# Gut Instincts: Feeding behaviour of the rock lobster, *Jasus edwardsii*

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A thesis submitted in fulfilment of the requirements

for the degree of Doctor of Philosophy,

The University of Auckland, 2021

*This thesis is dedicated to Nana and Da*

*May Hawkes & Neville Hawkes*

# Abstract

Predator-prey interactions play a critical role in structuring community dynamics, such as lobster predation, which has been shown to affect both soft sediment and rocky reef community structure. In recent years there have been major concerns regarding the over-exploitation of rock lobster stocks. The significant decline and sustained low lobster abundance have led to many populations becoming functionally extinct, resulting in large regime shifts in rocky reef habitats.

Despite the ecological importance of lobsters, conservation efforts in northeastern New Zealand are hindered by a lack of understanding concerning their nearshore feeding biology and sensory drivers. Therefore, this thesis aimed to assess the feeding behaviours and movements of the rock lobster, *Jasus edwardsii,* including the sensory mechanisms driving food selection.

Cafeteria experiments showed that large male lobsters exhibited a strong preference for soft-sediment bivalves over rocky-reef prey. Although urchins had the highest profitability, urchins were the least preferred when lobsters were presented with prey choice. Detection and selection of buried soft-sediment prey were primarily driven through chemoreception. The antennules, in particular, appeared to play a disproportionate role in prey detection.

Furthermore, lobsters play a key role in controlling urchin populations, whose intensive grazing can turn lush kelp forests into barren habitats. Predation pressure of male lobsters fluctuated throughout the year and was predominantly dictated by the moult stage and a preference for urchins with a high gonad index. This seasonal variability and selective predation may have implications in using lobsters as a mitigation tool to reduce the expansion of urchin barren habitats.

Lastly, foraging-associated movements validate the historically observed offshore migrations being food driven and suggest that lobster home ranges extend well beyond rocky reef margins. Unexpectedly, visually-impaired lobsters showed increased movement, and the associated energy expenditure may have cascading effects on foraging efficiency, shelter selection and predator avoidance.

Collectively, this thesis's findings have significant implications for fisheries and conservation management regarding marine protection design. In particular, ensuring that soft-sediment feeding habitats are better understood and protected remains critical for this valuable yet vulnerable predator.

# Acknowledgements

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Chapter two

Flood, A.S., Haggitt, T.R., Radford C.A. (under review). Setting healthy boundaries with diet: Feeding preferences of the rock lobster, Jasus edwardsii. Marine Ecology Progress Series.

| Nature of contribution by PhD candidate | Lead author and principle investigator |
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Chapter three

Flood, A.S., Haggitt, T.R., Radford C.A. (under review). Making sense of foraging behaviour: The role of chemoreception and vision in the rock lobster, Jasus edwardsii

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Chapter four

Flood, A.S., Haggitt, T.R., Radford C.A. (under review). Seasonal importance and consumptive abilities of the rock lobster, Jasus edwardsii, on the sea urchin, Evechinus chloroticus

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# CHAPTER ONE

# General Introduction

**Impacts of fishing**

Coastal marine habitats hold some of the most productive and diverse assemblages of organisms on earth (Suchanek 1994). Over the past century, the resources within these habitats have been subjected to increasing pressure from multiple stresses, such as overfishing, habitat degradation and climate change (Jackson et al. 2001, Hewitt et al. 2016). Globally, many marine fisheries have been declining since the 1980s and are exacerbated by significant increases in fishing effort (Pauly et al. 2002, Worm et al. 2006). The proportion of fish stocks within biologically sustainable levels decreased from 90 % in 1974 to 65.8 % in 2017 (a 1.1 % decrease since 2015), with 59.6 % classified as 'fully fished' (FAO 2020). It is widely recognised that fisheries impact species, habitats and ecosystems that go well beyond the direct impacts of fishing target species (Hobday et al. 2011). Furthermore, a large component of targeted fish species are predators (Lassalle et al. 2012), which can have cascading effects on lower trophic species. Severe overfishing drives species to ecological extinction, meaning the overfished population no longer interacts significantly with other species in the community (Jackson et al. 2001). Ecological extinction caused by overfishing precedes all other pervasive human disturbance to coastal ecosystems, including pollution, water

quality degradation, and climate change (Jackson 2008). Therefore, understanding an animal's ecological role is an essential component to the long-term management and preservation of marine animals, especially of top predators (Pikitch et al. 2004, Beddington et al. 2007).

## The role of predators

Predators are an important part of almost every known ecosystem and play a pivotal role in structuring food-webs (Terborgh & Estes 2013). The importance of predators to ecosystems has been highlighted through studying the effects of harvesting on many top-level terrestrial and aquatic predators (e.g. Pace et al. 1999). The rapid removal of top predators can alter food-web interactions causing a catastrophic regime shift where an ecosystem suffers from "trophic downgrading", switching to an alternative stable state dominated by intermediate-level organisms (Pace et al. 1999). These intermediate-level organisms overconsume lower-level organisms or resources, altering the ecosystem's overall structure and function (Myers et al. 2007, Estes et al. 2011). For example, a reduction in predation pressure on sea urchins has been attributed to urchin population outbreaks (Scheibling & Hamm 1991). High abundances of urchins are capable of structuring sub-tidal reefs through intensive grazing of kelp forests to create a desert of urchin barrens (Filbee-Dexter & Scheibling 2014). Subsequently, kelp forests have experienced widespread deforestation, in part, due to population explosions of herbivores in response to the removal of apex predators (Jackson et al. 2001).

**Selective predation**

When animals forage, a trade-off exists between maximising net energy and nutritional gain and minimising costs, such as predation, time and energy expenditure (Ford 1983, Ydenberg et al. 1994). Optimal foraging theory predicts which prey predators should include within their diet to maximise energy intake (Emlen 1966). Predators should, therefore, prefer foods that deliver the greatest value per unit effort or time expended acquiring them (Owen-Smith et al. 2010). As a result, most predator species do not feed on prey in proportion to their abundance but select prey of particular types and sizes.

Selective predation pressure can profoundly affect the structure of prey populations (Mascaro & Seed 2000, Rovero et al. 2000, Shears & Babcock 2003). For example, consumption of sea urchins by sea otters has a positive indirect effect on kelp forests, where sea otters predation of urchins releases recruiting kelp from grazing, thereby allowing the establishment of rich kelp forest habitat (Estes & Palmisano 1974). This trophic cascade has been altered by dramatic declines in sea otter populations beginning in the 1990s, attributed to dietary shifts in killer whales (Estes et al. 1998, Estes et al. 2004). Therefore, a shift in the apex predator's prey preference can create reciprocal changes in the relative populations of predator and prey through the food chain, often resulting in dramatic ecosystem structure changes. Consequently, understanding the behavioural mechanisms underlying prey selection by predators is an essential component for unravelling the processes that rule predator-prey dynamics (Fryxell & Lundberg 1994).

# Marine protection

No-take marine protected areas have been proposed as an effective way to maintain and manage fisheries while simultaneously preserving biodiversity and meeting other conservation objectives as well as human needs (Sumaila et al. 2000, Halpern 2003). For example, the abundance and size of fished species tend to increase within reserve boundaries (see review Halpern 2003). In some cases, reserves can slow or even reverse ecosystem-level fishing effects (Shears & Babcock 2002, Babcock et al. 2010). Despite the popularity of marine reserves as a management tool, marine reserve location and size are often determined through contentious negotiations between diverse stakeholders rather than by the application of sufficient ecological data (Guénette et al. 2000, Halpern 2003, Sale et al. 2005, Grüss et al. 2011, Voyer et al. 2014). As a result, most reserves are small (Leenhardt et al. 2013), with only 31 % of reserves meeting their management goals, primarily due to poor reserve design and placement (Sale et al. 2005).

The use of closed areas to meet various fishery management goals for temperate marine systems has had mixed results (Horwood 2000, Murawski et al. 2000). For example, lobsters have been shown to respond positively to the initial protection, in terms of both abundance and size (Cole et al. 1990, MacDiarmid & Breen 1993, Kelly et al. 2000a). However, due to insufficient reserve size, lobster populations are still exposed to fishing pressure, likely from extensive fishing on reserve boundaries (Kellner et al. 2007, Lester et al. 2009). This fishing pressure has led to population declines and, in some cases, lobster numbers approaching neighbouring fished areas (LaScala-Gruenewald et al. in press). This population

decline further emphasises that without a clear understanding of a species' life history and its role in the broader ecosystem, we cannot modify or adapt management plans to improve ecosystem and fishery stability (Zukowski et al. 2012).

## Rock lobster

The rock lobster (Palinuridae) is a family of morphologically, ecologically, and behaviourally diverse predatory benthic crustaceans. Rock lobsters (herein lobster) are widely distributed through temperate and tropical systems from shallow waters to extreme depths (Rios-Lara et al. 2007, Spanier et al. 2010). This family consists of eight genera and over 47 species, 33 of which are commercially harvested (Morgan 1980, Lipcius & Eggleston 2000). Lobster fisheries are some of the most economically valuable in the world, with significant fisheries located in New Zealand, Australia, USA, South Africa, and the Caribbean (Lavalli & Spanier 2010, Phillips et al. 2013). Lobsters additionally support several cultural and recreational fisheries worldwide (Lipcius & Eggleston 2000). However, from 2005 to 2009, there was a 20 % decline in global lobster landings (Jeffs 2010). This decline was likely due to a combination of overfishing, climate change, disease, habitat destruction, coastal pollution and a decrease in the recruitment for several species of lobster that support substantial commercial fisheries (Jeffs 2010).

## *Jasus edwardsii*

*Jasus edwardsii* (Hutton, 1875) supports large commercial fisheries in New Zealand and Australia and significant recreational and cultural fishing practices. In New Zealand, the average commercial catch from $2010 - 2015$ was 2,839 t, and the exports earn approximately \$268 million a year (MPI, 2018). The lobster fishery within New Zealand has been regulated using a Quota Management System (QMS) since 1990 (Miller & Breen 2010). This system sets total allowable commercial catches (TACCs) for nine management areas (CRA1- CRA9; Fig. 1.1). In recent years, the CRA2 management area in northeastern New Zealand has experienced large-scale declines in catch per unit effort (Webber & Starr 2018).

*Jasus edwardsii* populations within the CRA2 fishing zone have been described as functionally extinct; meaning lobsters no longer play a significant role in ecosystem function (Shears & Babcock 2002, MacDiarmid et al. 2013). Lobsters were considered the third most important benthic invertebrate before human arrival in New Zealand and, to date, are now considered one of the least (Pinkerton et al. 2015). This significant and continuous decline in this particular species and lobster in general signals for a greater understanding of their behaviour and ecology to better inform management decisions and marine protection area designs.
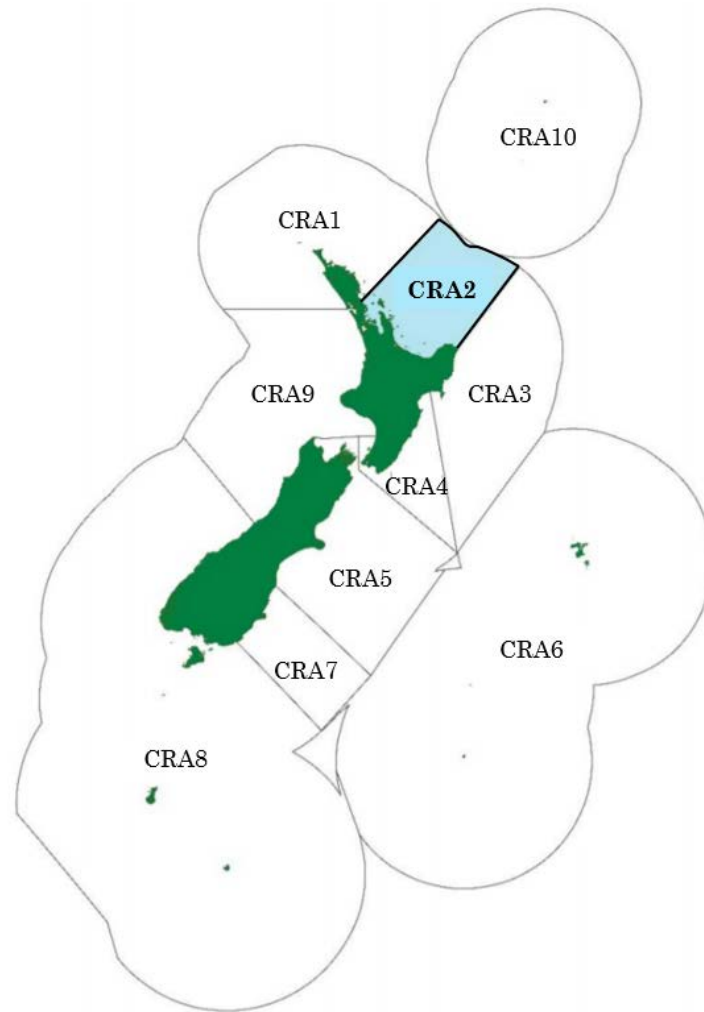
**Fig. 1.1.** Map of rock lobster Quota Management Areas. CRA2 stock shown in blue (Adapted from: mpi.govt.nz (Dec 2020)). CRA10 TACC is set at zero.

**Feeding behaviours**

Lobster occupy shallow-water habitats on rocky reefs and are considered high-level predators that consume a wide range of prey, including echinoids, molluscs, and bivalves (Haggitt & Kelly 2004). In turn, they are also prey for a suite of species, including octopus and various fish (Andrew & MacDiarmid 1999). Their potential influence on reef communities has been a significant theme for research on trophic interactions and community dynamics (Babcock et al. 1999,

Shears & Babcock 2002, 2003, Salomon et al. 2008, Shears et al. 2008, Babcock et al. 2010). In particular, the role lobsters play in supporting the health of coastal kelp forest ecosystems by reducing sea urchin (*Evechinus chloroticus*) abundances through predation and indirectly increase the abundance of macrophytes (Shears & Babcock 2002, 2003; Eddy et al. 2014).

Additionally, lobsters are incredibly accurate when localising and identifying potential prey (Kamio & Derby 2017). For example, lobsters can move considerable distances and were observed undertaking seasonal movements presumably to feed on offshore sand beds and patch reefs (MacDiarmid 1991; Kelly 2001; Kelly & MacDiarmid 2003). These offshore excursions of several hundred meters in the search for foraging grounds have the potential to influence soft sediment communities (Langlois et al. 2005). However, the sensory systems driving these foraging movements in *J. edwardsii* are not well understood.

This offshore movement was also a likely explanation into why lobster show mixed responses to protection (LaScala-Gruenewald et al. in press). It is believed that targeted fishing of lobster aggregations near reserve boundaries has contributed not only to population declines within reserves but also the decrease in the number of large individuals (Kelly et al. 2002, Kelly & MacDiarmid 2003). Therefore, limited knowledge of nearshore feeding biology and the drivers behind observed offshore movements have consequently hindered conservation efforts.

# Thesis Aims

This thesis aimed to examine the feeding behaviour of the rock lobster, *Jasus edwardsii,* to help provide a greater understanding of prey selection and the sensory mechanisms involved in these, foraging movements and consumptive capabilities. This perspective manifests itself in this research through:

(1) ***Assessing if lobster exhibit feeding preferences between common rocky reef and soft-sediment prey.*** This chapter (Chapter Two) aimed to enhance our current knowledge of nearshore feeding biology and the possible drivers behind observed offshore movements. Feeding preferences were determined through a series of cafeteria experiments and video analysis. Prey size, shell thickness and nutritional content were also analysed to determine the profitability of each prey.

(2) ***Investigating the importance of both chemoreception and vision in food selection and foraging movements.*** This chapter (Chapter Three) aimed to enhance our understanding of how lobsters locate and identify potential prey. Sensory mechanisms were analysed through a series of repeated cafeteria experiments under different sensory manipulations.

Lastly, (3) ***monitoring the seasonal consumption of the sea urchin (Evechinus chloroticus).*** This chapter (Chapter Four) aimed to assess if and to what extent lobster's consumptive capabilities fluctuated throughout the year and its implications on urchin populations. Lobster consumption was monitored in terms of food intake and urchin size preferences.

The findings of various components of this study were synthesised and discussed in the General Discussion (Chapter Five). The role of lobsters as top predators in temperate reefs and their influential consumptive capabilities were reviewed in light of this thesis's findings. The value and design of no-take marine reserves and ecosystem-level effects resulting from fishing pressure were also discussed.

# CHAPTER TWO

# Setting healthy boundaries with diet: Feeding preferences of the rock lobster, *Jasus edwardsii*

## Introduction

Predation is a significant force shaping community structure through both direct and indirect effects (Paine 1974, Hixon & Beets 1993). Directly, predators can limit, regulate or eliminate prey populations through consumption (Kavahagh 1988, Korpimäki & Krebs 1996, Gurevitch et al. 2000). These effects can then propagate indirectly through the community in various ways, including trophic cascades, indirect facilitation, and apparent competition (Wootton 1994, Shears & Babcock 2003). Direct and indirect effects of predation can produce quantitative and qualitative shifts in community composition. For instance, the effects of foraging tend to decrease with increasing distance from rocky reef habitats, with the potential to create halos of reduced prey density around reef structures (e.g. Langlois et al. 2005). The extent of these effects on the population and community composition depends on the rate of predation and prey preference (selection).

Preference is one of the most critical components that can influence the consumption patterns of food resources (Jackson & Underwood 2007). The existence of a preference requires some active behavioural choice causing non-

random consumption (Singer 2000). Components of optimal foraging theory (OFT) can help predict how animals behave when searching for food (Pyke, 1984). Although obtaining food provides the animal with energy, searching for and handling the food requires both energy and time (Smallegange et al. 2008). Factors such as exposure, risk of injury, nutritional gains, and taste can all influence predator-choice (Underwood & Clarke 2005). Thus, understanding the behavioural mechanisms that underlie prey selection and knowledge of predator-prey relationships is crucial for unravelling how marine ecosystems function.

Rock or spiny lobsters (Palinuridae, herein - lobsters) are ecologically important benthic predators that are considered opportunistic omnivores, where the surrounding habitat governs their diet and foraging range (Robles 1987, Robles et al. 1990, Pederson & Johnson 2006, Kintzing & Butler IV 2014). Lobsters are typically nocturnal foragers, moving between their dens (shelters within reefs) and surrounding benthic habitat (Herrnkind 1980, MacArthur et al. 2008). Foraging distance is likely to be influenced by the density and distribution of prey, energetics of locomotion, time constraints, and predators' density and activity patterns (Smith et al. 2001). Identification of food consumed by lobsters is, however challenging, as their stomach contents tend to be in a semi-digested condition soon after consumption (Berry 1971). Therefore, information on the natural diet and feeding behaviour of lobsters remains scarce. Lobsters were long considered scavengers due to their attraction to dead bait in fishing traps (Crawford & De Smidt 1922, Lindberg 1955). However, gut content analysis from field and laboratory-based studies have demonstrated that lobsters are somewhat selective in their feeding choice, feeding on mostly live or freshly killed material

(reviewed in Kanciruk 1980, Mayfield et al. 2000, Gnanalingam & Butler IV 2018). Moreover, their selective predation may be responsible for profound effects on species composition and surrounding benthic community structure (Langlois et al. 2005, Butler et al. 2016).

Lobsters are the focus of valuable fisheries worldwide and are among the most highly-priced seafood (Cau et al. 2019). In New Zealand, the rock lobster *Jasus edwardsii* (Hutton, 1875) has a high economic value (NZ$300m), and in many locations, such as the Hauraki Gulf, overfishing has influenced numbers substantially (Seafood New Zealand 2020; Fisheries New Zealand 2020). Sustained low lobster abundance has resulted in stocks becoming functionally extinct; meaning they no longer play a significant role in ecosystem function relative to historical population estimates (Shears & Babcock 2002, MacDiarmid et al. 2013). Trophic modelling of the Hauraki Gulf had also demonstrated that before human arrival, lobsters were considered the third most important benthic invertebrate species out of 12 groups (as both predator and prey) but are now considered one of the least (Pinkerton et al. 2015). This decline in abundance and consequent ecological role, in turn, resulted in large shifts in rocky reef habitat composition (Shears & Babcock 2003). The decline in these fundamental predators has put increased emphasis on the success of management options in restoring the abundance and functional role of lobsters.

There are various management approaches available to help restore trophic linkages include changing size limits (Linnane et al. 2011), translocations (Gardner & Putten 2008; Johnson et al. 2013) and temporal and spatial closures (Sloan et al. 2007). More specifically, no-take marine reserves are suggested to be

a useful tool for mitigating the effects of fishing (Sumaila et al. 2000). However, lobsters have displayed highly variable responses to protection, with a few populations showing a rapid recovery within MPAs and others showing little response even after a decade of protection (Freeman et al. 2012, LaScala-Gruenewald et al. in press). Cape Rodney to Okakari Point (CROP) Marine Reserve situated within the Hauraki Gulf is New Zealand's oldest no-take marine reserve, established in 1975, and has had an overall positive effect on lobster populations within protected area boundaries (Kelly et al. 2000b, Freeman et al. 2012). However, lobster populations have declined by approximately 87.5 % since 1995 (Cole et al. 1990, MacDiarmid & Breen 1993, Kelly et al. 2000b). It is believed that targeted fishing of lobster aggregations (predominantly large males) on the offshore boundaries of the relatively small CROP marine reserve have contributed not only to population declines within the reserve but also the decline in large individuals (Kelly et al. 2002, Kelly & MacDiarmid 2003).

Lobsters are capable of moving considerable distances; for example, several large male lobsters tagged by MacDiarmid (1991) on inshore reefs within the CROP Marine Reserve were caught in fishing traps over the seaward boundary of the reserve. This suggests that some lobsters make offshore excursions upwards of 500 m from rocky reef margins. Kelly et al. (1999) showed that lobsters from the CROP Marine Reserve undertake predictable seasonal movements between depth strata. Additionally, at certain times of the year (November – February), large numbers of predominantly male lobsters aggregated in offshore areas with little or no relief in seabed structure for extended periods (Kelly 2001). The observed offshore migration is speculated to be partly driven by increased feeding

opportunities, which enable males to offset the high metabolic costs associated with mating and ecdysis. This hypothesis is supported by observations of lobsters foraging on the sand flats at night and carrying prey items back over the sand towards their reef shelters (MacDiarmid 1991).

Despite both the ecological and economic importance of *J. edwardsii,* our overall understanding of nearshore feeding biology and the drivers behind inshore/offshore migration patterns, remain limited. This study aimed to assess if *J. edwardsii* exhibited feeding preferences between common rocky reef and soft-sediment prey species. This research identified essential feeding associations and provides context to support previously identified movement patterns between rocky reef and soft sediment environments.

## Materials & Methods

### Lobster collection and housing

To understand the motives behind large male lobster offshore movements, large (140 – 160 mm carapace length (CL)) male lobsters were collected from the local fishery (Lee Fish Ltd) and transported to the Leigh Marine Laboratory (36.2692° S, 174.7984° E). Only inter-moult individuals were used in these experiments, as feeding rates differ according to moult stage (Lipcius & Herrnkind 1982). Lobsters were housed in large 1,500 L (1.75 m diameter) tanks at ambient temperature and photoperiod and received aerated continuous flow-through seawater. Individuals were fed a combination of thawed squid (*Nototodarus sloanii*) and pilchards (*Sardinops neopolchardus*). Before the feeding experiments,

lobsters were withheld food for four days to standardise levels of starvation (Mills et al. 2016).

**Prey types**

Prey used in the feeding trials were chosen based either on "known" lobster prey types (Witman & Grange 1998, Jack et al. 2009) or inferred from faunal descriptions from current (Fig. 2.1) soft-sediment faunal sampling that overlapped historic lobster aggregations (Kelly et al. 1999). Six different prey species across three phyla (Mollusca; Echinodermata and Crustacea) were offered to individual *J. edwardsii*. Prey species were the sea urchin (*Evechinus chloroticus*); gastropod (*Cookia sulcata*); bivalves (*Tawera spissa*; *Tucetona laticostata*; *Myadora striata*), and the common hermit crab (*Pagurus novizealandiae*). These prey species were sourced from subtidal rocky reefs and adjacent sand habitats around the Leigh coast. Throughout the experiments, *M. striata* were difficult to collect in large enough numbers needed to maintain feeding regimes. Therefore, the wedge shell, *Macomona liliana,* was used as a proxy. Wedge shells are also soft-sediment deposit-feeding bivalves and have a similar shell architecture to the *M. striata* (Powell 1979). A pilot study indicated that handling times and feed intake were similar between the two species (One-way ANOVA handling: $F_{(1,180)} = 1.50$, $p = 0.22$; intake: $F_{(1,7)} = 0.02$, $p = 0.91$). Herein, the combination of these two species is referred to as 'wedge clam'.
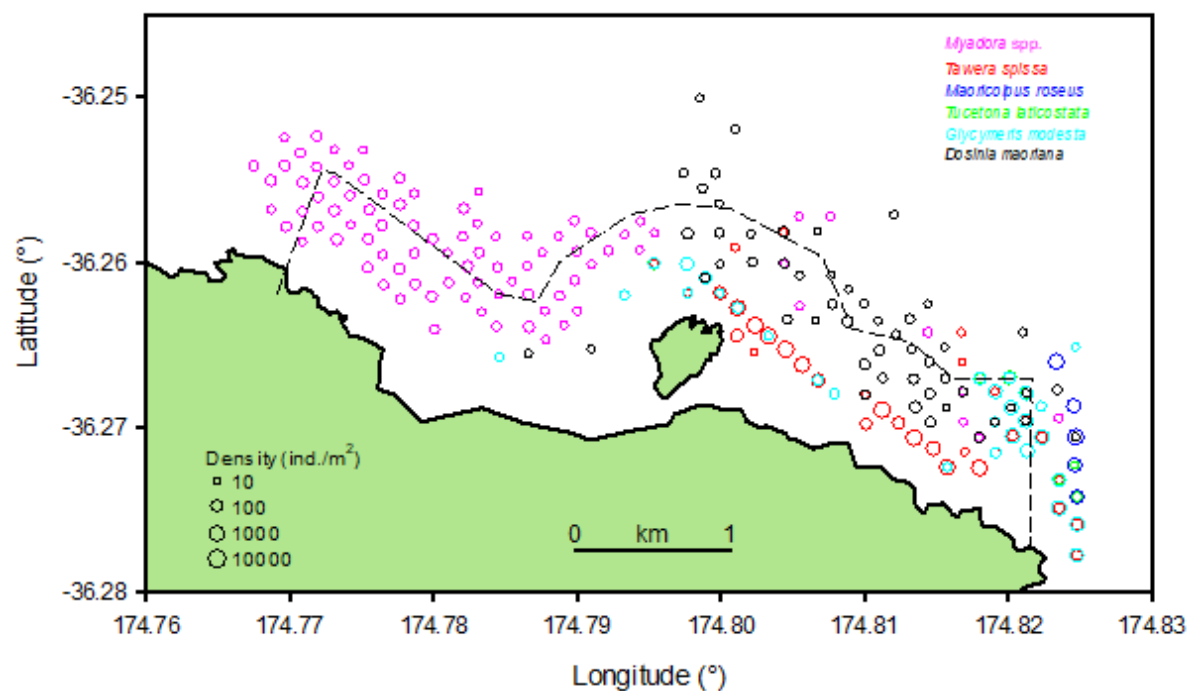
**Fig. 2.1.** Bivalve distribution bubble plots for the 2019 sediment grab survey completed at CROP marine reserve (see Schoensee 2020). Circle area indicates proportional to logged densities. The black line is indicative of reserve boundary. *Myadora spp.* (pink), *Tawera spissa* (red) and *Tucetona laticostata* (green).

**Characteristics and nutritional content of prey species**

Measurements of shell thickness (mm), dry mass (%), calories ($g^{-1}$), protein (%) and lipid content (%) were collected from 10 randomly selected individuals from each of the six prey types (n = 20 wedge clam; 10 *M. Liliana,* 10 *M. striata*). Shell thickness was measured using Vernier callipers to ± 0.5 mm and was taken from where lobsters initiate breakage. *Pagurus* and *Cookia* thickness measurements were taken from the outer shell lip or aperture (where breakage was commonly observed). *Evechinus* test thickness was measured by cracking the urchin open from the peristomial membrane and taking the measurement closest to the oral opening. Standard methods were used to determine dry matter after

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freeze-drying to constant weight (± 0.001 g). All samples were prepared for chemical analysis by grinding to a homogenous powder using liquid nitrogen and a hand mortar and pestle. Total lipid was measured by chloroform-methanol extraction (Bligh & Dyer 1959), protein content was determined using a modified Bradford (1976) protocol, and gross heat (calories ($g^{-1}$)) was estimated using bomb calorimetry (Siddon et al. 2013).

**Experimental design**

All feeding experiments were completed in 1,500 L tanks (1.75 m diameter, 0.5 m height) supplied with flow-through ambient seawater (Fig. 2.2). Tank water levels were maintained to ensure that prey items could not climb beyond the reach of lobsters. A layer of sand (~ 7 cm in height) was spread evenly across the bottom of the tank to mimic a more natural environment and allow soft-sediment prey species to burrow. Patches of rock rubble and cement blocks of various sizes were also added into the experimental tank to mimic a reef environment and allow reef-dwelling prey species to hide.

To observe lobster foraging behaviour, a CCTV camera (HiWatch IPC-B120) was mounted vertically in the centre of the tank 1.5 m above the water surface to track animals' movement. Red LED lights (iFlex LED Strip light) were fitted to the upper rim of the tank to allow video recordings to be undertaken at night when rock lobsters are most active (Herrnkind 1980). Crustaceans are known to have low sensitivity to red light (Johnson et al. 2002), and therefore, the presence of red light should have a negligible effect on their feeding behaviour.

To determine the quantity of each prey type required for feeding experiments, and to standardise for the difference in prey type weights, individual lobster (n = 9) were offered each of the six prey species once over a 24 hr period. Based on consumption rates from this pilot study the following amounts of each prey were used: *Evechinus* = 4; *Cookia* = 4; *Pagurus* = 6; *Tucetona* = 10; *Tawera* = 20; wedge clam = 16.
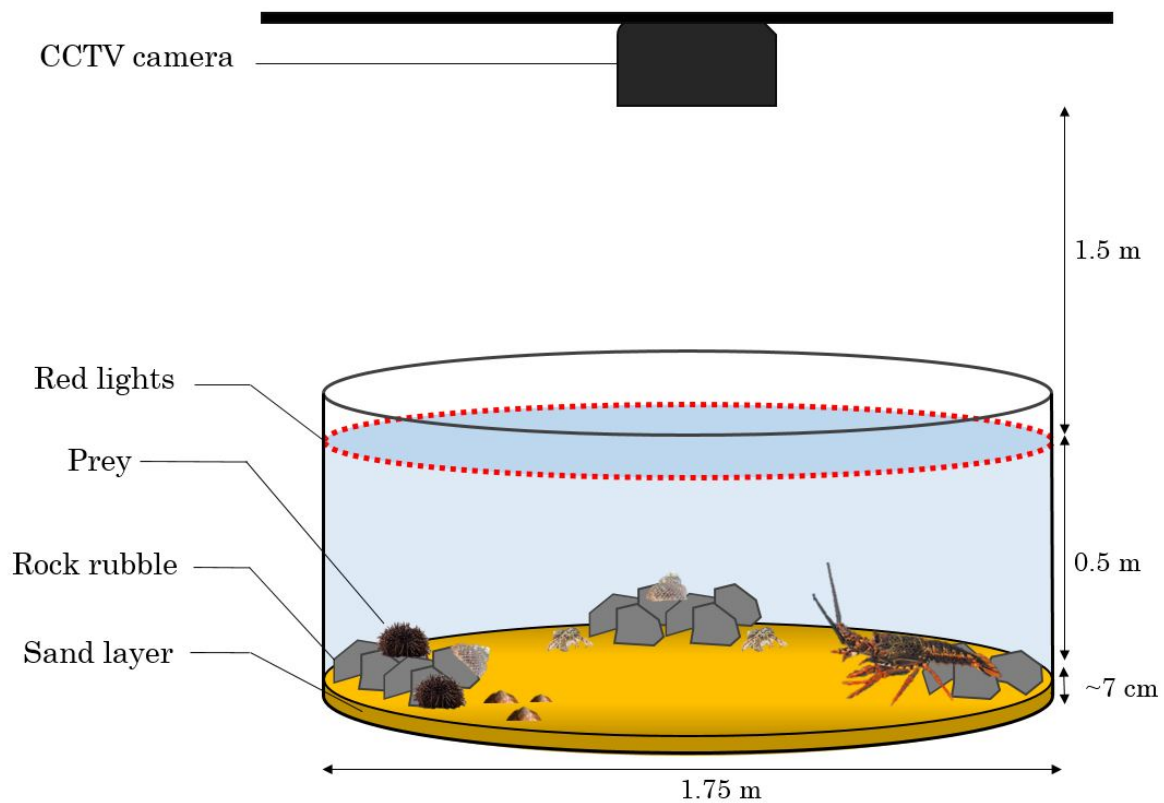


**Fig. 2.2.** Schematic diagram showing experimental tank set up

**Feeding preference tests**

Feeding experiments, of inter-moult lobsters commencing between Jan 2019 and Sep 2019, were conducted to evaluate prey feeding preference. All six prey types were offered simultaneously to each lobster; in total, five replicates of five lobster were completed to take into account variability with individuals. The size

(± 0.5 mm), and fresh weight (FW, ± 0.1 g) of each prey were recorded before being placed into the experimental tank. The size of each prey type was determined using Vernier callipers (± 0.5 mm) as follows: bivalve species - shell length (SL: maximum linear dimension of the shell); *Cookia* - widest opening of the base of the shell; *Pagurus* – shell height (SH: maximum linear dimension of the axis at right angles to SL); *Evechinus* – test diameter (TD).

Prey species were placed at random into the 1,500 L experimental tank at the beginning of the day and left for at least four hrs to allow prey to burrow/ hide to simulate their natural habitat. Prey species, such as *Tawera, Tucetona,* and wedge clams were placed in two groups to represent how they are found in the natural environment (Fig. 2.1). The location of these bivalves was recorded and randomised for each trial.

At 17:00 hrs an individual lobster was selected at random (from a pool of 5) and placed by hand into the centre of the experimental tank, and video recording commenced. Each feeding trial ran until 7:00 hrs the following day, i.e., 14 hrs.

**Apparent food intake and prey handling**

The amount of prey consumed at the end of each trial was counted to assess prey consumption. Any leftover shell and tissue remnants of each prey type weighed (± 0.1 g) to estimate apparent food intake (AFI). The AFI from each prey type were combined to get a trial AFI value. If a feeding trial had an AFI of ≤ 50 g it was discarded, as this was considered to represent a reduced feeding rate (Kelly et al. 1999). Using the video recordings, time of prey consumption and total handling time for each prey consumed were determined upon playback. Handling

time was defined as - the period starting from when a given lobster captured the prey until the point at which the lobster was no longer interacting with it for one minute (this time was subtracted from the total handling time). If the lobster were to return to a previously handled prey item this new time was treated to the same conditions as above and added to the original handling time to determine a total handling time. To determine prey profitability, the AFI of each prey type was multiplied by the associated calorific score and standardised to handling time for each trial as per the following equation:

$$profitability\ score = \frac{(AFI * Cal)}{HT}$$

**Movement**

To understand if lobster movements were associated with foraging, video recordings of the first three feeding trials of each of the five lobsters were compared to controls (prey absent) of the same lobsters and repeated three times. Based on video recordings when lobsters were actively searching for food, lobster would forage within the "inner tank". Therefore, as a proxy for foraging, an inner tank arena was defined as 20 cm in from the outer tank boundary (Fig. 2.3). The inner tank arena was plotted in a feeding trial video and the same inner tank parameters were mirrored in the associated control. Distance travelled (m) and the proportion of time spent within the inner tank was calculated.
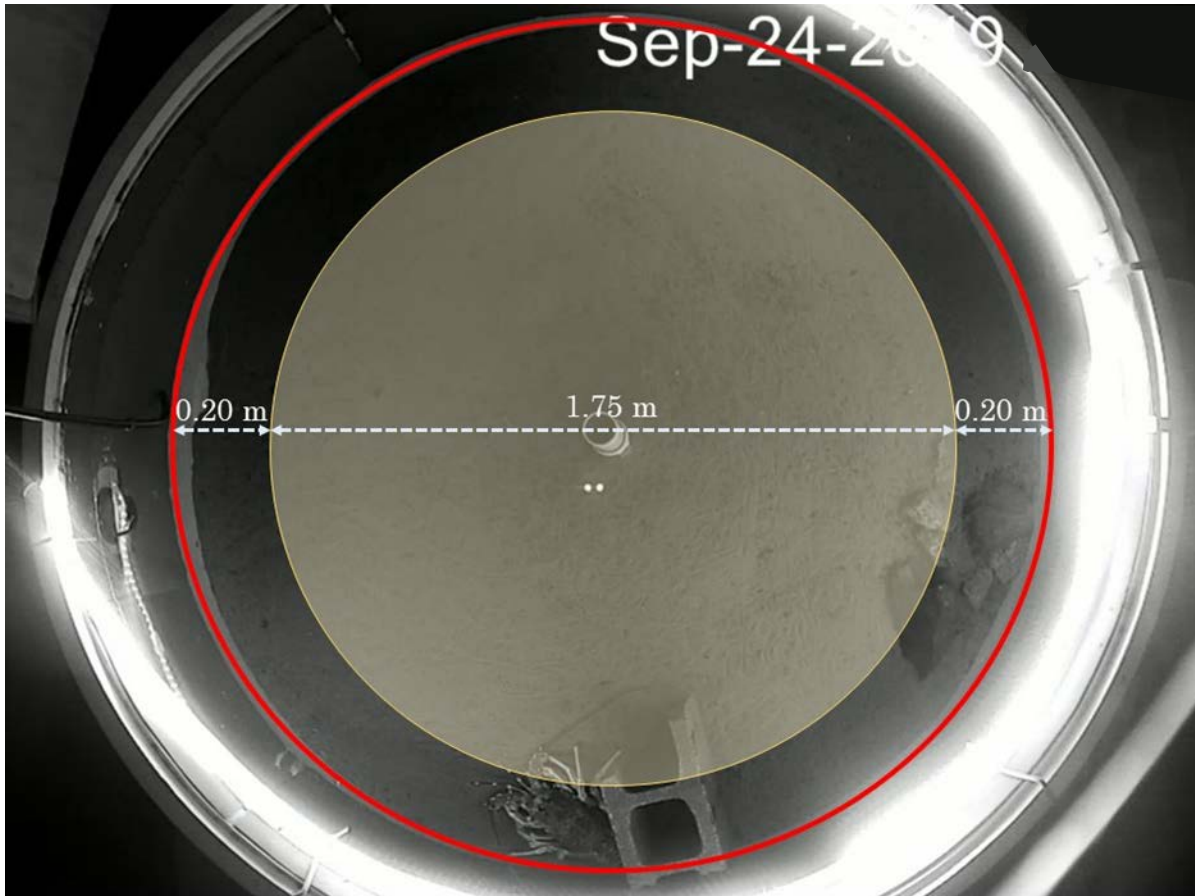
**Fig. 2.3.** Example of tank area zones used for analysing distances travelled (m) and proportion of time spent within the inner tank (yellow shaded area). The inner tank was set 20 cm in from the outer tank boundary (red). This eliminated edge effects (lobster resting – as seen in the above example).

**Data analysis**

Statistical analyses were conducted using PRIMER-E statistical software (V 7; Clarke & Warwick 2001) and PERMANOVA (Anderson et al. 2008) and R-Studio Software (v 1.2.5033, RStudio INC). All data were tested for normality and homogeneity of variance prior to analysis and overall statistical significance at the 0.05 level.

*Characteristics and nutritional content of prey species*

PERMANOVA was used to test differences in shell thickness and nutritional content (dry matter, lipid, protein, calorific values) among the six prey types. Analysis was run on normalised data and a Euclidean distance matrix. Principle Component Analysis (PCA) was then employed to visualise differences among prey in multivariate space.

*Feeding preference tests*

To evaluate lobster prey preference, Rodgers' index ($R_i$) for cafeteria type experiments was calculated for each prey type (Rodgers & Lewis 1985). $R_i$ ranged from 0 (avoidance) to 1 (preference). The area beneath the consumption curves accounts for the order, rate, and total amount of each prey item consumed (see Krebs 1989). The index considers the inability to replenish food during the experiments and allows for one or more food types to be completely consumed during the experiment. The Rodgers' index was calculated as $R_i = A_i/\max(A_i)$, where $A_i$ is the area under the curve of the proportion of species $i$ prey items consumed over time and max ($A_i$) is the largest value of $A_i$ per experimental unit (Krebs 1989). For this study, the amount of each prey consumed were binned into one-hour blocks.

The calculation of prey preference using Taplin's (2007) method assumes that the order in which prey is consumed discloses information about preference, with the more preferred prey being consumed first. The resultant null hypothesis would be that prey consumption is random. Each prey item was assigned a rank depending on the order of consumption, i.e., the first prey type eaten was assigned rank 1, the second prey rank 2 and so on until all prey had been ranked. When a

prey item was not consumed, it was considered least preferred, or if there were multiple prey types left unconsumed, they were considered tied for last and given an average rank.

Preference scores ($R_i$, Order of consumption) were averaged for each lobster (n = 5) prior to further analysis. The relationship between prey preference and prey type were analysed using a generalised linear model (GLM) back-fitted to a gaussian distribution with an identity link function. Additionally, preference indices from reef prey (*Evechinus, Cookia, Pagurus*) and soft-sediment prey (*Tucetona, Tawera, Wedge clam*) were pooled (habitat) and analysed. Tukey's Honest Significant Difference (Tukey's HSD) test was then used in pairwise-comparisons to determine the difference between the means, with confidence intervals based on the studentised range distribution.

*Apparent food intake and prey handling*

To test for differences within prey type AFI, and handling time, a one-way ANOVA was used. Tukey's HSD test was then used in pairwise-comparisons to determine the difference between the means, with confidence intervals based on the studentised range distribution. To test if feeding trial AFI was changed with month, a one-way ANOVA was completed. As data for profitability score did not meet the assumptions for parametric tests, the Kruskal–Wallis test was used to determine differences between prey types. A two-way repeated-measures AVOVA was conducted to evaluate the proportion of different prey types consumed over time. *P*-values were adjusted using the Bonferroni multiple testing correction method and a pairwise comparison, using paired t-tests were used to show individual differences in prey proportions consumed. Additionally, preference

indices from reef prey (*Evechinus*, *Cookia*, *Pagurus*) and soft-sediment prey (*Tucetona*, *Tawera*, Wedge clam) were pooled (habitat) and analysed.

*Movement*

Lobster movements were analysed in MATLAB (R2018a) using DLTdv digitising tool (Hedrick 2008; http://biomech.web.unc.edu/dltdv/). The raw video was converted into 1 fps, and the lobster's position was reordered for every frame. Distance travelled (m) were binned into one-hour blocks. Additionally, the proportion of time spent in the inner-tank zone was calculated by summing the position data points within a pre-determined arena and dividing this by the total position points for each hour bin. Each lobster's distance for each hour (n = 3) was averaged before further analysis. A two-way repeated-measures ANOVA was conducted to evaluate the differences in distance travelled and proportion within the inner-tank over time and between treatment groups. *P*-values were adjusted using the Bonferroni multiple testing correction method and a pairwise comparison, using paired t-tests were used to show individual differences in prey proportions consumed.

# Results

## Characteristics and nutritional content of prey species

There were statistically significant differences found among prey types for select characteristics (shell thickness and nutritional components) (PERMANOVA; *Pseudo-F*$_{5,45}$ = 21.2 $p$ < 0.002). Wedge clams had the thinnest shell of the six prey types and had the lowest dry mass, alongside the other two bivalves (Table 2.1). *Evechinus* had the highest dry matter, lipid, and caloric values compared to the other prey species (Table 2.1). Principal Components Analysis used to support PERMANOVA demonstrated clear differences among prey type with *Evechinus* and *Cookia* typically grouped to the left of the ordination positively associated with PCA Axis 1 and the other prey types generally negatively associated with PCA Axis 1. Together the ordination explained ~ 75% of the variation (Fig. 2.4). Main components responsible for the separation of prey types based on Pearson's Correlation Coefficients are also presented supporting the differences outlined in Table 2.1.

**Table 2.1.** Mean (± SE) of shell thickness (mm), dry mass (% fw), calories (-g) and lipid and protein concentrations (% dwt). Different letters equate to significant differences based on Tukey's HSD test. ST = shell thickness, DM = dry mass, Cal = calories

| Prey | ST (mm) | DM (%) | Lipid (%) | Protein (%) | Cal (-g) |
|------|---------|--------|-----------|-------------|----------|
| *Evechinus* | 2.3 ± 0.13ab | 41.14 ± 0.92a | 14.42 ± 1.16a | 24.76 ± 3.09a | 5066.53 ± 90.65a |
| *Cookia* | 2.35 ± 0.24ab | 31.26 ± 4.39a | 5.09 ± 0.01b | 39.28 ± 2.67b | 3698.71 ± 156.59b |
| *Pagurus* | 2.65 ± 0.26a | 31.84 ± 4.14a | 2.35 ± 0.32c | 12.64 ± 1.75c | 2911.83 ± 98.71bc |
| *Tucetona* | 2.57 ± 0.18a | 16.58 ± 0.34b | 2.41 ± 0.12c | 51.58 ± 3.80b | 4234.69 ± 436.08ab |
| *Tawera* | 1.66 ± 0.11b | 11.18 ± 0.87b | 3.66 ± 0.14b | 44.66 ± 2.55b | 4066.26 ± 673.81ab |
| Wedge Clam | 0.84 ± 0.06c | 14.56 ± 1.75b | 2.95 ± 0.28c | 17.19 ± 2.98ac | 2210.9 ± 186.73c |
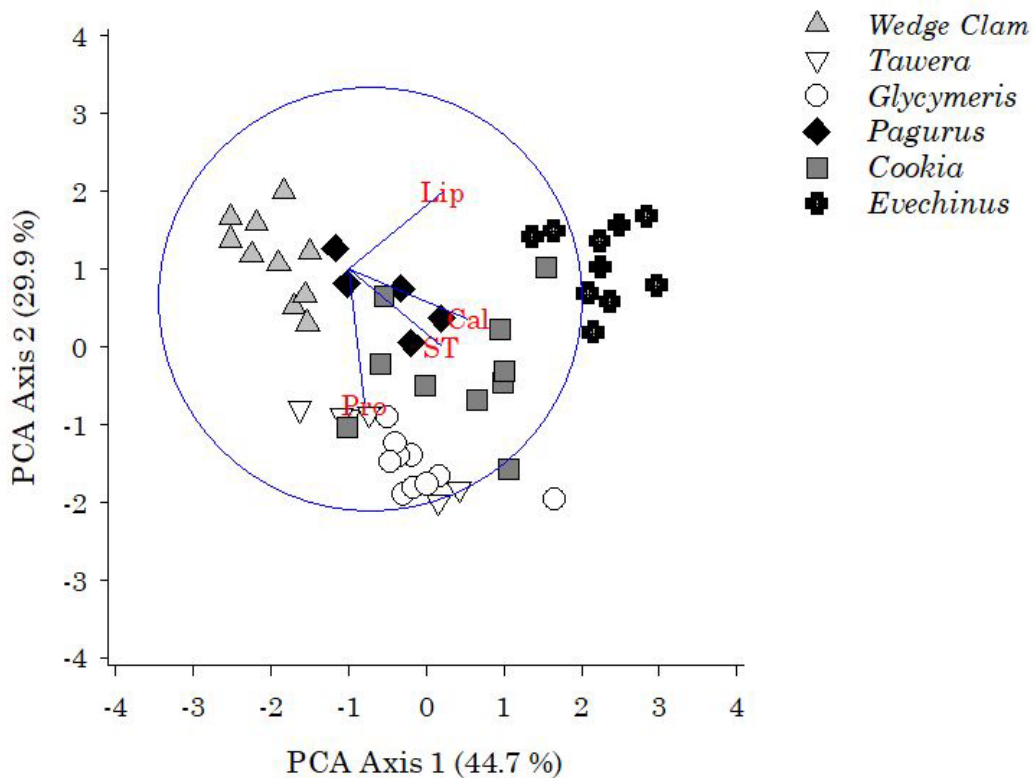
**Fig. 2.4.** Principle Components Analysis of nutritional components of prey types. Analysis is based on normalised data and Euclidean distance matrix. Vectors denote separation of main elements based on Pearson's Correlation Coefficients. ST = shell thickness, Cal = calories, Lip = Lipid, Pro = Protein.

**Feeding preference tests**

$R_i$ indicated that large male lobsters significantly preferred two of the six prey types offered, *Tawera* and wedge clams (Table 2.2a, Fig. 2.5a). The four remaining prey species had comparatively lower $R_i$ values. Overall, lobsters exhibited a significant preference for soft-sediment species over reef species (Table 2.2a).

Similarly, consumption order preference score showed that lobsters preferred *Tawera* and wedge clams, with the four remaining prey types having comparatively higher order ranks (Table 2.2b, Fig. 2.5b). Again, there was a

significant (Table 2.2b) preference for soft-sediment species compared to reef habitat

species based on order rank.

**Table 2.2.** Analysis of deviance for GLM model fitted to prey preference scores derived from **a)** Rodgers' Index ($R_i$) and **b)** Consumption order.

| Source | d.f. | Deviance | Resid. d.f. | Resid. Dev. | P(>\|Chi\|) |
|---|---|---|---|---|---|
| **a) Rodgers' Index** | | | | | |
| Prey | 5 | 2.20 | 24 | 0.65 | $4.62e^{-16}$ *** |
| Habitat | 1 | 1.49 | 28 | 1.36 | $3.26e^{-08}$ *** |
| **b) Consumption order** | | | | | |
| Prey | 5 | 75.97 | 24 | 14.72 | $2.2e^{-16}$ *** |
| Habitat | 1 | 59.36 | 28 | 31.32 | $3.22e^{-13}$ *** |
| **Signif. codes: *** < 0.001; ** < 0.01; * < 0.05** | | | | | |



a)
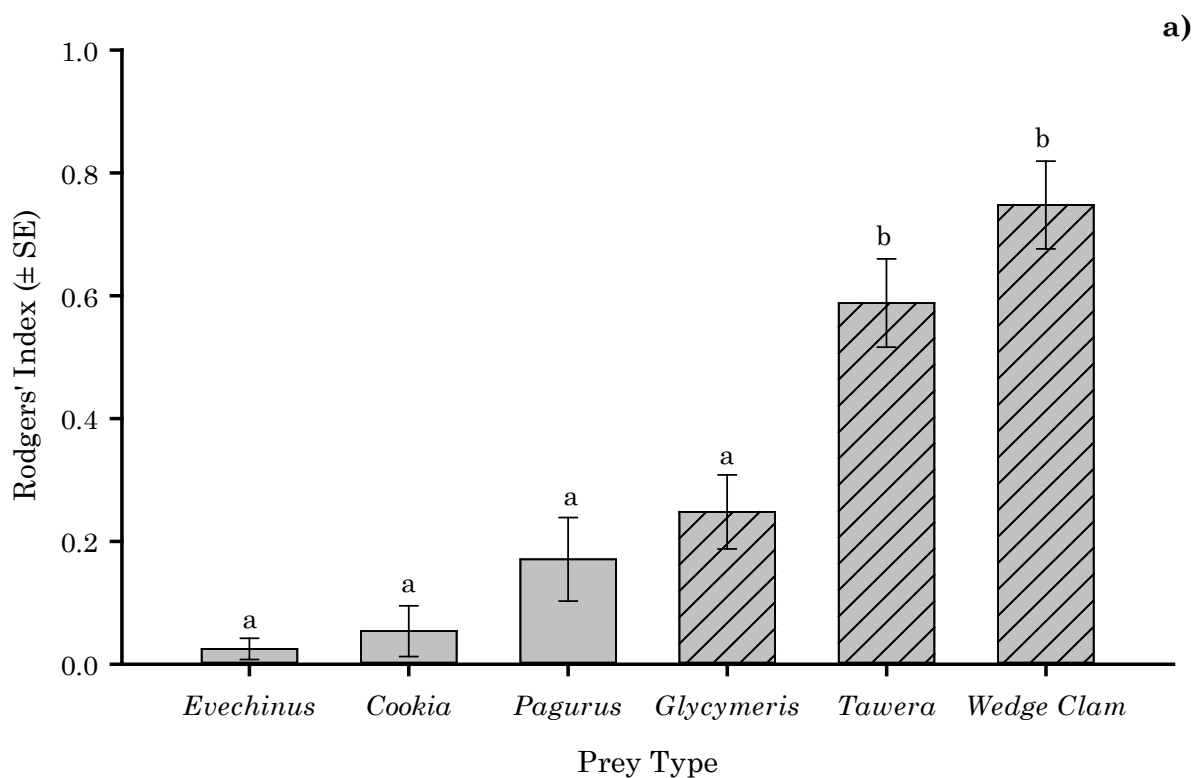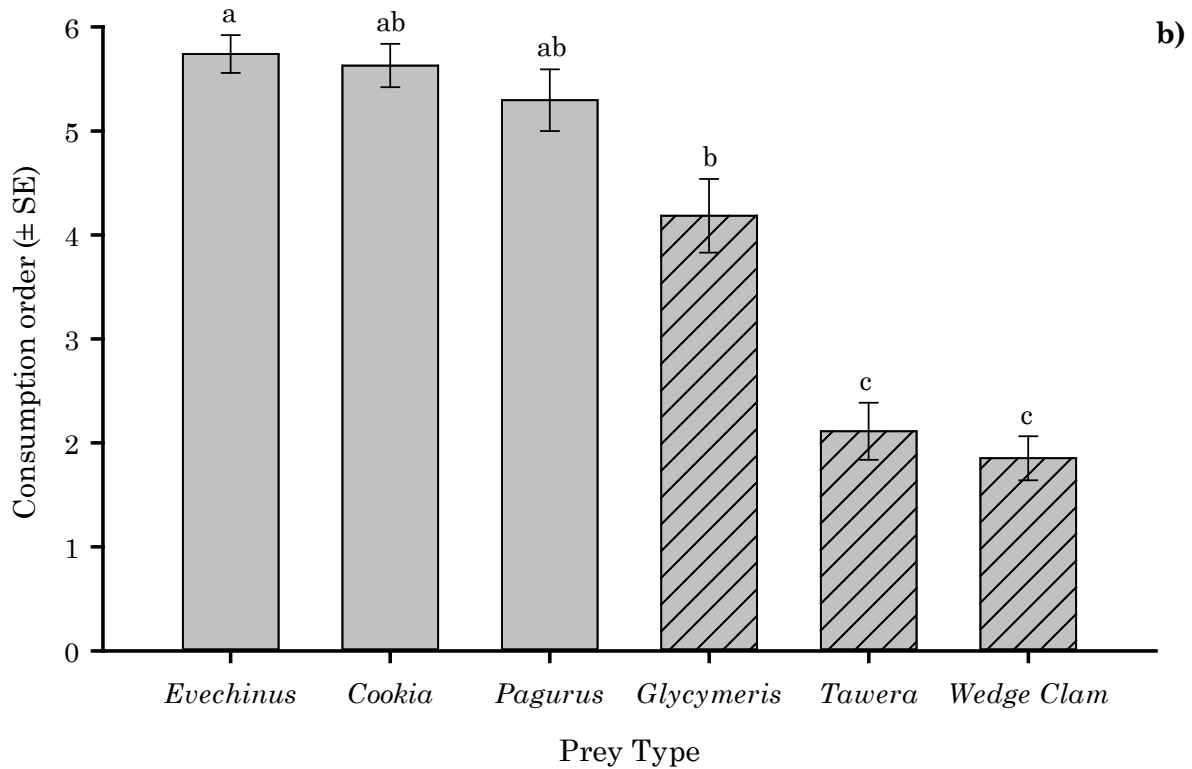
**Fig. 2.5.** Mean (± SE) **a)** Rodgers' Index ($R_i$) of preference for six prey types. The higher the $R_i$ the more preferred the prey type. **b)** Consumption order for six different prey types. The lower the order rank the more preferred the prey type. Solid bar = reef prey species; striped bar = soft-sediment prey species. Different letters equate to significant differences based on Tukey's HSD test.

**Apparent food intake and prey handling**

The average apparent food intake (AFI) of feeding trials in this study (January 2019 - September 2019) was 91.3 g ± 8.42 g, with no significant change over time (One-way ANOVA; $F_{1, 19}$ = 1.71, $p$ = 0.166). Two trials were discarded as they were under the predetermined 50 g consumption threshold (31.3 g; 46.5 g). There were differences in prey handling time (HT) (One-way ANOVA; $F_{5, 562}$ = 228.92, $p$ < 0.001), with *Evechinus* having the longest HT, and wedge clam and *Tawera* having the shortest HT (Table 2.3). *Evechinus* and the three bivalve prey types had the highest potential profitability (Fig. 2.6) ($H_5$ = 30.96, $p$ < 0.001) compared to *Cookia* and *Pagurus*. There was a significant interaction between the

proportion of prey consumed and prey type over time (Two-way RM ANOVA; $F_{75, 300}$, = 11.16, $p < 0.001$). The effects of prey type were significant at each time point ($p < 0.001$), with these differences primarily being driven by wedge clam and *Tawera*. The proportion of *Tawera* and wedge clams consumed increased steadily until most of them had been consumed. Overall, soft-sediment prey were the most consumed prey throughout the experiment (Two-way RM ANOVA; $F_{15, 60}$, = 39.19, $p < 0.001$; Fig. 2.7).

**Table 2.3.** Prey type and lobster feeding characteristics: Fresh weight (FW) and the size of each prey type used in feeding trials. Average intake and max intake are based on nine different lobsters (n = 9). Handling time (HT) and apparent food intake (AFI) are determined from preference feeding trials of five different lobsters (n = 25). *mean ± SE.

| Prey | FW (g)* | Size (mm)* | Intake (no.)* | Max intake (no.) | HT (min)* | AFI (g)* |
|---|---|---|---|---|---|---|
| *Evechinus* | 223.24 ± 10.69 | 82.28 ± 3.26 | 2.1 ± 0.23 | 3 | 57.8 ± 6.76 | 133.5 ± 40.72 |
| *Cookia* | 42.96 ± 4.18 | 50.26 ± 1.50 | 1.8 ± 0.64 | 3 | 37.48 ± 5.10 | 12.47 ± 2.29 |
| *Pagurus* | 26.41 ± 0.89 | 43.95 ± 1.52 | 3 ± 0.56 | 6 | 23.67 ± 3.27 | 8.74 ± 0.85 |
| *Tucetona* | 69.35 ± 2.85 | 46.25 ± 0.92 | 2.8 ± 2.20 | 9 | 19.44 ± 1.64 | 17.28 ± 1.20 |
| *Tawera* | 4.59 ± 0.08 | 22.73 ± 0.15 | 9.6 ± 2.78 | 20 | 2.68 ± 0.14 | 2.83 ± 0.17 |
| Wedge clam | 5.28 ± 0.21 | 32.0 ± 0.57 | 7.9 ± 2.32 | 16 | 2.91 ± 0.13 | 3.69 ± 0.32 |
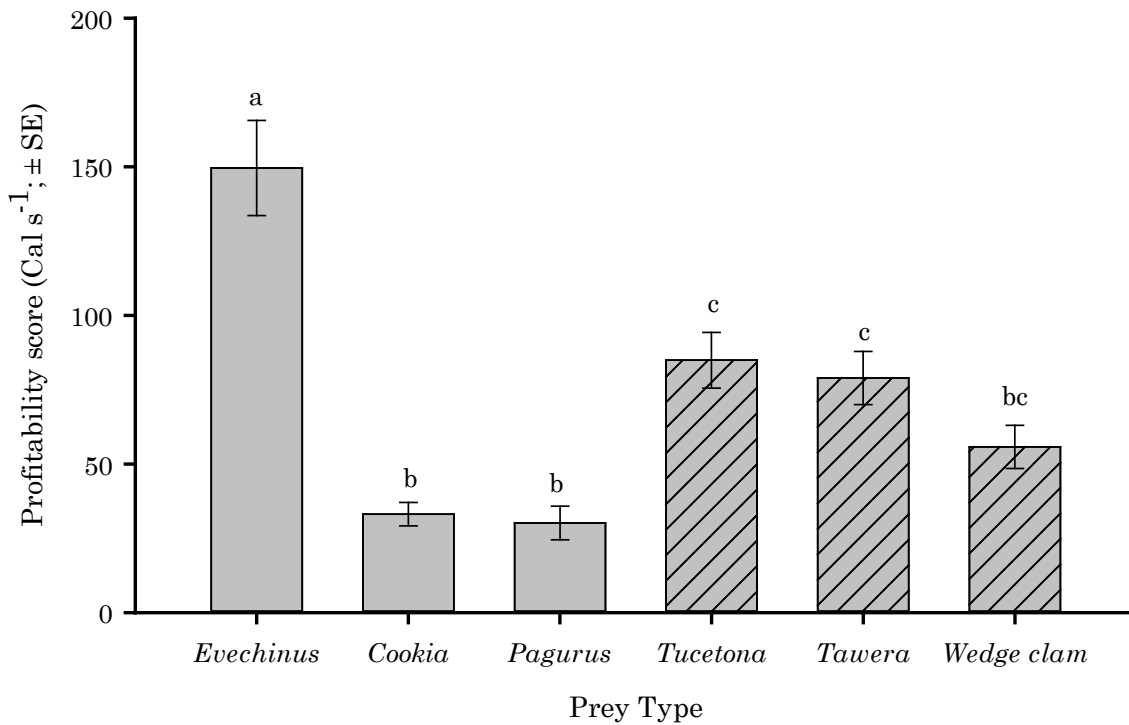
**Fig. 2.6.** Mean (± SE) profitability score (Cal s$^{-1}$). Solid bar = reef prey species; striped bar = soft-sediment prey species. Different letters equate to significant differences based on test. *Evechinus* n = 7; *Cookia* n = 6; *Pagurus* n = 7; *Tucetona* n = 1; *Tawera* n = 22; *Wedge clam* n = 622.
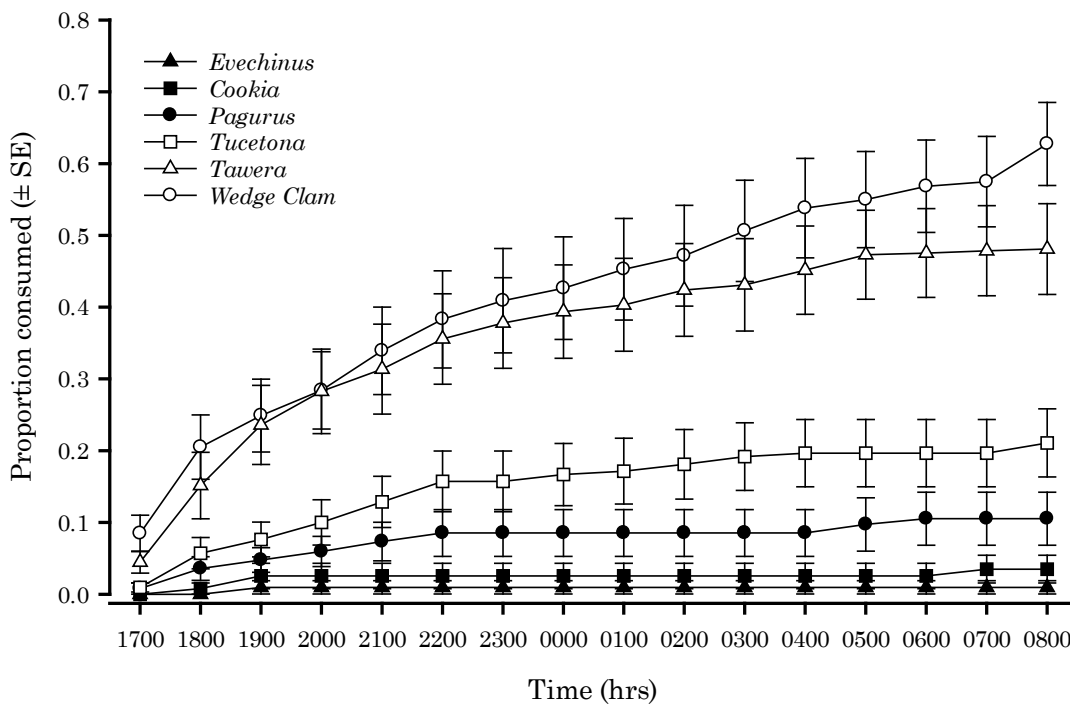


**Fig. 2.7.** Average proportion of prey consumption (± SE) over time (hrs). Black symbols = reef prey species; white symbols = soft-sediment prey species

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## Movement

The average distance travelled by lobsters in prey present (PP) trials were $613 \pm 42.3$ m and $310.9 \pm 51.8$ m in prey absent (PA) trials. The maximum distance a single lobster travelled overnight (12 hrs) was 1018.6 m (recorded in a PP trial). The distance travelled significantly increased (Two-way RM ANOVA; $F_{1, 4}$, $= 88.89$, $p < 0.001$) when prey was present in the tank (Fig. 2.8a). In the presence of prey, the proportion of time spent within the inner-tank arena significantly increased (Two-way RM ANOVA; $F_{1, 4}$, $= 11.14$, $p < 0.05$) and was observed at all time points (Two-way RM ANOVA; $F_{11, 44}$, $= 2.77$, $p < 0.01$; Fig. 2.8b).
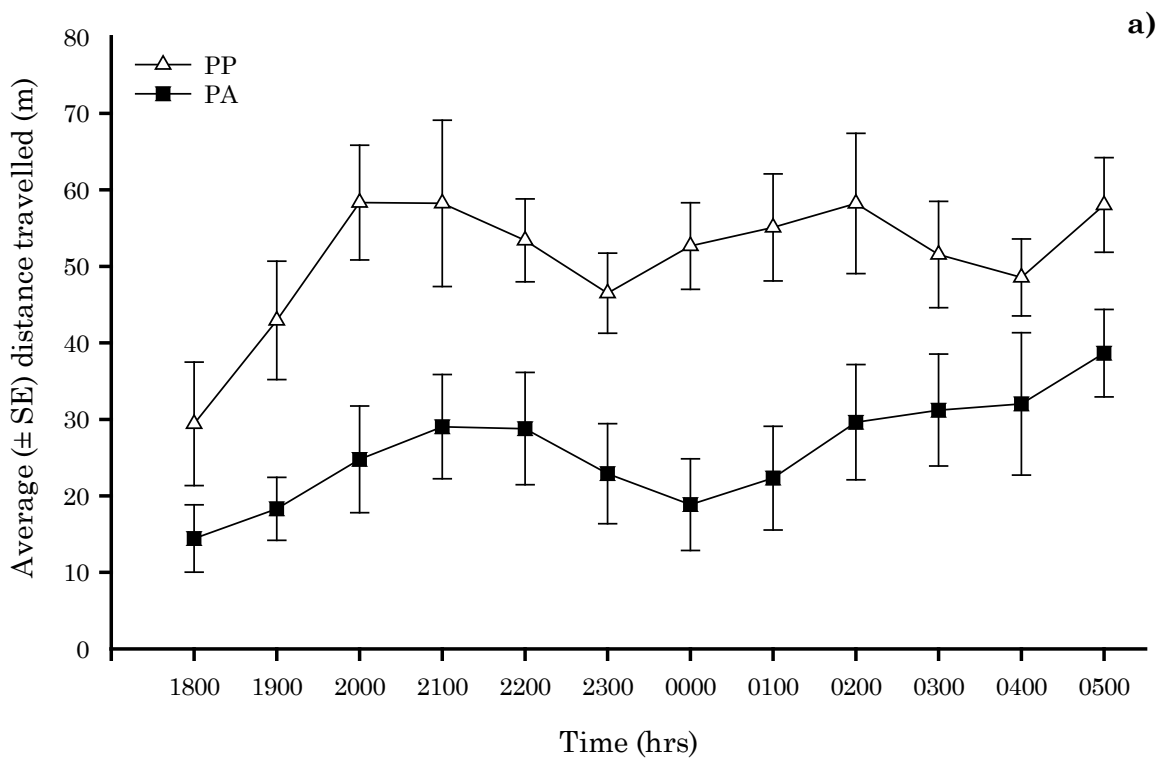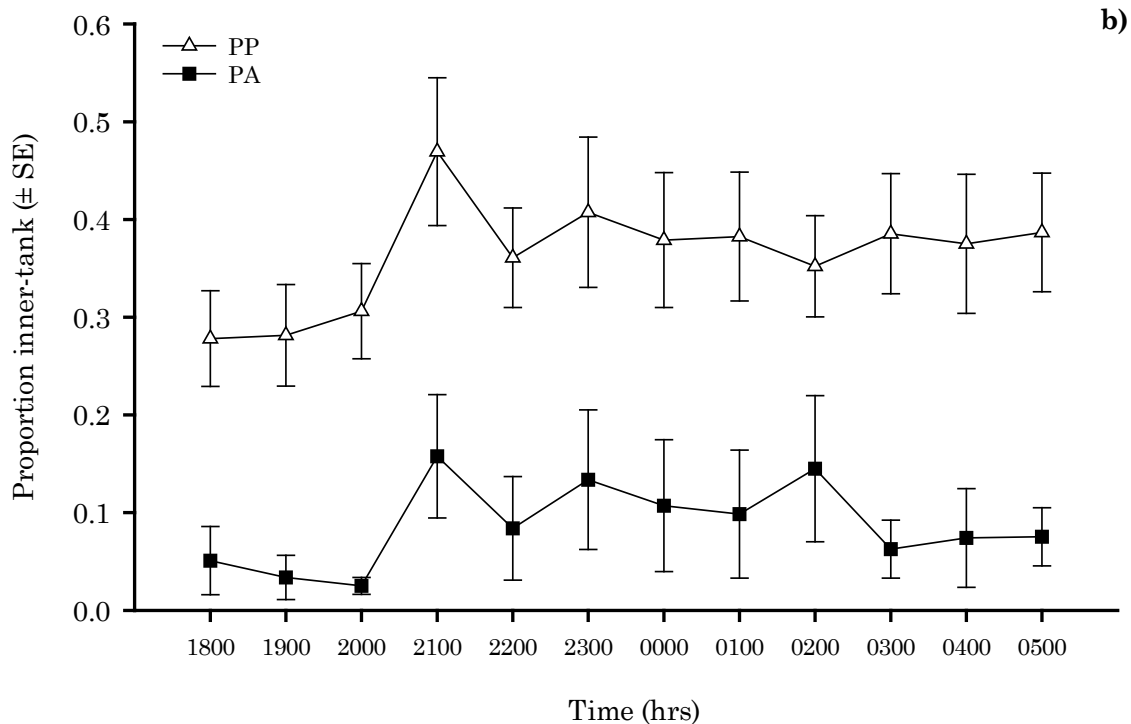
**Fig. 2.8.** Average (± SE) **a)** distance (m) travelled and **b)** the proportion of time spent within the inner-tank over time (hrs) for prey present and prey absent trials. PP = prey present; PA = prey absent (control) trials.

**General observations**

Feeding technique: *Evechinus* was consumed by turning the urchin over to attack it through the peristomial membrane. Once a large enough hole was achieved the lobster's first walking leg and third maxillipeds were used to pass soft tissue to the mandibles. The lobsters would revisit the urchin throughout the night and continue to consume the spines, test and entire Aristotle lantern. Lobsters used the pereiopods of the first walking leg to chip away *Pagurus* and *Cookia* shell until the meat was exposed. There were many attempts at catching *Pagurus*, but very few were successful. *Tucetona* were consumed by placing the ventral margin of the bivalves into the mandibles, which chip the shell before using the first walking leg and third maxillipeds to open the shell. *Tawera* and

wedge clams required minimal effort to consume (putting prey directly into mandibles) and lobsters would sometimes consume the entire prey without prior breaking of the shell.

Soft-sediment prey detection: Many of the wedge clams burrowed deep into the sand (~5 cm), *Tawera* and *Tucetona*, on the other hand, would usually burrow just below the surface (~1 cm). Lobsters would start by flicking their antennules in the water column, and once potential prey was identified in the sand, the antennules were then placed directly into or on the sand. The lobster would keep sampling the surrounding sand with the antennules until a potential site was located, which would initiate a digging behaviour (Fig. 2.9). Digging was achieved by a forward motion or 'lunge' that forced their first walking legs into the sand. This movement would be followed by a backwards pulling motion moving the sand towards the abdomen, making a crater. The antennules would then reassess the displaced sand and crater, and upon encountering a mollusc further assessed the prey with the antennules.
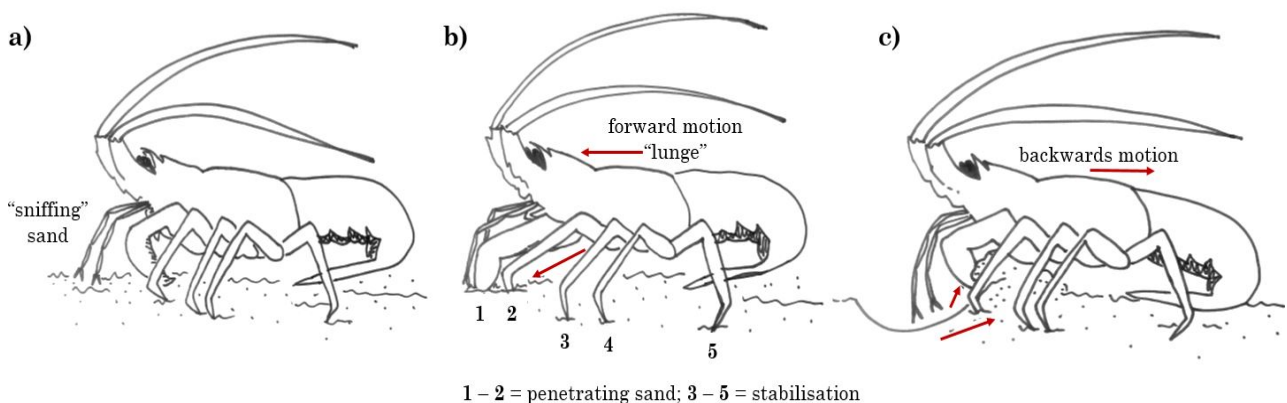


**Fig. 2.9.** Schematic breakdown of a digging movement: **a)** antennules 'sniffing' substrate; **b)** forward lunge and penetrates sand with legs 1 and 2, while $3 - 5$ act in stabilisation; **c)** creates a creator in sand with a backwards motion.

## Discussion

Lobsters are considered to be essential predator in many temperate coastal environments. They are capable of consuming a wide range of prey types (Shears & Babcock 2002, Langlois et al. 2005, Kintzing & Butler IV 2014) and have been shown to influence, both directly and indirectly, rocky reef and soft-sediment community structure and species abundances (Langlois et al. 2006). *Jasus edwardsii* are suggested to be opportunistic predators (Mayfield et al. 2000); however, within the context of coastal New Zealand, there is little known about lobster feeding behaviour and prey selection. This study has demonstrated that *J. edwardsii* have a strong preference for soft-sediment prey compared to common reef species. Strongest preferences were for the bivalves *Tawera spissa* and wedge clams (the combination of *Myadora striata* and *Macomona liliana*). Collectively, these species had the shortest handling times and thinnest shells, therefore, required minimal effort to consume. However, *Tawera* and wedge clams had the lowest dry mass, and wedge clams had comparatively low calorific value and lipid and protein content (Table 2.1). This apparent low nutritional value suggests that multiple individuals would need to be consumed to be profitable within the context of optimum foraging theory (OFT). Additional trade-offs following OFT for small prey types include reduced risk of injury, thereby increasing overall profitability (Hughes & Seed 1981, Juanes & Hartwick 1990).

Despite bivalve prey being buried, lobsters were still able to locate and dig for these prey species. When a lobster identified potential prey in the sand, the antennules would be placed directly into or on the sand, potentially 'smelling' for metabolites from buried bivalves (Thiel & Watling 2015). The lobster would keep

sampling the surrounding sand with the antennules until a potential site was located, which would initiate a digging behaviour (see section Results 3.5 for more details). On the tips of their pereiopod dactyl segments were setal tufts, which are used for 'contact' chemoreception (Lavalli et al. 2007). The lobster would proceed to place antennules into the displaced sand and repeat digging until prey were found. Similarly, Jones (1988) reports that *Thenus* spp. probe the substrate with their first two pairs of pereiopods, while at the same time raising and lowering the antennules above the substrate surface.

The least preferred prey types were *Tucetona laticostata* and the three rocky reef species (*Evechinus chloroticus*, *Cookia sulcata* and *Pagurus novizealandiae*). Low preference scores for *Tucetona, Pagurus* and *Cookia* could potentially be explained by their relatively thick shells resulting in higher handling times and correlated risk of injury (Table 2.1; Table 2.2). *Cookia* and *Pagurus* also had the lowest profitability score compared to the other prey types (Fig. 2.6), indicating that the energy required for consumption may exceed the nutritional gain (Kaiser et al. 1993). The lobsters also made many attempts at catching *Pagurus,* but very few were successful. Although not examined in this study, this may indicate that *Pagurus* have a deterrent mechanism to reduce predation.

*Evechinus* were the least preferred prey in both preference tests; this was surprising considering that lobsters are commonly referred to as 'reef predators', and their predation on sea urchins has been well documented (Mann & Breen 1972, Breen & Mann 1976, Shears & Babcock 2003, Pederson & Johnson 2006). *Evechinus* had the highest profitability score suggesting the profit or nutritional gain of *Evechinus* should theoretically outweigh the costs associated with handling

efforts (Fig. 2.6). Once *Evechinus* had been opened and partially consumed, the lobsters would revisit the urchin throughout the night and continue to consume the spines and test. Interestingly, the Aristotle's lantern was always consumed, which may provide a rich source of calcium carbonate. Interestingly, Ennis (1973) found that American lobsters (*Homarus americans*) changed to a slightly more calcium-rich diet during the moulting season. Further investigation into the nutritional content of the test, spines and Aristotle's lantern of the urchin is required to fully understand the potential importance of these structures in the diet of *J. edwardsii.*

Overall, despite this study indicating the *Evechinus* would be a favoured prey type, when given a choice lobsters prefer to feed on soft-sediment bivalves. These results highlight the potential importance of bivalve beds as feeding habitat of *J. edwardsii*. This preference may be a possible explanation as to why *J. edwardsii* within the CROP Marine Reserve were found migrating from the rocky reefs onto offshore sand beds forming large feeding aggregations (Kelly et al. 1999, Kelly 2001). Several large males tagged by MacDiarmid (1991) on inshore reefs within the CROP Marine Reserve were later caught in traps set by fishers over the reserve's seaward boundary. This suggested that some male lobsters were making offshore excursions of at least 500 m beyond the reef margin. Our study also indicated that this is well within the capabilities of the distance a lobster can travel overnight (Fig. 2.8a). The observed offshore migration is speculated to be partly driven by increased feeding opportunities, which enable males to offset the high metabolic costs associated with mating and ecdysis, the two life-history events these migrations appear to be associated with (Kelly 2001). The findings of

this study support this hypothesis. It is also complementary to Langlois et al. (2005), which found that sites with high densities of lobster had lower biomasses of several bivalve species immediately adjacent. Therefore, small reserve size can put lobster populations at risk of being fished and are also inadequate at ensuring the diet of the lobster is protected from fishing pressure (Guest et al. 2009). These results could have significant implications in considering conservation efforts for *J. edwardsii* and highlight the importance of protecting reef habitats and protecting reef habitats and adjacent bivalve beds as important feeding grounds.

In conclusion, our results indicate that *J. edwardsii* shows a strong preference for soft-sediment bivalves. This preference is likely associated with the low handling effort required to consume these prey types. It also highlights the importance of surrounding sand beds as an essential feeding ground for lobsters, potentially explaining the observed offshore migrations. Concerning the potential rebuilding of lobster stocks, incorporating these feeding habitats into MPA decision making and management should be of high priority.

# CHAPTER THREE

# Making sense of foraging behaviour: The role of chemoreception and vision in the rock lobster, *Jasus edwardsii*

## Introduction

The natural environment presents more information than an animal can perceive or process. As a response, animals filter relevant cues from the available information, in part through the functional constraints of their sensory systems (Wehner 1987). Acquiring and interpreting environmental cues is crucial to their survival since it provides information about the location and quality of food, mates, predators, shelters, and risks (Derby et al. 2001, Johnson & Atema 2005, Shabani et al. 2009, Mellon 2014). Marine invertebrates are extremely sensitive and accurate when identifying and navigating towards potential sources of food (Kamio & Derby 2017), homing to shelters (Horner et al. 2006) and identifying sick conspecifics (Behringer et al. 2006), despite living in turbulent environments.

Lobsters possess compound eyes with numerous square facets that increase in number and expand the area in which light can enter the eye with each moult (Meyer-Rochow 2001, Land & Nilsson 2002). One role of the eyes is to convey information on the impinging visible light's quality and quantity, covering

wavelengths ranging from 300 to 800 nm (Meyer-Rochow, 1994). The decapod eye is extremely light-sensitive with mirrors in the upper part of the eye to increase light collection efficiency (Land 2000). This feature is crucial for nocturnal animals or animals inhabiting dim-light environments (Palmer et al. 2018). Most crustacean eyes can withstand some degree of fluctuating light intensities; however, if exposure is too intense for prolonged periods, irreversible damage can result in anatomical and physical changes (Lindstrom et al. 1988, Meyer-Rochow 2001). Photoreceptor damage can also have a direct impact on behaviour, with individuals becoming less dominant and unable to locate suitable hiding places (Meyer-Rochow & Tiang 1984). In general, vision is not considered necessary in lobsters' feeding behaviour as they feed at night (Premke et al. 2006, Kawamura et al. 2017). However, studies have shown a preference for mobile prey types and blinded crustaceans had a decline in food detection (Hirtle & Mann 1978, Kawamura et al. 2017). This behavioural change suggests some involvement of vision in crustacean foraging may exist.

One of the primary ways crustaceans gain information about their surroundings is through chemoreception. In decapod crustaceans, such as lobsters, the role of chemical senses is important for feeding, locating shelter and sexual and social interactions (Atema 1986, Ratchford & Eggleston 2000, Derby et al. 2001, Briones-Fourzan et al. 2008). Foraging behaviour is driven by two sets of chemosensory organs used to detect and search for food. Firstly, unimodal chemosensory aesthetascs on the lateral antennule, which are connected to the olfactory pathway in the central nervous system (Derby et al. 1984, Mellon 2005). Secondly, bimodal chemo- and mechanical sensilla are present in dense tufts on

the dactyls and mouthpart, linked to the distributed sensory pathway (Derby and Atema, 1982 Garm et al. 2005). Extensive research on lobsters have distinguished "distance" chemoreception (smell) and "near" chemoreception (taste) (Atema 1977, Atema 1980, Schmidt & Ache 1992, Atema & Voigt 1995).

Lobsters smell their environment by flicking the lateral flagellum of the antennules through the water, taking discrete samples of the spatial and temporal distribution of fine-scale chemical plumes (Koehl et al. 2001, Goldman & Patek 2002, Koehl 2006). The antennules can detect food-related chemicals, including representatives of amino acids, organic acids, and other molecules (Kozma et al. 2018). Detection of these chemicals initiate searching, and by tracking the distribution of chemical concentrations, lobsters can orientate towards the source of distant chemical stimuli (Steullet et al. 2000, Schmidt & Mellon 2010). Once the lobster reaches an odour source's proximity, they taste for food-related molecules through chemoreceptors on the distal ends of the walking legs or pereiopods (Derby & Atema 1982). When these structures detect the food source, they stimulate search behaviours, such as probing the substrate and grabbing (Derby & Atema 1982, Lavalli et al. 2007). Sensilla on the mouthparts evaluate the potential food items' palatability and determine whether it gets ingested or rejected (Derby 1982, Derby & Atema 1982).

Rock or spiny lobsters (Palinuridae, herein called lobsters) are ecologically important benthic predators. The lobster, *Jasus edwardsii*, although commonly assumed to spend the majority of their time on rocky reefs, can travel considerable distances over adjacent sandy areas to locate potential feeding grounds (MacDiarmid 1991, Kelly et al. 1999, Langlois et al. 2005). This off-reef foraging

behaviour has the potential to alter soft-sediment communities and create 'infaunal halos' of reduced prey density (Langlois et al. 2005). The mechanisms and the sensory systems driving these movements are not well understood. Therefore, this study aimed to determine the importance of both vision and chemoreception in food selection and foraging movements of *J. edwardsii*.

## Materials & Methods

### Lobster collection and housing

To evaluate the role of vision and chemoreception in foraging behaviour, five large (140 – 160 mm carapace length (CL)) male *Jasus edwardsii* were collected from the local fishery (Lee Fish Ltd) and transported to the Leigh Marine Laboratory (36.2692° S, 174.7984° E). Only inter-moult individuals were used in these experiments, as feeding rates differ according to moult stage (Lipcius & Herrnkind 1982). Lobsters were housed at ambient temperature in 1,500 L (1.75 m diameter) tanks that received aerated, continuous flow-through seawater. Individuals were fed a combination of thawed squid (*Nototodarus sloanii*) and pilchards (*Sardinops neopolchardus*). Before feeding experiments, lobsters were withheld from food for four days to standardise levels of starvation.

### Prey types

Prey used in the feeding trials were chosen based on previous feeding experiments investigating lobster preferences (Chapter Two). Six different prey species across three phyla (Mollusca; Echinodermata and Crustacea) were offered to individual *J. edwardsii*. These were the sea urchin (*Evechinus chloroticus*);

gastropod (*Cookia sulcata*); bivalves (*Tawera spissa*; *Tucetona laticostata*; *Macomona liliana*) and the hermit crab (*Pagurus novizealandiae*). All prey was sourced from subtidal rocky reefs and adjacent soft-sediment habitats around the Leigh coast.

**Experimental design**

All feeding experiments were completed in 1,500 L tanks (1.75 m diameter, 0.5 m height) supplied with flow-through ambient seawater (Fig. 3.1). Tank water levels were maintained to ensure that the more mobile prey items could not climb beyond lobsters' reach. A layer of sand (approx. 7 cm in height) was spread evenly across the bottom of the tank to mimic the natural environment and allow soft-sediment prey species to burrow. Patches of rock rubble and cement blocks of various sizes were also added to allow reef-dwelling prey to hide.

Lobster foraging behaviour was observed via a CCTV camera (HiWatch IPC-B120) mounted in the centre of the tank 1.5 m above the water surface. Red (iFlex) LED strip lights were fitted to the tank's upper rim to allow video recordings to be undertaken at night when rock lobsters are most active (Herrnkind 1980). Crustaceans are known to have low sensitivity to red light (Johnson et al. 2002), the presence of red light should therefore have little effect on feeding behaviour.
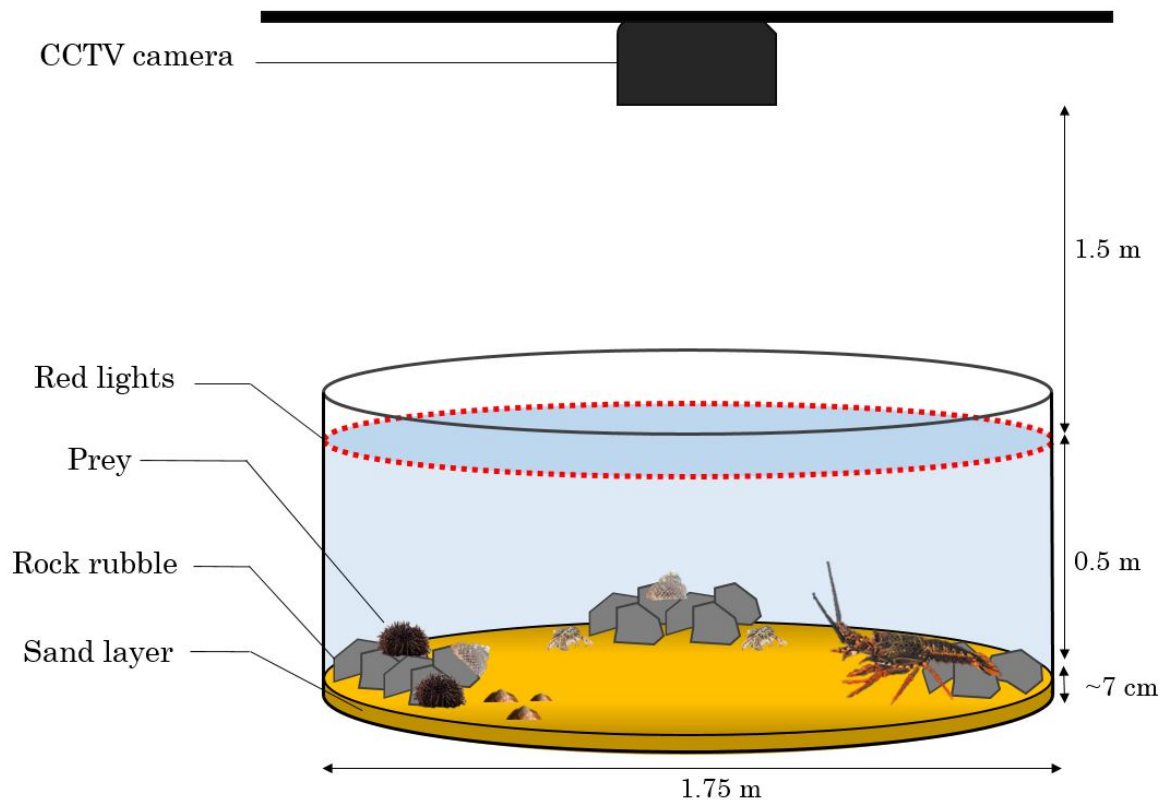
**Fig. 3.1.** Schematic diagram showing the experimental tank set up.

## Sensory-impairment procedure: vision

Vision was manipulated through the exclusion of visible light to investigate the role it plays in lobster feeding behaviour. Vision Exclusion Devices (VEDs) were constructed from black polyvinyl chloride (PVC) material (7.5 cm L x 4 cm W) that were cut to fit the curvature of the lobster carapace. Each end of the VEDs was blacked out using heavy-duty black duct tape. Individual lobsters were placed into a 32 L fish bin filled with enough fresh saltwater to cover the gills, leaving the carapace's dorsal portion exposed. The carapace just posterior to the supraorbital spine was dried thoroughly with paper towels, and VEDs were placed on the lobster. Care was taken to ensure that both eyestalks were covered, but not touching the VEDs in any way, which was then glued in place using an epoxy

adhesive (Selleys Araldite 90 Seconds Epoxy) and left to dry for approximately 5 mins.

Sham trials were undertaken to control for handling and lobsters having an artificial object attached to their carapace. Sham trials used the same VEDs construction but with open ends and several holes drilled into the top of the PVC material to allow lateral and dorsal vision (sham VEDs). Lobsters fitted with VEDs did not react to visual stimuli (hand waved over the lobster). In contrast, lobsters with sham VEDs responded to visual stimuli by backing away, moving the antenna forward or tail flipping.

Prior to the behavioural experiments, lobsters were placed in individual tanks to recover from VED fitting for approximately 30 mins. After this acclimation period, the animals appeared calm and sedentary behaviour was observed. Vision impaired (VI) and vision sham (VS) trials were completed on the same lobster. The order of VS and VI experiments was randomised among individual lobsters.

**Sensory-impairment procedure: chemoreception**

To investigate the role of chemoreception in feeding behaviour, sensory appendages (antennules and leg setae) were manipulated (n = 5). An individual lobster was placed into a 32 L fish bin filled with enough fresh seawater to cover the gills, and a damp towel was used to handle the lobster. Each antennule was fitted with a non-toxic silicon tube (each weighing > 2 g). The antennule tubes (ATs) extended beyond the flagellum by approximately 10 mm and glued (Selleys QuickFix) in place at the first antennule joint. All ATs were filled with fresh sterile seawater to keep the flagellum lubricated and later blocked using epoxy (Selleys

Araldite 90 Seconds Epoxy). Utmost care was taken to ensure the epoxy did not contact the flagellum; this was assessed visually. Sensory setae on the lobsters walking legs were also removed using a scalpel.

To control for both handing and an attached artificial object, sham trials (n = 5) were completed using the same AT construction without blocking the protruding end with epoxy. These sham ATs allowed the lobster to continue sampling the ambient seawater. To replicate the handling procedure of getting shaved, lobsters' sensory setae on the legs were rubbed with a bladeless scalpel.

Prior to the behavioural experiments, lobsters were placed in individual tanks to recover from the manipulation procedure for approximately 30 mins. Chemo-impaired (CI) and chemo-sham (CS) trials were completed on the same lobster. The destructive nature of shaving leg setae resulted in CS trials being completed before CI trials.

**Prey consumption and feeding preference tests**

Feeding experiments, commencing Sep 2019 till Feb 2020, were conducted to evaluate how vision and chemoreception influence prey consumption, selection and preference. All six prey types were offered simultaneously to each lobster. In total, five replicates were completed for each treatment and associated sham trials. The number of each prey type (*Evechinus* = 4; *Cookia* = 4; *Pagurus* = 6; *Tucetona* = 10; *Tawera* = 20; *Macomona* = 16), fresh weight (± 0.1 g), and their size (± 0.5 mm) were recorded before being placed into the experimental tank. Size of each prey type was determined using Vernier callipers as follows: bivalve species - shell length (SL: maximum linear dimension of the shell); *Cookia* - widest

opening of the base of the shell; *Pagurus* – shell height (SH: maximum linear dimension of the axis at right angles to SL); *Evechinus* – test diameter (TD).

Prey species were placed at random into the 1,500 L experimental tank at the beginning of the day and left for at least four hours to allow prey to burrow/hide. Bivalve prey was placed in two groups to represent how they are distributed in the natural environment (refer to Chapter two). The location of bivalve patches was recorded and randomised for each trial.

At 17:00 hrs, an individual lobster was placed by hand into the centre of the experimental tank, and video recording commenced. Each feeding trial ran until 07:00 hrs the following day, i.e., 16 hrs. To assess prey consumption, the amount of prey were counted at the end of each trial and any leftover shell, and tissue remnants weighed (± 0.1 g) to estimate apparent food intake (AFI).

**Foraging movement and behaviours**

The distance travelled by each lobster was calculated over a 12-hr period (18:00 – 06:00 hrs), to understand foraging movements in association with sensory manipulation. Additionally, from 18:00 to 00:00 hrs digging events (lobster lunging and pereiopods digging into the sand) were counted. After reviewing video footage of vision-impaired trials, lobsters were observed turning in circles on the spot (e.g. Appendix 3.A). These spinning events were counted under the same period as digging events. The distance travelled, and behavioural events were binned into one-hour blocks.

**Data analysis**

Statistical analyses were conducted in R-Studio Software (v 1.2.5033, RStudio INC). All data were tested for normality and homogeneity of variance prior to analysis and overall statistical significance at the 0.05 level. Vision and chemoreception treatment experiments were analysed separately.

*Prey consumption and feeding preference tests*

To evaluate lobster consumption, a one-way analysis of variance (ANOVA) was used to compare the effect of treatment on apparent food intake (AFI). *Aposterori* Tukey's Honest Significant Difference (Tukey's HSD) test was used for pairwise-comparisons to determine the difference between the means, with confidence intervals based on the studentised range distribution.

To determine feeding preferences, Rodgers' index ($R_i$) for cafeteria type experiments was calculated for each prey type (Rodgers & Lewis 1985). $R_i$ ranged from 0 (avoidance) to 1 (preference). The area beneath the consumption curves accounts for the order, rate, and total amount of each prey type consumed (see Krebs 1989). The index considers the inability to replenish food during the experiments and allows for one or more food types to be completely consumed during the experiment. The Rodgers' index was calculated as $R_i = A_i/\max (A_i)$, where $A_i$ is the area under the curve of the proportion of species i prey items consumed over time and $\max (A_i)$ is the largest value of $A_i$ per experimental unit (Krebs 1989). For this study, the amount of each prey consumed was binned into one-hour blocks.

The calculation of prey preference using Taplin (2007) method assumes that the order in which prey is consumed discloses information about preference, with

the more preferred prey being consumed first. The resultant null hypothesis would be that prey consumption is random. Each prey item was assigned a rank depending on the order of consumption, i.e., the first prey type eaten was assigned rank 1, the second prey rank 2 and so on until all prey had been ranked. When a prey item was not consumed, it was considered least preferred, or if there were multiple prey types left unconsumed, they were considered tied for last and given an average rank.

The relationship between prey preference and sensory impairment treatment were analysed using a generalised linear model (GLM) back-fitted to a gaussian distribution with an identity link function. Analysis of deviance of fitted models was performed separately for each sensory treatment. Additionally, preference indices from reef prey (*Evechinus*, *Cookia*, *Pagurus*) and soft sediment prey (*Tucetona*, *Tawera*, *Macomona*) were pooled (habitat) and analysed as above.

*Foraging movement and behaviours*

Lobster movements were analysed in MATLAB (R2018a) using DLTdv digitising tool (Hedrick 2008; http://biomech.web.unc.edu/dltdv/). The raw video was converted into 1 fs$^{-1}$, and the lobster's position was reordered for every frame. Position data were binned into one-hour blocks and analysed to calculate the distance travelled (m). A two-way repeated-measures ANOVA was conducted to evaluate the differences in distance travelled over time and between treatment groups. Tukey's HSD test was used for pairwise-comparisons to determine the difference between the means, with confidence intervals based on the studentised range distribution.

Digging events were analysed using a one-way ANOVA. Digging events for chemoreception did not meet the parametric tests' assumptions; the Kruskal-Wallis test was used to determine differences between treatments.

## Results

**Apparent food intake**

For vision impairment experiments, there was a marginally higher average apparent food index (AFI) in sham (140.1 ± 34.5 g) compared to impaired (141.6 ± 30.8 g) lobsters, but this was statistically similar (One-way ANOVA: $F_{1,9} = 0.223$, $p = 0.650$; Fig. 3.2a). Conversely, AFI was significantly lower (One–way ANOVA: $F_{1,9} = 13.864$, $p < 0.01$) for chemoreception impairment lobsters, equating to a 65 % reduction in food consumption relative to sham (Fig 3.2b).
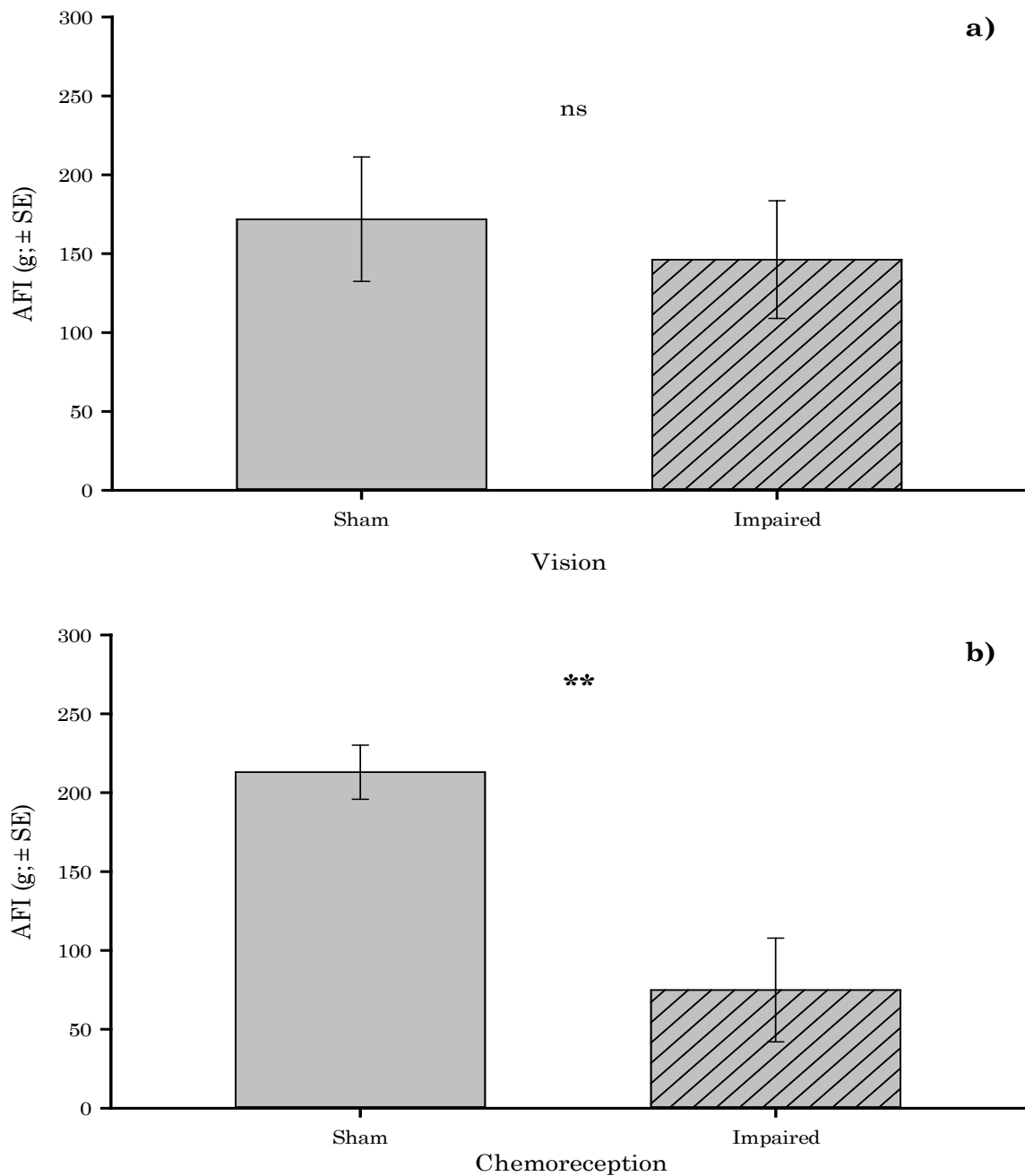
**Fig. 3.2.** Mean (± SE) apparent food intake (AFI) for **a)** vision and **b)** chemoreception treatments; (*) indicates significant difference between treatment type based on Tukey's HSD test; ns = not significant (p > 0.05), ** p < 0.01.

## Feeding preference: vision

Vision treatment had no apparent effect on prey preference scores derived from Rodgers' Index ($R_i$) (Table 3.1a) and the order of prey consumption (Table 3.1b). However, both preference indices suggest a statistically significant difference between prey types (Table 3.1a, b). *Macomona* was the preferred prey type, with an average $R_i$ of 0.87 ± 0.13 compared to the other tested prey, with $R_i$ score less than 0.3 (Fig. 3.3a). Similarly, *Macomona* was preferentially selected compared to *Cookia* and *Evechinus* (Fig. 3.3b). Overall, soft-sediment species were the most preferred prey type (Table 3.1a, b).

**Table 3.1.** Analysis of deviance for GLM model fitted to vision treatment and prey preference scores derived from **a)** Rodgers' index and **b)** Consumption order.

| Source | d.f. | Deviance | Resid. d.f. | Resid. Dev. | P(>\|Chi\|) |
|---|---|---|---|---|---|
| **a) Rogers' index** | | | | | |
| Prey | 5 | 4.6915 | 54 | 3.8847 | 7.84E-12*** |
| Treatment | 1 | 0.0014 | 53 | 3.8833 | 0.8917 |
| Prey × Treatment | 5 | 0.1869 | 48 | 3.6964 | 0.7875 |
| | | | | | |
| Habitat | 1 | 1.4016 | 58 | 7.1746 | 0.0009*** |
| Treatment | 1 | 0.0014 | 57 | 7.1732 | 0.9154 |
| Habitat ×Treatment | 1 | 0.0717 | 56 | 7.1014 | 0.4520 |
| | | | | | |
| **b) Consumption order** | | | | | |
| Prey | 5 | 88.611 | 66 | 221.17 | 0.0023** |
| Treatment | 1 | 0.889 | 65 | 220.28 | 0.6068 |
| Prey × Treatment | 5 | 18.944 | 60 | 201.33 | 0.3422 |
| | | | | | |
| Habitat | 1 | 40.017 | 58 | 218.83 | 0.0011** |
| Treatment | 1 | 0.150 | 57 | 218.68 | 0.8414 |
| Habitat × Treatment | 1 | 8.817 | 56 | 209.87 | 0.1251 |
| **Signif. codes: *** < 0.001; ** <0.01; * <0.05.** | | | | | |
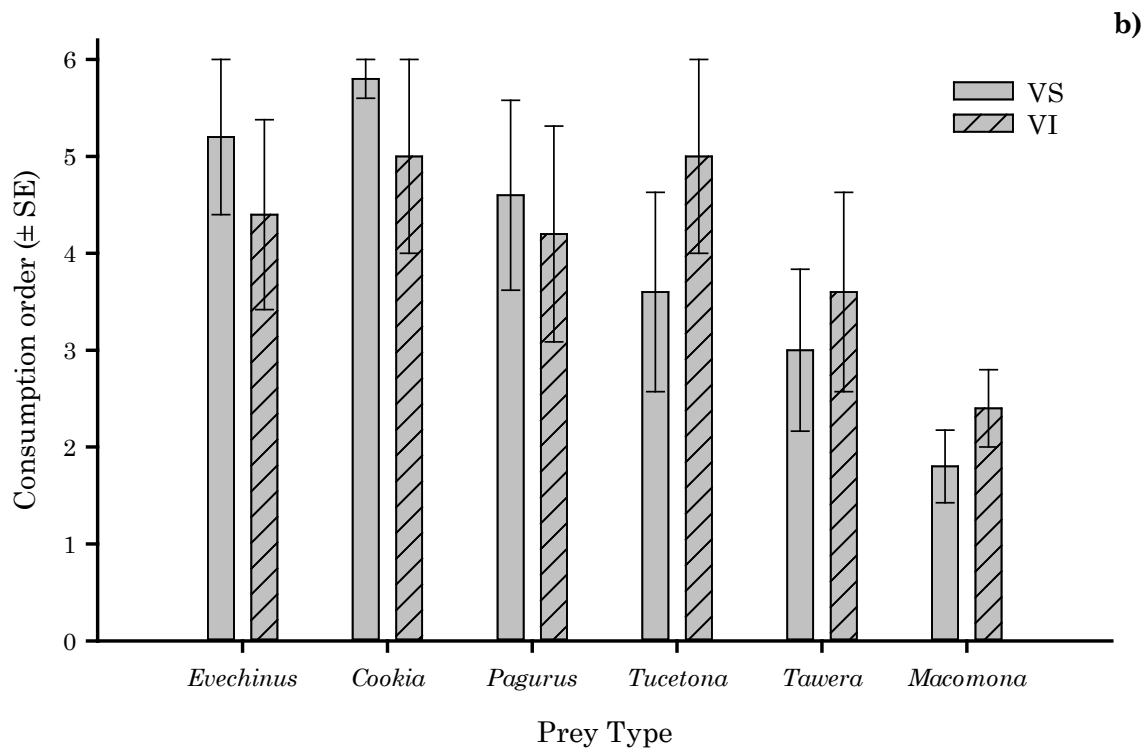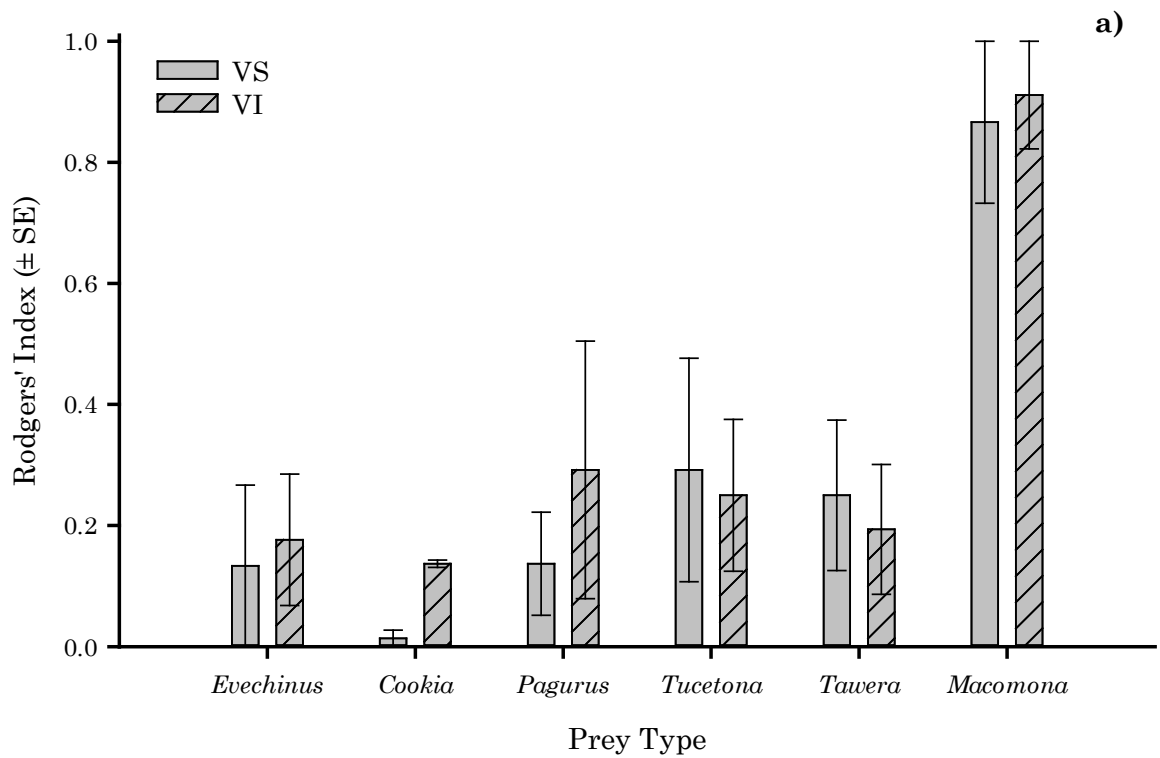
**Fig. 3.3.** Mean (± SE) **a)** Rodgers' Index ($R_i$) and **b)** consumption order preference score for six prey types (n = 5) under sham and impaired vision treatments. The higher the Ri, the more preferred the prey type. The lower the order score the more preferred the prey type. VS = Vision Sham; VI = Vision Impaired.

### Feeding preference: chemoreception

There was a decline in prey choice in CI lobsters, leading to a significant effect on $R_i$ preference scores (Table 3.2a). There was a significant difference in prey preference (Table 3.2a), with *Evechinus* being the most preferred prey type (Fig. 3.4a). Additionally, reef species were the most preferred prey types (Table 3.2a).

There was also a significant effect on the order of prey consumption when chemoreception was impaired (Table 3.2b). *Evechinus* was preferred over *Pagurus, Tucetona* and *Tawera* (Fig. 3.4b). However, when prey type was pooled into reef and soft-sediment species, there was no significant difference in preference (Table 3.2b).

**Table 3.2.** Analysis of deviance for GLM model fitted to chemoreception treatment and prey preference scores derived from **a)** Rodgers' index and **b)** Consumption order.

| Source | d.f. | Deviance | Resid. d.f. | Resid. Dev. | $P(>|Chi|)$ |
|---|---|---|---|---|---|
| **a) Rodgers' index** | | | | | |
| Prey | 5 | 2.5790 | 54 | 5.8521 | 0.0002*** |
| Treatment | 1 | 0.4732 | 53 | 5.3789 | 0.0333* |
| Prey × Treatment | 5 | 0.3668 | 48 | 5.0122 | 0.6215 |
| | | | | | |
| Habitat | 1 | 0.6478 | 58 | 7.7833 | 0.0248* |
| Treatment | 1 | 0.4732 | 57 | 7.3102 | 0.0551 |
| Habitat × Treatment | 1 | 0.1080 | 56 | 7.2022 | 0.3596 |
| | | | | | |
| **b) Consumption order** | | | | | |
| Prey | 5 | 61.550 | 54 | 181.30 | 0.0010*** |
| Treatment | 1 | 22.817 | 53 | 158.48 | 0.0059** |
| Prey × Treatment | 5 | 14.083 | 48 | 144.40 | 0.4560 |
| | | | | | |
| Habitat | 1 | 7.350 | 58 | 235.50 | 0.1582 |
| Treatment | 1 | 22.817 | 57 | 212.68 | 0.0129* |
| Habitat × Treatment | 1 | 6.017 | 56 | 206.67 | 0.2017 |
| **Signif. Codes: *** < 0.001; ** < 0.01; * < 0.05.** | | | | | |
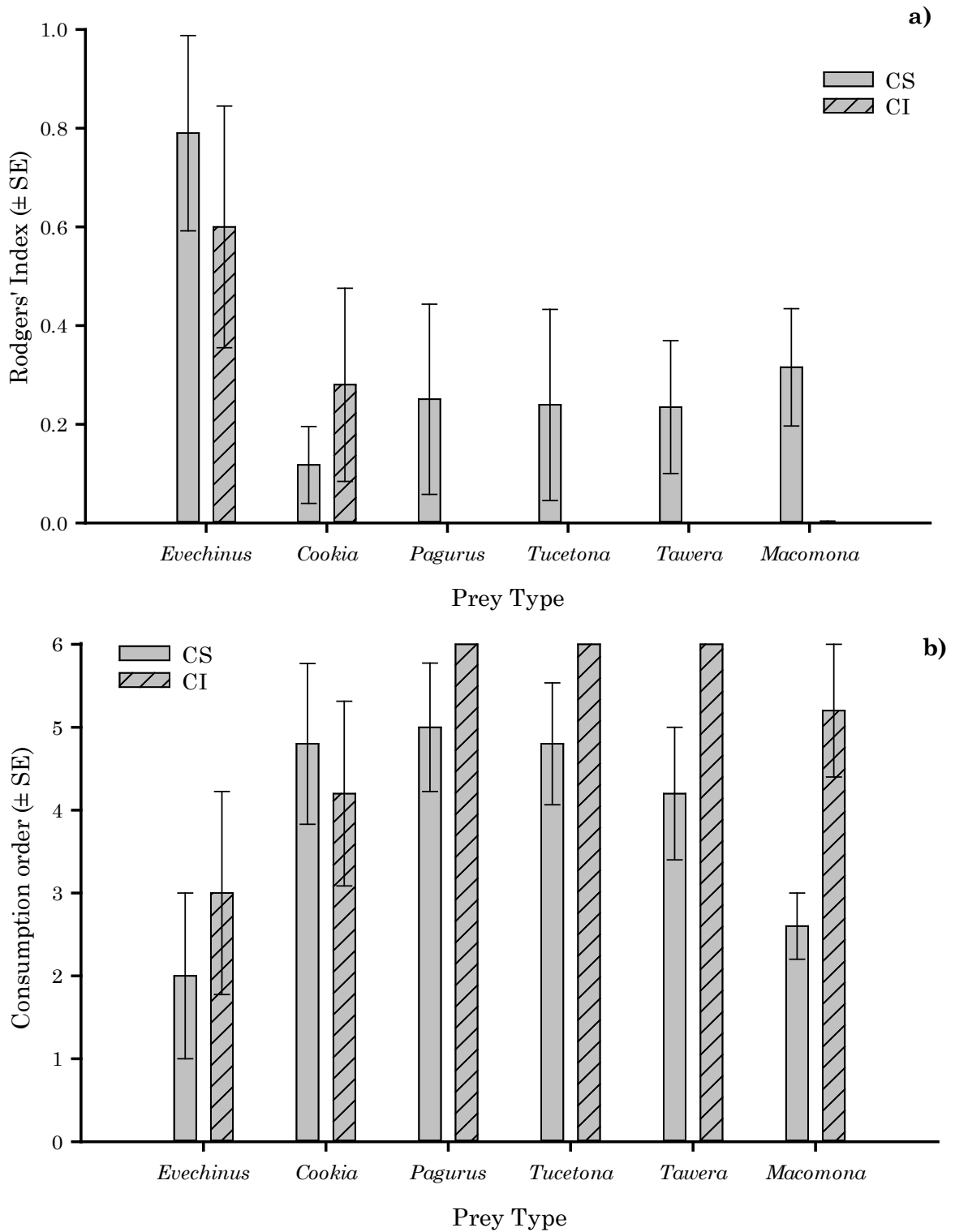
**Fig. 3.4.** Mean (± SE) **a)** Rodgers' index ($R_i$) and **b)** consumption order preference score for six prey types (n = 5) under sham and impaired chemoreception treatments. The higher the $R_i$, the more preferred the prey type. The lower the order score, the more preferred the prey type. The lower the order score, the more preferred the prey type. CS = Chemoreception Sham, CI = Chemoreception Impaired.

**Movement behaviour**

The distance travelled by VI lobsters was slightly greater than that of VS lobsters (VI = 1,271.2 ± 308.7 m; VS = 755.5 ± 167.4 m; (Fig. 3.5a, Fig. 3.6)), however they were statistically similar with only time having an effect (Table 3.3a). Every VI lobster was also observed spinning on the spot (see Appendix 3.A). These spinning events occurred at an average rate of 4.9 ± 1.7 hr$^{-1}$, with duration ranging from a few seconds to several minutes. There was no significant change in digging events with vision treatments (One-way ANOVA: $F_{1,9} = 0.07$, $p = 0.796$). On average, digging events were observed at a rate of 2.6 ± 0.4 hr$^{-1}$ for VI and 2.8 ± 0.6 hr$^{-1}$ for VS lobsters.

When chemoreception was impaired the distance travelled significantly declined (Table 3.3b; Fig. 3.5b). On average the total distance CS lobsters travelled was 681.7 ± 31.2 m and this reduced to 284.6 ± 78.8 m when chemoreception was impaired. The distance travelled had a significant time effect but no interaction with treatment was found (Table 3.3b; Fig. 3.5b). Additionally, digging events significantly (Kruskal–Wallis; $H_1 = 7.305$, $p < 0.01$) declined by 97 % when chemoreception was impaired (0.03 ± 0.03 hr$^{-1}$ for CI; and 1.0 ± 0.1 hr$^{-1}$ for CS lobsters).

**Table 3.3.** Two-Way Repeated Measures Analysis of Variance for **a)** vision and **b)** chemoreception.

| Source | d.f. | SS | MS | *F* | *P* |
|---|---|---|---|---|---|
| **a) Vision** | | | | | |
| Time | 11 | $4.8 \times 10^4$ | $4.4 \times 10^3$ | 2.38 | 0.021* |
| Treatment | 1 | $5.6 \times 10^4$ | $5.6 \times 10^4$ | 6.01 | 0.070 |
| Time × Treatment | 11 | $1.3 \times 10^4$ | $1.2 \times 10^3$ | 1.40 | 0.205 |
| | | | | | |
| **b) Chemoreception** | | | | | |
| Time | 11 | $3.2 \times 10^4$ | $3.2 \times 10^4$ | 14.04 | 0.020* |
| Treatment | 1 | $2.2 \times 10^4$ | $2.0 \times 10^3$ | 11.89 | < 0.001*** |
| Time × Treatment | 11 | $4.8 \times 10^3$ | $4.4 \times 10^2$ | 1.12 | 0.369 |

 **Signif. Codes: *** < 0.001; ** < 0.01; * < 0.05.**
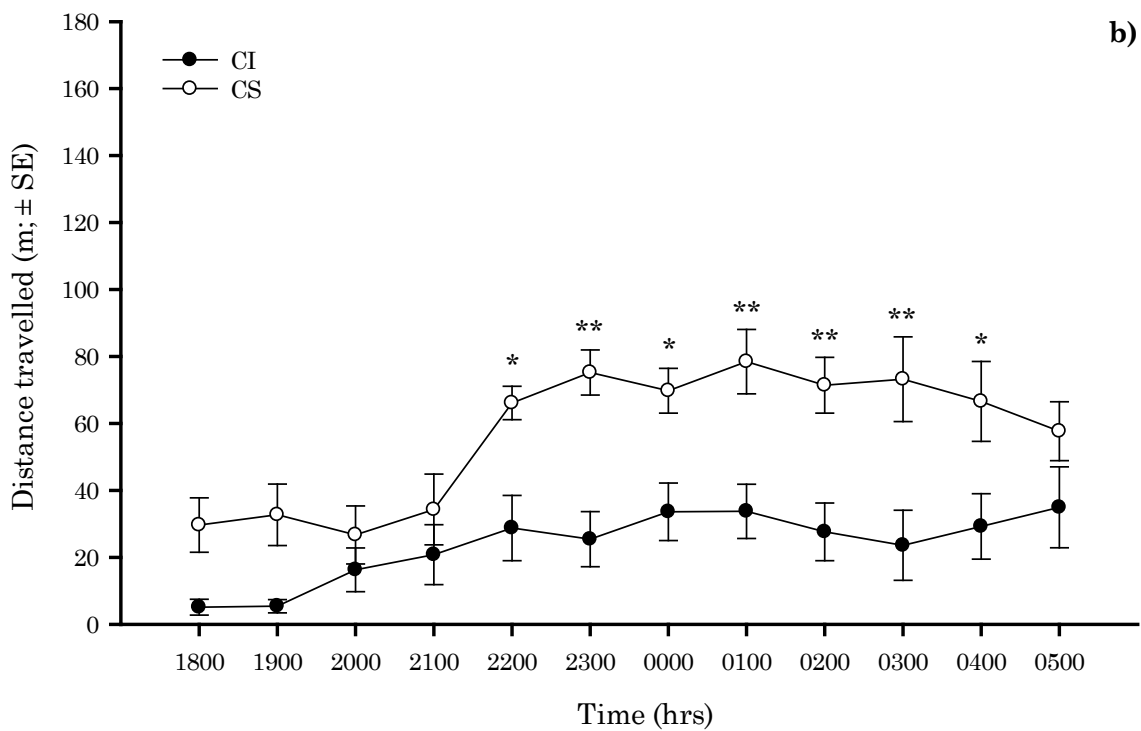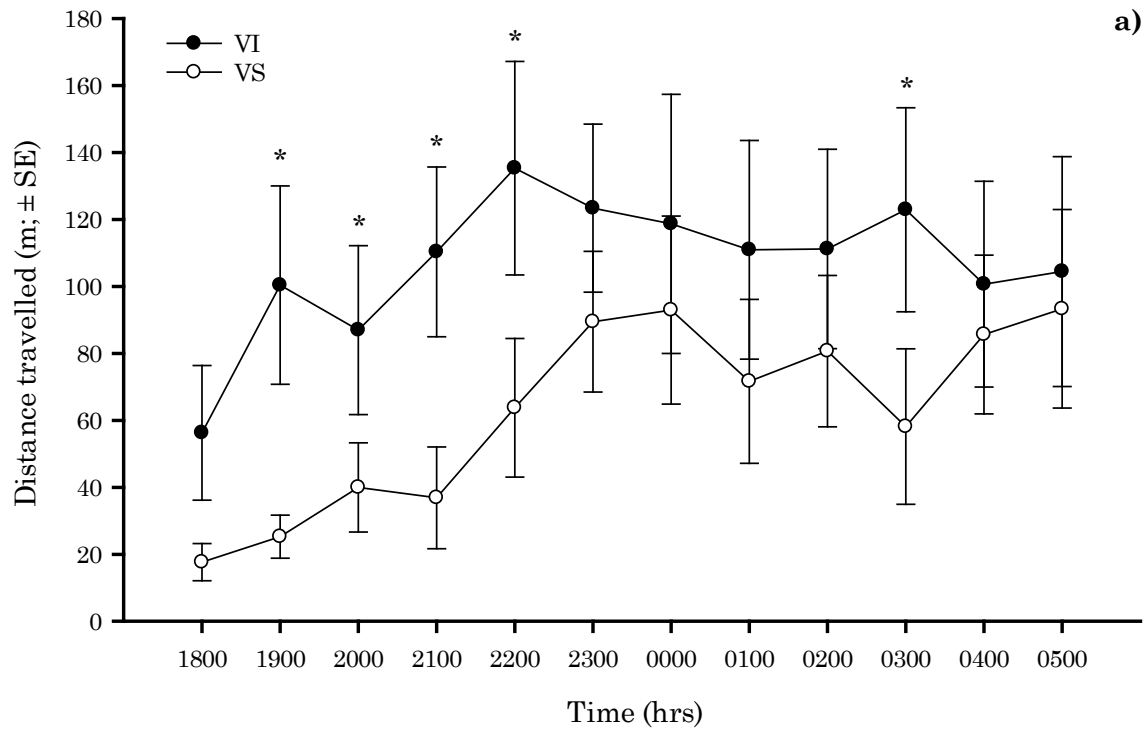
**Fig. 3.5.** Distance travelled (m ± SE) over time (hrs) for **a)** vision and **b)** chemoreception sensory treatments. VI = Vision Impaired; VS = Vision Sham; CI = Chemoreception Impaired; CS = Chemoreception Sham. (*) indicates significant difference between treatment type at each time point based on Tukey's HSD test; *p < 0.05, ** p < 0.01.
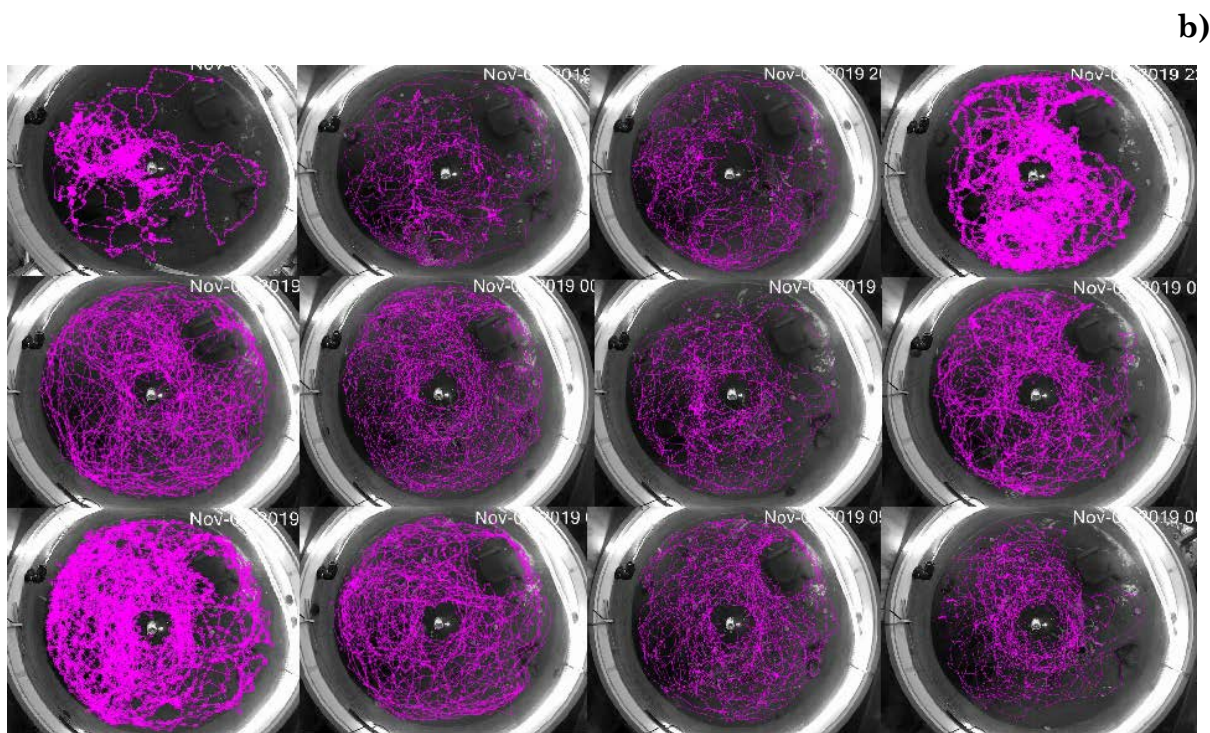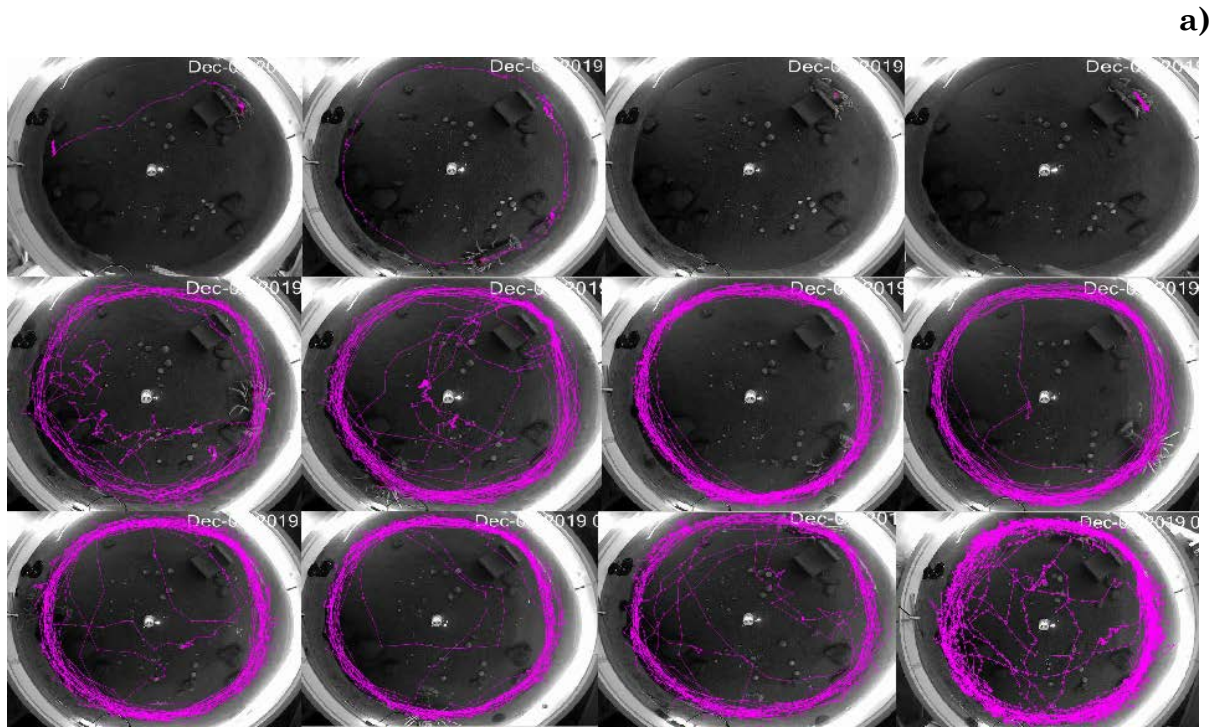
Fig. 3. 6 Exemplar tracking data of the same lobster under vision **a)** sham (total = 983.52 m) and **b)** impaired (total = 1525.31 m) treatment trials in one-hour blocks for 12-hours. Sequence starting at 18:00 hrs in the top left-hand corner going from left to right.

# Discussion

Lobsters are ecologically important benthic predators whose selective predation can strongly influence the surrounding soft sediment and rocky reef community composition and structure (Shears & Babcock 2002, Langlois et al. 2005, Butler & Kintzing 2016). Although commonly assumed to spend the majority of their time on rocky reefs, *Jasus edwardsii* have been shown to travel considerable distances over adjacent sandy habitats in search of prey (MacDiarmid 1991, Kelly et al. 1999, Langlois et al. 2005). This study indicates that vision plays a minor role in prey selection and consumption but is likely to be important in lobster foraging movements and efficiency. On the other hand, Chemoreception was found to play a significant role in prey localisation and selection, especially for buried soft-sediment prey, such as bivalves.

When vision was impaired, there was no significant change in food consumption and prey preference, and both vision treatments showed a strong preference for soft-sediment bivalves. This prey preference was in agreement with our previous experiments under no sensory manipulation (Chapter Two). Vision has been suggested to play a role in foraging behaviour through motion detection (Hirtle & Mann 1978). Mobile prey, such as moving hermit crabs, snails and sea urchins, should initiate an increased foraging response by the lobster compared to stationary bivalve prey (Hirtle & Mann 1978). On the contrary, there was a slight increase in mobile prey's consumption and preference in this study, especially *Cookia,* in visually impaired lobsters (Fig. 3.3a). This indicates that vision, in the form of motion detection, plays an insignificant role in influencing lobster prey choice and preference.

Vision may play a minor role in the localising and selection of prey but could influence foraging movements. Visually impaired lobsters showed an increase in distance travelled (upwards of 500 m), and their movements appeared to be somewhat random compared to associated sham treatments (Fig. 5.6). Although not statistically significant, this increase in energy expenditure without an increase in energy gain, through prey consumption, may result in an overall net loss for the lobster (Pyke 1984). Additionally, the spinning movement observed in visually impaired lobsters may be caused by a loss in orientation. These movement patterns and seemingly inefficient foraging paths may provide further evidence that lobsters use visual markers to assist short-range movements (Herrnkind and McLean, 1971).

Vision plays a critical role in shelter selection, navigation and predator avoidance in a range of benthic decapods. For example, the fiddler crab, *Uca rapax,* angles its body so that the burrow is always within visual range, providing a quick and direct escape route (Layne et al. 2003). Paul and Steneck (1993) found that adult American lobsters, *Homarus americanus,* inhabiting kelp forests remain on the outer edges of the kelp to keep shelter within visual range while they forage. While foraging, there is an increased risk of predation, therefore knowing possible escape routes through visual markers increase the chances of predator avoidance. This use of vision in other decapod species indicates that it is likely that *J. edwardsii* may be using visual cues to orientate and locate potential shelters or refuges (cement blocks in these experiments) whilst foraging. This hypothesis could explain the increased distance travelled and the random movements/ spinning observed in visually impaired lobsters.

Lobsters with impaired chemoreception (CI) demonstrated a significant decline in overall consumption, indicative of reduced prey detection and localisation. In particular, there was a significant decline in preference for the small buried bivalves *Tawera* and *Macomona*. A reduction in digging events also accompanied a significant reduction in the consumption of these prey types. Reduced digging events further supports the lack of prey detection and the use of dactyl setal tufts to stimulate behaviours, such as probing of the substrate (Derby & Atema 1982, Lavalli et al. 2007). The measured reduction in foraging agrees with similar studies evaluating the role of antennules in the initial stages of prey detection (Pacific white shrimp: Eap et al. 2020; Caribbean spiny lobster: Steullet et al. 2001).

Interestingly, lobsters with impaired chemoreception displayed a stronger preference for reef dominated prey types (especially *Evechinus*), indicating that lobsters may rely on visual cues to target mobile reef prey (Hirtle & Mann 1978). Although not statistically significant, our chemoreception sham trials also showed an elevated preference for reef prey types, namely *Evechinus*. This preference is not what we would have expected based on our previous experiments investigating lobster prey preferences with no sensory manipulations (Chapter Two). This reef dominated preference is further emphasised by an overall decline (~ 80 %) in digging events in both chemoreception treatments compared to vision treatments. A plausible explanation is that the protrusion of sham ATs beyond the antennule flagellum prevented lobsters from placing the flagellum directly onto the substrate; a behaviour observed in vision treatments and our previous experiments (Chapter Two).

Reidenbach & Koehl (2011) revealed that odour concentrations sampled by the legs increased as an animal neared an odour source, whereas antennule sampling decreased; thus, leg chemosensors should become more important in locating the odour source when an animal is in close proximity. However, foraging lobsters typically approached buried bivalves with their antennules down near the substrate, and upon encountering a mollusc, the lobster would further assess the prey with the antennules (Chapter Two). Antennule probing is unusual behaviour for rock lobsters. Their antennules are used to distantly 'chemo orientate' to the food source and the dactyl setal tufts for contact chemoreception (close range) (Nevitt et al. 2000, Derby et al. 2001, Lavalli et al. 2007). Using antennules for contact chemoreception has been observed in slipper lobsters (*Scyllarides*) (Derby & Atema 1982, Lavalli et al. 2007), which lack the dactyl setal tufts. It has been suggested that the antennules of slipper lobsters have partially filled this sensory void by taking on a contact chemoreception role (Lavalli et al. 2007). In this study, the antennules continued to examine the odour source directly throughout the feeding process, indicating that the dactyl setal tufts alone cannot obtain sufficient sensory feedback, similar to the behaviour observed in slipper lobsters. Furthermore, direct placement of antennules onto the substrate for prey localisation reinforces their role of 'contact' chemoreception. Therefore, based on these behaviours, it is proposed that the antennules of *J. edwardsii* are the primary mechanism used in orientation, localisation and identification of prey.

Our results show that chemoreception is crucial for detecting and selecting prey, especially for buried soft-sediment prey types. In particular, the antennules appear to play a disproportionate role in prey detection, further highlighting these

structures' importance. Chemoreception could potentially be the primary driver for detecting the presence of offshore soft-sediment prey. Vision may not have influenced food consumption and preference in these experiments but could play an important role in foraging efficiency since it is related to the overall movement. The observed increase in movement and associated energy expenditure during vision-impaired trials may have cascading effects on foraging efficiency, shelter selection and predator avoidance. Additionally, vision is likely to play a role in the migratory path and efficiency of movement towards these offshore foraging grounds and return to shelter. Overall, chemoreception and vision are both likely important sensory mechanisms guiding observed *J. edwardsii* offshore migrations.

# CHAPTER FOUR

# Seasonal importance and consumptive abilities of the rock lobster, *Jasus edwardsii,* on the sea urchin, *Evechinus chloroticus*

## Introduction

The importance of predation as a regulatory process in marine systems has been well documented and can dramatically influence population and community-level dynamics. Predators, such as sea otters, fish and rock lobsters play a critical role in structuring sea urchin populations and are often implicated in trophic cascades (Estes & Duggins 1995, Mayfield & Branch 2000, Mayfield et al. 2001, Shears & Babcock 2002, Shurin et al. 2002). The removal of such predators not only increases urchin abundance, but also causes an altered foraging behaviour, where urchins become less cryptic; further intensifying the overall grazing pressure (Steneck 1997, Jackson et al. 2001, Spyksma et al. 2017). Furthermore, the transition into barren habitat also appears difficult to reverse (Carnell & Keough 2019). Even when fishing pressure is reduced, there appears to be a significant time lag (> 5 years) before urchin numbers decline and kelp forests recover (Babcock et al. 2010).

This time lag could be explained by urchin cryptic anti-predator behaviour, such as remaining in crevices or burrows and size-specific predation on urchins (Pederson & Johnson 2006). For example, smaller urchins are the preferred prey of lobsters and other predators, but are more likely to be cryptic (Shears & Babcock 2002, Pederson & Johnson 2006). Conversely, although less likely to show cryptic behaviours, larger urchins are significantly less likely to suffer predation (Shears & Babcock 2002). Additionally, lobsters may be able to detect the quality of prey. Sea urchins occupying barren habitats, suffer from starvation and are forced to partition resources to other metabolic activities for survival, resulting in reduced gonad tissue production (Lawrence 2001, Stewart & Konar 2012). This reduction in gonad production reduces individual quality, resulting in predators avoiding urchins from barrens (Eurich et al. 2014).

The endemic sea urchin, *Evechinus chloroticus*, is widespread throughout New Zealand's subtidal rocky reefs. In addition to being a traditional food source, urchins play a crucial role as primary grazers of kelp, *Ecklonia radiata*. Early studies in northeast New Zealand documented the urchins' role as a habitat creator through kelp grazing (Choat & Schiel 1982, Grace 1983). However, at that time, it was thought that barren areas on the reef were a 'natural' characteristic of rocky reefs. In the subsequent decades, the dynamics between kelp forests, sea urchins and exploitation of sea urchin predators (mainly snapper, *Pagrus auratus*, and the palinurid lobster, *Jasus edwardsii* (herein lobster)) has been investigated in New Zealand (Shears & Babcock 2002, Shears et al. 2004).

Lobsters were discounted as playing a critical regulatory role in controlling urchin populations principally because they were not thought to occur, or forage,

in urchin barren habitats (Andrew & Choat 1982, Andrew & MacDiarmid 1991). However, through the establishment of no-take marine reserves in north-eastern New Zealand, lobster foraging was found to extend into urchin barren habitats (within marine reserve sites). Furthermore, a high proportion (> 46.2 %) of predation on large urchins (75 mm) were from lobsters (Shears & Babcock 2002). In particular, large lobsters are vital predators of the sea urchin as they are less restricted by urchin size (Pederson & Johnson 2006). Unfortunately, larger lobsters are of high demand, both commercially and recreationally, and are relatively rare in fished areas (Kelly et al. 2000a). Hence, placing further emphasis on restoring lobster populations, particularly large individuals. Knowledge of the seasonal importance and consumptive abilities of lobster, *J. edwardsii,* of the sea urchin, *E. chloroticus,* are lacking. Therefore, this present study aimed to assess the relative importance of *J. edwardsii* moulting periodicity and *Evechinus* gonad quality as drivers of lobster feeding behaviour.

## Material & Methods

### Animal collection and housing

To understand *Jasus edwardsii* feeding behaviour on the sea urchin, *Evechinus chloroticus*, large (150 – 170 mm carapace length (CL)) male lobsters were collected from the local fishery (Lee Fish Ltd) and transported to the Leigh Marine Laboratory (36.2692° S, 174.7984° E). Lobsters were housed in large 1,500 L (1.75 m diameter) tanks at ambient temperature and photoperiod and received aerated continuous flow-through seawater. Individuals were fed a combination of thawed squid (*Nototodarus sloanii*) and pilchards (*Sardinops neopolchardus*).

Before the feeding experiments, lobsters were withheld food for four days to standardise levels of starvation.

*Evechinus* were sourced from subtidal kelp forests around the Leigh coast, due to urchin quality and lobsters preference (Eurich et al. 2014). *Evechinus* were housed in holding tanks 1000 L (1 m diameter) tanks at ambient temperature and photoperiod and received aerated continuous flow-through seawater, fully stocked with kelp, *Ecklonia radiata.*

**Gonad Index**

*Evechinus* gonad index (GI) was measured for a 12-month period to evaluate whether seasonal changes in gonad condition influenced lobster consumption. During every *Evechinus* collection for the feeding trials, a minimum of 10 *Evechinus* each month were randomly selected for dissections. To avoid triggering spawning, *Evechinus* were measured to the nearest 0.5 mm test diameter (TD) using Vernier callipers and weighed to the nearest 0.1 g (total weight) and dissected immediately after collection. Gonads were removed from the test and weighed to the nearest 0.1 g (Fig. 4.1). GI was calculated as a ratio of gonad mass to the whole body wet mass: (gonad weight / total weight) x 100 and given as a percentage.
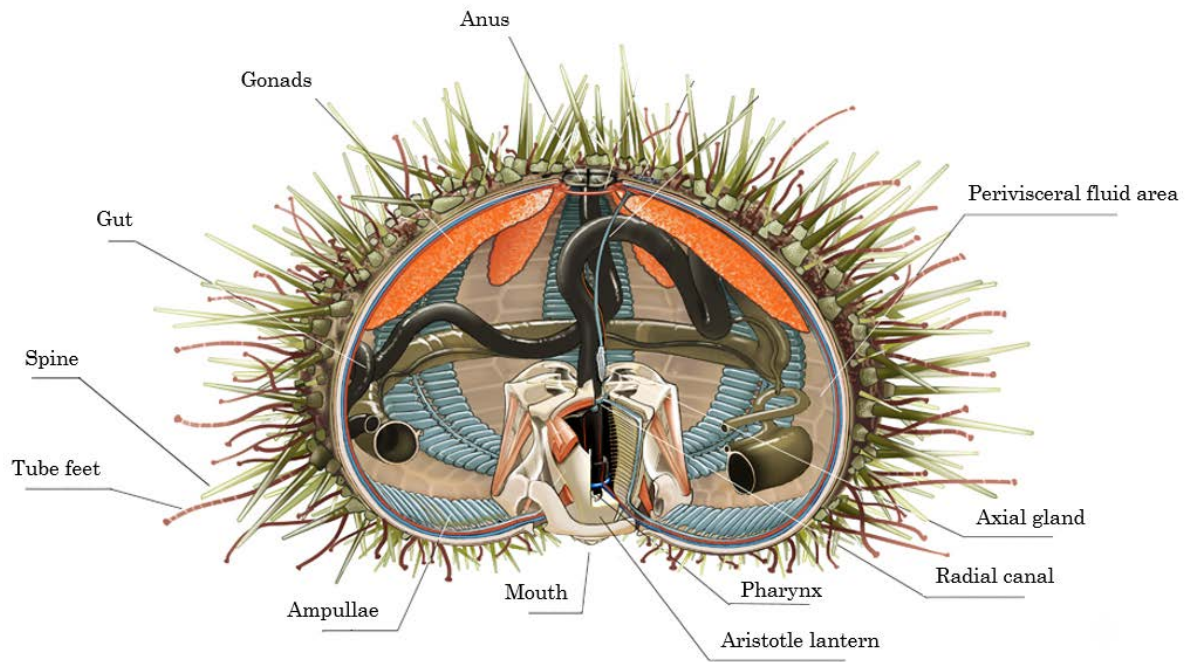
**Fig. 4.1.** Sea urchin anatomy (adapted from: Abiogenisis (Oct 2020)).

**Experimental Design**

All feeding experiments were undertaken in two identical 1,500 L tanks (1.75 m diameter, 0.5 m height) supplied with flow-through ambient seawater (Fig. 4.2). Tank water levels were maintained to ensure that *Evechinus* could not climb beyond the reach of lobsters. Patches of rock rubble and cement blocks of various sizes were added into the experimental tank to mimic a reef environment and allow *Evechinus* to hide. The tanks were covered with two layers of UV protected shade cloth (Number 8) to prevent direct sunlight damaging lobsters eyes (Meyer-Rochow 1994), while still providing a natural photoperiod.
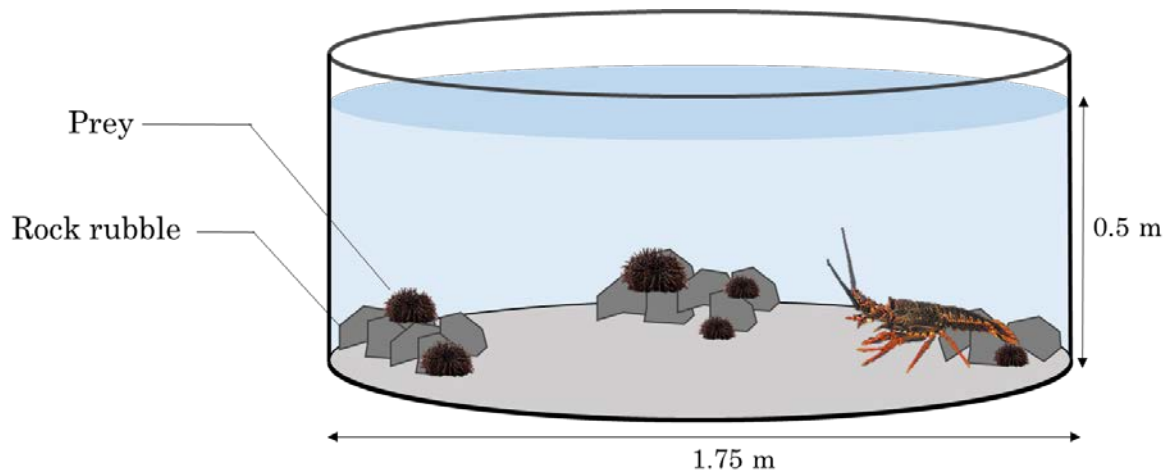
**Fig. 4.2.** Schematic diagram of the experimental tank set up.

### Feeding experiment

A 12-month study, commencing October 2019 till October 2020, was conducted to investigate the seasonal consumption of *Evechinus* by adult lobsters. Four lobsters were used, with two trials being completed each week (lobsters used were alternated), and the tank used was randomised. Each trial lasted for three nights (72 hrs).

The size (TD; ± 0.5 mm) and total weight (± 0.1 g) of *Evechinus* were recorded. Six *Evechinus* were used in these feeding experiments (three small "juvenile" (≤ 65.0 mm) and three large "adult" (> 65.0 mm)). Size classes were based on the approximate size of sexual maturity (McShane & Anderson 1997). *Evechinus* were placed at random into the 1,500 L experimental tank at the beginning of the day and left for at least two hrs to allow *Evechinus* to hide within the rock rubble. At 12:00 hrs (noon) an individual lobster was placed by hand into the experimental tank's centre. The experimental tank was monitored daily (morning) to record the number and size of *Evechinus* consumed. Consumed *Evechinus* were replaced with similar-sized individuals, ensuring six were always available throughout the trial period.

**Apparent food intake, consumption and size preference**

To assess the lobsters' *Evechinus* consumption abilities and size preferences, consumed *Evechinus* were identified. Any remaining test, spine and tissue remnants were weighed (± 0.1 g) to estimate apparent food intake (AFI). The AFI from each day were combined at the end of each trial to get a trial AFI value. To understand if lobsters not only showed a change in the number of *Evechinus* consumed, but a change in the proportion of each *Evechinus* consumed, the remaining weight was deducted from the wet weight.

A subsample of *Evechinus* (n = 72) was weighed (total weight) before being drained of perivisceral fluid and reweighed (drained weight; g) to achieve an accurate representation of AFI. The percentage of drained fluid was then subtracted from the total apparent food intake values. The average (± SE) perivisceral fluid equated to 21 ± 0.6 % of the total weight. Therefore, 21 % of the total AFI was subtracted prior to analysis.

**Sea Surface Temperature (SST)**

To investigate the relationship between sea surface water temperature (SST) and *Evechinus* GI and lobster AFI, SST was obtained from the University of Auckland's Leigh Marine Laboratory (N. Shears, unpub. data). Daily measures of SST (~1 m depth) taken at 0900 hrs were averaged (± SD) over each month. Austral seasons were defined as: Summer – December, January, February; Autumn – March, April, May; Winter – June, July, August; Spring – September, October, November.

**Lobster moulting**

To evaluate if moulting influences consumption rate, the date of moulting was noted. The presence of a moulted gastric mill structure was recorded for all available large male lobsters (n = 4). The new CL was measured using a measuring tape post moult, once carapace had hardened, to determine growth (± 1 mm).

**Data analysis**

Statistical analyses were conducted in R-Studio Software (v 1.2.5033, RStudio INC) using a univariate approach. All data were tested for normality and homogeneity of variance prior to analysis and overall statistical significance at the 0.05 level. Values are given as mean ± SE unless stated otherwise. The average (± SE) perivisceral fluid of *Evechinus* equated to 21 ± 0.6 % of the total weight. Therefore, 21 % of the total AFI was subtracted prior to analysis.

A generalised linear model (GLM) back-fitted to a Gaussian distribution with an identity link function was used to analyse the relationship between months and:

1. *Evechinus* gonad index score

2. Apparent food intake

3. Number of *Evechinus* consumed per trial

4. The proportion of each *Evechinus* consumed

Additionally, GI was averaged for each month and subsequently investigated for correlation with AFI, using Pearson correlation coefficients.

*Size preference: number of consumed individuals*

The number of large (> 65.1 mm) and small (< 65.0 mm) *Evechinus* consumed were compared using the chi-square goodness-of-fit test with Yates' correction for continuity.

*Size preference: apparent food intake and proportion of Evechinus consumed*

The associated AFI that a size class contributed and the proportion of a total *Evechinus* consumed for each month was analysed using GLM back-fitted to a Gaussian distribution with an identity link function to test for differences over months.

# Results

**Gonad Index**

*Evechinus* gonad index (GI), was found to vary significantly across months (Table 4.1). GI was significantly higher in late spring/ early summer (November – January) and declined rapidly over late summer (Feb). In winter months, GI did not fluctuate markedly (Fig. 4.3a).

**Apparent food intake and consumption**

Differences in rates of consumption were found to be statistically significant across months (Table 2.1). Following lobster moulting in 2019, the consumption of *Evechinus* steadily increased, peaking in December. After that, consumption steadily reduced through mid/late summer extending into winter months. Summer months had the highest consumption of $2.54 \pm 0.25$ *Evechinus* day$^{-1}$ compared to only $0.51 \pm 0.11$ *Evechinus* day$^{-1}$ consumed over winter months.

Negligible consumption was recorded in August and September, consistent with lobster pre-moult feeding behaviour (Fig. 4.3b). There was a significant positive correlation with lobster consumption (AFI) and GI (Pearson correlation: $r = 0.3$, $p < 0.01$; Fig. 4.4).

On average, 78.3 ± 1.1 % of an individual *Evechinus* was consumed throughout the experiment. The average proportion of an individual *Evechinus* consumed was dependent on month (Table 4.1); this was primarily driven by a significant decline observed in June (Fig. 4.5). The Aristotle's lantern was always consumed (n = 324), and in extreme cases (n = 16) Aristotle's lantern and test spines were the only part of *Evechinus* consumed (refer to Fig. 4.1). In these cases, the test spines appeared to look 'shaved' (see Appendix 4.A). This behaviour was primarily (75 %) observed within a month post-moulting.

**Table 4.1.** Analysis of deviance for GLM model fitted to **a)** GI and **b)** AFI **c)** number of *Evechinus* consumed and **d)** proportion of consumed *Evechinus*.

| Source | d.f. | Deviance | Resid. D.f. | Resid. Dev. | P(>\|Chi\|) |
|---|---|---|---|---|---|
| **a)  Gonad index (GI)** | | | | | |
| Month | 11 | 886.45 | 256 | 1083.4 | $2.2E^{-16}$ *** |
| | | | | | |
| **b)  Apparent food intake (AFI)** | | | | | |
| Month | 11 | $3.5E^5$ | 74 | $1.7E^5$ | $2.2E^{-16}$ *** |
| **c)  Number consumed** | | | | | |
| Month | 11 | 843.65 | 70 | 341.83 | $2.2E^{-16}$ *** |
| **d)  Proportion consumed** | | | | | |
| Month | 11 | 16744 | 305 | 102801 | $7.2E^{-7}$ *** |
| **Signif. codes: *** < 0.001; ** < 0.01; * < 0.05** | | | | | |

## Lobster moulting

The lobsters used in this feeding experiment (n = 4) moulted in late Sep/early October 2020. The median date of moulting was 6th October 2020. On average lobsters grew 6.75 mm in CL between 2019 and 2020 moulting events. Lobsters stopped eating *Evechinus* 61.8 ± 3.7 days before moulting, and this continued for an additional 18.3 ± 1.5 days after moulting. One lobster went a total of 90 days between consuming *Evechinus*. The gastric mill was identified in all lobster exuvia (n = 4).

**a)**
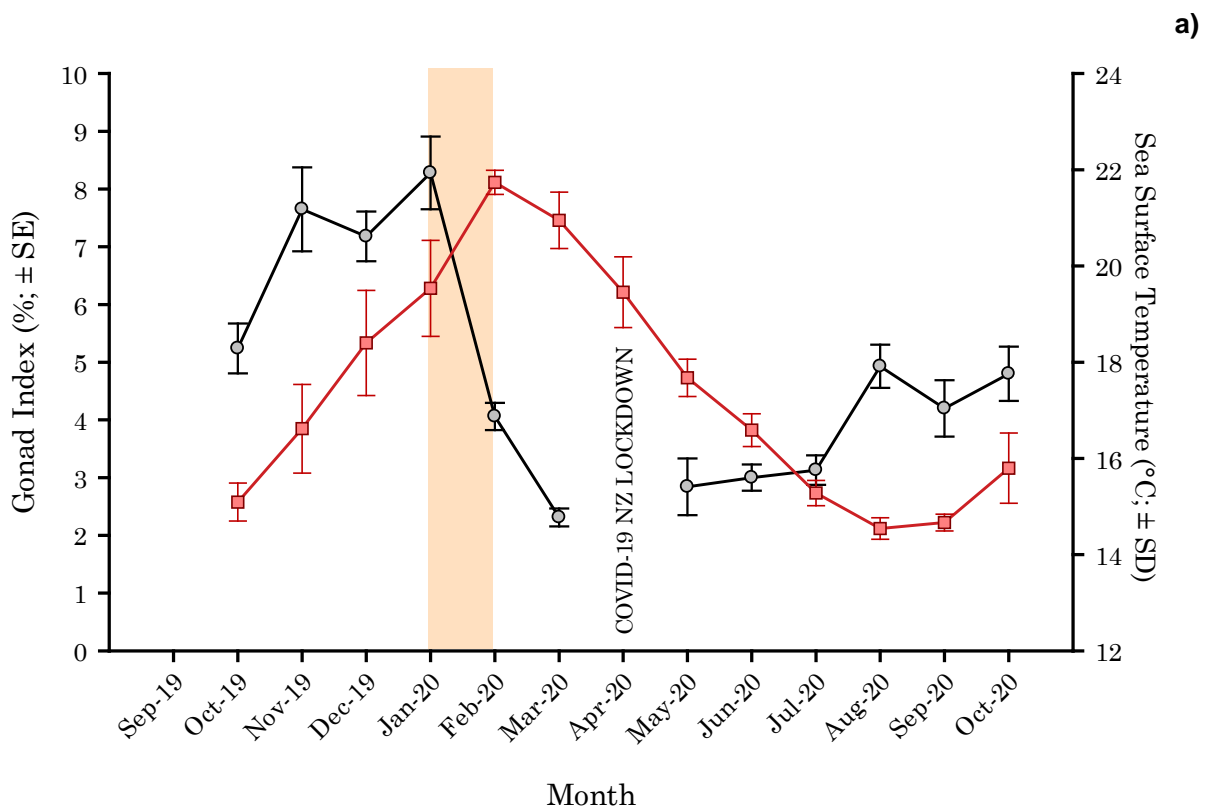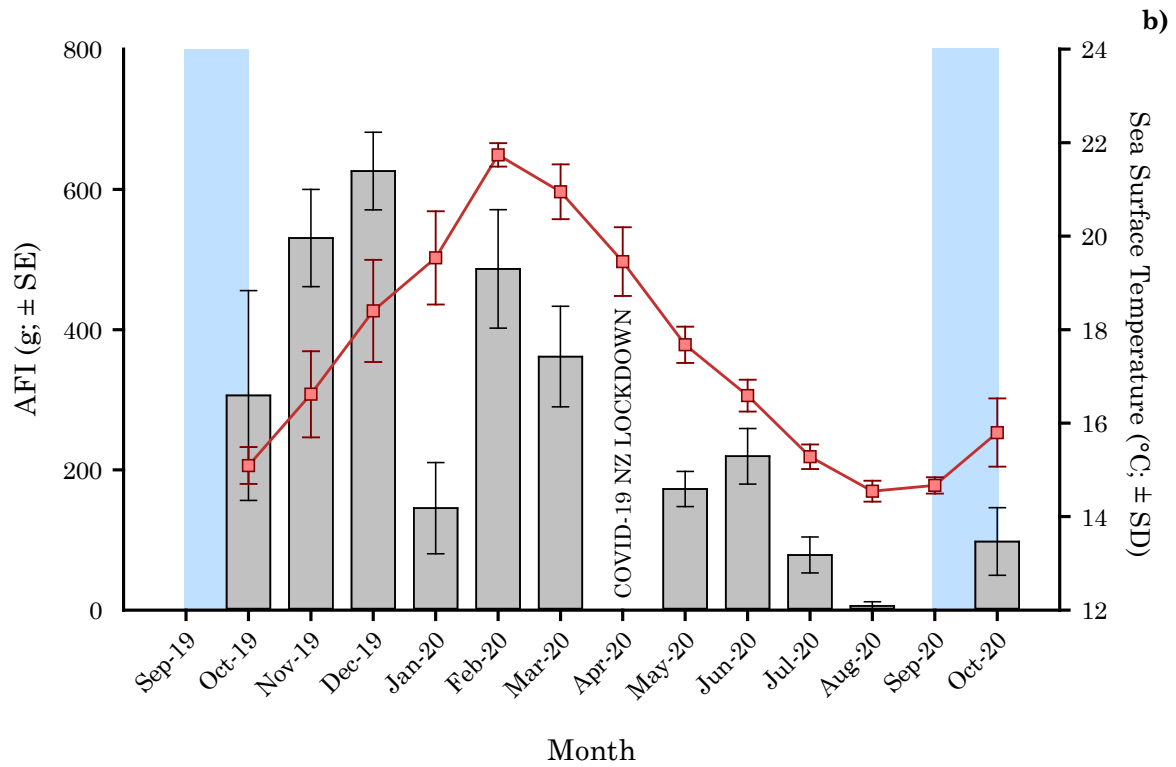
**Fig. 4.3.** Average sea surface temperature (SST) and **a)** *Evechinus* gonad index (GI), over each month and **b)** apparent food intake (AFI). Data for April-2020 missing due to Covid-19 New Zealand lockdown; Orange box = *Evechinus* spawning period; Blue box = timeframe that lobsters moulted.
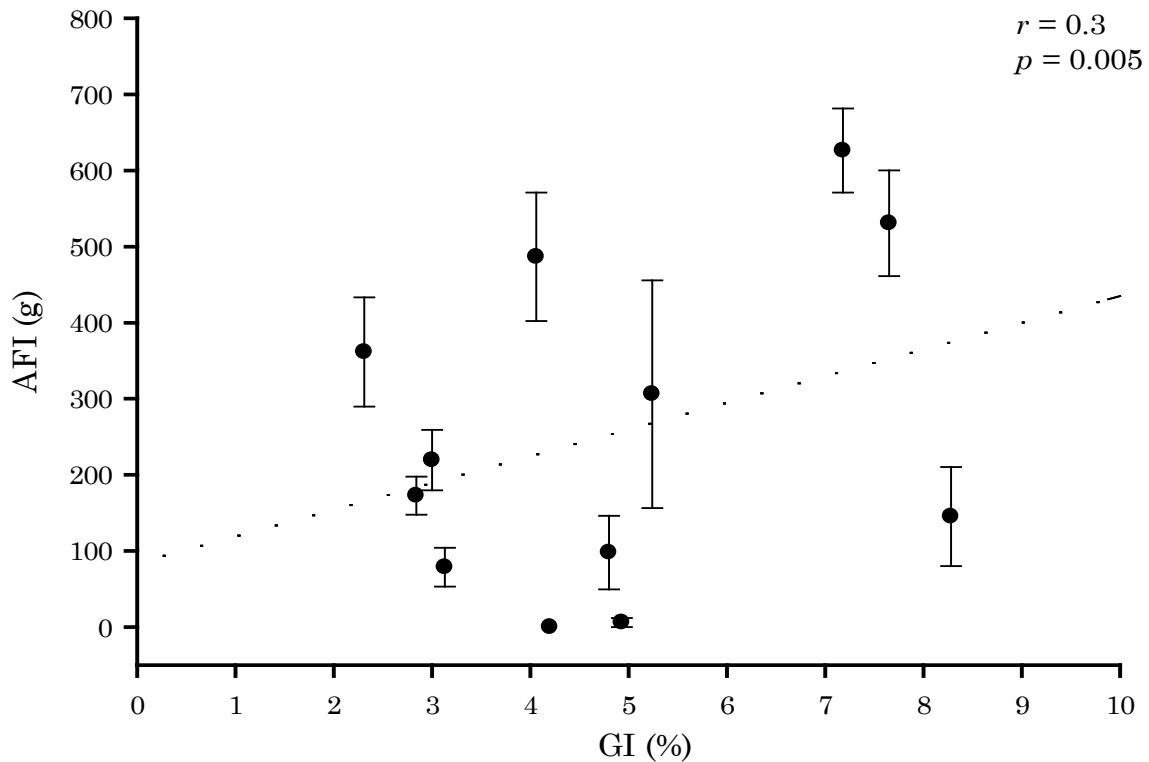
**Fig. 4.4.** Correlation between AFI and GI. Linear regression indicated by the black dashed line.

**Size preference: number of consumed individuals**

The largest *Evechinus* used in these experiments had a test diameter of 109 mm, while the smallest was 35 mm, both of which were consumed. In this experiment, 67.6 % of small *Evechinus* ($\leq$ 65.0 mm) used were consumed compared to 44.9 % of large *Evechinus* (> 65.0 mm), with small *Evechinus* comprising 62 % of all the consumed *Evechinus* (n = 324). Overall, lobsters showed a significant ($X^2$ = 29.353, $p$ < 0.001) preference for smaller *Evechinus* compared to large *Evechinus*.

**Size preference: apparent food intake and proportion of total *Evechinus* consumed**

From spring to late summer there was a trend from high consumption of large *Evechinus* relative to small *Evechinus*. In comparison, from late-summer through to mid-winter, typically the opposite was true (Fig. 4.5a). Post moult (2019)

consumption was variable among size classes. Overall differences in AFI were significant across months and between sizes, with a statistically significant interaction indicative of variability in small and large consumption across the experiment's duration (Table 4.2a).

The average (± SE) proportion of a small *Evechinus* consumed was $0.82 \pm 0.01$ compared to only $0.74 \pm 0.02$ in large size class. Overall, the proportion of *Evechinus* consumed was greater in small *Evechinus* than large *Evechinus* (Table 4.2b).

**Table 4.2.** Analysis of deviance for GLM model fitted to month and size category preference scores derived from **a)** AFI and **b)** Proportion consumed of *Evechinus*.

| Source | d.f. | Deviance | Resid. d.f. | Resid. Dev. | P(>|Chi|) |
|---|---|---|---|---|---|
| **c) AFI** | | | | | |
| Month | 10 | $5.2e^4$ | 313 | $5.5e^5$ | $1.14e^{-9}$ *** |
| Size | 1 | $2.5e^5$ | 312 | $2.9e^5$ | $2.2E^{-16}$ *** |
| Month × Size | 8 | $1.7e^4$ | 304 | $2.7e^5$ | 0.0132 * |
| **d) Proportion consumed of *Evechinus*** | | | | | |
| Month | 10 | $1.1e^4$ | 313 | 106421 | 0.0001 *** |
| Size | 1 | $8.1e^3$ | 312 | 98222 | $3.57e^{-08}$ *** |
| Month × Size | 8 | $2.0e^3$ | 304 | 96193 | 0.6011 |
| **Signif. codes: *** < 0.001; ** < 0.01; * < 0.05** | | | | | |
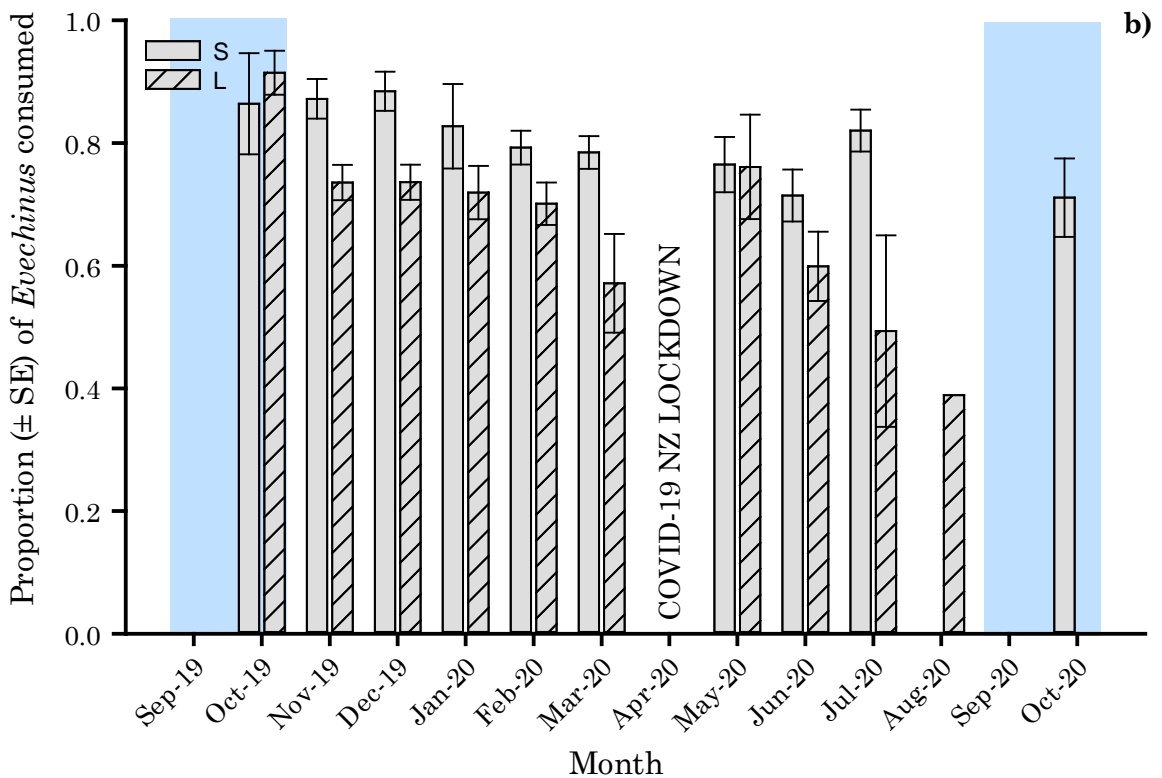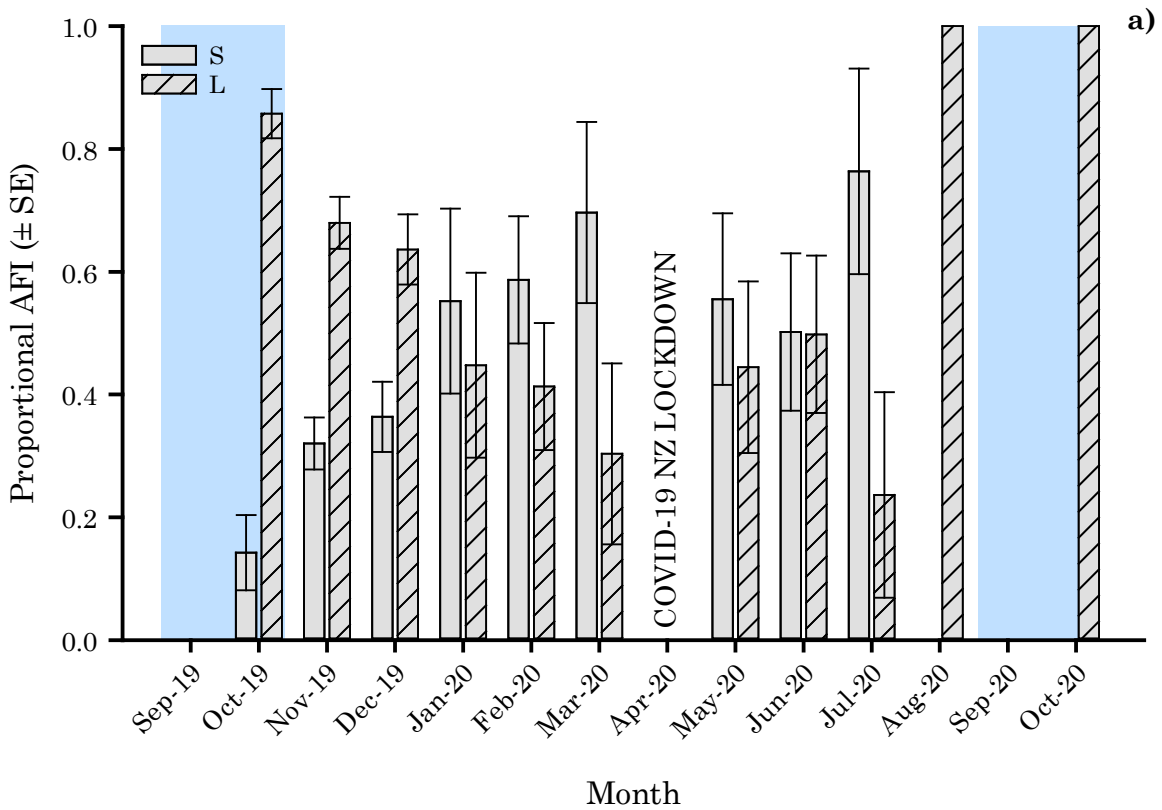
**Fig. 4.5.** Average proportion of **a)** apparent food intake (AFI) and **b)** total *Evechinus* consumed based on size category (S = ≤ 65.0; L = > 65.0 mm) for each month. April-2020 was missing due to Covid-19 New Zealand lockdown; Blue box = timeframe that experimental lobsters moulted.

## Discussion

It is well known that lobsters constitute significant predation pressures on the herbivorous sea urchin (Shears & Babcock 2002, Eurich et al. 2014, Selden et al. 2017). However, little is known about the rates and seasonality of consumption as they pertain to lobster life histories. This study indicates that *Jasus edwardsii* consumption of *Evechinus chloroticus* was highly dependent on the time of the year and was primarily dictated by moulting periodicity. Additionally, greater food intake (AFI) was correlated with *Evechinus* gonad mass in the months following moulting. This high consumption suggests an increased preference for higher quality urchins, especially in the months following moulting.

Consumption of *Evechinus* was significantly reduced in male lobsters during August through to October, which corresponds to male peak spring ecdysis (September/ October) (MacDiarmid 1991). During this time, lobsters ceased eating *Evechinus* for prolonged periods (up to 90 days). Here, it was observed that the gastric mill was also moulted during lobster ecdysis, providing a plausible explanation for the decline in feeding; suggestive of the gastric mills' limited functionality as a new replacement is being formed. Sheridan et al. (2016) found that the new medial tooth and lateral teeth were formed during the pre-moult period of the Norway lobster (*Nephrops norvegicus*). This gastric mill formation may also be the case for *J. edwardsii* as the majority of reduced feeding occurred before moulting events.

In addition to the carbon loss through the removal of exuviae, the need to compensate for the extended period without feeding could result in the high rate of *Evechinus* consumption recorded in the summer. Therefore, the greatest impact

male rock lobsters could be expected to have on wild populations of sea urchins would be during late spring and early summer. This increase in consumption also coincides with *Evechinus* quality (gonad index), which peaks in summer. Apart from the deviance during the moulting period, gonad index and lobster AFI follow a similar trend (Fig. 4.4). This consumption pattern provides evidence for the ability of lobsters to distinguish, and actively make a choice based on the nutritional status of the urchin. A similar scenario was identified in the California spiny lobster, *Panulirus interruptus*, which preferred higher quality urchins acquired from kelp habitats (Eurich et al. 2014). Selective predation can, therefore have profound effects on the rate of kelp forest restoration.

Furthermore, the proportion of *Evechinus* consumed (including test and spines) was highest in summer (~ 80 %), and instances of complete *Evechinus* consumption were more likely to occur within a month post-moult. Macro-minerals, calcium and magnesium, comprise a substantial percentage of sea urchins' dry matter content, primarily in the test, spines, and Aristotle's lantern (Lawrence 2013). The significant increase in *Evechinus* consumption post-moult may be due to calcium being reabsorbed into the carapace and other hard structures. During pre-moult stages, calcium is either resorbed from the carapace and stored within the body or, primarily, lost to the environment (Greenaway 1985). Recalcification begins immediately, or shortly after, ecdysis using calcium obtained from the water, food, exuviae, or a combination of all three (Greenaway 1985). Immediately after moulting lobsters are completely soft with limited mobility and unable to feed until the mouthparts and stomach ossicles are recalcified and able to cope with food. Therefore, calcium gained from food likely

plays a minor role in the early stages of recalcification. Nonetheless, in this study, the Aristotle's lantern was always consumed, indicating the nutritional importance of this structure and that calcium may be an essential mineral not limited to the post-moult cycle.

Although lobsters have significant consumptive pressure on urchins in summer, this study also highlights relatively low foraging rates for at least five months of the year, especially over winter. For example, in December lobsters were consuming an average of ten urchins each trial, compared to less than two urchins over the July – September period. If lobsters are not feeding on urchins for extended periods, there is reduced population control. During this time, kelp will not have a chance to become established, resulting in the system remaining in a barren state. This substantial decline in urchin intake over this period could have implications for the management of reserves. Reduced foraging may also provide insight into why there are lag periods in kelp forest recovery despite increases in overall lobster populations (Babcock et al. 2010).

However, despite the reduced direct predation of *Evechinus* by male lobsters during winter months, the mere cue of a predator can change prey behaviour. For example, sea urchins exposed to potential predators' odour ceased feeding or moved to different areas (Vadas Sr & Elner 2003, Matassa 2010, Morishita & Barreto 2011, Kintzing & Butler IV 2014). Therefore, despite the reduced direct consumption on urchins, lobsters' presence indirectly diminishes sea urchins foraging activities and their impacts as herbivores. Additionally, this study only investigated the feeding behaviour of male lobsters. In northern New Zealand, female lobsters usually moult in late April – June (MacDiarmid 1989). Therefore,

investigating females consumptive abilities of *Evechinus* could indicate high predation on urchins during the male moulting period. Female feeding behaviour could also help decipher if the primary driver of consumption rate is, in fact, moulting or *Evechinus* quality.

The size distribution of *Evechinus* in the natural environment in northeastern New Zealand are suggested to be bimodal, with a peak observed in small cryptic individuals (< 40 mm TD) and another larger peak between 60 and 70 mm TD (Andrew & MacDiarmid 1991). Lobsters were capable of consuming *Evechinus* upwards of 100 mm TD in this study, suggesting large lobsters will have a significant influence on the naturally occurring *Evechinus* population. Overall, small *Evechinus* (> 65 mm) were preferred in terms of number consumed, proportional AFI, and proportion of *Evechinus* consumed. This preference is likely due to maximising energy gain, as smaller *Evechinus* have relatively reduced crushing resistance and handling time (Tegner & Levin 1983, Mayfield et al. 2001). However, this preference depended on the month, with larger *Evechinus* seemingly preferred in October through December. This preference change is likely associated with the lobsters observed increased foraging rates and associated higher nutritional demands after moulting.

In conclusion, this study demonstrates the importance of large lobsters in sea urchin population control. Sea urchins can decimate kelp forests, turning biodiverse habitats into expansive areas of structurally simple and relatively unproductive barrens. Large lobsters are a pivotal predator of *Evechinus*, with high consumptive capabilities, especially of the larger sized *Evechinus* that are less likely to be predated on by fish (Shears & Babcock 2002). However, this

consumptive ability was seasonal, with significant declines during the lobsters' pre-moult cycle, followed by significant increases post-moult. Therefore, this study suggests that the potential impact lobsters can have on controlling urchin populations is relatively complex, as top-down pressure would fluctuate throughout the year.

# CHAPTER FIVE

# General Discussion

Globally, human activities are increasingly perturbing marine ecosystems, leading to impaired ecosystem functions and altered tropic structures (Branch et al. 2010, Hooper et al. 2012), and cascades (Frank et al. 2005, Shears et al. 2008). Worst-case scenario, these impacts can lead to ecosystem collapse (MacDougall et al. 2013). While ecosystems appear capable of withstanding some level of stress, "catastrophic shifts" in structure and function can occur once a critical stress threshold or tipping point is reached (Holling 1973, Scheffer et al. 2001). Significant stressors identified in marine ecosystems include changing climate, overfishing, habitat loss, invasive species and pollutants (Jackson et al. 2001, Airoldi et al. 2008, Gutt et al. 2015).

The exploitation of coastal marine resources affects not only the targeted species, but also other species and habitats in the ecosystem (Jackson et al. 2001, Pandolfi et al. 2003, Lotze et al. 2006, Hobday et al. 2011). For example, populations of apex predators in many natural systems have collapsed, due to humans' overexploitation, leading to significant structural and functional changes in coastal marine ecosystems (Jackson et al. 2001, Estes et al. 2011). Severe overfishing drives target species to ecological extinction, meaning the overfished

population no longer interacts significantly with other species in the ecosystem (Jackson 2008).

The establishment of marine protected areas (MPA) in temperate regions has revealed significant shifts in community structure, including increases in both population and the size of commercially important species (Kelly et al. 2000a, Halpern & Warner 2002), and the indirect 'flow-on' effects of these changes (Babcock et al. 1999, McClanahan et al. 1999). The increase in the abundance of predators, such as lobsters and demersal fish, on protected temperate reefs is well documented and associated with reducing sea urchin densities within reserves (McClanahan & Muthiga 1989, Babcock et al. 1999).

Lobsters are the focus of valuable fisheries worldwide and are among the most highly-priced seafood (Cau et al. 2019). This high value, however, has led to many stocks being overfished to meet global demands. Populations of rock lobster, *Jasus edwardsii,* are under significant pressure from fisheries and have been described as functionally extinct in northeastern New Zealand (Shears & Babcock 2003). Attempts to mitigate fishing pressure through MPAs have produced mixed responses, primarily attributed to poor MPA design by not incorporating essential habitats and the associated offshore movement patterns of adult lobster (LaScala-Gruenewald et al. in press). The plight of lobster in this region has been well publicised for several years, and there is no doubt that urgent management action is needed.

# Lobsters as an influential predator

Several factors may influence a predator's choice of prey. These include cost-benefits (Brunner et al. 1992), risk (Kacelnik & Bateson 1996), and considerations of long-term energy and mineral intake (Lankford Jr & Targett 1997). Predators can also make an active choice about what they consume based on prey quality (Mayfield et al. 2001, Eurich et al. 2014). Hence, selective predation is a significant force shaping community structure (Paine 1974, Hixon & Beets 1993). Predators unquestionably influence prey communities' composition, and in some circumstances, their trophic effects can cascade through the community (Paine 1980). So too can the indirect effects of predation, such as altering prey behaviour in response to predator cues (Trussell et al. 2003, Freeman 2006). Often the scent of a predator is enough to change prey behaviour. For example, sea urchins stop feeding and flee when exposed to lobster odour and injured conspecifics (Vadas Sr & Elner 2003, Matassa 2010, Kintzing & Butler IV 2014), which weakens their impact as aggressive herbivores. Not only can the presence of predators alter a prey's behaviour, but also induce morphological changes. For example, sea urchins within marine reserves (high food supply and predator cues) had more crush-resistant tests than individuals on nearby fished reefs where predators and food were relatively rare (Spyksma et al. 2017).

Historically, lobsters were at least four times more abundant and played a dominating predatory role in structuring temperate communities by directly impacting their prey's abundance and indirectly influencing their prey's prey (Eddy et al. 2014). However, reduced biomass, due to overexploitation, resulted in lobsters having a weakened influence on ecosystem trophic interactions. The

recovery of lobsters within marine protected areas has given an important insight into the potential consumptive capabilities, and ecological role lobsters play (Eddy et al. 2014). Lobster population recovery has also revealed important linkages between the reef and surrounding soft-sediment habitats (Langlois et al. 2005, Langlois et al. 2006).

**Influence on soft sediment communities and offshore foraging movements**

Lobsters showed a strong preference for offshore soft-sediment bivalves compared to common reef species. This preference is likely associated with low handling efforts and reduced risks of injury. This feeding behaviour highlights the importance of surrounding sand beds as an important feeding ground for lobsters, with the potential to alter soft-sediment communities and create 'infaunal halos' of reduced prey density (Langlois et al. 2005).

In addition to prey preferences, lobsters can travel considerable distances over adjacent sandy areas to locate potential feeding grounds (MacDiarmid 1991, Kelly et al. 1999, Langlois et al. 2005). This thesis strengthens this hypothesis, with evidence of food-motivated movements with considerable distances (upwards of 600 m) travelled overnight. This movement behaviour also suggests that lobster home ranges extend well beyond rocky reef margins.

The feeding preferences and the associated foraging movements described in this study gives a plausible explanation for the historically observed offshore movements (MacDiarmid 1991, Kelly 2001, Kelly & MacDiarmid 2003). These offshore movements have been recognised as a likely cause for declines of lobster abundance within the Cape Rodney to Okakari Point (CROP) Marine Reserve, with targeted fishing of lobster aggregations near reserve boundaries (LaScala-

Gruenewald et al. in press). Interestingly, anecdotal evidence suggests that these historical offshore movements and aggregation events no longer occur, or if so, to a lesser extent.

One suggested explanation for the decrease in offshore movements and aggregation behaviour, is the reduced density of lobsters, especially large males (LaScala-Gruenewald et al. in press). During these aggregations on exposed soft-sediment beds, lobsters would gather in large numbers (groups of 200 individuals) and form mutual defence aggregations (Kelly et al. 1999). Reducing lobster numbers within the CROP marine reserve may have hindered this anti-predator behaviours' overall effectiveness. Therefore, the benefit gained from making these foraging migrations no longer outweighs the associated costs of predation.

Additionally, this study indicated that small bivalves, such as *Tawera spissa* were a preferred prey type. Dense *Tawera* beds were found within the CROP marine reserve boundary, located along the 20 m depth contour (Schoensee 2020). The location of these preferred bivalve beds' further reduces the incentive to migrate offshore and beyond the reserve boundaries.

Furthermore, these large aggregations were observed two decades ago and coincided with historically abundant horse mussel, *Atrina zelandica,* beds (Kelly et al. 1999). Horse mussels were abundant in the CROP marine reserve in the 1980s and 1990s, where dense beds were located along the western reserve boundary (Mutch 1983, Grant-Mackie 1987, Kelly et al. 1999). Based on current (2019) benthic surveys, only one live horse mussel was discovered (Schoensee 2020). This significant loss of horse mussel beds indicates that a major soft-

sediment community change and the reason for the apparent loss is currently unknown.

**Influence on rocky reef communities**

The ecological effects of removing lobster from reef ecosystems have been unequivocally demonstrated, especially where lobsters are considered to be ecologically or functionally extinct (MacDiarmid et al. 2013). The removal of key predators through fishing has led to large increases in sea urchins, which have grazed down kelp forests and formed urchin barrens on many shallow reef systems.

Sea urchins are one of the most dominant and conspicuous habitat-structuring taxa on rocky reefs, and through their intensive grazing elicit phase shifts from dense macroalgal beds to comparatively structurally simple barren habitats (Andrew & MacDiarmid 1991, Sala et al. 1998, Johnson et al. 2005, Shears et al. 2008, Salomon et al. 2010, Blamey & Branch 2012). The magnitude of the influence that sea urchins exert is partly a function of their abundance. For example, when urchin abundance increases their primary food source (drift kelp) declines. Reductions in drift kelp then cause a shift from passive feeding to actively feeding on attached kelp (Vanderklift & Kendrick 2005, Kriegisch et al. 2019). Unlike most other herbivores, their high population density can persist long after overgrazing and maintain a comparatively unproductive barren ecosystem state (Johnson & Mann 1982, Ling et al. 2009).

Urchin barrens have had significant adverse environmental impacts as well as a reduction in commercial reef-dwelling species like the blacklip abalone, *Haliotis rubra,* in New South Wales and Tasmania (Bentley et al. 1998, Andrew

& O'Neill 2000, Ling et al. 2009). Additionally, there is rising concern over biodiversity loss due to the expansion of urchin barren habitats. This reduction in diversity reduces reef systems' ability to fulfil their natural role of fixing carbon, and a potential weakening in the reef systems' resilience to rapidly changing environmental conditions brought on by global warming (Steneck et al. 2002, Ling et al. 2009).

**Mitigation techniques and strategies**

Using lobsters as a potential tool to control the expansion of urchin barrens is receiving increased interest, and various management solutions have been implemented to bring degraded ecosystems back to a more natural "healthy" state. Relocation experiments of lobsters have proved successful, in terms of lobsters staying in the relocated area (Green et al. 2013), survivorship (Green & Gardner 2009), and an increase in growth rate (Chandrapavan et al. 2010). This study demonstrates the importance of large lobsters in sea urchin population control. Sea urchins can decimate kelp forests, turning biodiverse habitats into expansive areas of structurally simple and relatively unproductive barrens. Large lobsters are a pivotal predator of urchins, with an ability to consume large numbers, especially of the larger sized urchins that are less likely to be predated on by teleost fish (Shears & Babcock 2002). However, this consumptive ability is seasonal, with significant declines during the lobsters' pre-moult cycle, followed by significant increases post-moult. Therefore, we suggest that male lobsters' potential impact on controlling urchin populations is relatively complex, as top-down pressure would fluctuate throughout the year.

Most importantly, marine reserves have been recommended as a possible solution to initiate phase shifts to more desirable states by protecting key predators (Dayton et al. 2000, Lester et al. 2009, Ling & Johnson 2012). This thesis's findings suggest that marine reserves' efficacy is influenced by habitat quality in terms of the availability and abundance of food resources for lobsters. Lobsters show a strong preference for bivalve prey species, potentially driving offshore movements, especially during post-moult feeding events. Offshore foraging movements have influenced lobster abundance and distribution by increasing vulnerability to recreational and commercial fishing along offshore reserve boundaries. Likewise, the seasonality of male offshore feeding behaviours, emphasise the use of seasonal closures. Extending reserve boundaries offshore to include additional soft-sediment habitat will offer lobsters protection and allow safe access to these essential feeding grounds. This thesis highlights the importance of considering habitat quality for effective implementation of marine protection strategies.

Furthermore, it has been suggested that lobsters can detect urchin quality (Eurich et al. 2014). This was also indicative in our study, with a positive correlation between lobster consumption and *Evechinus* gonad quality; lobsters appear to consume fewer *Evechinus* during low gonad periods. In light of translocating lobsters into urchin barrens, sea urchins occupying barren habitats have reduced gonad tissue production compared to urchins within kelp forests (Lawrence 2001, Stewart & Konar 2012). This reduction in gonad production reduces individual quality, resulting in predators avoiding barren-urchins (Eurich et al. 2014). Optimal foraging theory suggests that predators will avoid low-quality

prey until their preferred prey's abundance is below a 'switching threshold' (Krivan & Sikder 1999). As a result, consumption of barren-urchins may not occur until the abundance of other more preferred prey declines below the switching threshold for a predator. Based on this study, when lobsters are given a choice, alternative prey to *Evechinus* was consumed in preference. Therefore, translocating lobsters into urchin barrens or the initial response to protection may have a significant time lag.

**Sensory mechanisms driving foraging movements**

This work identified that both vision and chemoreception are important sensory mechanisms guiding foraging movements. Vision may play a role in the migratory path and efficiency of movement towards these offshore foraging grounds and back to shelter. Lobsters with impaired vision showed an increase in movement, and this associated energy expenditure may have cascading effects on foraging efficiency. Chemoreception was found to be a crucial sense for detecting and selecting prey, especially for buried soft-sediment bivalves. In particular, the antennules appeared to play a disproportionate role in prey detection, further highlighting these structures' importance. Overall, this study's feeding behaviour indicates that chemoreception plays a significant role in detecting the presence of soft-sediment prey and possibly initiating offshore movements.

In New Zealand, fishers must discard all berried and undersized lobster (tail width: female = 60 mm; male = 54 mm; MPI 2020). Captured lobsters are brought to the water's surface and potentially exposed to direct sunlight. Lobsters eyes are adapted for low-light conditions, and light exposure can reduce lobster eyes' functionality (Meyer-Rochow 2001). If a lobster is returned to the water, there may be lasting negative implications. This study indicates that a released lobster with

impaired vision is likely to experience increased "randomised" movement, increasing overall energy expenditure, and reducing overall fitness. Lyons and Kennedy (1981), estimated that 12.3 % of lobsters (*Panulirus argus*) died after 30 minutes of exposure to direct sunlight. Furthermore, it is common for lobsters to have damaged and/ or missing appendages, which may be essential for foraging success, further reducing returned individuals' overall survivorship. Therefore, the total fishing-induced mortality of the population is greater than expected and can even result in recruitment overfishing.

## Future research directions

This study focused on large adult males, based on historically observed inshore-offshore movements in male lobsters (Kelly 2001, Freeman 2008). Male *J. edwardsii* moulting period overlaps with *Evechinus* increased gonad index (October through to November). It is therefore difficult to isolate if lobster consumption rate is driven by urchin quality or moulting periodicity. Alternatively, future studies would benefit by analysing the feeding behaviour of female *J. edwardsii* as they have a different moulting period (late April – early June). This offset of timing between moulting and low *Evechinus* GI may give a clearer indication of how prey quality influences lobster feeding behaviour. Additionally, few juvenile lobsters were observed in these offshore migrations and may display differences in feeding preferences. Prey selection of smaller lobsters are also more constrained by their prey's size (Gnanalingam & Butler IV 2018).

Furthermore, it has been suggested that the gastric mill could prove to be a useful tool in ageing lobsters (Gnanalingam et al. 2019). However, this study

suggests that the gastric mill is replaced during the moulting cycle. Therefore, the application as an ageing tool is doubtful, at least for this species. However, how the gastric mill is replaced is still unknown in this species. Understanding gastric mill regeneration may prove an interesting future research opportunity, especially if the gastric mill plays a role in intraspecific communication via sound production.

## Conclusions

Lobsters exhibited strong preferences for soft sediment bivalves over common reef species. This preference was most likely driven by short handling times and reduced risk of injury. Furthermore, lobster movements were shown to be food-motivated and were also capable of travelling considerable distances in search of food (> 500 m a night). These results highlight the importance of soft sediment bivalve beds as an essential feeding habitat for *J. edwardsii* and validate observed offshore movements. The presence of the food-driven movements provides further impetus for implementing more drastic management measures to prevent further fishing on the offshore boundaries of relatively small reserves.

Collectively the findings of this research have significant implications for both fisheries management and conservation management in terms of marine protected area design. In particular, ensuring that soft-sediment feeding habitats/grounds are better-understood and protected remains critical for this valuable yet vulnerable predator.

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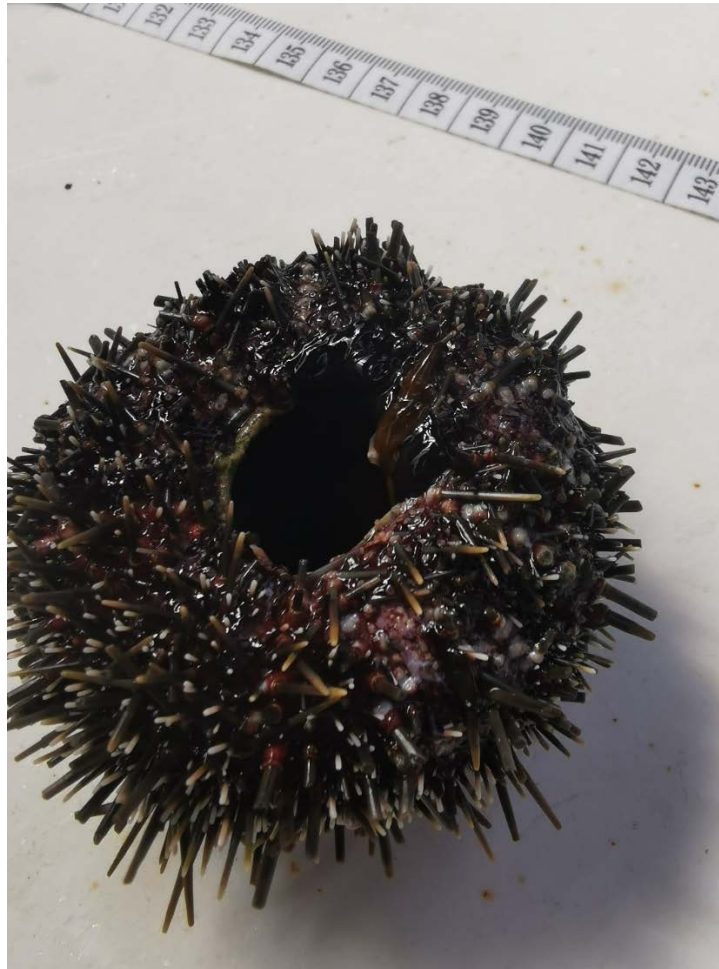
# Appendices

**Appendix 3.A**
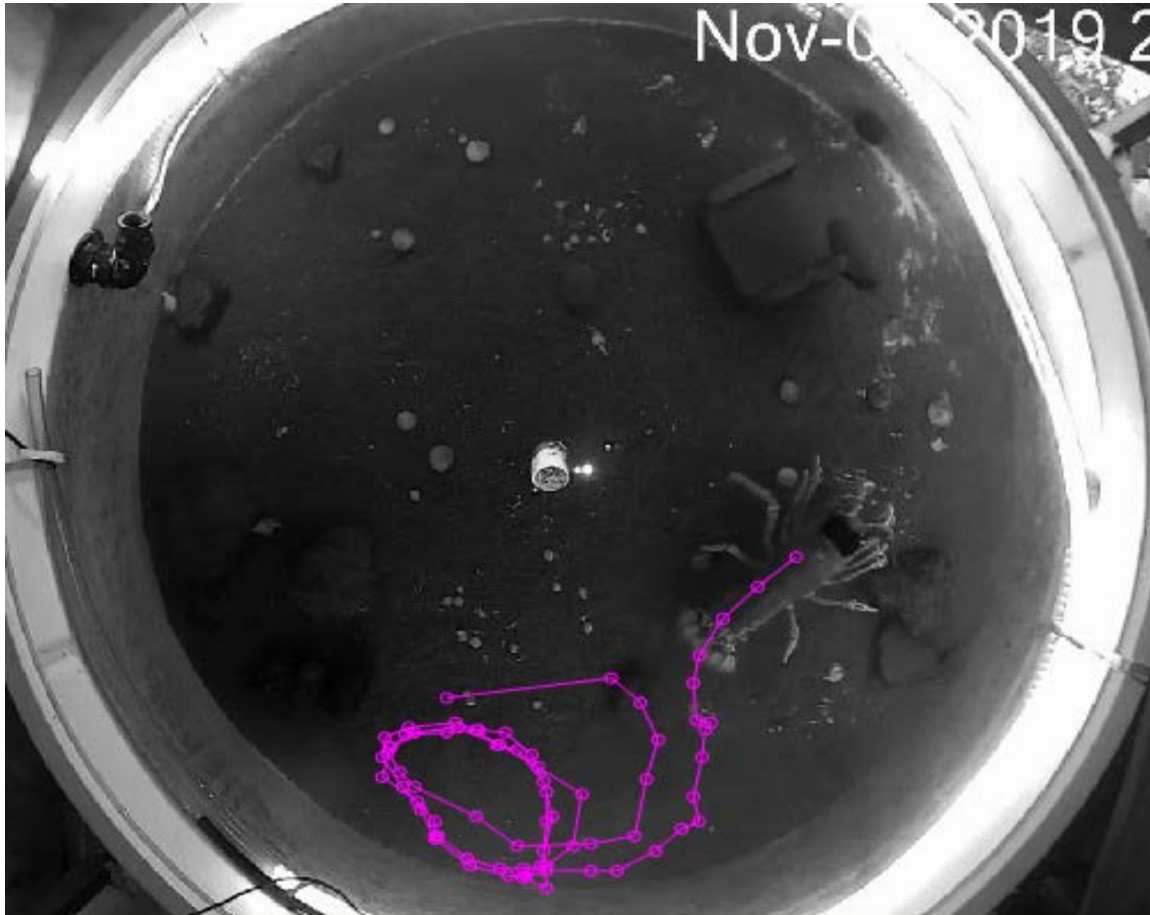


Example of individual lobster doing circles on the spot (single spinning event). The pink line shows tracking output from MATLAB (R2018a) using DLTdv digitising. The below image is a snapshot of approximately 60 seconds, with each point representing one frame, with four 360° spins completed.

**Appendix 4.A**



Small urchin (58 mm TD) with 'shaved' spines and Aristotle lantern
consumed. Date = 08 Oct 2020.

**Appendix 4.B**
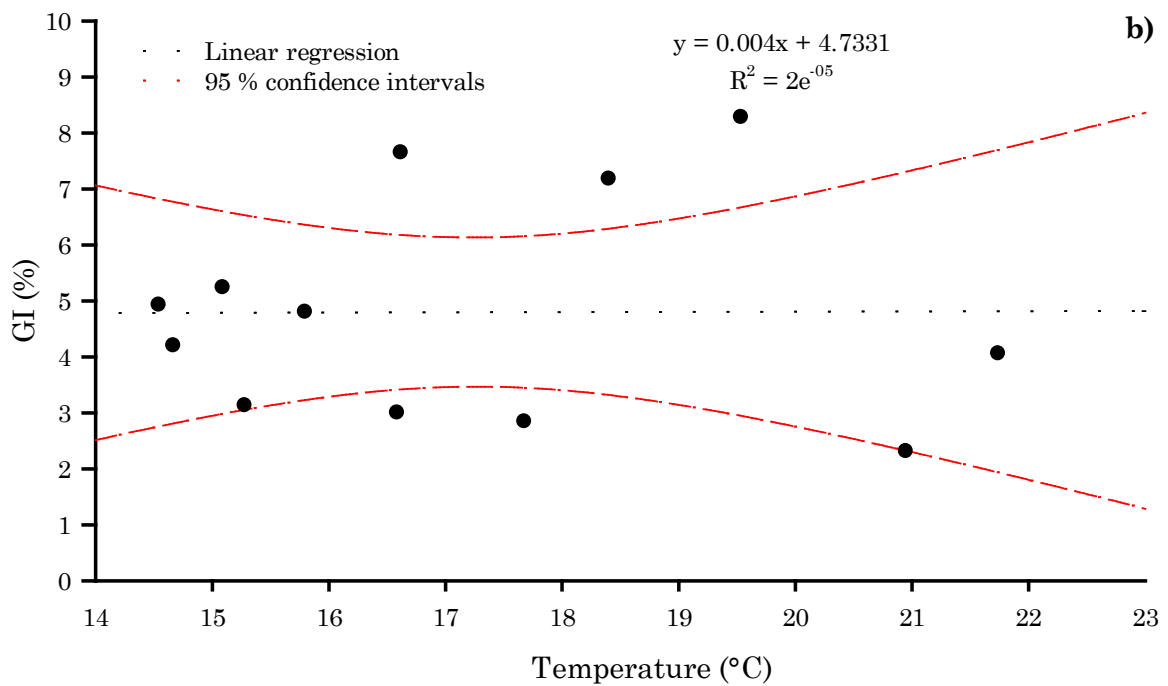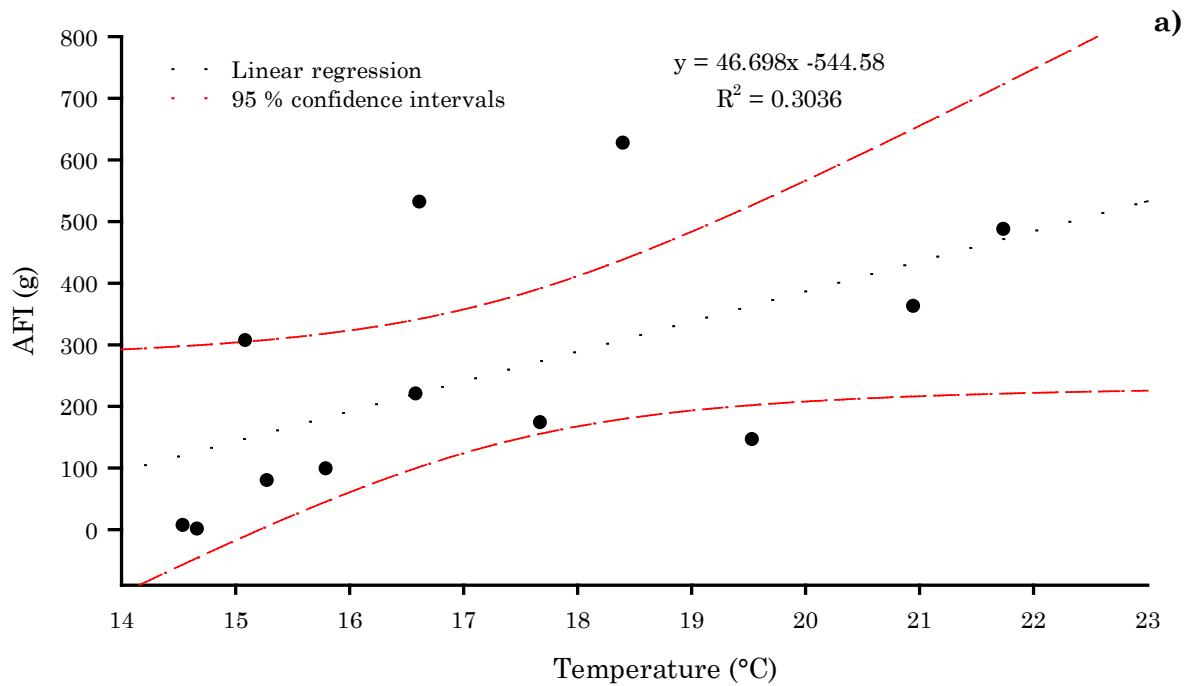


Linear regression analysis of average monthly **a)** apparent food intake (AFI; n = 83) and **b)** gonad index (GI), paired against the associated sea surface temperature (SST). Confidence intervals (95 %) around the slope are indicated by red dashed lines