

Handling times for *Haliotis iris* were significantly correlated with shell length, while handling times for *Cookia sulcata*, and *Perna canaliculus* were not (Table 4.2). *C. sulcata* again displayed large variation in handling times resulting in a poor linear regression ($r^2 = 0.0002$) (Table 4.2 Figure 4.3). Comparatively *P. canaliculus* and *H. iris* demonstrated strong linear relationships ($r^2 = 0.7404$ and 0.7524 respectively) despite this, *P. canaliculus* handling times were not significantly related to shell length (Table 4.2, Figure 4.3).

Equations representing the linear fit of prey shell length to handling time were calculated to adjust apparent diet to actual diet in field surveys (Ref. Chapter 5) (Table 4.2).
Table 4.1: Results from general linear model which tested the effect of prey species, tissue weight consumed and shell length on handling time. Significant results are denoted by *.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prey</td>
<td>2</td>
<td>37.4484</td>
<td>&lt; 0.0001*</td>
</tr>
<tr>
<td>Weight consumed</td>
<td>1</td>
<td>0.4641</td>
<td>0.5002</td>
</tr>
<tr>
<td>Shell length</td>
<td>2</td>
<td>0.0748</td>
<td>0.7856</td>
</tr>
<tr>
<td>Prey*Weight consumed</td>
<td>1</td>
<td>0.4553</td>
<td>0.6369</td>
</tr>
<tr>
<td>Prey*Shell length</td>
<td>2</td>
<td>0.1954</td>
<td>0.8232</td>
</tr>
</tbody>
</table>

Table 4.2: Results from general linear model which tested the effect of shell length and consumed weight on handling times for *Haliotis iris*, *Perna canaliculus* and *Cookia sulcata*. Significant values are denoted by *.

<table>
<thead>
<tr>
<th>Prey species</th>
<th>Source</th>
<th>DF</th>
<th>F</th>
<th>p</th>
<th>r²</th>
<th>Linear equation</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Haliotis iris</em></td>
<td>Weight consumed</td>
<td>1</td>
<td>101.4286</td>
<td>&lt; 0.0001*</td>
<td>0.9354</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Shell length</td>
<td>1</td>
<td>5.0486</td>
<td>0.0324*</td>
<td>0.7524</td>
<td>$y = 6.6299x - 14.306$</td>
</tr>
<tr>
<td><em>Perna canaliculus</em></td>
<td>Weight consumed</td>
<td>1</td>
<td>0.0079</td>
<td>0.9305</td>
<td>0.6793</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Shell length</td>
<td>1</td>
<td>2.8301</td>
<td>0.1183</td>
<td>0.7404</td>
<td>$y = 6.9988x + 27.268$</td>
</tr>
<tr>
<td><em>Cookia sulcata</em></td>
<td>Weight consumed</td>
<td>1</td>
<td>0.0000</td>
<td>0.9984</td>
<td>0.0002</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Shell length</td>
<td>1</td>
<td>0.0005</td>
<td>0.9827</td>
<td>0.0002</td>
<td>$y = 0.609x + 172.46$</td>
</tr>
</tbody>
</table>
Figure 4.2: *Astrostole scabra* handling times for *Haliotis iris*, *Perna canaliculus* and *Cookia sulcata*. Tissue weight consumed refers to the difference in prey weight succeeding digestion. Linear trend lines are fitted to *H. iris* (short dash line), *P. canaliculus* (solid line) and *C. sulcata* (long dash line) handling times. Letters represent significant differences in handling time between prey species.

Figure 4.3: *Astrostole scabra* handling times for *Haliotis iris*, *Perna canaliculus* and *Cookia sulcata*. Linear trend lines are fitted for *H. iris* (short dash line), *P. canaliculus* (solid line) and *C. sulcata* (long dash line). Letters represent significant differences in handling time between prey species.
4.3.3. Effect of prey size on profitability

The energetic benefit of each prey species was determined as the grams of tissue consumed per hour of handling time, referred to here as prey profitability. *Haliotis iris* and *Perna canaliculus* were significantly more profitable prey than *Cookia sulcata* (Figure 4.4, Table 5.3). Prey profitability increased in relation to shell length for all three prey species a trend that was statistically significant in all cases (Figure 4.4, Table 4.3).

4.3.5. Effect of *Astrostole scabra* size on profitability

Prey profitability was used to determine whether large *Astrostole scabra* digested prey more efficiently than small individuals (Figure 4.4). Prey profitability was significantly affected by prey species, but was not affected by *A. scabra* size and therefore large *A. scabra* do not appear to digest prey more quickly (Table 4.4).

Table 4.3: Results from general linear model which tested the effect of shell length on profitability for *Haliotis iris*, *Perna canaliculus* and *Cookia sulcata*. Significance is denoted by *.

<table>
<thead>
<tr>
<th>Prey species</th>
<th>Source</th>
<th>DF</th>
<th>F</th>
<th>p</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Combined prey</td>
<td>Prey species</td>
<td>2</td>
<td>0.3345</td>
<td>0.0013*</td>
<td></td>
</tr>
<tr>
<td><em>Haliotis iris</em></td>
<td>Shell length</td>
<td>1</td>
<td>25.3773</td>
<td>&lt; 0.0001*</td>
<td>0.4583</td>
</tr>
<tr>
<td><em>Perna canaliculus</em></td>
<td>Shell length</td>
<td>1</td>
<td>9.4645</td>
<td>0.0088</td>
<td>0.4213</td>
</tr>
<tr>
<td><em>Cookia sulcata</em></td>
<td>Shell length</td>
<td>1</td>
<td>5.9572</td>
<td>0.0373</td>
<td>0.3983</td>
</tr>
</tbody>
</table>

Table 4.4: Results from general linear model which tested the effect of prey species and *Astrostole scabra* size on prey weight consumed per hour. Significance is denoted by *.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prey</td>
<td>2</td>
<td>12.0200</td>
<td>&lt; 0.0001*</td>
</tr>
<tr>
<td><em>A. scabra</em> size</td>
<td>1</td>
<td>0.3613</td>
<td>0.5504</td>
</tr>
<tr>
<td>Prey*A. scabra size</td>
<td>2</td>
<td>0.6873</td>
<td>0.5075</td>
</tr>
</tbody>
</table>
Figure 4.4: Relationship between prey profitability (grams of tissue consumed per hour) and shell length for *Haliotis iris*, *Perna canaliculus* and *Cookia sulcata*. Linear trend lines are fitted for *H. iris* (short dash line), *P. canaliculus* (solid line) and *C. sulcata* (long dash line) handling times. Letters represent significant differences between species.

Figure 4.5: Relationship between profitability (grams of tissue consumed per hour) and *Astrostole scabra* size. Markers represent prey species *Haliotis iris* (short dash line), *Cookia sulcata* (long dash line) and *Perna canaliculus* (solid line). Letters represent significant differences in profitability between prey species.
4.4 Discussion

4.4.1. Variation in handling times

Astrostole scabra handling times of prey were significantly dependant on the prey species being consumed. Haliotis iris and Perna canaliculus handling times were not significantly different, however handling times of Cookia sulcata significantly longer and contained greater variation than the other prey species. H. iris handling times were significantly affected by both shell length and weight consumed. Conversely, P. canaliculus and C. sulcata handling times were not significantly affected by weight consumed or shell length. Fairweather and Underwood (1983) examined handling times of the whelk Morula maginalba and found prey species was the greatest determinant of handling time. Prey size was not as important as prey species and was a significant factor in only one of the three species tested. Similar results were obtained here with prey species greatly influencing handling time while prey size appeared to be a less important factor and was only significantly for only H. iris.

4.4.2. Handling time and protective mechanisms of:

4.4.2.1. Haliotis iris

It was hypothesised that Haliotis iris would record the lowest handling times as H. iris possesses little structural protection so the stomach of Astrostole scabra would make direct contact with H. iris tissue as soon as feeding began. Handling times of small H. iris (< 25 g minus shell) were shorter than similarly weighted Perna canaliculus. However, in larger prey P. canaliculus recorded the shortest handling times. The large foot size of adult H. iris may have meant that the cardiac stomach of A. scabra could not completely cover large individuals, while small individuals could be fully encased by stomach folds. Menge (1972) postulated that Asteroid handling times were likely related to the surface area to biomass ratio of a particular prey species. As H. iris tissue is essentially a solid body, and therefore the surface area to biomass ratio of the species would be low in large individuals. Furthermore, during digestion H. iris tissue was more exposed than other species tested, which had shells to confine A. scabra’s cardiac stomach and digestive acid. Therefore sea water intrusion may have diluted stomach resulting in slower break down of H. iris tissue.

The three prey species tested in the present study utilise different mechanisms for avoiding Asteroid predation. H. iris is mobile and possesses an efficient escape response which it
relies upon to escape from Asteroids before capture can occur (Feder 1963, Harrold 1982, Schiel and Welden 1987, Donovan and Carefoot 1997, Blancala 2009). Therefore the predator avoidance strategy of *H. iris* depends upon escape prior to capture as no structural mechanisms exist to reduce handling time subsequent to capture. In this experiment, *A. scabra* experienced great difficulty when capturing large *H. iris*, even when *H. iris* were turned upside down with *A. scabra* placed on top. Therefore the *H. iris* escape response appears to become more effective as size increases. Schiel and Welden (1984) observed that the Asteroid *Pycnopodia helianthoides* consumed a greater proportion of small abalone *Haliotis rufescenes* compared to large individuals in a laboratory experiment, suggesting that the escape response of larger individuals was more effective at reducing Asteroid predation.

4.4.2.1. *Perna canaliculus*

Overall, *Perna canaliculus* handling times were shortest of the three species tested. As stated above, small *Haliotis iris* (< 25g minus shell) were consumed more quickly than similarly sized *P. canaliculus* but for larger individuals the opposite was true. An explanation for this may be that it takes *Astrostole scabra* some time to force its stomach inside the closed shells of *P. canaliculus*. The process of pushing the cardiac stomach inside shells is required for mussels of any size. Therefore the time for *A. scabra* to enter the shells of *P. canaliculus* is probably short relative to the overall handling time required for large individuals but comprises a greater proportion of the handling time for small individuals. Once inside *P. canaliculus* shells, the high surface area to biomass ratio of mussel tissue results in short digestion times (Menge 1972). Furthermore the shells of *P. canaliculus* form a concealed area for digestion to occur with minimal intrusion of sea water to dilute digestive enzymes.

*P. canaliculus* possesses greater shell protection than *H. iris*, however this strategy does not appear to be particularly effective in deterring Asteroid predation, as mussels are the common prey for many Asteroid species (Castilla 1972, Paine 1976, Penny and Griffiths 1984, Tokeshi *et al.* 1989, Laudien and Wahl 2004, Blanchette *et al.* 2005, Addison 2009). Mussels are known to reach a size refuge from Asteroid predation (Paine 1976) however no size refuge was observed here as the largest *P. canaliculus* tested (157mm) was still consumed by *A. scabra*.
4.4.2.1. Cookia sulcata

The prolonged handling time of *Cookia sulcata* was likely a result of the calcareous operculum which is closed at the time of capture and prevents the cardiac stomach of *A. scabra* from making direct contact with tissue (Vermeij and Williams 2007). The operculum of *C. sulcata* acts as a shield from digestive acid and resulted in handling times that were not dependent of prey size or weight consumed. Therefore handling times of *C. sulcata* may be dependent on other factors such as the closeness of fit of operculum or *A. scabra* experience in consuming this species. Experience in digesting *C. sulcata* may have been represented by the occasional rotation observed in some *A. scabra* during feeding, which may have allowed digestive enzymes to reach deeper into the shell so that the operculum could be breached.

The Asteroid predator avoidance strategy of *C. sulcata* appears to depend on its long handling times to make it a low quality and therefore unattractive food source (Vermeij and Williams 2007). Only thick calcareous opercula used by Turbinid snails are thought to impede Asteroid predation. Close relatives from the family Trochidae have flexible opercula and have retained fleeing responses when encountered by Asteroids (Vermeij and Williams 2007). In the case of Asteroid predation, this mechanism of defence would be sacrificial of the individual but effective on an evolutionarily time scale. A calcareous operculum may completely deter predation in faster moving predators such as crabs, however, *A. scabra* is still capable of consuming *C. sulcata* if it is willing to concede a prolonged handling time.

4.4.5. Effect of prey species and size on nutritional profitability

Prey profitability was defined as grams of tissue consumed per hour for each of the prey species, in which case *Perna canaliculus* and *Haliotis iris* were found to be the highest quality food sources. Profitability also increased with increasing prey size for each species. Therefore *Astrostole scabra* should prefer to consume large *H. iris* and *P. canaliculus* individuals (Menge 1972). Town (1981) observed that *A. scabra* consumed larger prey species and larger individuals of the same species as their size increased. Large *A. scabra* become more capable at capturing larger prey and do so to acquire greater nutrition, required for the increased cost of self-maintenance and growth in large individuals (Menge 1972, Town 1981). Calories per gram of tissue may differ between prey species and may have an additional effect on prey profitability, however this is expected to be minor compared to the influence of prey size and handling time (Menge 1972).
4.4.6. Field data adjustments to account for prey handling times

The following chapter will investigate the diet of *Astrostole scabra* in field surveys. It is important to consider biases created by handling time when the effect of a predator on a prey community is investigated (Fairweather and Underwood 1983). Equations for the linear regression of shell length and handling time of prey will be used to adjust field data to gain more accurate estimates of *A. scabra* prey consumption. Linear equations calculated for each prey species will be used to adjust field survey results despite non-significant relationships between shell length and handling time for *Perna canaliculus* and *Cookia sulcata*. Linear regressions for *P. canaliculus* show that handling time was explained well by shell length \( (r^2 = 0.7404, y = 6.9988x + 27.268) \). The linear regression for handling time and shell length for *C. sulcata* was poor due to high variability in handling time \( (r^2 = 0.0002, y = 0.609x + 172.46) \). However, it is clear that *A. scabra* require a far longer time to digest *C. sulcata* than other species. Therefore this data will still be used to adjust prey consumption rates of field data for each species including *C. sulcata* as it will produce more accurate results than not to doing so.

Prey species which appear in field survey and were not tested here will be adjusted based on handling times of *Haliotis iris* or *P. canaliculus* as it seems these species represent near maximal handling times and probably represent most species which lack a significant defence to *A. scabra* digestion. Any other species recorded which possess a thick calcareous operculum, such as *Turbo smaragdus* will be adjusted using values obtained for *C. sulcata*.

4.4.7. Effect of Astrostole scabra size on handling time

*Astrostole scabra* size had no significant effect on the handling times of prey. Therefore it appears that large *A. scabra* are not able to increase feeding efficiency as they become larger. Fairweather and Underwood (1983) proposed that a source of variation in whelk handling time is probably predator size, this seems untrue for Asteroids. *A. scabra* may increase feeding efficiency by capturing larger prey which are more nutritionally profitable or by gaining predatory experience as seen in rotation behaviour while feeding on *Cookia sulcata*. 
4.4.8. Conclusions

_Haliotis iris_ and _Perna canaliculus_ represent the best quality food items for _Astrostole scabra_ as they are quicker to consume than _Cookia sulcata_. Larger prey individuals were of greater energetic benefit per unit of time than small individuals for all prey species tested. _A. scabra_ size did not affect the efficiency of prey digestion. As _H. iris_ and _P. canaliculus_ were identified as a high quality prey species, it is likely that they are selected for by _A. scabra_ in the East Otago Taiāpure. Data collected here will be used to adjust field survey data to adjust the apparent diet of _A. scabra_ to its actual diet.
Chapter 5

Field survey of *Astrostole scabra* distribution and diet

*Astrostole scabra* on the move. Taken from Puketeraki within the East Otago Taiāpure (Courtesy Chris Hepburn).
5.1 Introduction

5.1.1. Astrostole scabra diet

*Haliotis iris* is a culturally and commercially important species and is one of the largest remaining abalone fisheries in the world, as many other abalone fisheries have suffered serial decline (McShane 1996, Hauck and Sweijd 1999, Karpov et al. 2000, Woodby et al. 2000, Roberts *et al.* 2007). The present study surveys several sites within the East Otago Taiāpure where restrictions in the catch limit of *H. iris* have already been enforced to counteract a recognised decline in stocks (Satyanand 2010). When working with wild populations of commercially important species, it is important to understand the role of that species in its ecosystem, so that managers may determine how overfishing may result in trophic imbalance (Ortiz *et al.* 2003). *Astrostole scabra* is an acknowledged predator of *H. iris* and was the main source of adult *H. iris* mortality in a population observed over an annual period (McShane and Naylor 1997). Although *A. scabra* are capable of preying on adult *H. iris*, it is assumed here that *A. scabra* predation is focused on juvenile *H. iris*, as the escape response of adult *H. iris* should limit predation on large individuals, thereby creating a size refuge from *A. scabra* (Penny and Griffiths 1984, Schiel and Welden 1987, Barbeau and Scheibling 1994, Ross *et al.* 2002, Brewer and Konar 2005). Asteroids have been shown to select for smaller sized abalone, as prey escape responses become more effective with increasing prey size (Schiel and Welden 1987). This trend has also been shown to occur in other prey species with effective escape responses, such as scallops (Barbeau and Scheibling 1994, Ortiz *et al.* 2003).

The present study aimed to determine the density of *A. scabra* populations within the East Otago Taiāpure and gauge their threat to recovering *H. iris* populations. Some Asteroid species are recognised as important controlling forces in marine ecosystems and regulate the size and distribution of prey populations (Brewer and Konar 2005, Blanchette *et al.* 2005). It would have been desirable to determine whether *A. scabra* densities are increasing and now exert higher levels of mortality on recovering *H. iris* stocks. However, the identification of any increase in *A. scabra* abundance would have required a comparison with historic records of local *A. scabra* density, to allow a before and after impact assessment (Barret *et al.* 2009). Although this survey was not capable of recognising increasing *A. scabra* abundance, it did obtain baseline data which can be used by Taiāpure management to monitor future changes in *A. scabra* population size (Barret *et al.* 2009).

5.1.2. Possible influences on Astrostole scabra size structure and population density:

5.1.2.1. Depth

Asteroid distribution is regularly stratified by depth and generally associated with the depth distribution of prey species (Town 1979, Gaymer et al. 2001, Lamare 2009). Town (1979) observed numerous small individuals living in the intertidal and larger Astrostopole scabra living subtidally. A. scabra may move into deeper water to search for larger prey (Ref. Chapter 3) (Town 1981). Juvenile Haliotis iris are thought inhabit shallow water habitat when young then migrate to deeper water when a size refuge is reached (McShane and Naylor 1995, Roberts et al. 2007). Therefore it was expected that large A. scabra would occur at greater depths and prey on larger prey compared to A. scabra occurring in shallow habitat.

5.1.2.2. Wave action

Astrostopole scabra were less effective predators when subjected to water motion due to reduced locomotion speed and capture success when subjected to faster flowing currents (Ref. Chapter 3). Therefore A. scabra living in wave exposed areas are expected to have fewer encounters with prey and be less effective at capturing mobile prey when encounters do occur (Ref. Chapter 3). Water motion is a common source of disturbance in marine environments (Bell and Denny 1994), and can inflict mortality via dislodgement or suppress feeding when individuals are forced to shelter during periods of high swell (Bell and Denny 1994, Barahona and Navarrete 2010). The predatory Asteroid Heliaster helianthus could not forage during days of high swell, as a result, individuals living on reefs which received frequent wave exposure were observed to feed less often (Barahona and Navarrete 2010). Therefore lower
densities of *A. scabra* and smaller sized individuals were expected to occur at wave exposed reefs.

5.1.2.3. Prey availability and quality

Prey abundance is another factor likely to affect the distribution and size of Asteroids (Barbeau and Scheibling 1994). *Astrostole scabra* inhabiting food rich areas should occur in higher densities and grow to a greater maximum size (Menge 1972). In the present study, prey abundance at study sites was calculated from a survey of invertebrate populations within the East Otago Taiāpure conducted in 2008 (Richards 2009). *A. scabra* growth may also be affected by the quality of prey species present in a community (Menge 1972). The prolonged handling time of *Cookia sulcata* results in this species being of reduced energetic value to *A. scabra* when compared to species with comparatively short handling times, such as *Haliotis iris* and *Perna canaliculus* (Ref. Chapter 4) (Fairweather and Underwood 1983). Handling times can create bias in field surveys as species with longer handling times are observed disproportionately more often than those with short handling times (Fairweather and Underwood 1983). Therefore, the present study will adjust ‘apparent’ proportions of prey species consumed to ‘actual’ proportions, based on the handling times for *H. iris, C. sulcata* and *P. canaliculus* (Ref. Chapter 4) (Fairweather and Underwood 1983). Optimal foraging theory predicts that species of greatest energetic value should be selected for (Menge 1972, Barbeau and Scheibling 1994). Therefore it was expected that *C. sulcata* would be selected against because of its prolonged handling time and reduced nutritional value to *A. scabra*.

5.1.3. Hypotheses

It was hypothesised that sites with less favourable foraging conditions such as wave exposed reefs and reefs with limited food resources would contain sparser populations of *Astrostole scabra* and individuals of smaller mean size. Furthermore, *A. scabra* diet was expected be composed of a greater proportion of easy to capture immobile prey species such as *Perna canaliculus* at wave exposed shores, as mobile species would stand a greater chance of escape in such conditions. *Cookia sulcata* was expected to be a more common prey in areas where nutritionally valuable species were less common.
Based on observations made by Town (1979, 1981), it was hypothesised that *A. scabra* residing in deep water would be larger and consume larger prey than those recorded in shallow habitat. Lastly it was expected that juvenile *Haliotis iris* would constitute some part of *A. scabra*’s diet and *H. iris* would be preferably selected for at sites where both *H. iris* and *Cookia sulcata* were abundant.

### 5.2 Methods

#### 5.2.1. Experimental design

*Astrostole scabra* density, size, distribution and feeding status were measured at three locations within the East Otago Taiāpure (Figure 5.1). Each site was comprised of two, paired sub-sites which occurred in close proximity to each other (Figure 5.1). These paired sub-sites were characterised as being wave sheltered or wave exposed based on the presence of macroalgae indicator species (Hepburn *et al.* 2007). The bull kelp *Durvillaea antarctica* indicated that sites were wave exposed while stands of bladder kelp *Macrocystis pyrifera* indicated sites were wave sheltered (Hepburn *et al.* 2007). Sites were further divided into shallow subtidal and deep subtidal surveys. Surveys were conducted by snorkelling along 30 m transects, aligned parallel to the shore. Shallow surveys began at the mean low water mark and comprised of 2 - 3 transects, each separated by 6 m. Deep surveys began six meters beyond shallow transects and comprised of 3 - 5 transects, each separated by 10m. Depth was measured at four locations (0, 10, 20 and 30 m) along each transect so that the general bathymetry of each site could be plotted. Depths were later adjusted to account for tide height at the time surveys were conducted. One meter either side of the fixed transect line was intensively searched for *A. scabra*, so that a total area of 60 m² was observed by each transect. Snorkelers swept away any macroalgae obscuring view and searched as much cryptic habitat as possible without lifting rocks. When *A. scabra* were located, their size, position along transects and feeding status was recorded. If feeding *A. scabra* were discovered, the prey species was identified and shell length measured.
5.2.2. Survey sites

Figure 5.1: Wave exposed (top) and wave sheltered (bottom) sites used in the present surveys. Site names from right to left are Big Rock, Puketeraki and Huriawa.
5.2.3. Prey surveys

Prey surveys of *Haliotis iris*, *Perna canaliculus* and *Cookia sulcata* populations were conducted in 2008, four years prior to *A. scabra* surveys (Richards 2009). Prey surveys were conducted at the same sites used for *A. scabra* surveys. Prey surveys comprised of ten 1 m$^2$ quadrats placed at random positions along 30 m transect lines aligned parallel to the shore. Five transects were conducted at each site and ran along five depth contours. For this study three of the transects (0 m, 0.5 m and 1 m depth) were considered shallow, and two (2 m and 5 m depth) were considered deep. The abundance of *Haliotis iris*, *Cookia sulcata* and *Perna canaliculus* within each quadrat was recorded. Rocks were lifted to count animals living in cryptic habitat.

5.2.4. Data analysis

Statistics for *A. scabra* surveys were conducted in JMP 9. General linear models were used to determine whether *A. scabra* size and density was affected by site pair (wave exposed and sheltered pair), depth or exposure. Site pair was crossed with exposure to investigate differences within each site. Statistics for prey surveys also conducted used general linear models to test whether prey and density was affected by site pair, depth and exposure. Again, site pair was crossed with exposure and depth to investigate differences within each site.
5.3 Results:

5.3.1. Overall Astrostole scabra density and distribution

The mean density of Astrostole scabra across the six study sites was one individual per 25 m$^2$, but varied greatly between sites from 0.01 to 0.09 m$^2$. The positions of A. scabra were plotted on the bathometric profile of each site to visually analyse the distribution of A. scabra (Figures 5.2, 5.3, 5.4).

5.3.1.1. Big Rock sites

Both Big Rock sites recorded high densities (one individual per 20 m$^2$ and 11 m$^2$ respectively) of Astrostole scabra, despite differences in wave exposure and bathometry (Figures 5.2). At Big Rock Exposed the distribution of A. scabra was concentrated in deeper habitat while at Big Rock Sheltered distribution was spread evenly throughout the sample site (Figure 5.2). Big Rock Exposed increased in depth rapidly, falling to a depth of 5 m, whereas Big Rock Sheltered remained shallow (< 2 m) throughout transects (Figure 5.2). Few individuals were recorded in the shallow transects of Big Rock Exposed where the shore gradient was steepest. Sampling at Big Rock Exposed also began higher in the intertidal than at other sites (Figure 5.2).

5.3.1.2. Puketeraki sites

Puketeraki sites also held relatively high densities (one individual per 33.3 m$^2$ and 16.7 m$^2$ respectively) of Astrostole scabra, with the majority of individuals occurring close to the shore at both sites (Figures 5.3). At Puketeraki Exposed the bulk of A. scabra recorded were clumped in an area close to shore under a dense canopy of Durvillaea antarctica (Figure 5.3). It was noted during the survey that a dense aggregation of H. iris occurred in this area. At Puketeraki Sheltered A. scabra distribution was concentrated close to shore in shallow habitat (Figure 5.3).

5.3.1.3. Huriawa sites

Astrostole scabra densities were low at both Huriawa sites (one individual per 100 m$^2$ and 50 m$^2$ respectively) (Figures 5.4). All A. scabra recorded at Huriawa Sheltered occurred along one side of transects where reef became shallow as it followed a rock platform along the side of the bay as seen in site photos (Figure 5.4). A. scabra were not observed in any shallow surveys at Huriawa Sheltered (Figure 5.4). A. scabra at Huriawa Exposed occurred uniformly throughout the site (Figure 5.4).
Figure 5.2: Bathymetric profiles of Big Rock survey sites with *Astrostole scabra* positions overlaid. *A. scabra* observed within a two meter section of the transect line were recorded. Individual transects are represented by numbers representing distance from shore along the x axis. Shallow transects are separated by 6 meters and deep transects by 10 meters. Depth of substrate is displayed relative to the mean low-tide mark and is represented by different colours according to the key.
Figure 5.3: Bathymetric profiles of Puketeraki survey sites with *Astrostole scabra* positions overlaid. *A. scabra* observed within a two meter section of the transect line were recorded. Individual transects are represented by numbers representing distance from shore along the x axis. Shallow transects are separated by 6 meters and deep transects by 10 meters. Depth of substrate is displayed relative to the mean low-tide mark and is represented by different colours according to the key.
Figure 5.4: Bathymetric profiles of Huriawa survey sites with *Astrostole scabra* positions overlaid. *A. scabra* observed within a two meter section of the transect line were recorded. Individual transects are represented by numbers representing distance from shore along the x axis. Shallow transects are separated by 6 meters and deep transects by 10 meters. Depth of substrate is displayed relative to the mean low-tide mark and is represented by different colours according to the key.
5.3.2. Size structure of Astrostole scabra populations

When analysed across all sites Astrostole scabra size frequency demonstrated a normal distribution, with the most frequent A. scabra size being 40 – 44 cm (Figure 5.5). Diameters ranged from 25 – 56 cm therefore no small individuals (< 25 cm) were recorded by these surveys (Figure 5.5).

Sites with a larger sample sizes (Big rock Sheltered and Puketeraki, Sheltered) also appeared to have normally distributed size ranges. A. scabra size differed significantly between sites (p = 0.0027) (Table 4.1, Figure 5.6). Individuals from Puketeraki Sheltered were significantly smaller than all other sites except Huriawa Sheltered (Figure 5.6). The greatest abundance of large individuals (+ 50 cm) occurred at Big Rock Exposed (Figure 5.6). Figure 5.5 should not be used to infer about A. scabra abundance as graphs do not account for differences in sample size.

Figure 5.5: Size frequency distribution of Astrostole scabra. Bars represent the number of A. scabra found within each size class. Black triangle represents A. scabra size class containing the mean diameter.
Figure 5.6: Size structure of *Astrostole scabra* populations at each site surveyed. Bars represent the number of *A. scabra* found within each size class, at each site. Letters represent significant differences between sites. Black triangles represent *A. scabra* size class containing the mean diameter.
5.3.3. Effects on Astrostole scabra populations

5.3.3.1. Depth

Astrostole scabra diameter did not vary between shallow and deep transects overall (Figure 5.7). Depth failed to significantly explain A. scabra density, however significant differences were observed between deep and shallow transects within two site pairs (Table 5.2, Figure 5.7). A. scabra density was significantly greater in deep transects than shallow transects at Big Rock sites (Figure 5.7). Conversely A. scabra density at Puketeraki sites was greater in shallow transects (Figure 5.7). Density did not differ between shallow and deep transects at Huriawa. A. scabra were not observed in shallow transects at the Huriawa Sheltered (Figure 5.7).

5.3.3.2. Wave exposure

Exposure did not have a significant effect on Astrostole scabra diameter across combined sites (Table 4.1, Figure 5.8). When analysed among sites, individuals from Puketeraki Sheltered were significantly smaller than individuals from Puketeraki Exposed and all other sites except Huriawa Sheltered (Figure 5.8).

Exposure had a significant effect on A. scabra density across all sites (p = 0.0064) (Table 5.2, Figure 5.8). Significant differences in A. scabra density were observed between individual sites (Table 5.2, Figure 5.8). Big Rock Sheltered and Puketeraki Sheltered recorded significantly greater densities of A. scabra than Puketeraki Exposed and both Huriawa sites (Figure 5.8). Big Rock paired sites contained significantly different A. scabra densities (Table 5.1, Fig 5.8). Geographical location had the greatest overall effect on A. scabra density (p < 0.0001) (Table 5.2).
Table 5.1: Results from general linear model used to test the significance of location, depth and exposure on *Astrostole scabra* diameter. Individual sites are represented by Site pair*Exposure. Significance is denoted by *.

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Table 5.2: Results from general linear model used to test the significance of location, depth and exposure on *Astrostole scabra* density. Individual sites are represented by Site pair*Exposure. Significance is denoted by *.

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Figure 5.7: *Astrostole scabra* density (bars) and mean diameter (points) for deep and shallow transects at each site pair and overall. Letters represent significant differences between paired sites. No *A. scabra* were recorded in shallow Huriwa transects.

Figure 5.8: *Astrostole scabra* density (bars) and mean diameter (points) for exposed and sheltered paired sites and overall. Letters represent significant differences between sites.
5.3.4. Observed diet of Astrostole scabra

5.3.4.1. Diet composition

The most common prey species recorded were *Haliotis iris* and *Cookia sulcata* which made up 43% and 36% of the ‘apparent’ diet respectively (Table 5.3). The remaining 21% of the diet was made up of two further gastropod species, including a whelk (*Lepsithais lacunosus*), and a ducks bill limpet (*Scutus breviculus*), as well as the camouflage crab (*Notomithrax peronei*) (Table 5.3).

Many prey species being consumed by *Astrostole scabra* were small (shell length < 30 mm) apart from *H. iris*, which were comparatively much larger (100 – 124 mm). *S. breviculus* was of a similar size of *H. iris* despite having a short shell length (38 mm). The body length of a similar *S. breviculus* with a similar shell length (41 mm) was measured and found to be 70 mm long.

5.3.4.2. Adjustment from apparent to actual diet

The apparent observations of *Haliotis iris* and *Cookia sulcata* were adjusted by considering handling time and prey size to calculate their ‘actual’ prevalence in *Astrostole scabra* diet (Table 5.4). The greater handling time and small size of *C. sulcata* meant that the observed frequency and importance to *A. scabra* of this species was overestimated (Table 5.4). Post adjustment, *H. iris* and *C. sulcata* made up 55% and 18% of the diet respectively (Table 5.4).

The average energetic benefit to *A. scabra* was calculated as grams consumed per hour and was several orders of magnitude higher for *H. iris* (5.77 g h$^{-1}$) than *C. sulcata* (0.02 g h$^{-1}$) (Table 5.4)

5.3.4.3. Feeding activity

Overall, feeding activity was low with only 14 out of a total of 114 *Astrostole scabra* observed feeding (Table 5.3). The proportion of individuals feeding differed greatly between sites, from 0% of *A. scabra* recorded feeding at Huriawa Sheltered to 60% at Huriawa Exposed (Table 5.3). Tide conditions did not have an obvious effect on feeding status, with individuals found feeding at all points of the tidal cycle (Table 5.3).
Table 5.3: Observed levels of *Astrostole scabra* feeding status and diet for each site. Instances of one prey being consumed by two *A. scabra* are marked *. Tide conditions represent the tide state at the time of survey as well as the direction of tidal flow, for example Mid – High is an incoming tide.

<table>
<thead>
<tr>
<th>Site</th>
<th>Tide conditions</th>
<th>n <em>A. scabra</em></th>
<th>n <em>A. scabra</em> feeding</th>
<th>proportion feeding</th>
<th>Prey Species</th>
<th>Astrostole scabra diameter (cm)</th>
<th>depth of feeding (m below average low tide mark)</th>
<th>Mean Prey shell length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Big Rock Exposed</td>
<td>Mid - High</td>
<td>24</td>
<td>6</td>
<td>0.25</td>
<td><em>Haliotis iris</em></td>
<td>47</td>
<td>1.83</td>
<td>108</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Haliotis iris</em></td>
<td>42</td>
<td>1.83</td>
<td>108</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Haliotis iris</em></td>
<td>58</td>
<td>2.70</td>
<td>124</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Haliotis iris</em></td>
<td>50</td>
<td>0.06</td>
<td>112</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Cookia sulcata</em></td>
<td>56</td>
<td>2.70</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Cookia sulcata</em></td>
<td>41</td>
<td>2.70</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Cookia sulcata</em></td>
<td>42</td>
<td>2.88</td>
<td>21</td>
</tr>
<tr>
<td>Big Rock Sheltered</td>
<td>Mid - Low</td>
<td>44</td>
<td>1</td>
<td>0.02</td>
<td><em>Haliotis iris</em></td>
<td>48</td>
<td>0.25</td>
<td>100</td>
</tr>
<tr>
<td>Puketeraki Exposed</td>
<td>High - Mid</td>
<td>13</td>
<td>2</td>
<td>0.15</td>
<td><em>Haliotis iris</em></td>
<td>38</td>
<td>0.37</td>
<td>107</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Haliotis iris</em></td>
<td>49</td>
<td>0.37</td>
<td>107</td>
</tr>
<tr>
<td>Puketeraki Sheltered</td>
<td>Mid - Low</td>
<td>22</td>
<td>2</td>
<td>0.09</td>
<td><em>White welk</em></td>
<td>37</td>
<td>1.94</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Cookia sulcata</em></td>
<td>28</td>
<td>1.14</td>
<td>16</td>
</tr>
<tr>
<td>Huriawa Exposed</td>
<td>Low</td>
<td>5</td>
<td>3</td>
<td>0.60</td>
<td><em>Notomithrax peronii</em></td>
<td>49</td>
<td>0.93</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Cookia sulcata</em></td>
<td>42</td>
<td>1.40</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Scutus breviculus</em></td>
<td>53</td>
<td>0.73</td>
<td>38</td>
</tr>
<tr>
<td>Huriawa Sheltered</td>
<td>High</td>
<td>6</td>
<td>0</td>
<td>0.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Overall</td>
<td></td>
<td>114</td>
<td>14</td>
<td>0.12</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 5.4: Adjusted *Astrostole scabra* diet based on handling time for the two most frequent prey species, *Haliotis iris* and *Cookie sulcata* (Ref. Chapter 4). Relative proportions consumed are based on the handling time of *H. iris* and refers to the number of *C. sulcata* consumed for every *H. iris*. The contribution of other species to the diet was given the same relative proportion as *H. iris* as no other species possessed a calcareous operculum which may lengthen handling time (Ref. Chapter 4).

<table>
<thead>
<tr>
<th>Species</th>
<th>Average prey length (mm)</th>
<th>Average estimated handling time (hr)</th>
<th>Estimated weight (g) consumed per hour for each prey individual</th>
<th>Relative consumption rate</th>
<th>Apparent contribution to diet</th>
<th>Adjusted/actual contribution to diet</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Haliotis iris</em></td>
<td>109.4</td>
<td>86.78</td>
<td>5.77</td>
<td>1</td>
<td>43%</td>
<td>55%</td>
</tr>
<tr>
<td><em>Cookie sulcata</em></td>
<td>21.2</td>
<td>173.75</td>
<td>0.02</td>
<td>0.50</td>
<td>36%</td>
<td>18%</td>
</tr>
<tr>
<td>Other</td>
<td></td>
<td>1</td>
<td>21%</td>
<td></td>
<td>21%</td>
<td>27%</td>
</tr>
</tbody>
</table>
5.3.5. Distribution and abundance of prey species

Surveys of prey density revealed individual sites had a significant effect on the distribution of *H. iris* and *P. canaliculus*, while *C. sulcata* did not vary significantly between sites (Table 5.3, Figure 5.9). The high densities of *A. scabra* at Big Rock sites coincided with high abundances of *H. iris* and few *C. sulcata* (Figure 5.9). *H. iris* was also the major prey species at Puketeraki Exposed, where they occurred in low abundance overall but were observed to form a dense aggregation in shallow habitat beneath a thick *Durvillaea antarctica* canopy (Figure 5.9). At Puketeraki Sheltered, the dominant prey species was *Cookia sulcata*. All prey species were numerous at Huriawa Exposed despite low densities of *A. scabra* (Figure 5.9). At Huriawa Sheltered a low *A. scabra* density was coupled with low prey availability (Figure 5.9).

Depth significantly affected the distribution of *H. iris* and *P. canaliculus* with both species occurring in higher densities in shallow quadrats (Table 5.4 Figure 5.10). The only site that *H. iris* density did not significantly vary between deep and shallow transects was Big Rock Exposed (Figure 5.10). *H. iris* and *P. canaliculus* distribution was significantly affected by exposure, with denser populations occurring at wave exposed sites. Conversely *C. sulcata* distribution was not significantly affected by depth or exposure (Table 4.4 Figure 5.10).

### Table 5.5: Results from general linear model which tested the effect of location, depth and exposure on *Haliotis iris*, *Cookia sulcata* and *Perna canaliculus* density. Values representative of individual sites are depicted by Site pair*Exposure. Significance is denoted by *.

<table>
<thead>
<tr>
<th>Species</th>
<th>Source</th>
<th>DF</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>H. iris</em></td>
<td>Site pair</td>
<td>2</td>
<td>7.189</td>
<td>0.0009*</td>
</tr>
<tr>
<td></td>
<td>Depth</td>
<td>1</td>
<td>20.6747</td>
<td>&lt; 0.0001*</td>
</tr>
<tr>
<td></td>
<td>Exposure</td>
<td>1</td>
<td>4.4195</td>
<td>0.0364*</td>
</tr>
<tr>
<td></td>
<td>Site pair*Depth</td>
<td>2</td>
<td>5.8395</td>
<td>0.0033*</td>
</tr>
<tr>
<td></td>
<td>Site pair*Exposure</td>
<td>2</td>
<td>2.4008</td>
<td>0.0924</td>
</tr>
<tr>
<td><em>C. sulcata</em></td>
<td>Site pair</td>
<td>2</td>
<td>1.7060</td>
<td>0.1834</td>
</tr>
<tr>
<td></td>
<td>Depth</td>
<td>1</td>
<td>0.0177</td>
<td>0.8943</td>
</tr>
<tr>
<td></td>
<td>Exposure</td>
<td>1</td>
<td>1.4128</td>
<td>0.2356</td>
</tr>
<tr>
<td></td>
<td>Site pair*Depth</td>
<td>2</td>
<td>0.0464</td>
<td>0.9546</td>
</tr>
<tr>
<td></td>
<td>Site pair*Exposure</td>
<td>2</td>
<td>3.0432</td>
<td>0.0492*</td>
</tr>
<tr>
<td><em>P. canaliculus</em></td>
<td>Site pair</td>
<td>2</td>
<td>9.8375</td>
<td>&lt; 0.0001*</td>
</tr>
<tr>
<td></td>
<td>Depth</td>
<td>1</td>
<td>10.3514</td>
<td>0.0014*</td>
</tr>
<tr>
<td></td>
<td>Exposure</td>
<td>1</td>
<td>16.2636</td>
<td>&lt; 0.0001*</td>
</tr>
<tr>
<td></td>
<td>Site pair*Depth</td>
<td>2</td>
<td>9.0785</td>
<td>0.0001*</td>
</tr>
<tr>
<td></td>
<td>Site pair*Exposure</td>
<td>2</td>
<td>14.6994</td>
<td>&lt;0.0001*</td>
</tr>
</tbody>
</table>
Figure 5.9: Density of prey species *Haliotis iris*, *Cookia sulcata* and *Perna canaliculus* (bars) and *Astrostole scabra* (points) for Exposed (E) and Sheltered (S) site pairs at Big Rock (BR), Puketeraki (P) and Huriawa (H). Density is calculated as average number of animals per m$^2$. Letters denote significant difference in *H. iris* and *P. canaliculus* density between sites. Numbers denote significant difference in *A. scabra* density between sites. *C. sulcata* density did not differ significantly between sites.
Figure 5.10: Density of *Haliotis iris*, *Cookia sulcata* and *Perna canaliculus* in shallow (white bars) (0 – 1 m) and deep (grey bars) (3 – 6 m) quadrats for Exposed (E) and Sheltered (S) site pairs at Big Rock (BR), Puketeraki (P) and Huriawa (H). Letters represent significant differences in prey density.
Discussion

5.4.1. Overall Astrostole scabra distribution, size structure and density

The overall size frequency of *Astrostole scabra* was normally distributed, as observed in other Asteroid population surveys (Scheibling 1980, Duggins 1983, Penny and Griffiths 1984, Ortiz *et al.* 2003). Asteroid growth is generally indiscriminate of age and relies more on accessibility to prey resources (Menge 1972, Tokeshi *et al.* 1989). The lack of dependant growth or any visible size modes makes it impossible to determine any age structure in this Asteroid population.

The smallest *A. scabra* recorded was 25 cm and therefore this survey method failed to sample small individuals. Asteroids living at rocky shores are thought to recruit to cryptic habitat making encounters with small individuals rare (Duggins 1983, Tokeshi *et al.* 1989, Ortiz *et al.* 2003, Blanchette *et al.* 2005). The limited *A. scabra* size range recorded here makes it difficult to compare results with Town’s (1981) study which investigated the diet of small (4 – 30 cm), intertidal *A. scabra*. Intertidal *A. scabra* feed mainly on chitins and trochid snails, with *H. iris* constituting < 1% of prey consumed (Town 1979).

The present survey recorded an overall *A. scabra* density of 0.04 m$^{-2}$. *A. scabra* distribution was far from homologous and varied significantly among sites from 0.01 to 0.09 *A. scabra* per m$^2$. The average density of the predatory Asteroid *Marthasterias glacialis* on mussel beds was at 5.65 m$^2$, greater than *A. scabra* densities observed here (Penny and Griffiths 1984). However, Asteroids feeding on mussel beds may be expected to occur in dense aggregations as their prey exist in spatially distinct patches. The density of six Sub Antarctic Asteroid species ranged from 0.4 to 1.5 m$^2$ (Beckley and Branch 1992), and *Oreaster reticulatus* varied between sites from 0.02 – 0.14 m$^2$ in a sandy bottom habitat. Such densities are similar to those recorded in the present study for *A. scabra*.

5.4.2. Effect of depth on Astrostole scabra populations

Deep transects were expected to contain larger *Astrostole scabra* than shallow transects, however *A. scabra* size did not vary according to depth overall. Town (1979, 1981) found that larger *A. scabra* occurred in deeper water. However, as previously mentioned, the present survey did not record any *A. scabra* smaller than 25 cm and therefore it is likely that
all observed *A. scabra* were non-cryptic adults and may not be affected by depth. Depth did not significantly affect the overall density of *A. scabra*, however *A. scabra* density did vary in relation to depth at individual sites.

### 5.4.2.1. Big Rock sites

At Big Rock, significantly more *Astrostole scabra* occurred in deep transects. *A. scabra* may occur more frequently in deep habitat at Big Rock Exposed because the distribution of *Haliotis iris* extended deeper at this site than at other sites. Large *H. iris* (100 – 124 mm) were the most common *A. scabra* prey and adult *H. iris* individuals generally reside in deeper water (McShane and Naylor 1995, McShane and Naylor 1997, Roberts *et al.* 2007). Therefore it is likely that large *A. scabra* may move into deeper water to search for large *H. iris* in areas where their distribution is extended. Other factors may have also contributed to greater *A. scabra* abundance in deep transects at Big Rock Exposed, such as the steep bathometric profile of the site, which is known to increase the wave force experienced by animals (Denny 1995). Transects at Big Rock Exposed also began higher above the mean low tide mark than other sites and therefore the shallowest transect may have been unlikely to contain *A. scabra*, reducing the average density observed in shallow transects. At Big Rock Sheltered none of the prey species were recorded by deep prey surveys yet the majority of *A. scabra* were found in deep *A. scabra* survey transects. This may be an effect of the low slope gradient of the site, meaning that only depths < 2 m were searched in *A. scabra* surveys. Comparatively, deep prey surveys were conducted from 2 – 5 m. Therefore majority of deep transects likely still covered areas with high prey abundance.

### 5.4.2.2. Puketeraki sites

At both Puketeraki sites *Astrostole scabra* occurred at significantly greater densities in shallow transects. *A. scabra* at Puketeraki Exposed were recorded consuming adult *Haliotis iris* despite a low abundance of *H. iris* recorded in prey surveys. At Puketeraki Exposed *A. scabra* were observed to occur in dense aggregations beneath a thick canopy of *Durvillaea antarctica*, where aggregations of *H. iris* were also observed. Therefore it seems likely the distribution of *H. iris* influences the depth distribution of *A. scabra* at Puketeraki Exposed. At Puketeraki Sheltered *A. scabra* were concentrated in shallow transects which may be a
result of the small size of *A. scabra* observed at this site. The smaller *A. scabra* from Puketeraki Sheltered may prefer to live intertidally where small prey which are easy to catch are more common (Town 1981).

### 5.4.2.3. Huriawa sites

At Huriawa, low densities of *Astrostole scabra* make it difficult to draw any conclusions about whether distribution was affected by depth. *A. scabra* distribution at Huriawa Sheltered was most dense along the side of transects where reef became shallow and substrate turned to boulders. This area likely provide higher levels of prey as boulder substrate is thought to be preferable habitat for most reef dwelling gastropod species (Alexander *et al.* 2009).

### 5.4.3. Effect of wave exposure on Astrostole scabra populations

The present survey hypothesised that *Astrostole scabra* would be less effective predators at wave exposed shore as their ability to locate and capture mobile species would be reduced by water motion (Gagnon *et al.* 2003, Weissburg *et al.* 2003, Barahona and Navarrete 2010, Muller *et al.* 2011). Therefore *A. scabra* were expected to occur in greater abundance and be of a larger mean size at wave sheltered shores.

*A. scabra* size was not affected by exposure when analysed across all sites but did vary within some site pairs. As mentioned prior, Puketeraki Sheltered contained significantly smaller individuals than other sites, contrary to the hypothesis. The small size of *A. scabra* at Puketeraki Sheltered is likely a result of a low quality diet, as the dominant prey species here was *Cookia sulcata*.

Wave exposure significantly affected overall *A. scabra* distribution, with greater densities observed at wave Sheltered sites. The greatest densities of *A. scabra* were recorded at Big Rock Sheltered and Puketeraki Sheltered. Wave exposure is an important source of mortality in marine ecosystems (Bell and Denny 1994, Denny 1994), and is an important factor in generating heterogeneity in ecosystems, as it creates areas where predation pressure is reduced (Duggins 1983). Patches of low predation can allow a preferred prey species to exist in an ecosystem which is otherwise controlled by predation and resulted in greater *H. iris* and
P. canaliculus abundance at wave exposed sites (Petraitis 1990, Duggins 1983). The abundance of A. scabra was not significantly different between Huriawa Exposed and Sheltered sites which may be a result of few A. scabra being recorded at both of these sites.

5.4.4. Observed Astrostolet scabra diet

5.4.4.1. Diet composition

Haliotis iris and Cookia sulcata were identified as major prey species across most sites. Perna canaliculus was not once observed as an Astrostolet scabra prey item, even at Huriawa Exposed where they occurred in high abundance and the greatest proportion of feeding activity was recorded. H. iris was the most common prey overall and with adjustments to account for the prolonged handling time of C. sulcata, constituted over half (55%) of the observed diet. Differences in handling time mean that the prevalence of some prey are underestimated when predator diet is surveyed, as observations are biased towards more slowly digested prey (Fairweather and Underwood 1983, Petraitis 1990).

5.4.4.2. Prey size

Astrostolet scabra consumed larger Haliotis iris than expected (100 – 124 mm), with no juvenile H. iris recorded by feeding surveys. Most other prey species were comparatively much smaller than H. iris, with the one exception of a single medium sized Scutus breviculus (70 mm body length). It was hypothesised that the strong escape response of adult H. iris would limit predation and therefore juvenile H. iris would be common prey (Ref. Chapter 3). The diet of the Asteroid Asterais vulgaris comprises mainly small individuals of the scallop Plactopecten magellanicus, because large P. magellanicus escape more regularly, despite similar encounter rates with all prey sizes (Barbeau and Scheibling 1994, Ortiz et al. 2003). In the Asteroid Pycnopodia helianthoides predation was focused on smaller size classes of the Red abalone (Haliotis rufescens) when the two species were left together in captivity (Schiel and Welden 1987). A. scabra diet is known to change as it increases in size (Town 1981). As predator size increases a wider range of prey species and sizes become available (Menge 1972). Large A. scabra recorded by the present survey are evidently capable of capturing adult H. iris on a regular basis.
5.4.4.3 Prey quality

Food quality can be determined as the weight of prey tissue consumed per hour of handling time (Menge 1972). The large size and short handling time of *Haliotis iris* makes this species high quality food source for *Astrostole scabra* (Ref. Chapter 4). Due to the common presence of *H. iris* in diet surveys and large size compared to other prey species it is expected that *H. iris* is a major dietary component of *A. scabra* living in the East Otago Taiāpure.

5.4.4.4 Feeding activity

Surveys were conducted in summer when feeding activity was expected to be high so that the diet of *A. scabra* could be defined as accurately as possible (Town 1980b). Evidently feeding activity was low (12%) and highly variable between sites, ranging from 0% to 60%. Town (1979) observed feeding to vary between 20% and 40% during any time of year and the predatory Asteroid *Leptasterias hexactis* ranged in feeding activity form 28.9% to 62.0% (Menge 1972). As surveys could only be conducted on calm days it does not seem that wave action is to blame for suppressed feeding activity. Feeding activity also occurred evenly throughout all sectors of the tidal cycle. Furthermore as handling times for the prey observed encompass a period of several days it should be expected that feeding events would be observed irrespective of tidal state. Low feeding activity observed in the present study may be linked to the large size of prey (Menge 1972). Large prey species are considered high quality food sources as weight consumed per hour increases with increased prey size (Ref. Chapter 4) (Menge 1972). Menge (1972) observed that feeding activity was highest where poor quality prey were abundant and lower at sites where high quality prey was abundant. Therefore an abundance of high quality prey such as *H. iris* may compensate for the observed low feeding activity (Menge 1972). Conversely, at Huriawa Exposed feeding activity was greater than other sites (60%) which may be due to a lower quality *A. scabra* diet.

5.4.5 Prey abundance at survey sites

Prey distribution is acknowledged as a factor that can affect Asteroid distribution (Menge 1972, Gaymer *et al*. 2001, Lamare *et al*. 2009). Asteroids move short distances and take long times to consume prey, therefore they are found within close proximity to prey populations.
In the present prey surveys, *Haliotis iris* were the most common prey species and were present at all sites, but occurred in significantly greater abundance at Big Rock sites and Huriawa Exposed. High *H. iris* densities at Big Rock may explain the high densities of *A. scabra* at this site. *Astrostole scabra* from Big Rock sites also recorded the greatest proportion of large (+50 cm) individuals which suggests high food quality (Menge 1972). *A. scabra* were observed in aggregations around areas of suspected high *H. iris* abundance at sites Puketeraki Exposed and Huriawa Sheltered. Therefore it is likely that *A. scabra* increase their chances of encountering high quality prey by living in areas where quality species occur in high abundance. Oddly, at Huriawa Exposed where the greatest proportion of *A. scabra* feeding activity was recorded, no *H. iris* were identified as prey. Huriawa Exposed is also in close proximity to a river outlet and therefore it is likely that low salinity may suppress capture ability (Wing and Leichter 2011). Areas of low salinity are known to attract elevated abundances of mussels as observed at Huriawa exposed (Wing and Leichter 2011). Wing and Leichter (2011) examined the effect of low salinity on mussel interactions with predators and identified that *Perna canaliculcus* gained refuge from predation from red rock lobsters (*Jasus edwardsii*) and Asteroids (*Coscinasterias muricata*) in the low salinity layer of a New Zealand fiord system. It is likely that *A. scabra* predation is negatively affected by the low salinity at Huriawa and making it especially difficult for *A. scabra* to capture species with effective escape responses such as *H. iris*. If *H. iris* were unobtainable at Huriawa Exposed, it may also explain the high levels of feeding activity recorded, as *A. scabra* would be forced to shift their diet to lower quality food sources which require higher levels of consumption (Menge 1972).

*Cookia sulcata* were recorded at multiple sites but occurred in greatest densities at Puketeraki Sheltered. The elevated densities of *C. sulcata* at Puketeraki Sheltered may be linked to the significantly smaller sized *A. scabra* observed at this site. Menge (1972) recorded smaller individuals of the Asteroid *Leptasterias hexactis* at a site which contained mainly small, energy poor prey species. The operculum of *C. sulcata* prolongs handling time and reduces the prey’s energetic benefit which is dependent on the weight consumed per hour (Ref. Chapter 4) (Menge 1972, Fairweather and Underwood 1983, Vermeij and Williams 2007). When *Leptaasterias hexactis* was fed abundant food in captivity, it grew to a much larger size than observed in natural conditions (Menge 1972). Therefore, food is expected to limit growth in Asteroids and explains why *A. scabra* are smaller at Puketeraki sheltered (Menge
Surprisingly, *A. scabra* density remained high at Puketeraki sheltered despite low food quality.

Optimal foraging theory predicts that species of greatest calorific importance should be preferably consumed (Menge 1972, Town 1981, Barbeau and Scheibling 1994). *H. iris* were consumed at higher levels than other, lower quality prey species. However, even when energy rich species such as *H. iris* were abundant at sites such as Big Rock, the comparatively energy poor *C. sulcata* remained an occasional dietary component. Prey selection in Asteroids can be active, where predators select a preferred species more often than others or passive, where selection is random and based on factors such as encounter rate and capture success (Menge 1972, Barbeau and Scheibling 1994). As *H. iris* constituted 55% of *A. scabra* prey it seems selection is largely active. However as *A. scabra* did not always reject the energy poor species *C. sulcata*, selection also appears to also be somewhat passive. Menge (1972) proposed that Asteroids will always attempt to capture energy rich species which are often difficult to catch, but when individuals become hungry they will be more likely to consume easy to capture, energy poor species. Therefore foraging behaviour may switch from active to passive based on *A. scabra*’s level of hunger at a single point in time (Menge 1972). This theory explains the diet observed in *A. scabra* and fits with the generalist nature of the species. A generalistic foraging strategy may ensure that the species can thrive no matter what type of prey are available and allows *A. scabra* to overcome the limiting effect of food availability (Menge 1972, Town 1980b). *A. scabra* at Puketeraki Sheltered appeared to have adapted to a diet different than other sites, as their small size suggested their diet comprised of lower quality prey, yet they remained in high abundance. Similarly the Asteroid *Meyenaster gelatinosus* was able to survive by feeding on other prey species when its preferred prey, the scallop *Argopecten purpuratus* was fished to low levels (Ortiz et al. 2003) and *Heliaster helianthus* achieved similar levels of food intake across different localities by adjusting foraging behaviour to local conditions (Menge 1972). Generalisation allows a species to thrive in unstable environments, where prey composition can vary spatially or seasonally (Menge 1972).

5.4.6. Effect of multiple factors on Astrostole scabra populations

Prey abundance and distribution seems to be the major contributor to the distribution and size structure of *Astrostole scabra* populations, more so than wave exposure or depth. Sites that
recorded significantly lower densities of *A. scabra* (Puketeraki Exposed and Huriawa Sheltered) contained low abundances of the three prey species recorded. Conversely, sites that recorded the highest densities of *A. scabra* (Big Rock Sheltered, Exposed and Puketeraki Sheltered) contained higher levels of prey abundance. Puketeraki Sheltered recorded a significantly higher abundance of *C. sulcata* which coincided with significantly reduced *A. scabra* size. Huriawa Exposed recorded low densities of *A. scabra* despite having abundant prey populations, which is likely attributed to low salinity negatively impacting *A. scabra* prey capture success, resulting in a diet of lower quality prey requiring greater feeding activity (Wing and Leichter 2011).

Although prey availability is thought to be the primary factor controlling *A. scabra* abundance and distribution it is likely that many others factors interact with one another and also affect *A. scabra* populations. Reef substrate and water flow interact to create different assemblages of biota and by create refuge for prey species (Alexander et al. 2009). Therefore while wave action had a direct negative effect on *A. scabra* distribution, it also affects algae growth and the distribution of invertebrate species (Hepburn et al. 2007, Donovan and Taylor 2008). *A. scabra* occurred at significantly greater densities in wave sheltered sites while *H. iris* significantly favoured wave exposed sites. Therefore wave exposure also likely has indirect positive influences on *A. scabra* such as increased abundance of high quality prey species such as *H. iris*. This was shown here by the fact that Puketeraki Sheltered contained low abundances of *H. iris* which coincided with *A. scabra* of significantly smaller size, while Big Rock Exposed which held high abundances of *H. iris* and contained the largest *A. scabra* recorded. Furthermore the highest densities of *A. scabra* were observed at Big Rock Sheltered where both favourable conditions are present, namely high *H. iris* abundance and low wave action. Depth is also known to affect *H. iris* distribution, with larger individuals residing in deeper water (Cornwall et al. 2009). In the present study, at Big Rock where the depth distribution of *H. iris* was extended *A. scabra* colonised deeper waters. Therefore multiple factors likely interact to affect *A. scabra* distribution.

5.4.7. Conclusion

Overall, prey abundance, distribution and quality were the greatest determinants of *Astrostole scabra* density, distribution and size. *A. scabra* density and size did not appear to be affected by depth when analysed overall. However depth did significantly affect *A. scabra*
distribution at individual sites, most likely as a result of prey species depth distribution. *A. scabra* were significantly more common at wave Sheltered sites than wave Exposed sites as *A. scabra* is expected to be a more effective predator and experience lower levels of mortality in low water motion conditions. Immobile prey *Perna canaliculus* were not observed being eaten by *A. scabra* and therefore were not selected more often at wave exposed sites as predicted. *H. iris* were identified as major dietary component of *A. scabra* with results indicating that approximately half of the *A. scabra* diet consists of *H. iris*. Lastly *A. scabra* were observed to feed on large *H. iris* (100 – 124 mm), rather than juvenile *H. iris*, contrary to expectation.
Chapter 6

Isotope analysis of *Astrostole scabra* diet

*Astrostole scabra* in separated feeding tanks used in isotope turnover experiments.
6.1 Introduction

6.1.1. Stable isotope analysis of Astrostole scabra diet

Stable isotope analysis allows the diet of predator species to be estimated if the isotopic signature of a predator and its prey are known (Post 2002, Newsome et al. 2007). Astrostole scabra are generalist predators and may consume a wide range of prey species (Town 1981). Town (1981) identified juvenile A. scabra consumed a diverse diet, however, field surveys conducted in the present study observed adult A. scabra consuming only five prey species, with a large proportion of their diet comprising of H. iris (Ref. Chapter 5). Field surveys were conducted at one point in time and recorded a low overall level of feeding activity, limiting the accuracy of results and conclusions made about A. scabra diet. In this chapter, estimates of A. scabra diet will be made based on the isotopic signatures of A. scabra and the three prey species H. iris, Cookia sulcata and Perna canaliculus, in order to cross-check conclusions made about A. scabra diet during field surveys.

Stable isotope signatures reflect average diet consumed by an animal over a period of months or years (Post 2002, Newsome et al. 2007). The period of time an isotopic signature reflects varies depending on the species sampled, the animal’s age and the type of tissue sampled (Post 2002). Therefore, the rate of isotopic turnover in A. scabra was calculated experimentally to identify the time period represented by isotope signatures in the field and examine the level isotopic fractionation in A. scabra.

6.1.2. Using stable isotopes in ecology

Two of the most common isotope ratios used in marine ecology today are $^{13}$C/$^{12}$C and $^{15}$N/$^{14}$N (Post 2002). Stable isotopic signatures are generally denoted in delta notation and express the difference between the isotopic ratio of the sample and that of a standard (Pee belemnite limestone for δ$^{13}$C and atmospheric nitrogen for δ$^{15}$N) (Peterson and Fry 1987, Post 2002). Results are derived using the following equation:

$$\delta = \left[ \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 1000$$

Where R is the absolute ratio of isotopes ($^{15}$N / $^{14}$N or $^{13}$C / $^{12}$C) and $\delta$ is expressed as deviation per ml from the standard (‰).
Stable isotope analysis allows the movement of organic matter through an ecosystem to be estimated and relies on the dependable trophic discrimination of isotopic ratios as they move up the food web (Post 2002). As atoms move through food webs lighter isotopes (\(^{14}\)N and \(^{12}\)C) are incorporated into tissues more slowly than heavy isotopes (\(^{15}\)N and \(^{13}\)C) (Peterson and Fry 1987, Post 2002). As a consequence, higher trophic level animals become enriched with heavy isotopes (Peterson and Fry 1987, Post 2002). Trophic discrimination of \(\Delta^{13}\)C is relatively small (typically \(\sim 0.4\)‰ per trophic level) as carbon is transferred up through food webs (Peterson and Fry 1987, Post 2002). Therefore carbon isotopes are often used to indicate the important primary producers in an ecosystem, referred to as organic sources (Peterson and Fry 1987, Post 2002). Trophic discrimination of nitrogen \(\Delta^{15}\)N is relatively large (typically \(\sim 3.4\)‰ per trophic level) as nitrogen is transferred up through food webs (Peterson and Fry 1987, Post 2002). Therefore nitrogen isotopes are good indicators of an animal’s trophic level (Peterson and Fry 1987, Post 2002). The combined use of carbon and nitrogen isotopes complement each other and allow both the carbon source and trophic level of an animal to be identified.

6.1.3. Isotopic turnover rates

The \(\delta^{13}\)C and \(\delta^{15}\)N isotope signatures of a predator’s tissue represent the predator’s diet over a period of days, months or years (Suring and Wing 2009). This period of time depends on the isotopic turnover rate in an animal’s tissues, which varies depending on the metabolic rate of the species and the type of tissue sampled (Peterson and Fry 1987, Suring and Wing 2009). Research for this thesis failed to locate any experiments that tested isotopic turnover in Asteroids and therefore, the time period represented by the isotope signature of Asteroid tissue was unknown. The tube feet of *Astrostole scabra* are comprised of soft muscle tissue and were expected to turnover quickly, representing an isotope signature representative of recent diet. Rates of isotopic turnover in *A. scabra* tube feet were calculated experimentally in this study and used to identify the time period represented by \(\delta^{13}\)C and \(\delta^{15}\)N signatures of *A. scabra* in the wild. Furthermore, if complete isotopic turnover occurred within the duration of the study, difference between the \(\delta^{13}\)C and \(\delta^{15}\)N signatures of *A. scabra* and its prey could be used to calculate the amount of fractionation that occurs when isotopes are sequestered by *A. scabra*. When the amount of trophic discrimination for an animal is determined, then the pathway of source carbon through the food web can be more accurately resolved.
6.1.3. Hypotheses

It was hypothesised that the isotope signature of *Astrostole scabra* fed a single species for a period of six months would change to reflect that of its diet. Furthermore if two treatments comprising of different prey species, each with different carbon isotope signatures were feed to *A. scabra* the carbon signatures of *A. scabra* would diverge to reflect the same difference in isotopic signature represented by the prey species themselves. It was also hypothesised that isotope signatures of wild *A. scabra* would reflect differences in diet between field survey study sites and provide a test for conclusions already made about *A. scabra* diet (Chapter 5).

6.2 Methods:

6.2.2. Isotope turnover experiment

Sixteen *Astrostole scabra* were feed a constant diet of *Cookia sulcata* or *Perna canaliculus* for six months to investigate isotopic turnover. Eight *A. scabra* were collected by snorkel from the Puketeraki wave exposed site and eight from Aramoana Mole which was categorised as a wave sheltered site (Ref. Chapter 1, Figure 1.3). Four individuals from each site were fed *C. sulcata* and four were fed *P. canaliculus*. Therefore four treatments existed of each site and diet combination. *P. canaliculus* and *C. sulcata* were selected as food as they consume different organic matter sources and as a result should be isotopically distinct from one another. *P. canaliculus* consumes SPOM (suspended particulate organic matter), while *C. sulcata* is assumed to consume macroalgae. Originally *Haliotis iris* were to be used rather than *C. sulcata*, however this would mean taking large numbers from already reduced populations, also, other studies have already identified high variation in the isotopic signatures of *H. iris* which makes them inappropriate for this type of study (Suring and Wing 2009).

*A. scabra* were collected from sites which experienced different levels of wave exposure as it was hypothesised that *A. scabra* living at wave exposed reefs would consume greater amounts of immobile animals feeding on SPOM such as *P. canaliculus*. Therefore isotope signatures of *A. scabra* from Puketeraki Exposed would represent a high level of SPOM sourced carbon, and when fed *P. canaliculus* *A. scabra* would represent a predominantly phytoplankton-derived diet in a short space of time. Conversely individuals from Puketeraki Exposed fed *C. sulcata* would require more time to reflect a vastly different diet and would demonstrate a greater change in isotopic signature. The exact opposite was expected to occur with individuals from The Mole wave sheltered site. In light of results from the field survey,
bivalves may represent only a small proportion of A. scabra diet, however this was not known at the beginning of the experiment (Ref. Chapter 5).

A. scabra were held alone in tanks (56 cm x 46 cm x 30 cm) while feeding. Because of space limitations A. scabra were held together in larger tanks (140 cm x 70 cm x 35 cm) when not feeding. When an A. scabra finished feeding it would be taken to the large holding tank and replaced with a new A. scabra. All tanks were maintained with a flow through water system from Otago harbour and experienced constant aeration. A. scabra were morphologically different in colour, size and number of arms and could therefore be tracked using a photo ID system. One A. scabra died during the experiment and two others stopped feeding in winter when sea water temperature reached 5°C, therefore a further individual was removed from the study so that sample size remained equal between treatments at n = 3. The length and weight of C. sulcata and P. canaliculus was measured before and after being fed to A. scabra. The shells of C. sulcata and P. canaliculus were cracked with a blunt object to reduce handling time, which is often lengthy when feeding on C. sulcata (Ref. Chapter 4). Isotope samples of A. scabra tissue were taken monthly over a six month period by removing tube feet which were sealed in Eppendorf tubes and frozen at -80°C until processed.

6.2.2. Collection of prey isotope samples

Prey isotope samples were collected from two sites within the East Otago Taiāpure. Haliotis iris were collected from Warrington and Cookia sulcata and Perna canaliculus from Matainaka (Ref. Chapter 1, Figure 1.3). Collection sites were chosen based on their close proximity to A. scabra survey sites and high abundances of prey species at the respective sites. Two collections of C. sulcata and P. canaliculus took place at 10/3/11 and 18/7/11. H. iris were collected at 22/11/11. Prey were held alive in tanks to be used for food in turnover and handling time experiments before being sampled. Prey isotope sampled were collected at the conclusion of isotope turnover experiment 30/11/11 and frozen at -80°C until processed. The same prey isotope results were used for both the turnover experiment and the investigation of wild Astrostole scabra populations.
6.2.3. Collection *Astrostole scabra* field samples

Field isotope samples of *Astrostole scabra* were collected from the same locations and at the same time field surveys were conducted (Ref. Chapter 5). Therefore six sites were sampled and comprised of three wave exposed/sheltered pairs. Samples were taken from *A. scabra* systematically so that one sample was generally collected in each survey transect, however, in sites where *A. scabra* were rare, more than one *A. scabra* was sampled per transect. This method allowed multiple depths to be sampled to give a stratified estimate of the population. The number of samples collected varied from 3 to 12 per site and depended on the abundance of *A. scabra* at sites. *A. scabra* tissue samples were collected by removing tube feet which were sealed in Eppendorf tubes and frozen at -80°C until processed.

6.2.4. Preparation of isotope samples

Tissue samples were freeze dried at Portobello Marine Lab before being ground to a fine powder using a mortar and pestle. Ground samples were weighed to 1 mg (± 0.05 mg) and sealed inside tin capsules. Carbon and nitrogen isotope ratios were calculated by Iso-trace NZ in the Department of Chemistry at the University of Otago on a Europa 20-20 Update stable isotope mass spectrometer (Europa Scientific, Crewe, UK) interfaced to a Carlo Erba elemental analyser (NA1500; Carlo Erba, Milan Italy) in continuous flow mode (precision: 0.5‰ for δ¹⁴C, 0.6‰ for δ¹⁵N). Primary standards for analysis were calibrated to EDTA laboratory standard reference (Elemental Microanalysis, Cheshire, UK) and standardised against international standards (IAEACH-6 for canyon IAEAN1 and IAEAN2 for nitrogen). The primary standard for δ¹⁵N was atmospheric air and Pee Dee limestone was the standard for δ¹³C.

6.2.5. Data analysis

A general linear model was used to examine the effect of time, diet treatment and site treatment on the δ¹³C and δ¹⁵N signatures of *Astrostole scabra* over the six month period of the turnover experiment and also tested for significant differences in isotopic signatures of prey. A general linear model was used to test the effect of site, exposure and site*exposure on δ¹³C and δ¹⁵N of wild *A. scabra* and a post-hoc Tukey test identified significantly differences in between means following general linear models.
Three organic matter sources (Rhodophyta, SPOM and Phaeophyta) were fitted on plots of isotope signatures. The trophic position primary produces was estimated based on average levels of trophic discrimination in marine organisms ($\delta^{13}C + 0.4$, $\delta^{15}N + 3.4$) minus the trophic position of primary consumers (Post 2002, McCutchan et al. 2003).

Fractionation of $\delta^{15}N$ and $\delta^{13}C$ in $A$. scabra was calculated from turnover experiments as the difference between $A$. scabra and the prey species from individuals on the sixth month of the turnover experiment.

### 6.3 Results

#### 6.3.1 Isotopic turnover experiment

##### 6.3.1.1. Astrostole scabra site treatments

There was no significant change in the $\delta^{15}N$ or $\delta^{13}C$ isotopic signatures of Astrostole scabra fed a constant diets of Cookia sulcata or Perna canaliculus over the six month period for either site treatment (Table 6.1, Figures 6.1). At the beginning of the study the $\delta^{15}N$ isotope signatures of $A$. scabra were on average greater in individuals from the wave sheltered Aramoana Mole site than those from the wave exposed Puketeraki site (Figure 6.1). $A$. scabra $\delta^{15}N$ signatures fluctuated over time rather than reaching a distinct level and remaining constant (Figure 6.1). The $\delta^{15}N$ signatures of $A$ scabra from different site treatments fluctuated in unison for both of the diet treatments (Figure 6.1).

The $\delta^{13}C$ signature of $A$. scabra from different site treatments were significantly different, with more enriched $\delta^{13}C$ in individuals from the wave sheltered site Aramoana Mole (Table 6.2). $\delta^{13}C$ signatures of $A$. scabra from different site treatments that were fed Perna canaliculus also seemed to fluctuate in unison, however, those fed Cookia sulcata did not (Figure 6.2). Instead the $\delta^{13}C$ signatures of $A$. scabra fed $C$. sulcata diverged in the first month, remained at a constant distance for the following four months then began to converge in the final month (Figure 6.2).

More than double the amount of prey tissue was consumed on average by $A$. scabra individuals in the $P$. canaliculus (871 g) treatment than the $C$. sulcata (418 g) (Figure 6.5).
6.3.1.2. Isotope analysis of diet treatments

When the $\delta^{15}\text{N}$ signatures of *Astrostole scabra* from each site were combined the $\delta^{15}\text{N}$ of individuals fed different prey diverged after one month and remained apart for the duration of the experiment (Figure 6.3). The difference in $\delta^{15}\text{N}$ between *A. scabra* fed *Cookia sulcata* and those fed *Perna canaliculus* reflected the difference in $\delta^{15}\text{N}$ of *C. sulcata* and *P. canaliculus* themselves (Figure 6.3).

The when compared irrespective of site the $\delta^{13}\text{C}$ signatures of *A. scabra* fed different diets did not separate from each other and fluctuated slightly over time (Figure 6.4). The $\delta^{13}\text{C}$ signatures of *C. sulcata* and *P. canaliculus* were not significantly different from one another (Figure 6.4).

6.3.1.3. Isotopic fractionation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in *Astrostole scabra*

Isotopic fractionation of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopes in *A. scabra* after the six month period was 3.65‰ and 3.20‰ respectively (Figure 6.6). As the isotope signatures of *A. scabra* did not change significantly during the six months, the turnover time of *A. scabra* tube feet is assumed to be long and therefore will not be used for the analysis of wild populations.

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Table 6.1: Results from general linear model which tested the effect of time, site and diet on *Astrostole scabra* $\delta^{15}\text{N}$ signature.

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Table 6.2: Results from general linear model which tested the effect of time, site and diet on *Astrostole scabra* $\delta^{13}\text{C}$ signature.
Figure 6.1: Average $\delta^{15}$N signatures of *Astrostole scabra* fed sole diets of *Perna canaliculus* (circles) or *Cookia sulcata* (triangles) over a six month period. *A. scabra* originated from two separate populations, Puketeraki (black fill) and Aramoana Mole (clear fill) Data points are averages ± S.E. ($n = 3$ for each treatment).

Figure 6.2: Average $\delta^{13}$C signatures of *Astrostole scabra* fed sole diets of *Perna canaliculus* (circles) or *Cookia sulcata* (triangles) over a six month period. *A. scabra* originated from two separate populations, Puketeraki (black fill) and Aramoana Mole (clear fill) Data points are averages ± S.E. ($n = 3$ for each treatment).
Figure 6.3: Average $\delta^{15}$N signatures of *Astrostole scabra* fed sole diets of *Perna canaliculus* (clear circles) ($n = 6$) or *Cookia sulcata* (clear triangles) ($n = 6$) over a six month period. Average isotopic signatures of prey are represented by the black circle (*P. canaliculus*) ($n = 7$) and black triangle (*Cookia sulcata*) ($n = 7$). Points are averages ± S.E.

Figure 6.4: Average $\delta^{13}$C signatures of *Astrostole scabra* fed sole diets of *Perna canaliculus* (clear circles) ($n = 6$) or *Cookia sulcata* (clear triangles) ($n = 6$) over a six month period. Average isotopic signatures of prey are represented by the black circle (*P. canaliculus*) ($n = 7$) and black triangle (*Cookia sulcata*) ($n = 7$). Points are averages ± S.E.
Figure 6.5: Cumulative weight of prey tissue consumed (g) by *Astrostole scabra* in turnover experiment each month. *A. scabra* diets treatments include *Perna canaliculus* (circles) and *Cookia sulcata* (triangles), and site treatments Puketeraki (solid fill) and The Mole (clear fill). Data are averages ± S.E. (*n* = 3 for each treatment).

Figure 6.6: δ¹³C (Light grey) and δ¹⁵N (Dark grey) fractionation calculated for *Astrostole scabra*. Values are the average difference between *A. scabra* isotopic signature and the isotopic signature of respective prey species (*Perna canaliculus* and *Cookia sulcata*) ± S.E. (*n* = 6 for individual treatments and 12 overall).
6.3.2 Variation in $\delta^{13}C$ and $\delta^{15}N$ signatures of field samples for:

6.3.2.1. Prey species

Each of the three prey species sampled, *Haliotis iris*, *Cookia sulcata* and *Perna canaliculus* were significantly different from one another in $\delta^{15}N$ signature (Table 6.3, Figure 6.7). There was little variation in $\delta^{15}N$ within individual species (Figure 6.7). The $\delta^{13}C$ signatures of prey species varied significantly between *C. sulcata* and *H. iris* (Table 6.3, Figure 6.7). *P. canaliculus* was not significantly different from either *C. sulcata* or *H. iris* in $\delta^{13}C$ (Figure 6.7). There was large variation in $\delta^{13}C$ signatures of *H. iris* and *C. sulcata* and little variation in *P. canaliculus* samples (Figure 6.7).

As *H. iris* retained the lowest trophic position and was highly variable in $\delta^{13}C$ but not in $\delta^{15}N$ the position of Rhodophyta and Phaeophyta organic matter sources were positioned either side of, and one trophic level ($\delta^{15}N = 2.5$, $\delta^{13}C = 0.4$) below the distribution of *H. iris* $\delta^{13}C$ values (Figure 6.6). *C. sulcata* was also expected to feed on macroalgae however their signatures occurred at a greater trophic position than those of *H. iris* (Figure 6.7).

6.3.2.2. *Astrostole scabra*

$\delta^{15}N$ values were not significantly different between sites or wave exposure categories (Table 6.4, Figure 6.7). The average trophic level of *Astrostole scabra* was 2.13 (Figure 6.7). The $\delta^{13}C$ signatures of wild *A. scabra* differed significantly between study sites and between the two wave exposure categories (Table 6.5, Figure 6.7). *A. scabra* sampled at Puketeraki exposed and Big Rock sheltered were significantly reduced in $\delta^{13}C$ (Figure 6.7). *A. scabra* from Huriawa sheltered and exposed were more enriched in $\delta^{13}C$ than other sites although not to a significant degree (Figure 6.7).
Table 6.3: Results from general linear model which tested for differences in $\delta^{15}$N and $\delta^{13}$C of prey species *Haliotis iris*, *Cookia sulcata* and *Perna canaliculus*. Significant differences between species identified by the post hoc Tukey test are displayed in Figure 6.7.

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Table 6.4: Results from general linear model which tested the effect of site and exposure on *Astrostole scabra* $\delta^{15}$N signatures.

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<td>Site</td>
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<td>0.9461</td>
<td>0.3989</td>
</tr>
<tr>
<td>Exposure</td>
<td>1</td>
<td>0.3087</td>
<td>0.5823</td>
</tr>
<tr>
<td>Site*Exposure</td>
<td>2</td>
<td>0.4086</td>
<td>0.4086</td>
</tr>
</tbody>
</table>

Table 6.5: Results from general linear model which tested the effect of site and exposure on *Astrostole scabra* $\delta^{13}$C signatures.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
<td>2</td>
<td>21.1836</td>
<td>&lt; 0.0001*</td>
</tr>
<tr>
<td>Exposure</td>
<td>1</td>
<td>11.3324</td>
<td>0.0020*</td>
</tr>
<tr>
<td>Site*Exposure</td>
<td>2</td>
<td>18.7818</td>
<td>&lt; 0.0001*</td>
</tr>
</tbody>
</table>
Figure 6.7: Isotope signatures of *Astrostole scabra* (Circles) and prey species *Cookiea sulcata*, *Perna canaliculus* and *Haliotis iris* (squares). Estimates of organic matter sources: Rhodophyta, SPOM and Phaeophyta are also plotted (triangles) (Bode et al. 2006, Jack et al. 2009, Hepburn et al. 2010). Fractionation is estimated as ($\delta^{13}C + 3.4$, $\delta^{15}N + 0.4$) (Post 2002). Significant differences in $\delta^{15}N$ and $\delta^{13}C$ isotopic signature among *A. scabra* from different sites is denoted by letters beside the key and differences among prey species are denoted by numbers.
The mean *A. scabra* trophic position is ~2.1 levels above Rhodophyta and Phaeophyta organic matter sources (Figure 6.8). Spatially separate *A. scabra* populations vary in $\delta^{13}$C but not $\delta^{15}$N between populations (Figure 6.8). Averages of $\delta^{13}$C values for Puketeraki exposed and Big Rock sheltered indicate that diet is more reliant on Rhodophyta carbon pathway than other populations (Figure 6.8). Conversely *A. scabra* from Huriawa sites appear to be more dependent on Phaeophyta carbon pathways (Figure 6.8).

Figure 6.8: Average isotopic signatures ± S.E. for each *A. scabra* population and prey species. Exposed and sheltered survey sites are represented by abbreviations for Big Rock (BRS and BRE), Puketeraki (PS and PE) and Huriawa (HS and HE). Data are plotted in relation to estimates of organic matter sources Rhodophyta, SPOM and Phaeophyta (triangles) (Bode *et al.* 2006, Jack *et al.* 2009, Hepburn *et al.* 2011). Fractionation is estimated as $(\delta^{13}C + 3.4, \delta^{15}N + 0.4)$ (Post 2002).


6.4 Discussion

6.4.1 Astrostole scabra isotopic turnover experiment:

6.4.1.1. Site treatments

This experiment aimed to test isotopic turnover of Astrostole scabra by collecting specimens from reefs which receive different levels of wave exposure and were therefore expected to have different isotope signatures at the beginning of the study. The isotope signatures of A. scabra from different study sites were expected to converge to reflect the standard diet over the six month study period. A. scabra from the wave sheltered site Aramoana Mole, were on average more enriched in $\delta^{15}N$ than individuals from the wave exposed site Puketeraki, however, because the $\delta^{15}N$ signature of Perna canaliculus falls between that Haliotis iris and Cookia sulcata it cannot assumed that A. scabra from exposed sites consume greater amounts of immobile bivalve species. Likewise the isotopic signature of A. scabra from The Mole is more enriched in $\delta^{13}C$, however there is no significant difference in the $\delta^{13}C$ of P. canaliculus from other prey species sampled.

Site treatments did not appear to converge with each other to represent the diet of new prey species or remain at a constant level. Therefore the isotopic turnover time of A. sabra tube feet is likely longer than the six month period predicted, especially in the case of $\delta^{13}C$ signatures in the C. sulcata treatment which diverged at the beginning and only came closer together at the end of the experimental period. It is likely this is an effect of the considerable variation in the $\delta^{13}C$ signature of C. sulcata would mean a longer time would be required for A. scabra tissue to reflect the average C. sulcata $\delta^{13}C$ signature. This is reason that H. iris was not used as a food source in the experiment, as Suring and Wing’s (2009) study of isotopic turnover in Jasus edwardsii and Parapercis colias found that H. iris tissue was highly variable in isotopic composition. Furthermore C. sulcata tissue was consumed at less than half the rate of P. canaliculus tissue further prolonging the time to reflect prey isotopic signatures.

The isotopic signatures of A. scabra from different site treatments fluctuated in unison over the six month period. The fact that both site treatments fluctuated in the same way suggests that seasonal fluctuations in either the isotopic signatures of prey or A. scabra were responsible for this effect. Changes in prey isotopic signatures of C. sulcata may have occurred when it was fed a new food source on entering the lab, or in the case of P. canaliculus as SPOM composition changed seasonally. Ideally prey tissue samples should
have been sampled throughout the experiment to track seasonal changes. However, the fact that *A. scabra* isotope signatures did not change to represent the diets they were fed suggest that these seasonal fluctuations are not those of prey as it a very fast *A. scabra* turnover rate would be required to observe such seasonal changes in *A. scabra*. Therefore it seems more likely that the seasonal changes may be related to physiological changes in *A. scabra*. As this experiment was conducted from autumn to spring, changes in composition of protein, lipids or carbohydrates may occur to account for changes in temperature and expected periods of starvation during winter (Gannes et al. 1998). Ross geese (*Chen rossi*) become enriched in $\delta^{15}N$ as a consequence of physiological changes to account starvation which occurs during the incubation of eggs (Gannes et al. 1998). Furthermore, changes in tissue composition may have occurred as an effect of spawning. Only one individual was observed to spawn during the experiment however others may have still prepared for a spawning event.

6.4.1.2. Diet treatments

When the isotope signatures of *Astrostole scabra* from site treatments were combined the increased sample size clarified trends. The $\delta^{15}N$ signatures of *A. scabra* diet treatments diverged in the first month so that error bars were not overlapped and remained separated for the remaining five months. The separation of *A. scabra* $\delta^{15}N$ signatures between the diet treatments appears to reflect the difference between the isotopic signatures of *Perna canaliculus* and *Cookia sulcata*. However, it would not seem this is a true reflection of prey diet as *A. scabra* turnover seemed to be very slow, demonstrated by the fact that *A. scabra* $\delta^{13}C$ signatures remained at 3.2‰ above those of prey at the conclusion of the experiment, vastly greater than the expected level of $\delta^{13}C$ fractionation of 0.4‰. The $\delta^{13}C$ signatures of *A. scabra* in the two diet treatments did not diverge and would not be expected to diverge as the $\delta^{13}C$ signatures of *C. sulcata* and *P. canaliculus* were not significantly different. It was expected that the isotopic signatures of *P. canaliculus* and *C. sulcata* would be further separated than they were, based on the different organic matter sources utilised by the respective species (SPOM and macroalgae). In hindsight an unnatural food source with a vastly different isotope signature, such as fish tissue, may have demonstrated changes in *A. scabra* isotopic signatures more dramatically (Newsome et al. 2007). However, $\delta^{13}C$ values did not fall to reflect a difference of 0.4‰ between prey $\delta^{13}C$ signatures and therefore turnover was not observed.
Results obtained by the present study cannot be compared with other Asteroid species as no other study has investigated isotopic turnover in Asteroids. It is also difficult to compare these results as isotopic turnover was not observed, however, it is expected turnover in *A. scabra* occurs over a long time period. It is common for invertebrates to have fast isotopic turnover (Suring and Wing 2009). The Hemolymph from the red rock lobster *Jasus edwardsii* displayed an isotopic turnover rate more than five times that of the blue cod *Parapercis colias* (Suring and Wing 2009). The Holothurian *Apostichopus japonicas* recorded $\delta^{13}C$ half-lives of between 11.22 – 53.73 days for intestine tissue and 21.39 – 105.03 days for body wall (Sun *et al.* 2012). As isotopic turnover of tissue is generally fast in invertebrates and more specifically in Echinoderms the results obtained here of a slow turnover rates were unexpected and require further examination.

### 6.4.1.3. Isotopic fractionation

Isotopic fractionation in *Astrostole scabra* was calculated as the difference between the isotopic signatures of *A. scabra* and their respective diet treatment. Calculated levels of fractionation in *A. scabra* ($\delta^{13}C + 3.20$ and $\delta^{15}N + 3.65$) are larger than those typically observed in marine ecosystems ($\delta^{13}C + 0.4$ and $\delta^{15}N + 3.4$). Post (2002) states that the fractionation of $\delta^{13}C$ is between 0‰ and 1‰ per trophic level and therefore the value of fractionation recorded here (3.20‰) is substantially greater and therefore results from the turnover experiment not used in the analysis of wild populations.

### 6.4.2. Isotope analysis of wild populations:

#### 6.4.2.1. Organic matter sources

Organic matter sources were positioned in relation to the isotopic signatures of appropriate primary consumers and based on findings from other stable isotope studies. The position of SPOM could be plotted with confidence due to the low degree of variation in the isotopic signatures of *Perna canaliculus*. The position of Phaeophyta was plotted at the intercept of *Cookia sulcata* and *Haliotis iris* $\delta^{13}C$ distributions which is in concordance with other isotopic studies which generally observe Phaeophyta to be enriched $\delta^{13}C$ and slightly reduced in $\delta^{15}N$ compared with SPOM (Jack *et al.* 2009). Rhodophyta is known to have reduced $\delta^{13}C$ and $\delta^{15}N$ signatures when compared to other organic matter sources (Bode *et al.* 2006, Hepburn *et
al. 2011) and was fitted at the other end of the H. iris $\delta^{13}$C continuum as H. iris are known to feed on both Rhodophyta and Phaeophyta algae (Cornwall et al. 2009). Chlorophyta was not plotted here, as an organic matter source as the $\delta^{13}$C signatures of Phaeophyta and Chlorophyta are generally similar although Chlorophyta is generally more enriched in $\delta^{15}$N (Bode et al. 2006). It is possible that Chlorophyta is also consumed by H. iris and C. sulcata but it is not obvious what position Chlorophyta would occupy and therefore was not plotted.

6.4.2.2. Primary consumers

The $\delta^{15}$N signatures of primary consumers displayed little variation within each species, there were however significant differences between each species. Conversely the $\delta^{13}$C signatures of Haliotis iris and Cookiea sulcata were highly variable, while the isotopic signatures of Perna canaliculus displayed little variation. High variation in $\delta^{13}$C signatures of H. iris and C. sulcata indicate that more than one organic matter source is regularly consumed by individuals (Jack et al. 2009). H. iris occupies the lowest primary consumer trophic level and therefore is occupies a trophic position of ~1. The distribution of $\delta^{13}$C signatures forms a distinct line linking the two dominant organic matter sources Rhodophyta and Phaeophyta. The position of Rhodophyta is generally greatly reduced in $\delta^{13}$C (Bode et al. 2006, Hepburn et al. 2011). H. iris is known to feed on Rhodophyta, Phaeophyta and Chlorophyta, with some studies stating that Chlorophyta is preferred (Poore 1972), while others conclude that Phaeophyta is preferred (Taylor and Steinburg 2005, Cornwall et al. 2009). Adult H. iris are largely immobile feed predominantly on drift algae, it is therefore reasonable to assume that wild diet reflects the algae available rather than a preference for any one species (Cornwall et al. 2009). It was assumed that the isotopic signatures of C. sulcata would be similar to H. iris however they occupied a higher trophic position (~1.2) and the distribution of $\delta^{13}$C appeared to run between Phaeophyta and an organic matter source enriched in $\delta^{15}$N and depleted in $\delta^{13}$C. Therefore the other organic matter source for C. sulcata has not been plotted here as it is difficult to know what this secondary source is. Epiphytic algae may be the second organic matter source utilised by C. sulcata which has been shown to have a variable isotopic signature with two studies recording depleted $\delta^{15}$N levels compared to SPOM and macroalgae (Riera et al. 2000, Moncreiff and Sullivan 2001), and one recording enriched $\delta^{15}$N levels (Bode et al. 2006). Therefore it is possible that epiphytic algae is enriched in the present setting and is responsible for enriched $\delta^{15}$N isotopic signatures in C. sulcata. It is possible but unlikely that the increased trophic position on C. sulcata is due to a physiological difference
with *H. iris* as it still seems that one end of the *C. sulcata* δ\(^{13}\)C continuum points towards the same Phaeophyta organic matter source consumed by *H. iris*, therefore it is unlikely that a physiological difference exists. Another possibility is that *C. sulcata* consumes some sessile animals while grazing, resulting in an increased enriched δ\(^{15}\)N signature.

Isotopic signatures of *H. iris*, *C. sulcata* and *P. canaliculus* used here were each collected from one site only. Post (2002) recommends collecting isotopic signatures of primary consumers over a wide spatial range to account for geographical variation in δ\(^{13}\)C. As there was considerable variation in the δ\(^{13}\)C signatures of *C. sulcata* and *H. iris* it would have been beneficial to have taken samples from all survey sites. Unfortunately resources limited a wider sampling effort and the decision was made to concentrate on acquiring numerous samples of *A. scabra* rather than prey.

### 6.4.2.3. Astrostole scabra

The δ\(^{13}\)C signatures of *Astrostole scabra* were significantly different among study sites suggesting differences in diet between sites. *A. scabra* from Puketeraki exposed and Big Rock sheltered sites were significantly depleted in δ\(^{13}\)C compared to other sites, suggesting that they rely more heavily on Rhodophyta derived δ\(^{13}\)C pathways and consume more *H. iris* than other populations. Diet surveys of these sites recorded *Haliotis iris* as the only prey species consumed by *A. scabra* at each of these sites and therefore *H. iris* was likely a major dietary constituent at each of these populations. Diet surveys also suggested that *A. scabra* from Huriawa sites consumed a different diet than other sites (Ref. Chapter 5). Field survey observations are supported by these results although not to a significant degree. It appears that the diet of *A. scabra* at Huriawa is more dependent on Phaeophyta pathways and may indicate a more kelp-forest based ecosystem. The isotope signatures of *A. scabra* from Puketeraki sheltered and Big Rock exposed study sites are positioned between the two extremes and therefore likely rely on both Phaeophyta and Rhodophyta δ\(^{13}\)C pathways more equally than the other sites. Again these results are supported by diet surveys as *A. scabra* from Big Rock exposed were observed to feed on both *H. iris* and *Cookia sulcata*, while *A. scabra* from Puketeraki sheltered were observed feeding on *C. sulcata* and a whelk species (Ref. Chapter 5). *A. scabra* δ\(^{13}\)C signatures were more depleted than expected if feeding purely on the prey species recorded or those observed in field surveys. It is likely that *A. scabra* diet changes seasonally and incorporates a greater proportion of Phaeophyta grazing species in winter. Seasonal changes in diet have been observed in other Asteroids such as
Leptasterias hexactis and Astereis rubens (Menge 1972, Castilla and Crisp 1973) As isotopic turnover of A. scabra appears to occur over a long time period and therefore A. scabra signatures would be expected reflect the diet consumed over a full year. A. scabra locomotive speed was observed to decrease in cooler temperatures (Ref. Chapter 2) and locomotive speed was shown to impact A. scabra capture rates of H. iris (Ref. Chapter 3) therefore cooler water temperatures may mean that energy rich species such as H. iris become unobtainable during winter forcing a change in diet. A. scabra δ13C signatures were significantly affected by the wave exposure of sites, further supporting field survey results which demonstrated A. scabra distribution was reduced in wave exposed areas.

Overall, field survey results were supported by isotopic analysis of wild A. scabra populations. δ13C signatures of A. scabra were significantly affected by wave exposure as identified as also recorded in field surveys, however the largest contributing factor was study site itself. Therefore the same conclusion given from field surveys is applicable here in that the major contributor to A. scabra diet is most likely prey abundance which is in turn affected by multiple factors such as wave exposure, habitat, salinity and temperature.
Chapter 7

General Discussion

Astrostole scabra found amongst the remains of Evechinus chloroticus in Doubtful Sound, New Zealand.

7.1 Introduction
The primary objective of this thesis was to investigate aspects of Astrostole scabra biology and ecology to predict the influence of A. scabra predation on local prey populations. Several ecological aspects of A. scabra examined in four lab based experiments which were then further examined using field surveys of wild populations. The second aim of this study was to examine the distribution, abundance and diet of wild A. scabra populations within the East Otago Taiāpure. Wild A. scabra populations were examined by field surveys and isotope analysis with the aim of determining the impact A. scabra may have on commercially important species such as Haliotis iris. The following section synthesises the results of this study to communicate the key findings and discuss the threat of A. scabra to H. iris populations.

7.2 Prey preference in Astrostole scabra

Astrostole scabra prey preference was examined using a two stage tank set-up which allowed water to flow over prey before coming in contact with A. scabra. A. scabra was required to move towards one of two water plumes which had previously flowed over different prey species. Despite regularly moving towards water plumes, A. scabra was not capable of discriminating between prey species as there were no significant preferences for any species were identified. A. scabra appears to utilize a rheotactic foraging strategy which consists of movement against a current to approach prey from an inconspicuous position. Prey odors are likely to be highly diffused in turbulent water conditions and hence the adaption of a foraging strategy which does not require high fidelity determination of prey scents is understandable. The locomotive speed of A. scabra was observed to change with fluctuations in water temperature with reduced movement speed occurring in cooler temperatures. Water temperature did not appear to affect A. scabra motivation to forage.

7.3 Effect of water motion on Astrostole scabra locomotion and predation

The effect of water motion on the locomotive speed and predation ability of Astrostole scabra was examined within a flume which generated a unidirectional current. Because of the rheotactic behavior exhibited by A. scabra, individuals would reliably move upstream so that locomotive speed could be calculated and a juvenile Haliotis iris would be encountered. Both locomotive speed and capture success of A. scabra was reduced as water motion increased,
indicating that *A. scabra* living in areas which receive high levels of water motion may be less successful predators as they would take longer to locate prey and have a reduced chance of successfully capturing prey. *A. scabra* may also experience higher levels of mortality at wave exposed reefs as a result of detachment to the substrate. As escape rates only occur in mobile prey species it was expected that greater proportions of immobile prey would be consumed at wave exposed reefs. The escape response of *H. iris* was observed to change with increasing water motion. The running response became more common with increased water motion because *H. iris* could sense *A. scabra* before tube feet were attached to the shell. *H. iris*'s response to release from the substrate was only effective during high levels of water motion when *H. iris* could be carried away by the current subsequent to releasing from the substrate.

### 7.4 Astrostole scabra handling times

*Astrostole scabra* feeding behavior was observed when feeding on *Haliotis iris, Cookia sulcata* and *Perna canaliculus* by time lapse video to examine the effect of prey species and prey size on handling time. *A. scabra* recorded short handling times when feeding on *H. iris* and *P. canaliculus* compared with *C. sulcata*, which took significantly longer to digest. From this information it was concluded that *C. sulcata* provided less energetic value to *A. scabra* as fewer grams of tissue were consumed per hour of handling time. Therefore it was predicted that *A. scabra* should only feed on *C. sulcata* in areas where higher quality prey species were not available. Results from the handling time experiment were later used to adjust field survey results to account for bias in the number of prey individuals consumed, as species with long handling times are recorded disproportionately more often than those with short handling times.

### 7.5 Isotopic turnover and fractionation in Astrostole scabra

*Astrostole scabra* were kept in captivity and fed a diet of a single prey species to investigate isotopic turnover and fractionation in the species. Turnover in *A. scabra* appeared to occur slowly as signatures did not diverge to reflect prey diets significantly or change to reflect the isotopic fraction expected. *A. scabra* isotope signatures fluctuated seasonally which likely represent physiological changes in tissue composition to account for cooler winter
temperatures or spawning. The isotopic signatures of wild *A. scabra* probably represent the diet of an *A. scabra* over a period of years.

### 7.6 Examination of wild Astrostole scabra populations

Wild populations of *Astrostole scabra* were examined using field surveys and isotopic analysis. Field surveys recorded the distribution, and abundance of *A. scabra* at wave exposed and wave sheltered sites and across a range of depths. Wave exposure had a significant effect on *A. scabra* distribution with greater densities occurring at wave sheltered reefs. Depth did not have a significant effect on abundance or distribution. The most significant determinant of *A. scabra* density was study site itself which was likely the result of several interacting factors including wave exposure, substrate, salinity and prey abundance. Diet surveys highlighted *Haliotis iris* as a major dietary component, comprising 55% of the diet overall and 100% at some sites. Interestingly, *A. scabra* was not observed consuming any *H. iris* smaller than 100 mm in length and therefore seemed to target larger individuals. *A. scabra* distribution was compared to the distribution of prey species, which was found to contribute to the size structure of and abundance of *A. scabra* populations. Denser *A. scabra* populations occurred at sites where high densities of *H. iris* or *Cookia sulcata* were present. There were a greater number of large *A. scabra* at sites where *H. iris* were abundant. Conversely, at sites which contained high abundances of *Cookia sulcata* *A. scabra* were significantly smaller in size, demonstrating the difference in prey quality between *H. iris* and *C. sulcata*.

Field surveys obtained quality information on *A. scabra* abundance and distribution, however, estimates of diet were less reliable, as only 12% of individuals were recorded as feeding at the time of survey. Therefore it was important to verify the accuracy of field results using stable isotope analysis. Isotope analysis of *A. scabra* identified differences in diet between sites which correlated with field survey results. Sites which were recorded as having sole diets of *H. iris* displayed a significantly depleted δ¹³C signature and therefore fed had diets consisting of a large amount of *H. iris*, which were themselves depleted in δ¹³C. There was no significant difference between the other populations recorded, however, *A. scabra* from Huriawa Peninsular, which were observed to consume a different diet in field surveys, also seemed to utilize a different diet in isotope analysis. *A. scabra* signatures were also more enriched in δ¹³C than expected and therefore may consume a different diet than observed in field surveys during winter.
Findings from the present study were generally in accordance with Town’s (1979, 1980a, 1980b, 1981) studies of *A. scabra* biology and ecology. The size range of *A. scabra* recorded in the two studies had implications for comparisons between the studies as Town (1980b) examined the diet and prey preference of juvenile *A. scabra* living intertidally, whereas the present study investigated adult *A. scabra* living subtidally. For this reason the diet of *A. scabra* recorded here contained a smaller range of larger bodied prey species. Town (1980b) did observe that diet varied between reefs, as observed here, which is likely connected with variations in prey abundance between study sites and is related to the abiotic conditions of particular reefs.

7.7 The threat of Astrostole scabra to the recovery of Haliotis iris populations

Surveys of wild *Astrostole scabra* populations highlighted *Haliotis iris* as a major dietary component of *A. scabra* at several sites within the east Otago Taiāpure. *A. scabra* were often numerous in areas of high *Haliotis iris* abundance or concentrated around small pockets of high *H. iris* abundance. Although adult *H. iris* have an effective escape response and may be difficult to capture, they are a high quality food source for *A. scabra*. Although *H. iris* was found to be a major *A. scabra* food source, this study is not capable of estimating quantitatively how many *H. iris* are consumed by *A. scabra*, due to a small sample size in diet analysis and a lack of seasonal data.

It is plausible to predict that as *H. iris* populations continue to recover within the East Otago Taiāpure the abundance of *A. scabra* will also increase as *A. scabra* abundance was linked to prey abundance. An increase in *A. scabra* abundance would likely have a negative effect on the recovery of *H. iris* populations. If increases in *A. scabra* abundance were to reach high densities *H. iris* populations may be seriously threatened, as this study suggests *H. iris* do not have a size refuge from *A. scabra* predation. The lack of a size refuge means that large breeding individuals may be removed from the population, limiting reproductive input, further impacting recovery. It is advised that the East Otago Taiāpure committee to continue to monitor *A. scabra* abundance within the reserve so that any increases in *A. scabra* abundance are identified.

Increases in the abundance of *A. scabra* may be a consequence of a decline in the abundance of their only known predator *Jasus edwardsii*. If *A. scabra* populations were to increase within the East Otago Taiāpure it may be wise to aid the recovery of *J. edwardsii* by reducing
the take of this species to help re-establish top down control in the ecosystem. It should be mentioned however, that an increase in the numbers of *J. edwardsii* will likely also have a negative effect on the recovery of *H. iris*. In a Tasmanian marine reserve a rise in the abundance of *J. edwardsii* resulted in reductions of Asteroid and Gastropod species (Alexander et al. 2009). Although re-establishment of *J. edwardsii* may have a negative effect on *H. iris* abundance, greater ecosystem stability would exist and reduce the likelihood of dramatic increases in *A. scabra* abundance. Therefore it is advised that the abundance of *A. scabra* is monitored and if it is seen to increase then action should be implemented through either the direct removal of *A. scabra* individuals or the introduction of a ban on the take of *J. edwardsii*.

7.8. Conclusions

- *Astrostole scabra* is not capable of chemoreception in turbulent water and instead applies a rheotactic foraging strategy, moving up-current to encounter prey from an inconspicuous position.
- *A. scabra* locomotive speed was reduced in cooler temperatures however motivation to forage was not observed to be affected by temperature
- *A. scabra* locomotion and prey capture success is negatively affected by water motion. Coincidentally *A. scabra* were less common at wave exposed shores in field surveys.
- *A. scabra* handling times were short for *Perna canaliculus* and *H. iris* but long for *Cookia sulcata*. As a result *C. sulcata* was deemed to be an energy poor species for *A. scabra* to consume
- Adult *H. iris*, rather than juvenile *H. iris*, were observed as a major dietary component of *A. scabra* within the East Otago Taiāpure.
- *A. scabra* isotopic turnover is likely to occur over a period of years.
- *A. scabra* is a generalist predator, capable of consuming a wide range of species. It is likely that *A. scabra* prefers to capture large, high quality prey species such as *Haliotis iris* when available, but will also predare lower quality species such as *Cookia sulcata* when better quality prey are not obtainable.
- The abundance and diet of *A. scabra* within the East Otago Taiāpure is dependent on no one factor but rather a range of factors including wave exposure, substrate type, salinity, temperature and prey abundance.


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