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Nature of contribution by PhD candidate	Experimental design, data collection, analysis and production of the manuscript
Extent of contribution by PhD candidate (%)	95%

CO-AUTHORS

Name	Nature of Contribution
Shaun Ogilvie	Leadership of overall research programme, editing and comments on manuscript
Andrew Jeffs	Supervision, editing and comments on manuscript

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The undersigned hereby certify that:

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- that the candidate wrote all or the majority of the text.

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Shaun Ogilvie		10 April 2017
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Nature of contribution by PhD candidate	Experimental design, data collection, analysis and production of the manuscript
Extent of contribution by PhD candidate (%)	95%

CO-AUTHORS

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Andrew Jeffs	Supervision, editing and comments on manuscript

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Andrew Jeffs	Supervision, editing and comments on manuscript

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Chemoattraction in New Zealand scampi (*Metanephrops challengeri*): Identifying effective baits to develop a potting fishery

By

Robert Neil Major

A thesis submitted in fulfilment of the requirements for the degree of PhD in Marine Sciences

Institute of Marine Science, University of Auckland, New Zealand

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Abstract

New Zealand scampi (*Metanephrops challengeri*) is a commercially important deep-water lobster species that is caught by bottom trawling on areas of muddy seafloor on the continental shelf below 300 m in areas around New Zealand. Bottom trawling is a fishing method that typically produces high levels of bycatch and is associated with extensive benthic habitat damage. Pots (also known as creels or traps) tend to have a lower environmental impact when used as an alternative harvesting method to trawling in a number of crustacean fisheries, and may have potential application for scampi. A key component of pot fisheries are effective and economic baits. Therefore, the aim of the research presented in this thesis was to identify effective baits for a scampi potting fishery, by firstly understanding the chemically-mediated food search behaviour of scampi.

To achieve this aim the research followed a framework previously identified in the literature;1) characterising the phases of food search behaviour of scampi (presented in Chapter 2); 2) investigating the effect of different hydrodynamic regimes on this behaviour (presented in Chapter 3), and 3) utilising a binary-choice flume to compare the attractiveness of different potential baits (presented in Chapter 4). Additionally, a field experiment was undertaken to assess how baits influenced the operation of pots targeting scampi, especially in terms of their interaction with pot design and the resulting bycatch (presented in Chapter 5). The results of the research showed that the time scampi spent during each of the phases of chemically-mediated food search behaviour was highly variable regardless of the bait tested. However, scampi are more efficient at searching for food in turbulent versus laminar flow conditions. The New Zealand pilchard (*Sardinops neopilchardus*) baits were identified as being more attractive to the scampi than a number of alternative natural seafood baits. Homogenised pilchard tissue that was diluted (1 & 10% by wet weight) and set in an alginate binder were as attractive to scampi as both the natural pilchard tissue and a positive control to which scampi have previously been conditioned to respond to. This suggests that artificial baits utilising diluted fish tissue may be a practical approach for reducing the amount of fish that would be required for baits in developing a potting fishery for scampi. The advances in the understanding of scampi behaviour made by this research highlight that scampi are likely to feed on a range of food items, and are likely to be more efficient searching for food during periods of higher tidal flow associated with greater turbulence near the seafloor. The results of the potting study showed that the type of bait used did not affect the quantity of composition of the bycatch caught in pots, and that

bycatch can be reduced in pots through appropriate pot design and spatially targeted fishing. Overall the results of this research provide a valuable foundation for advancing the potential for developing a more environmentally benign potting fishery for New Zealand scampi.

Ka pū te ruha, ka hao te rangatahi

As an old net withers another is remade

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Chapter One: General Introduction

1.1 Scampi

Scampi is the common name used to describe the members of two genera of clawed lobsters *Nephrops* and *Metanephrops* (Crustacea: Decapoda: Nephropidae). The sole representative of the *Nephrops* genus is *Nephrops norvegicus* (hereafter referred to by its common name, Norway lobster), which lives in the North-Eastern Atlantic Ocean and parts of the Mediterranean Sea, whereas *Metanephrops* is represented by 18 extant species found in waters from Japan to the Subantarctic Islands of New Zealand. All members of *Nephrops* and *Metanephrops* genera are marine, reptant, elongate crustaceans with a cephalothorax, a 6-segmented abdomen and 10 walking legs (Bell et al., 2013). The genera are separated by a number of small morphological differences, rather than any one major feature (Tshudy, 2013). Prior to 1972 all *Metanephrops* species were considered to be members of the *Nephrops* genus, however, the discovery of a fossil on a New Zealand beach prompted a sweeping taxonomic review and the creation of the *Metanephrops* genus (Jenkins, 1972). Subsequent DNA analysis has further separated the two genera, suggesting that *Nephrops* is more closely related to the clawed lobsters of the genus *Homarus* rather than *Metanephrops* species (Tshudy et al., 2009). From here on, the term scampi will be used for New Zealand scampi, *Metanephrops challengeri* (Fig. 1.1).

Figure 1.1 Photograph of New Zealand scampi (*Metanephrops challengeri*).

1.2 Ecology of New Zealand scampi

1.2.1 Habitat

New Zealand scampi, *Metanephrops challengeri*, is the sole representative of the *Metanephrops* genus in New Zealand. They inhabit the continental slope from the Bay of Plenty to the Subantarctic Islands and live at depths of 140-600 m (Fig. 1.2, (Ministry for Primary Industries, 2013). Scampi prefer muddy or silt-covered sediments in which they can burrow and consequently their distribution is strongly influenced by seafloor sediment (Cryer et al., 2001). These burrows are key to the life history of scampi, as they use them to avoid their primary predators, ling and skate (Dunn et al., 2010; Forman & Dunn, 2012), and even trawl nets (Tuck et al., 2015). Studies of Norway lobster and *Metanephrops* species suggest that they spend the majority of their life either inside, or at the entrance, of their burrow and only leave the shelter to forage for food, to moult, or for social interactions, such as mating (Chapman & Howard, 1979; Chapman & Rice, 1971; Farmer, 1974b).

The analysis of catch rates in commercial fisheries has identified that scampi emergence patterns vary due to reproductive and moulting cycles, as well as diel and tidal cycles (Aguzzi et al., 2003; Tuck, 2010; Tuck, et al., 2015; Ward & Davis, 1987). Consequently, to estimate the density of scampi and Norway lobster, photo-survey techniques analysing the number of burrow entrances have been developed, and the application of these methods suggest a wide ranging natural density of 0.03-0.13 m^{-2} (Cryer, et al., 2001).

1.2.2 Diet

The diet of scampi has not previously been studied. However, the foregut contents of other *Metanephrops* species living in similar habitats have identified crustaceans, fish, molluscs, annelid worms and foraminifera as dominant prey items (Choi et al., 2008; Sahlmann et al., 2011; Wassenberg & Hill, 1989). Collectively, these studies suggest that *Metanephrops* species are opportunistic scavengers or predators, potentially attacking and consuming mobile benthic prey (Wassenberg & Hill, 1989). This pattern of feeding is consistent with studies of Norway lobsters, which are scavengers and only make short foraging expeditions from their burrows (Chapman & Howard, 1979; Chapman & Rice, 1971). Examination of the foreguts and feeding ecology of Norway lobster have identified that they non-selectively consume a variety of crustaceans, fish and mollusc (Cristo, 1998; Cristo & Cartes, 1998).

1.2.3 Life cycle

Little is known about the life cycle and reproduction of scampi, with most of our knowledge being based on assumptions from studies of Norway lobster. Scampi moult several times per year in early life and about once a year after sexual maturity, which is reached at about 30 mm orbital carapace length (OCL) in females, although this varies among areas around New Zealand (Cryer et al., 2005). In comparison Norway lobster achieves sexual maturity between 23-36 mm OCL with animals living in shallower waters maturing at a smaller OCL (Bell, et al., 2013). No estimates have been made for the life span of scampi, however, growth rates are thought to be similar to Norway lobster, taking 3-4 years to grow to 30 mm OCL (Cryer, et al., 2005). Therefore, it is also reasonable to assume that scampi will have a similar life span of 15-20 years. The pelagic larval period is thought to be between 3 and 4 days and consist of only a single zoeal stage before settling as post-larvae, suggesting that scampi have limited pelagic larval dispersal (Wear, 1976).

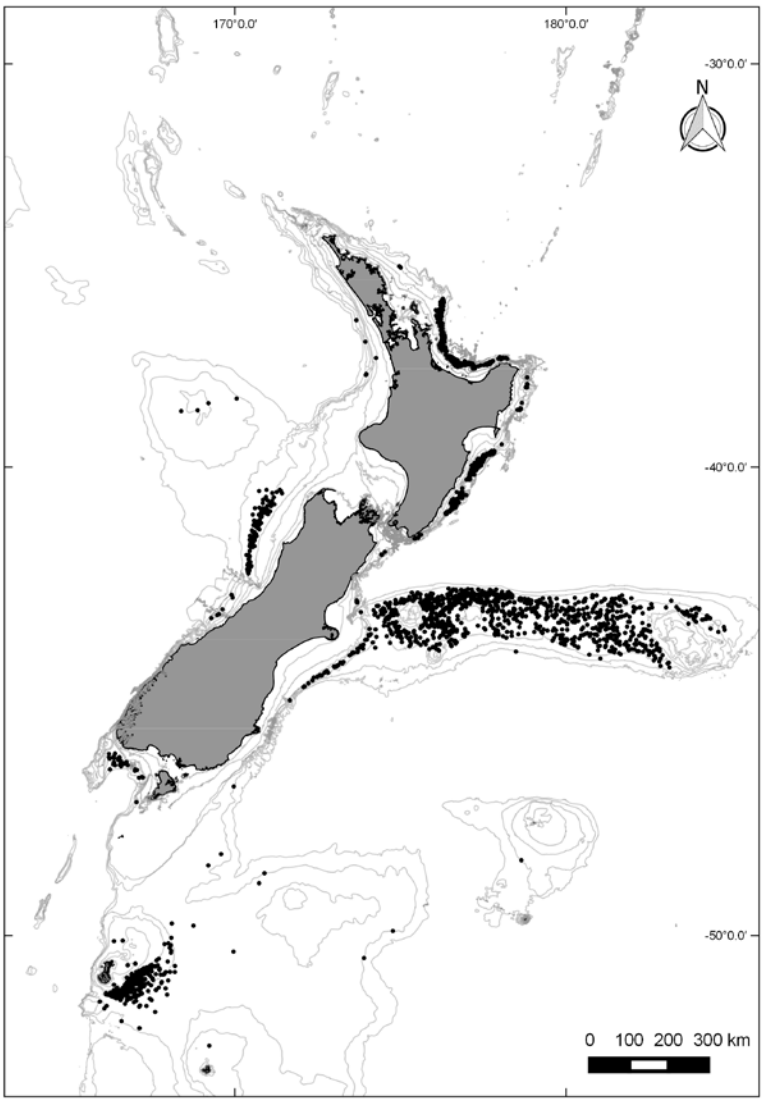

Figure 1.2 Map of locations where *Metanephrops challengeri* have been caught by research trawls undertaken by NIWA around New Zealand 1964-2008. Generated using data from www.iobis.org

1.3 Scampi fisheries

Scampi species that are commercially important in their natal regions include Norway lobster, *M. armatus* (Taiwan), *M. andamanicus*, *M. australienes*, *M. velutinus* (N.W. Australia) *M. formosanus* (Taiwan), *M. japonicas* (Japan), *M. mozambicus* (S.E. Africa), *M. thomsoni* (Korea, Taiwan) and *M. challengeri* (New Zealand) (Holthuis, 1991). Norway lobster supports the highest value commercial crustacean fishery in Europe, with fisheries in Ireland, the United Kingdom, Portugal, Italy, Spain, Greece, Sweden, and Norway having a combined annual production valued at around US$270 million

(Bell, et al., 2013). In 2010 global landings of Norway lobster were 66,500 t, with the majority caught in UK waters (58.1%) (Ungfors et al., 2013). Norway lobster is primarily caught in mixed fisheries by bottom trawlers using single or double rigged otter nets, although pot fisheries operate in Scotland, Sweden and Portugal. These fisheries operate at depths from 20 m in the lochs of northern Scotland, to over 500 m on the shelf ridge of the Hebrides Islands (Ungfors, et al., 2013).

1.3.1 New Zealand scampi fishery

The scampi trawl fishery developed in the 1980's and the first recorded landings were in 1986-1987. Initially most landings came from two areas off the North Island. As new fishing grounds in the Chatham Rise were developed, landings doubled from 450 t in 1990-91 to 900 t in 1991-1992 (Bell, et al., 2013). Landings were maintained at this level until they recently declined. The value of the scampi fishery varies depending on the amount of catch, for example in the 2008 – 2009 period 600 t of scampi where caught in New Zealand and generated NZD$11 million in exports (Anderson, 2012). Access to the scampi fishery in New Zealand is managed by the Quota Management System (QMS), and the fishing fleet consists of vessels that are 20-40 m in length that fish with double or triple-rigged bottom trawled otter nets. The major fishing grounds are the Chatham Rise, Bay of Plenty, Hawkes Bay, off the Wairarapa Coast and the Subantarctic Islands (Ministry for Primary Industries, 2013).

1.3.2 Issues with bottom trawling

The existing bottom trawl method for catching scampi raises substantial sustainability and efficiency issues (Suuronen et al., 2012). Environmental damage is caused by benthic disturbance from the trawls contacting the seabed and a high level of bycatch (Anderson, 2012; Cryer et al., 2002). The efficiency of the fishery is reduced by damaging the captured scampi with the fishing gear, low catches per unit effort (CPUE), and high fuel costs involved with bottom trawling in relatively deep water (Leocádio et al., 2012; Morello et al., 2009). Scampi account for only 17% of the estimated catch in observed scampi targeted trawls since 1990-1991, the highest rate of bycatch in any New Zealand trawl fishery (Anderson, 2012). Additionally, as with all New Zealand trawl fisheries, the bycatch of sea-birds and marine mammals is a significant issue. In 2008 -2009, 19 seabirds, 1 New Zealand fur seal and a Hooker's sea lion were reported as bycatch in commercial scampi trawls on which independent observers were present (Abraham & Thompson, 2011). As observers only monitor 10% of the trawls, it is estimated that as many as 182 seabirds, 6 fur seals and 15 Hooker's sea lions

were captured as bycatch in this period by the entire scampi fleet. The impact of trawling gear on benthic environments has been widely recognised (Thrush & Dayton, 2002). In a New Zealand context otter trawls, including those used in scampi fisheries, are known to have significant impacts on the benthic environment in the Bay of Plenty, by modifying the benthic community structure (Cryer, et al., 2002). Only about 20% of the scampi that are caught in trawls are harvested at the surface in an intact state (pers. comm. Waikawa Fishing Company). The remainder of the scampi are often damaged or of variable sizes and are consequently worth less than the premium grade whole frozen scampi, which sells for up to NZD$250 per kg in China (Oravida, 2017). CPUE of scampi in the four main fishing areas has been decreasing since 1995 (Ministry for Primary Industries, 2013). The low CPUE combined with high fuel costs of up to 9 l of diesel kg^{-1} of scampi landed indicates that there is a clear need to increase the efficiency and sustainability of the scampi fishery.

Trawled Norway lobster fisheries also have issues with benthic damage and bycatch. Additionally, due to a minimum landing size in Europe, undersized live Norway lobsters are discarded. The north-eastern Atlantic Norway lobster fishery has the fifth-highest discard rate of any fishery in the world, primarily due to the unselective trawl methods catching significant quantities of undersized Norway lobster and non-target vulnerable fish (Catchpole et al., 2008). Landed Norway lobster are required to have a minimum OCL of 20 mm on the west coast of Scotland and 40 mm in areas of Sweden, consequently the mesh size of the net is adjusted appropriately to minimise the number of undersize scampi caught. Strict regulations in Europe have driven innovations in trawl designs to reduce the number of discarded animals caught. Innovations include, square mesh panels placed at set distances from the cod-end (Catchpole et al., 2006b), windows of larger mesh sizes in the upper panel of the net (Revill et al., 2007), structures to separate the trawl into horizontal layers (Main & Sangster, 1985; Rihan & McDonnell, 2003), and using firm grids (Nordmøre grids) to physically remove larger fin-fish species and sieve scampi through to the cod-end (Catchpole, et al., 2006b; Catchpole, et al., 2008).

Efforts have been made to introduce these European trawl design innovations to the scampi fishery and reduce the amount of bycatch (Hartill et al., 2006). Nordmøre grids and varying mesh sizes in the main body and cod-end of nets were trialled in 1992 and 1996 respectively. The Nordmøre grids were observed to divert 80% of large fish and 30% of small fish from the trawl. The three cod-end mesh

sizes trialled were 35, 55 and 65 mm, with all the cod-ends retaining the most abundant scampi length classes, but only the 65 mm cod-end allowed the majority of bycatch fish to pass through. Less bycatch was caught per kilogram of scampi using a mesh size of 80 mm rather than 100 mm. Since 1992, the minimum legal sizes for cod-end mesh has been 55 mm and 80 mm for the main body of the net, although fishing companies have been known to experiment with larger mesh sizes in cod-ends and the body of the net, however, there is no consistency in the mesh sizes currently used by the scampi industry. Nordmøre grids were not adopted in the scampi fishery due to concerns with losing scampi, crew safety, and difficulties with deployment (Hartill, et al., 2006).

1.3.3 Potting for scampi: a sustainable alternative to bottom trawling

An alternative method of catching scampi is by pots, also known as traps or creels. Pots are a versatile and effective fishing technique that is globally responsible for significant landings of many species of high value crustaceans (Miller, 1990). Across Europe pots accounts for < 5% of the Norway lobster caught, however, the percentage of pot landings are much higher in areas such as Western Scotland (20%) and the Swedish west coast (25%) (Ungfors, et al., 2013). Pots are predominately fished in areas where there are regulations against using mobile trawl gear, including inshore areas, sea lochs, or areas with large boulders and soft muddy substrate where trawlers cannot normally operate (Leocádio, et al., 2012). Pot fisheries have been observed to have little to no impact on the benthic environment, have less bycatch, and the lobsters caught are typically larger and in better condition and able to attract higher prices in fresh and live export markets (Leocádio, et al., 2012; Morello, et al., 2009). On the Swedish coast fishers deploy 300-400 pots a day, which are left to soak for up to two and a half days. The number of pots a fisher can deploy in a day is regulated. For example, in Sweden fishers are limited to 800 pots per day, while in Scotland fishers are limited to 400 pots per day (Ungfors, et al., 2013). A potting trial for scampi was conducted in the Eastern Bay of Plenty in the 1980's and proved unsuccessful due to large bycatch of hagfish (*Eptatretus cirrhatus*) and sea-lice (Olsen & Aitken, 1987).

Fishing using baited traps also has problems, especially with natural bait, which tends to be expensive, difficult to handle and can require freezing. The cost of using and storing bait is significant to fishers using traps (Chanes-Miranda & Viana, 2000; Dellinger et al., 2016), who often use fish products that are suitable for human consumption (Vazquez-Archdale & Kawamura, 2011). For

example, in Norway lobster pot fisheries the cost of bait is estimated to contribute 5-10% of total fishing expenses, using on average 1.1 kg of salted herring per kg of lobster caught (Ungfors, et al., 2013). Pots have been observed to catch non-target species as well, such as hagfish, conger eels, curled octopus, poor cod, squat lobsters, sea-lice and crabs (Morello, et al., 2009). Variations in catch rates of pots are commonly observed, with lower than expected catch rates typically due to poor capture efficiency of the pot and the loss of bait due to scavengers (Morello, et al., 2009)

Traps are a passive method of fishing that operate by attracting the target species into the trap by using bait, conspecifics or shelter (Miller, 1990). Crustaceans rely on their chemosensory systems to track odours released into the water column by potential food items used as bait (Derby & Sorensen, 2008). This chemosensory system is typically 'tuned' to specific mixtures of stimuli that are present in the tissues of preferred prey (Barbato & Daniel, 1997; Carr et al., 1996; Derby, 2000).

Traditional bait and chums are usually chosen after many years of trial and error. However, choosing the most effective bait or chum may be accelerated when the processes of chemoattraction and feeding behaviour are properly understood in the context of the individual species (Atema, 1980). Therefore, to develop effective baits for a developing scampi potting fishery, an understanding of the feeding behaviour of scampi and their behavioural responses to a range of chemical stimuli are required.

1.4 Review of crustacean chemoattraction

1.4.1 Understanding chemoreception

Crustaceans use water-borne chemical cues to find food, mates and avoid predators (Hay, 2011). The sophisticated chemosensory systems of many crustaceans enables them to distinguish specific chemical cues from the background 'noise' of chemicals in the aquatic environment (Atema, 1988; Carr & Derby, 1986). While there has been no research into the chemosensory system or chemoattractants for scampi, decapod crustaceans have been subject to numerous chemoattractant investigations. The American lobster (*Homarus americanus*) and the Caribbean spiny lobster (*Panulirus argus)* are commonly used as model organisms in such studies (Caprio & Derby, 2008). Morphological similarities between Norway lobster, *Metanephrops* species and these model organisms suggest similar chemoreceptive functionality (Katoh et al., 2013).

1.4.2 Location and function of chemosensory receptors

Crustaceans detect chemicals with small cuticular sensory organs called sensilla. These sensilla have a variety of external structures, but they can ultimately be divided into two classes, bimodal sensilla and aesthetascs (Hallberg & Skog, 2011). Bimodal sensilla are innervated by 1-2 mechanoreceptor neurons and 1-22 chemoreceptor neurons, which project down the shaft of the setae to a pore on the tip (Garm et al., 2003). The bimodal sensilla vary in external structure and are unevenly distributed across the entire body with dense arrays on the walking legs (pereopods), mouthparts (maxillipeds) and as 'guard hairs' on the antennules (Derby & Atema, 1982). In contrast, aesthetascs are innervated by 40-500 chemoreceptor neurons, which project into the wide lumen of thin walled setae (Hallberg et al., 1992) and are morphologically homogenous and primarily located on the lateral filament of the antennules (Devine & Atema, 1982; Schmidt & Mellon, 2011).

The receptor-neurons at the base of the sensory setae project to anatomically distinct neuropils within the central nervous system and are referred to as the sensory pathways (Horner et al., 2004). The first is the distributed chemosensory pathway that is linked to the bimodal sensors, while the olfactory pathway is linked to the aesthetascs (Horner, et al., 2004; Schmidt & Mellon, 2011). Early studies attempted to define the distributed chemosensory system as relating to taste or gustation, similar to that of mammals or contact chemoreception in insects (Johnson et al., 1985). However, due to the range of behaviours mediated by the bimodal sensilla (food search, ingestion, antennular grooming and mating), defining this pathway simply as taste is thought to be inaccurate (Schmidt & Mellon, 2011).

The functions of the two sensory pathways are dictated by the structure of the sensilla. As the aesthetascs of the olfactory pathway have numerous chemoreceptor neurons, they provide a detailed picture of the chemical environment, and detect a variety of potentially interesting odours (food, conspecifics, predators, landscape) (Hallberg, et al., 1992; Steullet et al., 2001). Conversely, the bimodal sensilla contain few chemoreceptor neurons coupled with mechanoreceptors and are distributed throughout the body, allowing for chemoreception of a few key chemicals with an understanding of where on the body the chemicals are being sensed (Atema, 1996; Mellon, 2012). This enables the pin-pointing of chemical stimuli and can be used to control movements of the

stimulated appendage, such as the handling of food or prey items by pereopods (Schmidt & Mellon, 2011).

1.4.3 Chemoattractants in food items

Chemoattractants are defined as chemical stimuli that cause an animal to orientate and then move towards the source (Lee & Meyers, 1996; Lindstedt, 1971). There are variations in which chemicals crustacean species respond to, however, feeding behaviour appears to be regulated by the same general classes of chemicals; i.e., amino acids, nucleotides, low molecular weight amines, organic acids, and hexoses (Carr & Derby, 1986; Lee & Meyers, 1997). These compounds are common metabolites in the tissues of marine animals and occur at high concentrations of 10^{-3} to 10^{-1} M (Atema, 1988; Carr, et al., 1996). Electrophysiological studies have observed that specific chemoreceptor neurons are tuned to specific or small ranges of chemicals, and specific chemoreceptor neurons have been identified for glutamate, glycine, ammonia, hydroxyproline, taurine, small peptides, small amines nucleotides and pyridine (Garm et al., 2005). However, the most attractive cues have been complex mixtures of these cues, usually in the form of extracts from preferred prey (Derby & Sorensen, 2008).

1.4.4 Chemosensory thresholds of activity

The concentration of an attractant at which a crustacean responds is called the response threshold (Harpaz et al., 1987). Response thresholds are separated into a threshold of detection, the lowest concentration of an attractant that an animal can detect, and a behavioural threshold, the concentration required for movement subsequent to detection (Lee & Meyers, 1997). This is because physiological detection of chemical stimuli is a separate process from the initiation of a subsequent behavioural response, and triggering a behavioural response typically requires a significantly higher concentration of the specific chemical than is required for detection (Coman et al., 1996; Zimmer-Faust, 1991). For example antennule flicking is an observable behaviour associated with chemical detection in lobsters (Goldman & Patek, 2002; Schmitt & Ache, 1979). However, food search behaviour is not always triggered once antennule flicking or antennule grooming has been initiated, requiring a more intense stimulus (Atema, 1996; Derby & Atema, 1982). Thresholds of behaviour can vary greatly depending on the chemical compound being tested, and can vary among natural food extracts versus single chemicals, and can be affected by chemical synergies and mixture suppression (Carr & Derby, 1986). The internal state of the animal also effects how they respond to stimuli, with

hunger, reproductive status, diel rhythms, territoriality and previous experiences also potentially influencing their behavioural response to specific cues (Løkkeborg et al., 2014).

1.4.5 Chemically-mediated food search behaviour

Crustaceans, such as lobsters, use the receptors of both chemosensory pathways to gather information about food (Steullet, et al., 2001). As the receptors connect differently within the central nervous system, the behaviour influenced by each sensory pathway can be observed (Derby & Sorensen, 2008). The highly sensitive aesthetascs are usually first to detect a chemical stimulus in the water column. Lobsters and crabs respond to chemical stimuli by flicking their antennules, which flays out the aesthetascs, breaking down the boundary layer around them and improving the sampling of odour chemicals (Moore et al., 1991a). Both the aesthetascs and bimodal sensilla on the antennules are used to orientate the animal to the odour, as the mechano-receptors of the bimodal sensilla provide information about turbulent flow to help the animal locate the source of the chemical plume (Mellon, 2012; Pravin & Reidenbach, 2013; Webster & Weissburg, 2009). Once detected the crustacean must decide whether or not to search for the food source, which is typically dependent on the quantity and quality of the stimulus, physiological state of the crustacean, food preference, prior ingestive conditioning, and presence of any conspecifics or predators (Daniel & Derby, 1988; Derby et al., 2001; Moir & Weissburg, 2009; Tran, 2014). As the animal orientates towards the chemical source, typically into the current, it is continually sampling the environment with its antennules and maxillipeds (Atema, 1996). In some species of crustaceans searching behaviour in the immediate area is initiated by probing, raking and digging into the substrate with the dactyls of the pereopods prior to locomotion (Derby & Atema, 1982).

Lobsters move towards a food source by tracking the released plume of odorant chemicals from the source (Moore et al., 1991b). These plumes are influenced by the local hydrodynamics (Webster & Weissburg, 2009), creating complex three-dimensional structures containing filaments of high-concentration attractant chemicals interspersed with clear water (Atema, 1996; Moore & Crimaldi, 2004; Zimmer & Butman, 2000). Crustaceans use a range of orientation strategies which depend on the structure of odour plumes (Weissburg & Zimmer-Faust, 1994), the hydrodynamics of their environments (Jackson et al., 2007), the morphology of their sensory systems (Keller et al., 2003), and their locomotor abilities (Vasey et al., 2015).

1.4.6 Chemoattraction methodologies

Quantifying the behavioural response of crustaceans to chemoattractants is the key variable when comparing stimuli, such as different types of bait. The methods to investigate chemoattraction can be split into laboratory and field studies, with laboratory studies predominating in the published literature (Lee & Meyers, 1997). The most commonly used methods for researching chemoattraction have focused on introducing stimuli into simple static or flow-through tanks (Carr, 1978; Coman, et al., 1996; Krång & Rosenqvist, 2006; Nunes et al., 2006; Pittet et al., 1996), although Y-mazes or divided tanks with multiple choice options have also been used (Nunes, et al., 2006; Rebach, 1996; Sherba et al., 2000) . Stimuli which have been tested in these ways include singular and mixtures of amino acids (Coman, et al., 1996), artificial feeds, natural extracts and animal tissues (Krång & Rosenqvist, 2006; Nunes, et al., 2006). Investigations of the molecular nature of species-specific chemoattractants have used behavioural bioassays to either identify the bioactive molecules in preferred prey items (Kreider & Watts, 1998), or to compare behavioural responses to a number of natural products and then examine more closely the chemoattractive properties of the most attractive items (Zimmer et al., 1999).

Descriptions of chemoreceptive behaviour have been used to develop a behavioural model of crustacean feeding behaviour (Lee & Meyers, 1996). These behaviours have been classified into five distinct phases of chemoattraction; (1) detection, (2) orientation, (3) locomotion, (4) initiation of feeding, and (5) continuation of feeding. This behavioural model has been explicitly used by studies investigating feeding behaviour in penaeid shrimp, *Penaeus* spp. (Pittet, et al., 1996), Pacific white shrimp, *Littopenaeus vannamei* (Nunes, et al., 2006), and southern rock lobsters, *Jasus edwardsii* (Tolomei et al., 2003). Behavioural responses of crustaceans have been quantified primarily through timing phases of behaviour (detection, waiting and locomotion) and measuring rates of antennular flicking and sweeping or maxilliped and cheliped movement (Coman, et al., 1996; Krång & Rosenqvist, 2006; Pittet, et al., 1996). Other approaches have been to quantify movement towards the stimulus and grasping the source (Carr, 1978). Y-mazes or multiple choice chambers can remove the influence of rheotaxis from the study, as the only variable is the presence or absence of the chemical stimuli in an arm of the Y-maze (Boudreau et al., 1993; Lee, 1992). The choice of a stimulus by the animal can be clearly interpreted as chemoattraction, and this makes Y-mazes a powerful method for identifying chemoattractants.

Identifying feeding behaviour of crustaceans has been an issue for some studies, resulting in low levels of reproducibility (Moore, et al., 1991b; Pittet, et al., 1996; Ryan et al., 2014). The most successful studies have used multiple experimental approaches and measures of behaviour, including temporal and spatial measurements (Moore et al., 2015). A key point is to distinguish between detection and attraction behaviours with reaching the source of the chemoattractant chemicals ultimately being the desired result. This suggests the need for a hierarchy of experiments to identify effective chemoattractants for crustaceans that consistently stimulate this moement towards and reaching of the source. Therefore, to identify or develop an effective chemoattractant for NZ scampi a study must determine a method for reliably attributing observed behaviours to chemoattraction so that differences in observed behaviours can be associated with corresponding differences in the effectiveness of potential chemoattractants.

1.4.7 Developing chemoattractive bait

Bait is a key factor in trap fishing, and is highly dependent on stimulating feeding behaviour of the target species, especially food searching behaviour (Miller, 1990). The important aspects of stimulating feeding behaviour are; the chemoattractive compounds released, rate of release of compounds at a similar rate to natural prey, and developing an odour plume that exceeds the chemosensory response threshold of the target species at a distance from the source, so that movement towards the source is initiated (Zimmer, et al., 1999). Common natural baits used in fisheries around the world, such as squid, mackerel and herring meet these criteria. For example, mackerel baits used in long-lining can attract fish from up to 700 m away over the course of 7 hours (Løkkeborg, 1998). However, these baits are also suitable for human consumption and the populations of bait species are under increasing pressure from harvesting (Dellinger, et al., 2016; Driscoll & Tyedmers, 2010). This is leading to a growing demand on these food sources, resulting in increasing bait prices (Chanes-Miranda & Viana, 2000). Artificial baits using either synthetic chemicals or fish by-products as attractants have been proposed as a solution to this problem. Ideally, artificial baits should have good catch rates, be species-specific, cost effective, and practical for storage and baiting (Daniel & Bayer, 1989; Løkkeborg, et al., 2014; Vazquez-Archdale & Kawamura, 2011).

Artificial baits using fish by-products or extracts have targeted economically important decapod crustaceans such as crabs (Dale et al., 2007; Vazquez-Archdale & Kawamura, 2011), spiny lobster (Chanes-Miranda & Viana, 2000), freshwater crayfish (Beecher & Romaire, 2010), and homarid lobsters (Daniel & Bayer, 1989; Mackie et al., 1980). These baits have been reported to have varying levels of success. For example, more crabs per gram of fish were caught with an experimental artificial bait, containing fish and squid waste mixed with wheat starch and garlic, than natural bait (Vazquez-Archdale & Kawamura, 2011). Likewise, a low cost artificial bait made with by-products from tuna processing was found to be as effective as natural baits used in a spiny lobster pot fishery (Chanes-Miranda & Viana, 2000). Reportedly the only formulated bait currently being used commercially for crustaceans is in freshwater crayfish aquaculture during the harvest process (Beecher & Romaire, 2010). However, an increasing number of artificial baits are being investigated for use in commercial fisheries due to increasing constraints on the supply and price of natural baits (Dellinger, et al., 2016).

Artificial baits using synthetic attractants have not been as thoroughly investigated as natural extracts. However, a synthetic mixture of chemicals designed to replicate squid extract caught an acceptable number of European lobsters (*Homarus gammarus*) in pots during field experiments (Mackie, et al., 1980). Synthetic mixtures that mimic the chemical profile, concentration and release rate of natural prey extracts have been observed to be as effective as natural extracts for attracting the mud snail (*Ilyanassa obsolete*) (Zimmer, et al., 1999). The most successful synthetic attractants have been when they have been used in conjunction with low quality fish products such as fish meal (Mackie, et al., 1980). This approach has also been widely used by incorporating amino acid mixtures into fishmeal to make it more attractive and palatable for use in the formulation of feeds for aquaculture species (Nunes, et al., 2006; Williams et al., 2005).

1.5 Research aims and thesis structure

The main objective for the research presented in this thesis was to identify effective baits to assist with the development of a potting fishery for scampi. To do so, the chemosensory behaviour of scampi was investigated in a series of laboratory based behavioural assays as a method to distinguishing between candidate baits. Additionally, a field experiment was undertaken to assess

how baits influenced the operation of pots targeting scampi, especially in terms of the interaction with pot design and the resulting bycatch.

This thesis is structured into six chapters as follows:

Chapter 1: General Introduction

This introductory chapter provides an overview of the ecology of scampi, the status of the fishery and a review of the chemosensory systems of decapod crustaceans, and how this knowledge can be used to identify and develop baits. The research aims for the study are outlined.

Chapter 2: Laboratory investigations of the foraging behaviour of New Zealand scampi

This chapter presents research that quantifies the phases of chemically-mediated food search behaviour in scampi in the laboratory as a potential route towards more efficiently resolving potential differences in the attractiveness of different baits. In doing so, this research represents the first description of the foraging behaviour of a member of the *Metanephrops* genus.

This chapter has been published as:

Major, R. N., Ogilvie, S. C., & Jeffs, A. G. (2017). Laboratory investigations of the foraging behaviour of New Zealand scampi. *Journal of Experimental Marine Biology and Ecology*, 497, 99-106.

Chapter 3: Orientation and food search behaviour of a deep-sea lobster in turbulent versus laminar odour plumes

The specific aims of the research presented in this chapter was to determine how the foraging behaviour of scampi changes in response to two candidate baits for both turbulent and laminar flow regimes in an experimental seawater flume. Animal tracking techniques were used to calculate the efficiency of the scampi search paths within the flume.

This chapter has been published as:

Major, R. N., & Jeffs, A. (2017). Orientation and food search behaviour of a deep sea lobster in turbulent versus laminar odour plumes. *Helgoland Marine Research*, 71(1), 9.

Chapter 4: Laboratory comparison of potential baits for potting New Zealand scampi

This chapter presents the results of the use of a binary-choice flume to identify potentially attractive bait materials for a scampi potting fishery, and to examine the potential for baits consisting of reduced amounts of fish tissue set in an alginate binder. Additionally, the research compares the attractiveness of the baits in relation to measures of the free amino acids released over the course of the experiment.

Chapter 5: Factors affecting bycatch in a developing New Zealand scampi potting fishery

The research presented in this chapter examined the factors influencing the bycatch of non-target species in experimental pots targeting scampi and deployed in two commercial scampi fishing grounds. The quantity of bycatch in experimentally deployed pots were assessed in relation to the bait species, pot design, pot soak time, deployment event, individual string on which any pot is deployed, and effectiveness of the design of the bait containers as assessed by the presence of sea lice and residual bait in the container.

This chapter has been published as:

Major, R.N., Taylor, D.I., Connor, S., Connor, G., Jeffs, A.G., 2017. Factors affecting bycatch in a developing New Zealand scampi potting fishery. *Fisheries Research,* 186: 55-64.

Chapter 6: General Discussion

This chapter presents a summary of the key findings from the previous chapters, including recommendations for the way forward for identifying more effective baits for developing a potting fishery for scampi.

Chapter Two:

Laboratory investigations of the foraging behaviour of New Zealand scampi

2.1 Introduction

2.1.1 Chemically-mediated foraging behaviour

Motile animals must forage efficiently in order to procure food resources to grow and survive (Pearce-Duvet et al., 2011; Stephens & Krebs, 1986). Lobsters, and other decapod crustaceans, use their chemosensory systems to detect and identify food items remotely, a distinct advantage in how they make foraging decisions (Zimmer-Faust, 1987). These foraging decisions are based on the 'quality' of the attractant chemicals, i.e. the similarity of the attractant chemicals to dietary items, and internal factors that affect how risk adverse the animal is (Steele et al., 1999; Zimmer-Faust, 1987).

The quality of the odorant chemicals is dictated by the mixtures of stimuli that the chemosensory system of the crustaceans is 'tuned to', primarily, what is present in the tissues of preferred dietary items, for example herbivorous crabs are attracted to sugars (Barbato & Daniel, 1997; Derby, 2000; Steullet & Derby, 1997; Vazquez-Archdale & Anraku, 2005; Vazquez-Archdale & Nakamura, 1992). The chemical nature of the stimulants of crustacean feeding behaviour have been suggested to be common metabolites of low molecular weight, primarily amino acids, but also quaternary ammonium bases, nucleotides, nucleosides and organic acids (Carr, 1988; Carr, et al., 1996; Zimmer & Butman, 2000). Mixtures of these compounds that simulate prey odours are considered to be of higher quality, than single chemical stimuli as they get stronger responses from crustaceans (Carr & Derby, 1986; Mackie & Shelton, 1972). These chemicals are transported as a filamentous plume that varies both spatially and temporally, to the lobster by the local hydrodynamics (Zimmer & Butman, 2000).

The foraging behaviour of lobsters and other decapod crustaceans is driven by two sets of chemosensory organs, which they use to detect and search for food. Firstly, the unimodal chemosensory aesthetascs, which are present on the lateral antennule, and are linked into the olfactory pathway in the central nervous system (Derby et al., 1984; Mellon, 2005). Secondly, bi-modal chemo-and mechanical sensilla, which are present in dense tufts on the mouthparts and

dactyls, and unevenly distributed on other parts of the body, which are linked to the distributed sensory pathway (Derby & Atema, 1982; Garm, et al., 2005). This diverse range of sensory organs mediates a diverse range of behaviours (Derby & Sorensen, 2008). The aesthetascs and olfactory pathway have been shown to dictate distance chemoreception, alarm cues and social interaction (Derby, et al., 2001; Horner et al., 2008; Shabani et al., 2009). Whereas, the bimodal sensilla are primarily contact driven and used to find food when the animal is within close proximity of source, for example digging and raking with the walking legs (Derby & Atema, 1982; Garm, et al., 2005). The function and behaviour mediated by this distributed sensory pathway can overlap with the olfactory pathway (Schmidt & Mellon, 2011), and decapods have been shown to detect and orientate to distant food odours just using these organs (Horner, et al., 2004; Keller & Weissburg, 2004; Steullet, et al., 2001). While there is overlap between these systems, it is between the aesthetascs and the bimodal sensilla also present on the antennules, and studies have shown that with the antennules completely ablated (i.e., all sensilla removed) lobsters cannot locate food sources (Horner, et al., 2004; Steullet et al., 2002). Therefore, by observing how lobsters use their appendages (i.e., antennules for distance chemoreception, walking legs direct nearfield food search and mouthparts to determine whether a food item should be eaten) (Caprio & Derby, 2008), studies have been able to quantify aspects of their food search behaviour and compare response to different food odours and concentrations (Pittet, et al., 1996; Steele, et al., 1999).

In addition to this foraging behaviour, crustaceans must also be able to respond appropriately to repellent or adverse cues (Weissburg et al., 2012). Crustaceans typically respond to this risk by suppressing foraging behaviour, or being less motivated to forage. However, risk sensitivity is suggested to be costly, as it diminishes the opportunity for foraging (Chivers & Smith, 1998). Risk sensitivity of an animal is related to a number of internal factors such as hunger level (Kidawa et al., 2004), size (Moir & Weissburg, 2009), and moult cycle (Lipcius & Herrnkind, 1982).

2.1.2 Metanephrops species

The genus *Metanephrops* is comprised of 18 extant species of clawed lobsters that are typically found on areas of muddy sediment on the upper slope of the continental slope in depths between 50-700 m in a number of oceans around the world (Bell, et al., 2013). Important commercial trawl fisheries exist for New Zealand scampi, *Metanephrops challengeri* (New Zealand), *M. armatus, M. formosanus*

(Taiwan), *M. andamanicus, M. australiensis, M. velutinus* (North-West Australia), *M. japonicas* (Japan), *M. mozambicus* (South-East Africa) and *M. thomsoni* (Korea, Taiwan) (Bell, et al., 2013; Holthuis, 1991), while *M. binghami* (Venezuela, Colombia) has been suggested as the target of a new deep sea fishery (Paramo & Saint-Paul, 2012). The majority of our knowledge of the ecology and behaviour of members of this genus is derived indirectly from catch data from trawl fisheries (Paramo & Saint-Paul, 2012; Tuck, 2014; Ward & Davis, 1987), photographic surveys (Cryer, et al., 2001; Cryer et al., 2004), biological investigations of deceased animals (Choi, et al., 2008; Sahlmann, et al., 2011; Wassenberg & Hill, 1989), and recent studies of burrow emergence behaviour using acoustic tags (Tuck, 2015). Additional information has been inferred from laboratory behavioural studies of the ecologically similar, but taxonomically more distant (Chan et al., 2009; Tshudy, et al., 2009), Norway lobster, *Nephrops norvegicus.* In this species there are studies of their sensory biology (Farmer, 1974a; Krång & Rosenqvist, 2006; Newland et al., 1988) emergence behaviour (Sbragaglia et al., 2013; Sbragaglia et al., 2015), and social interactions (Katoh et al., 2008).

The diets and feeding ecology of *M. australiensis*, *M. andamanicus, M. boschmai* (Wassenberg & Hill, 1989), and *M. thomsoni* (Choi, et al., 2008) species have been studied through gut content analyses, while *M. formosanus* and *M. armatus* have been subject to studies of the morphology of their mouthparts, gut content and tank based videos of their feeding behaviour (Sahlmann, et al., 2011). Gut contents studies of *Metanephrops* species have found both fish and crustacean items in the foregut (Choi, et al., 2008; Wassenberg & Hill, 1989). Morphological studies of *M. formosanus* and *M.* andamanicus, observed that the second maxilliped, first and second maxilla and mandible of the *Metanephrops* species were more slender in form than that of another deep-water lobster, *Puerulus angulatus,* and suggest that they are predators and/or scavengers on small crustaceans (Sahlmann, et al., 2011). These findings are similar to studies of Norway lobster, which have suggested that they non-selectively consume a variety of crustaceans, fish and mollusc species as an active predator or scavenger (Cristo, 1998; Cristo & Cartes, 1998). However, one key aspect of the feeding ecology of *Metanephrops* species that has not been studied is their foraging behaviour. An improved understanding of their foraging behaviour can help with the development of more sustainable methods for harvesting members of this genus, such as through the use of potting versus the status quo of sea bed trawling (Major et al., 2017b; Suuronen, et al., 2012). There are currently no potting fisheries for any *Metanephrops* species*.* Pots have been commonly used to harvest Norway lobster*,*

for the past 30-40 years in parts of Sweden, Scotland and Portugal where they can account for up to 25% of the local Norway lobster catch, overall pots account for 5% of the total European catch of Norway lobster (Ungfors, et al., 2013).

2.1.3 Aims and objectives

The aim of the work presented in this chapter was to identify and quantify the phases of chemically-mediated food search behaviour of this scampi species in a laboratory-based behavioural assay. Specific objectives to achieve this aim are: (1) to describe and quantify the foraging behaviour of scampi, (2) To observe if the foraging behaviour of scampi varies in response to different tissues from a range of marine taxa that have been identified as being part of the diet of different *Metanephrops* species, (3) To observe if a number of motivational factors (sex, size and starvation state) affect this food search behaviour. The study hypothesised that the food search behaviour of scampi would vary among the different tissues, and that sex, size and starvation state would not affect these behaviours.

2.2 Materials and methods

2.2.1 Experimental animals

The scampi used in the experiments were obtained from a depth of 300 m off the Cape Palliser coast of the North Island of New Zealand (40° 38' S; 176° 50'E) in October 2014 using a a short duration, 2 hour bottom trawl at slow speed of 2.8 km h^{-1}. One hundred and twenty scampi that were in good condition upon landing were transferred into aquaria with seawater chilled to their ambient temperature at point of capture (10°C). The scampi were transported to the laboratory at the Cawthron Aquaculture Park in Nelson, New Zealand, where they were held in a recirculating aquaculture system at 10.5°C with a salinity of 36 ppt. The seawater for the aquaculture park and recirculating system is obtained from Tasman Bay. The scampi were held in individual enclosures in plastic tanks under red light (λ > 600 nm) for at least a week to acclimatise prior to commencing experiments. During acclimatisation, the scampi were fed every three days with a mix of squid, mackerel and ProChaete pellets, a polychaete-based aquaculture feed, (ProChaete Innovations Ltd, U.K.). Food was withheld from scampi for 5-7 days (starvation period) before they were used in behavioural experiments to ensure they were responsive to food odour cues

2.2.2 Behavioural assay

Individual scampi were transferred in a darkened container and placed behind a removable, solid divider 30 cm from the end of the experimental polyethylene tank (1.8 × 0.56 × 0.54 m) filled to a water height of 0.25 m, a volume of approximately 390 l (Fig. 2.1). Freshly filtered (5 µm, UV sterilised) seawater was supplied to the opposite end of the tank at 30 ml s^{-1} via a PVC manifold and through a corrugated plastic collimator to smooth the flow of seawater, with the water flowing past a bait station in the centre of the tank and 10 cm from the collimator. Water flow in the experimental tank was visualised using food-colouring dye prior to any experiments occurring. A faster flow was observed in the middle of the tank compared to the edges, due to hydrodynamic drag on the sides of the tank. The dye visualisations were characterised by a plume arising from the position of the bait that was comprised of turbulent filaments that moved at a consistent speed, taking 1 min to flow along the length of the experimental arena of the tank (flow velocity of 1.8 cm s^{-1} at the centre of the plume).

The tank was emptied and cleaned after all flow visualisations. Beyond the bait station, the water flowed over the length of the tank and discharged at the outlet. The scampi was allowed 30 min to recover from handing stress behind the divider before the experiment began. If the scampi showed signs of stress or abnormal behaviour, such as extended tail flapping, prior to, or during, transfer to the experimental tank then it was returned to the holding tank, and an alternative scampi used. After the 30 min recovery period, 5 g of the bait treatment was placed, with a gloved hand, into the tank floor 1.1 m upstream of the divider, and then the divider was removed.

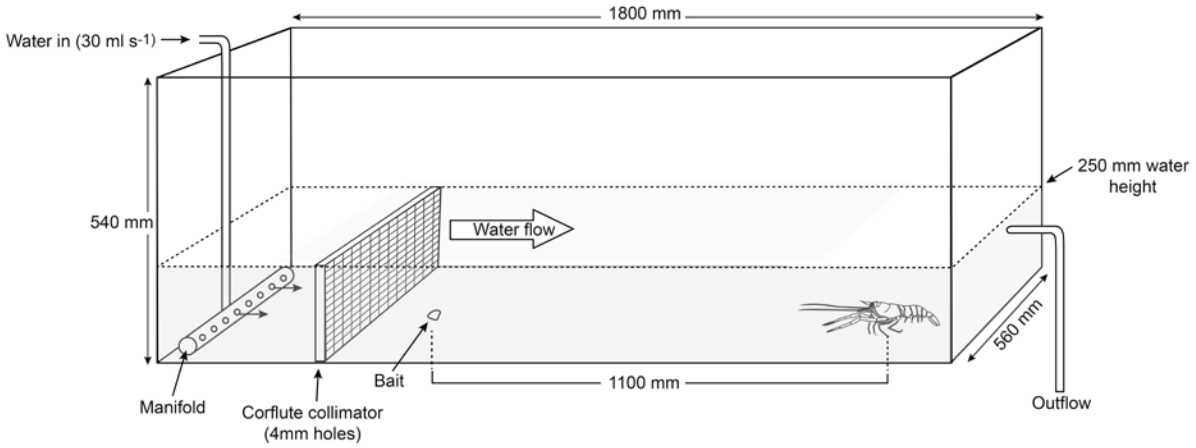

Figure 2.1 Diagram of the experimental behavioural chamber used to record the chemically-mediated food search behaviour of scampi. Experiments were run under infrared lighting and were filmed from an overhead video recorder.

The five bait treatments were comprised of a 5 g glass control and four natural baits, being jack mackerel flesh (*Trachurus declivis*), New Zealand arrow squid mantle (*Nototodarus sloanii*), green-lipped-mussel gonad (*Perna canaliculus*), and crushed whole New Zealand porcelain crab (*Petrolisthes elongates*). Each of the bait treatments were replicated 15 times (n = 15, a total of 75 experiments). The mackerel, squid, and mussel treatments were prepared by cutting fresh tissue into 5 g portions while the crab treatment consisted of whole specimens, both of which were frozen until required, and defrosted immediately prior to the experiment commencing.

The behaviour of the scampi was recorded in human visual spectrum darkness with an overhead video camera (Brinno TLC200Pro in ASAP mode) with infrared lighting for the 30 min experimental period. After each experiment, the tank was drained and thoroughly cleaned using a scrubbing brush to remove any residual bait odours before being re-used. The timing of the recovery and experimental periods are based on similar experiments with Norway lobster (Krång & Rosenqvist, 2006). If the scampi did not leave the starting area during the experimental time-frame the video was not used in the analysis. Only five experiments were rejected (2 from the squid, 2 from the mackerel and 1 from the mussel gonad treatments) due to inactive scampi.

Due to a limited supply of scampi a true 50:50 sex ratio could not be achieved, this resulted in a total of 61 male and 14 female scampi with orbital carapace lengths (OCL) ranging from 21.86 – 54.84 mm

(mean = 40.8 ± 0.8 mm) used in the experiments. No gravid females were used and any scampi that had recently moulted (i.e. were still soft to touch) were excluded from experiments. The OCL of each scampi was measured (mm) using callipers after the experiment and no scampi were subjected to repeated experiments.

2.2.3 Video analyses

Phases of behaviour have been used in investigations of feeding behaviour of a number of decapod crustaceans including, penaeid shrimp, *Penaeus* spp. (Nunes, et al., 2006; Pittet, et al., 1996), freshwater prawns, *Macrobrachium rosenbergii* (Mendoza et al., 1997), red swamp crayfish, *Procambarus clarkii* (Montemayor et al., 2002) and Australasian red spiny lobsters, *Jasus edwardsii* (Tolomei, et al., 2003). These studies have typically identified the phases as; 1) detection, 2) orientation, 3) locomotion, and 4) initiation of feeding (Lee & Meyers, 1997). However, during the experiment the scampi did not display the orientation behaviour as described by this framework, therefore, phases (2) and (3) were integrated into one phase called 'Search Period'. The 30 min digital video recordings of scampi food search behaviour were replayed and analysed in relation to the following parameters;

1) **Time to detection** - the time taken from when the divider restraining the scampi was lifted until detection of the bait odour by the scampi. Time to detection has been observed as an important measure of the release of chemicals from baits in previous studies (Keller and Weissburg, 2004). Observable behaviours in scampi were; a marked increase in the movement of appendages that contain the chemosensitive sensilla, including flicking or grooming of the antennae and antennules, beating of mouthparts and digging with, and wiping of dactyls.

2) **Wait period** - the time from the commencement of detection behaviour until the beginning of the search period. The scampi would typically continue to display detection behaviour during this period.

3) **Search period** - from when the scampi started locomotion or orientated into the water current, to the time it arrived at the bait.

4) **Time to reach bait** - time for all of the other behavioural phases combined, i.e., from the time the barrier was lifted to when the scampi reached the bait.

2.2.4 Statistical analyses

Fisher's exact tests were used to analyse contingency tables (5 rows × 2 columns) comparing the proportion of scampi which completed each of the phases of behaviour (West & Hankin, 2008). Where there was overall significance ($P < 0.05$), post-hoc pairwise Fisher's exact test were used to compare all of the treatments (10 pairwise comparisons) as 2 × 2 tables, a Benjimani-Hochberg correction was used to control the familywise error rate while making multiple comparisons (McDonald, 2014).

The time for each phase of chemically-mediated food search behaviour was analysed using linear models that incorporated the influence of the bait treatment, scampi size, sex, and length of the prior starvation period (5 - 7 days). Assumptions of data normality and homoscedasticity were tested for measures of the time taken to complete each behavioural phase using Shapiro's and Levene's tests respectively. The raw data did not meet these assumptions and was therefore log transformed. When a significant effect was observed for any of the factors on the length of a behavioural phase, post-hoc Tukey's tests were used for pairwise comparisons among treatment means. All means are presented with ± standard errors (S.E.). All analyses were done using R software and multiple comparisons of models using the Multcomp package (Hothorn et al., 2008; R Core Team, 2016).

2.3 Results

2.3.1 Generalised behaviour

During the experiments a number of general behaviours were observed that were not part of the hypothesised model of chemically-mediated food search behaviour. The most common behaviours were exploration of the sides of the tank and interaction with the collimator. This typically happened before the scampi detected the odour plume, or if it was at the edge of the tank where the flow velocity was much lower than in the centre. General behaviours also occurred during the search period, when some of the scampi would move towards the bait, then retreat back to where they started from and either explore the sides of the tank, or walk past the bait and back into a corner close to it.

2.3.2 Time to detection

Once the divider enclosing the scampi in the tank was lifted and the scampi encountered the odour plume, they would commence odour detection behaviour. This was primarily comprised of flicking and

grooming of the antennules, rotating on the spot, as well as raking and attempting to dig with their dactyls. Movement of the chelipeds was a common behaviour, which occurred when the scampi were fanning their maxillipeds to generate a water current over their antennules, a behaviour which improves their ability to sample the odour plume (Breithaupt, 2001; Denissenko et al., 2007).

The bait treatment was observed to affect the proportion of scampi that exhibited odour detection behaviour ($P < 0.001$). All of the scampi displayed detection behaviour when presented with the four different natural baits, which was significantly higher than the percentage of scampi (53%) that exhibited detection behaviour in the control treatment (pairwise comparisons for all natural baits vs control, $P = 0.014$) (Fig. 2.2). The mean time to detection was shortest for the mackerel treatment (159 ± 21 sec) and longest for the control treatment (1080 ± 99 sec) (Fig. 2.3). The mean time to detection was found to be significantly influenced by the bait treatment ($F = 8.0$, $P < 0.001$), however, sex, starvation period and animal size did not have any significant influence (Table 2.1). Scampi started displaying detection behaviour significantly faster in response to the mackerel ($t = 4.68$, $P < 0.001$), mussel gonad (350 ± 62 sec; $t = 3.12$, $P = 0.009$), squid (324 ± 74 sec, $t = 4.50$, $P < 0.001$), and crab treatments (383 ± 71 sec, $t = 2.71$, $P = 0.022$) than to the control treatment (1080 ± 99 sec). Among the natural bait treatments, scampi displayed detection behaviour significantly faster in response to the mackerel treatment than to the crab bait treatment ($t = 2.47$, $P = 0.03$).

2.3.3 Wait period

The mean length of wait period was shortest for the mackerel treatment (121 ± 25 sec), and longest for the mussel gonad (530 ± 49 sec) (Fig. 2.3). The length of the wait period was found to be significantly affected by the bait treatment ($F = 3.51$, $P = 0.013$), however, sex, starvation period and size of the scampi were found to not affect the length of the wait period (Table 2.1). Scampi presented with the mackerel and squid (202 ± 49 sec) treatments had significantly shorter wait periods than scampi presented with the mussel gonad treatment (530 ± 49 sec) (mackerel vs mussel gonad: $t = 3.04$, $P = 0.036$; squid vs mussel gonad: $t = 2.75$, $P = 0.040$).

2.3.4 Search period

Bait treatment significantly affected the proportion of scampi that searched for the bait ($P < 0.001$). Scampi searched for the natural baits at significantly higher (all natural baits $P < 0.001$) proportions (all 100%), than in response to the control treatment (33%) (Fig. 2.2).

The type of bait was observed to not significantly affect the time that the scampi spent searching for the bait (F = 0.177, P =0.17). Regardless, scampi had the fastest search period in response to the squid treatment (195 ± 83 sec) versus the mussel gonad, which had the slowest search period (341 ± 144 sec) (Fig. 2.3). None of the experimental factors analysed (i.e. sex, starvation period and size of the scampi) were found to significantly influence the search period (Table 2.1).

2.3.5 Reaching the bait

As none of the scampi reached the control treatment, the type of bait was observed to significantly affect the proportion of scampi that reached the bait in the experiments (P < 0.001). Among the natural baits the proportion of scampi that reached the bait station was highest for the mackerel treatment (80%), and lowest for the mussel gonad (40%) (Fig. 2.2). The scampi reached the crab (P = 0.003), mackerel (P < 0.001) and squid (P = 0.007) treatments at significantly higher proportions than the control bait. However, no significant differences were observed in the proportion of scampi that reached the natural baits.

Squid had the lowest mean time to reach the bait amongst the natural bait treatments (500 ± 169 sec), and the mussel gonad had the highest (1005 ± 258 sec) (Fig. 2.3). Bait treatment (F = 3.62, P = 0.026) and starvation period (F = 4.34, P = 0.023) were both found to significantly influence the time taken for the scampi to reach the bait, while sex and size of the scampi did not (Table 2.1). Among the natural bait treatments the scampi reached the squid treatment significantly faster than the crab (939 ± 137 sec; F = 3.05, P = 0.015) and mussel gonad bait treatments (F = 3.44, P = 0.011). Scampi that were starved for 7 days were observed to be significantly faster to the bait than the scampi starved for 6 days (t = 2.59, P = 0.039), but not the scampi starved for 5 (t = 2.36, P= 0.064).

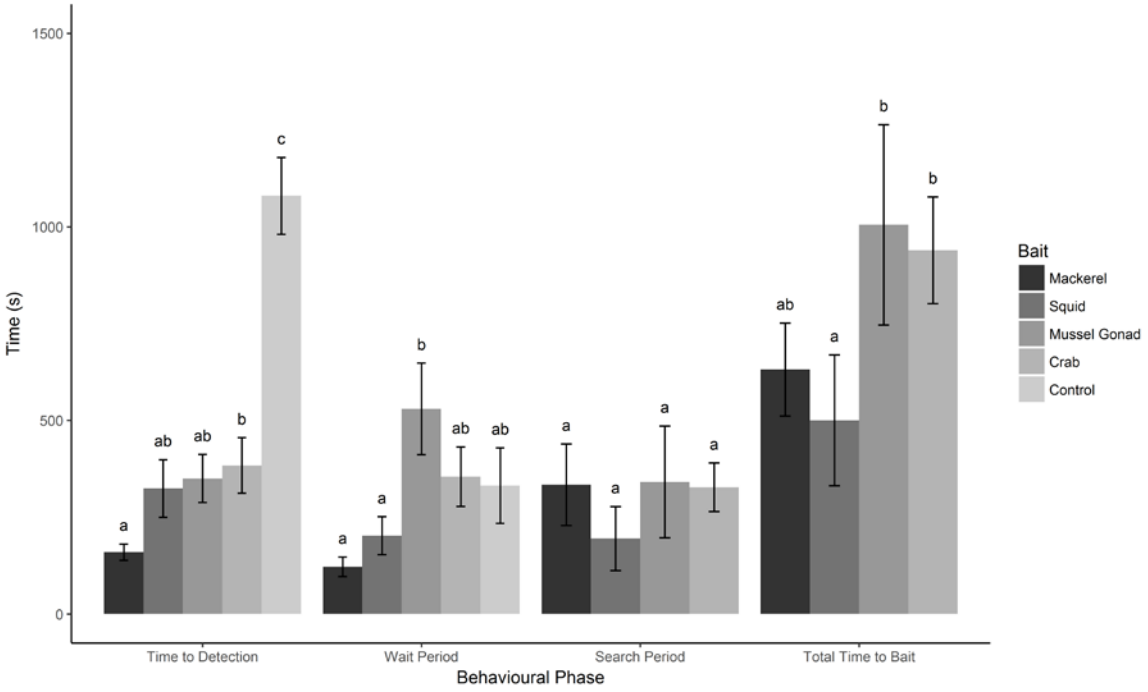

Figure 2.2 The mean time (±S.E.) that it took the scampi to complete each behavioural phase, and the total time to reach the bait, for the five bait treatments. Letters denote significant differences among baits within behavioural categories as determined by a post hoc Tukey test ($P < 0.05$). N = 15 for each treatment.

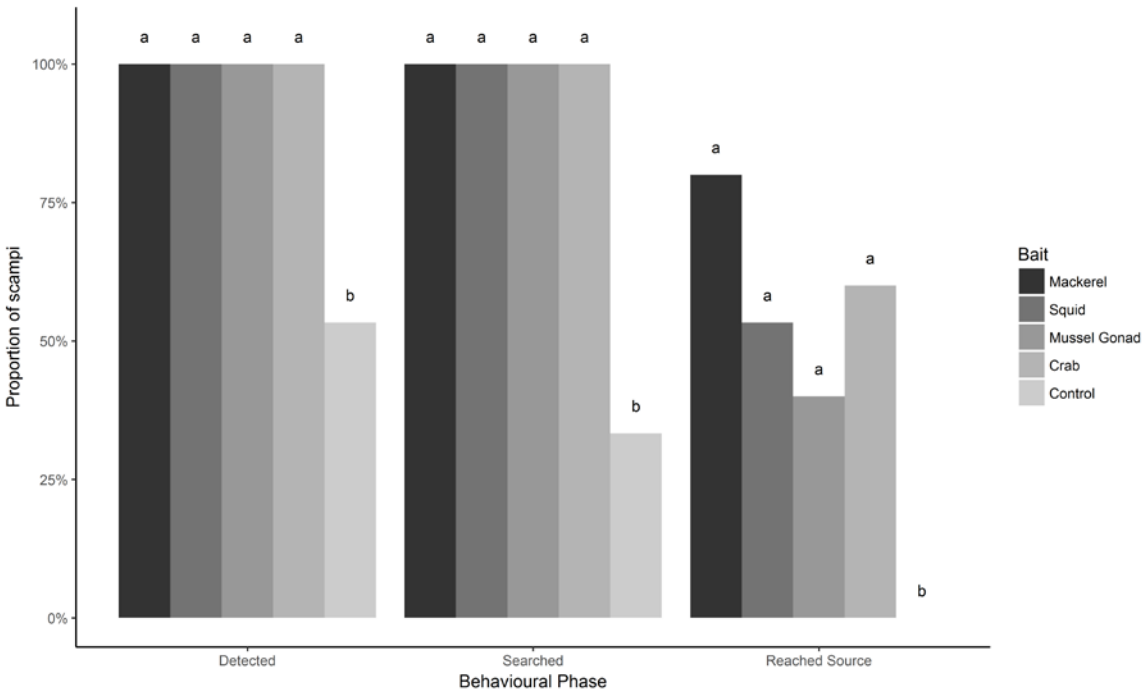

Figure 2.3 Percentage of scampi which detected, searched for, and reached the bait for each bait treatment; Letters denote significant differences ($P < 0.05$) among baits within behavioural categories as determined by pairwise Fisher's exact tests. N = 15 for each treatment.

Table 2.1 Results from an ANOVA of a multiple regression accounting for the influence of the bait treatment, size, sex and starvation period on each phase of chemically-mediated food search behaviour in scampi in relation to four natural bait treatments and an inert control.

		df	SS	MS	F	P
Time to detection						
	Bait treatment	4	23.7	5.9	8.0	<0.01
	Size	1	0.4	0.4	0.5	0.5
	Starvation period	2	0.1	0.07	0.1	0.9
	Sex	1	2.3	2.3	3.1	0.08
	Residuals	59	43.5	0.7		
Wait period						
	Bait treatment	4	17.5	4.4	3.5	<0.01
	Size	1	0.2	0.2	0.2	0.7
	Starvation period	2	3.0	1.5	1.2	0.3
	Sex	1	0.03	0.03	0.03	0.9
	Residuals	56	69.9	1.3		
Search period						
	Bait treatment	3	5.3	1.8	1.8	0.2
	Size	1	1.0	1.0	1.0	0.3
	Starvation period	2	5.2	2.6	2.6	0.09
	Sex	1	0.4	0.4	0.4	0.5
	Residuals	27	26.9	1.0		
Total time to bait						
	Bait treatment	3	5.5	1.8	3.6	0.03
	Size	1	0.2	0.2	0.4	0.5
	Starvation period	2	4.2	2.1	4.2	0.03
	Sex	1	0.3	0.3	0.7	0.4
	Residuals	27	13.7	0.5		

2.4 Discussion

2.4.1 Chemically-mediated food search behaviour

The study was able to identify and quantify the phases of chemically-mediated food search behaviour of scampi by observing how they used their chemosensory appendages. By doing so, the study found that scampi detected, searched for and reached the natural bait treatments at significantly higher proportions than an inert control treatment. However, no differences in the proportion of scampi that displayed these behaviours were observed among the four natural baits. Scampi did show differences in the time to detection, wait period, and total time to reach bait among the four natural bait treatments; however, these differences were not consistent. Therefore, the study shows that scampi do not show a higher level of attraction to any of the food types presented in this experiment. The range of tissues used in the experiments were determined from previous studies of *Metanephrops* diets, and this suggests that scampi have similar diets to that of other deep-water lobsters and potentially act as generalist feeders, consuming what is within reach of their burrows, similar to Norway lobster (Cristo & Cartes, 1998). Additionally, as fish in the diet of deep-water lobsters would primarily be available as discards from trawl fisheries and found via scavenging, whereas crustacean, mollusc and cephalopod tissue would come from predation (Berry 1969; Choi, et al., 2008; Wassenberg & Hill, 1989). By displaying chemoattractive behaviour in response to all of these tissues may indicate that scampi have some plasticity in their modes of foraging and feeding ecology (Trott & Robertson, 1984). Responding similarly to a range of tissues could be an ecological advantage for scampi as it would allow the scampi to spend less time foraging outside of their burrows and be able to avoid their primary predators, ling and skates (Dunn, et al., 2010; Forman & Dunn, 2012).

The differences observed in the phases of chemically-mediated food search behaviour due to the different bait treatments, allow conclusions to be drawn about how scampi search for food and their feeding ecology. Firstly, detection behaviour is known to occur when the concentration of odorant chemicals in the water is higher than the physiological detection threshold (Mackie & Shelton, 1972; Zimmer-Faust, 1991). Therefore, as there was no difference in the time to detection among the baits, the results suggest that all of the natural baits released chemicals at concentrations that the scampi were able to detect. The wait period is the time from detection to the initiation of search behaviour characterised as locomotion. This latency has been suggested to occur as the lobsters discriminate among attractive and adverse signals and decide to search (Derby, et al., 2001). Learning and

conditioning has been shown to be a key factor in the decision to search and experiments have shown that crustacean search latency can be affected by previous experiences (Daniel & Derby, 1988; Derby, 2000; Steullet & Derby, 1997; Weissburg, et al., 2012). As the scampi had a shorter wait period in response to the mackerel and squid bait treatments than the mussel gonad, this may potentially be due to the feeding of these tissues in captivity prior to the experimentation. Of the factors investigated by the study that would affect the risk-aversion behaviour of the scampi, only starvation period was observed to significantly affect the total time to the bait, with scampi starved for 7 days being faster to the bait than scampi starved for 5. Starvation is its own risk for animals, and longer starvation periods have been found to reduce the risk-sensitivity of blue crabs (Moir & Weissburg, 2009). The other factors have been used to show how crustacean species respond in reaction to predators, and as there would be no predatory signals in the experimental tank, there would be nothing for them to sense and display aversion behaviour to. Interestingly, the size of scampi did not influence their chemically-mediated food search behaviour. Size along with age are ontogenic factors that typically affect the risk aversion of crustaceans, as larger animals are more likely to be able to avoid predation (Moir & Weissburg, 2009). In this study, sex was also not observed to significantly influence any of the phases of chemically-mediated food search behaviour for the natural baits in scampi. This result is consistent with a study which found similar food search behaviour of both male and female *Macrobrachium rosenbergii* in response to food extracts and single chemicals (Mendoza, et al., 1997).

Crustacean search success has been attributed to the flow dynamics which create the plume and the rate at which the attractant chemicals are released from the bait (Keller & Weissburg, 2004; Moore, et al., 1991b; Page et al., 2011a, 2011b; Webster & Weissburg, 2001). Therefore, the differences observed may be related to the rate of release of the attractant chemicals from the tissues. The release rate of chemicals has been observed to decrease rapidly over time, and baits which have a greater ratio of their surface area exposed to the water release attractants at a higher rate (Løkkeborg, 1990; Westerberg & Westerberg, 2011). In the experiment, the squid was in a single piece and the crab was crushed. This may have resulted in a larger surface area of crab being exposed to the water currents, and a single large burst of attractants being released resulting in a plume which was harder to track (Keller & Weissburg, 2004). Additionally, the whole crushed crab

would have released different types of chemicals than the pieces of tissue, and may not have been as attractive to the scampi (Carr, et al., 1996).

Some of the potential variability in the results could be related to the flow of water within the experimental tank and the uncontrolled release of the odour from the source (Moore, et al., 1991b). For example, lifting the divider separating the experimental arena from the starting area may have interrupted the flow within the tank for a number of minutes. However, as the tank conditions were the same for every replicate, And acclimatising the scampi in the full tank, rather than behind a solid divider, would have avoided the exploratory behaviour of the scampi. Additionally, the small size of the experiment tank may have resulted in the lack of differences between the bait types as encountering the bait becomes a factor of activity rather than attraction (Ryan, et al., 2014). This highlights the need for future fieldwork with the baits that would identify which are the most attractive.

2.4.2 Application to identifying a bait for fisheries

Although the results of the study could not consistently separate all of the baits, mackerel and squid baits stand out as the leading candidates. Consequently, these baits could be a useful starting point for a developing potting fishery. Unfortunately, both mackerel and squid are expensive and potentially used for human consumption. However, if scampi are generalist feeders as observed by the results of the study, there is the potential for a wide range of baits to be used to effectively target this species and other *Metanephrops* species in potting fisheries. Future research should investigate the attractiveness of alternative baits to scampi, with the additional aim of enhancing the sustainability and cost-effectiveness of the fishery through bait choice (Vazquez-Archdale & Kawamura, 2011). For example, previous studies have investigated the use of fish meal (Daniel & Bayer, 1989), synthetic molecules (i.e., putrescine and cadaverine) (Mendoza, et al., 1997) , aquaculture and fish processing by-products (Chanes-Miranda & Viana, 2000; Dale, et al., 2007; Vazquez-Archdale & Kawamura, 2011), and pheromones (Aquiloni & Gherardi, 2010) as sustainable baits for crustaceans. Aspects of potential baits that may also warrant further examination include the extent of their attractive odour plume and the duration of their continued attractiveness to scampi given the extended pot soak times of 2.5 days on average used in *Nephrops* potting fisheries (Ungfors, et al., 2013; Westerberg & Westerberg, 2011). Studies of a range of marine species have used multi-choice flumes to compare

chemically-mediated search behaviour to locate both mates and food (Bushmann & Atema, 2000; Lee, 1992; Nunes, et al., 2006), and may be a suitable approach to identifying baits for scampi.

2.4.3 Conclusions

This study represents the first investigation of the foraging behaviour of a member of the *Metanephrops* genus, describing and quantifying the food search behaviour of scampi and determining attraction to a range of food types. The results highlight that scampi use their chemosensory system to detect, search for, and find, mackerel, crab, and squid at significantly higher proportions than in response to an inert control. However, few differences were observed in the time it took for scampi to progress through the phases of chemically-mediated food search behaviour in response to the four natural bait treatments and the differences that were observed were not consistent among the different phases. These results potentially indicate that this species is a generalist feeder consuming a wide range of taxa. Future directions for this work include the use of these baits in field studies to observe differences in catch of scampi. Additionally studies of the gut content of scampi would identify their actual dietary items, which may provide insight to natural tissues with high attraction to scampi, while studies using binary-choice flumes would enable the food preference of scampi to be examined more closely. The high levels of variability observed for some of the phases of behaviour and the total time to bait show that more control over the hydrodynamics in the tank are required. Therefore to aid with the development of a binarychoice flume, a study of the effect of different flow regimes (i.e. turbulent versus laminar) on the food search behaviour of scampi is required.

Chapter Three:

Orientation and food search behaviour of a deep sea lobster in turbulent versus laminar odour plumes

3.1 Introduction

New Zealand scampi (*Metanephrops challengeri*) is a commercially valuable lobster species that lives in depths of 200-600 m around much of the New Zealand coast (Bell, et al., 2013; Ministry for Primary Industries, 2013). Scampi are the target of a deep sea trawl fishery which has an annual catch quota of 1191 t and generates an estimated NZ$11 million per year of sales (Ministry for Primary Industries, 2013; Tuck, 2015). Deep sea bottom trawling for scampi damages the sea floor, has high levels of bycatch and uses large quantities of fuel (Anderson, 2012; Cryer, et al., 2002; Leocádio, et al., 2012). Pots (also known as creels) are used in northern hemisphere fisheries to target the ecologically similar Norway lobster (*Nephrops norvegicus*) (Bell, et al., 2013; Ungfors, et al., 2013). The proposed development of a potting fishery for scampi, replicating the northern hemisphere pot fishery, would result in a more sustainable method for harvesting scampi by reducing the collateral environmental impacts and improving the fuel efficiency (Major, et al., 2017b; Suuronen, et al., 2012). In addition, live scampi landed by using potting methods can be sold into higher-value markets for live seafood (Leocádio, et al., 2012; Morello, et al., 2009; Ungfors, et al., 2013). Effective baits need to be identified for a potting fishery to be economic (Miller, 1990). Initial laboratory experiments to identify superior baits for scampi found behavioural responses were inconsistent among candidate baits (Major et al., 2017a).

Scampi, like other lobsters, search for food by tracking attractant chemicals that are released from the food source and transported to the animal as plumes of chemical odour by the localised hydrodynamics (Major, et al., 2017a; Zimmer-Faust & Case, 1982; Zimmer & Butman, 2000). Diffusion disperses chemicals in fluids that are not moving, which creates a concentration gradient away from the source (Vickers, 2000). Advection is the dominant force governing the transportation of the odour chemicals in moving fluids. The variations in the velocity of the moving fluids create small-scale hydrodynamic features, such as eddies, which are collectively known as turbulence (Vickers, 2000; Webster & Weissburg, 2009). The complexity of the odour plume is affected by the

characteristics of the turbulence of the fluid movement (Webster & Weissburg, 2001). Consequently, particles of different molecular weights can be distributed throughout the plume in similar concentrations and ratios to what was originally released from the bait (Vickers, 2000). This creates filaments of the attractant chemicals in high concentrations interspersed with areas without attractants, forming a three-dimensional distribution of odorant chemicals (Atema, 1996; Moore & Crimaldi, 2004; Zimmer & Butman, 2000). The spatial variations in odour concentrations are more pronounced in higher turbulence conditions and there are shorter periods between the passage of high concentration filaments of chemicals past a fixed point (known as intermittency), when compared to low turbulence (Mead, 2003; Vickers, 2000).

In order to navigate the odour landscapes that they live in, crustaceans use a range of orientation strategies which depend on the structure of odour plumes (Weissburg & Zimmer-Faust, 1994), the hydrodynamics of their environments (Jackson, et al., 2007), the morphology of their sensory systems (Keller, et al., 2003), and their locomotory abilities (Vasey, et al., 2015). The simplest of these orientation strategies is odour-gated rheotaxis, which is when an animal moves upstream after being stimulated by the attractant chemical (Webster & Weissburg, 2009). This has been suggested to be the primary orientation strategy for blue crabs (*Callinectes sapidus*) and is used in combination with spatial comparisons of the chemical signals (chemo-tropotaxis) to maintain contact with the plume and progress toward the source (Weissburg & Dusenbery, 2002). In contrast, lobsters have been suggested to use a form of eddy-chemotaxis, simultaneously employing the chemosensors and mechanoreceptors on the antennules to make spatial and temporal comparisons of eddies of odorant chemicals (Atema, 1996; Moore, et al., 1991b; Pravin & Reidenbach, 2013). As turbulence affects the spatial complexity of odour plumes and the intermittency that crustaceans encounter the filaments of odorant chemicals in the plume, it has a significant effect on the foraging behaviour of a number of crustacean species, which are tuned to the turbulence they encounter in their natural habitat (Keller et al., 2001; Moore, et al., 2015; Moore & Grills, 1999).

Scampi are similar to other endobenthic crustaceans that either burrow or bury themselves in the sediment and must emerge from their burrows in order to search for food (Bell, et al., 2013; Katoh, et al., 2013). Emergence behaviour in Norway lobster and scampi has been investigated through variations in catch rates (Aguzzi, et al., 2003; Bell et al., 2008; Tuck, 2010), as the lobsters avoid

capture by benthic trawls when they are either inside or at the entrance of their burrows versus emergent and foraging on the open seabed (Chapman & Rice, 1971). The emergence patterns of Norway lobsters are typically driven by the diel cycle. In shallow areas on the continental shelf (0-200 m) Norway lobster emerge nocturnally with crepuscular peaks, and in deeper areas, on the continental slope (400 m), emergence patterns are weakly diurnal (Aguzzi et al., 2009; Aguzzi, et al., 2003). Other studies have observed Norway lobster catch rates to vary in relation to tidal state (Bell, et al., 2008). Similarly, the emergence patterns of scampi, which only live on the continental slope (> 200 m), have been observed to peak at dawn and potentially during periods of higher tidal flow in both tagging studies and investigations of catch rate variation (Tuck, 2010; Tuck, et al., 2015). As scampi may be foraging for food during periods of change in tidal flows, which generates turbulence at the seafloor (Kawanisi & Yokosi, 1994; Nimmo Smith et al., 1999), there is the potential that the chemosensory systems and orientation strategies of scampi may be tuned to turbulent rather than laminar flow.

Therefore, the aim of this research is to improve our understanding of the behavioural response of scampi to odours from two types of bait (mackerel and mussel) in both turbulent and laminar flow regimes in an experimental seawater flume in the laboratory.

3.2 Methods

3.2.1 Experimental animals

A total of 100 scampi were obtained from a depth of 300 m on the Chatham Rise, 250 km off the east coast of New Zealand (42-43°S, 176-177°E) in July 2015 using a short duration, 2 hour bottom trawl at slow speed of 2.8 km h^{-1}. Scampi in good condition upon landing were transferred into aquaria with seawater adjusted to their ambient temperature at point of capture (10°C). The scampi were transported to the laboratory at the Cawthron Aquaculture Park in Nelson, New Zealand, where they were held in a recirculating aquaculture system at 10.5°C with a salinity of 36 ppt. The scampi were held in individual enclosures in plastic tanks under red light (λ > 600 nm) for at least a week to acclimatise to the system prior to commencing experiments. During acclimatisation the scampi were fed every three days with squid. Food was withheld from the scampi for 7 days before they were used in behavioural experiments to ensure they were responsive to food odour cues.

3.2.2 Behavioural assay

The flume was 1.5 × 0.5 × 0.3 m (L× W × D), and supplied with 10 µm and carbon filtered seawater at 10.5°C, pumped into the manifold at 10 l min^{-1}, flowing at 1 cm s^{-1} and passed through a corflute collimator before reaching the behavioural arena (Fig. 3.1). The experimental arena was a 1 m long section of the flume containing seawater 30 cm deep, which extended from the end of the collimator to a weir at the opposing end of the flume that the seawater flowed over and discharged through an outlet. Individual scampi were transferred in a darkened container from their holding tanks to the experimental flume nearby. The scampi was then placed at the end of the flume arena next to the outflow weir and allowed to move around the entire arena for a 30 min acclimatisation period. The scampi were then gently ushered back to the starting point immediately in front of the outflow weir using a mesh gate to ensure the scampi were in the correct position for the experiment to start. Five grams of defrosted bait material was placed in a polyvinyl chloride (PVC) mesh bag and suspended at the antennule height of the scampi, 2 cm above the floor of the tank. If the scampi displayed any stress-related behaviour, such as tail flicking, during the transport or acclimatisation period the scampi was replaced with another animal and the acclimatisation process was repeated.

Once the bait was in position a further 30 sec was allowed for an odour plume to develop in the flume, then the mesh gate was carefully removed so as not to disrupt the plume or scampi and the experiment was allowed to run for 30 min. The experiments were conducted under infrared light and filmed from an overhead position using a Brinno TLC1200 time-lapse camera in ASAP mode. The flume was completely emptied and thoroughly cleaned between experiments.

Two baits were tested in the flume, the gonad of green-lipped mussel (*Perna canaliculus*) and tissue of New Zealand jack mackerel (*Trachurus declivis*). These baits were chosen because previous experiments had observed that scampi responded to the mackerel bait faster during the detection period than to the mussel gonad indicating differences in their chemical attractiveness to scampi (Major, et al., 2017a). Fifteen replicates were conducted for each combination of bait type (mussel versus mackerel) and flow regime (turbulent versus laminar) for a total of 60 experiments. Captive male and female scampi were randomly selected for use in the experiments from the 100 scampi available, however, given the limited supply of scampi maintaining an exact 50:50 sex ratio for the experiment was difficult and therefore a total of 28 females and 32 males were used. No gravid

females were used and any scampi that had recently moulted were excluded from experiments. The orbital carapace length (OCL) of each scampi was measured (mm) after the experiment, and no scampi were subjected to repeated experiments.

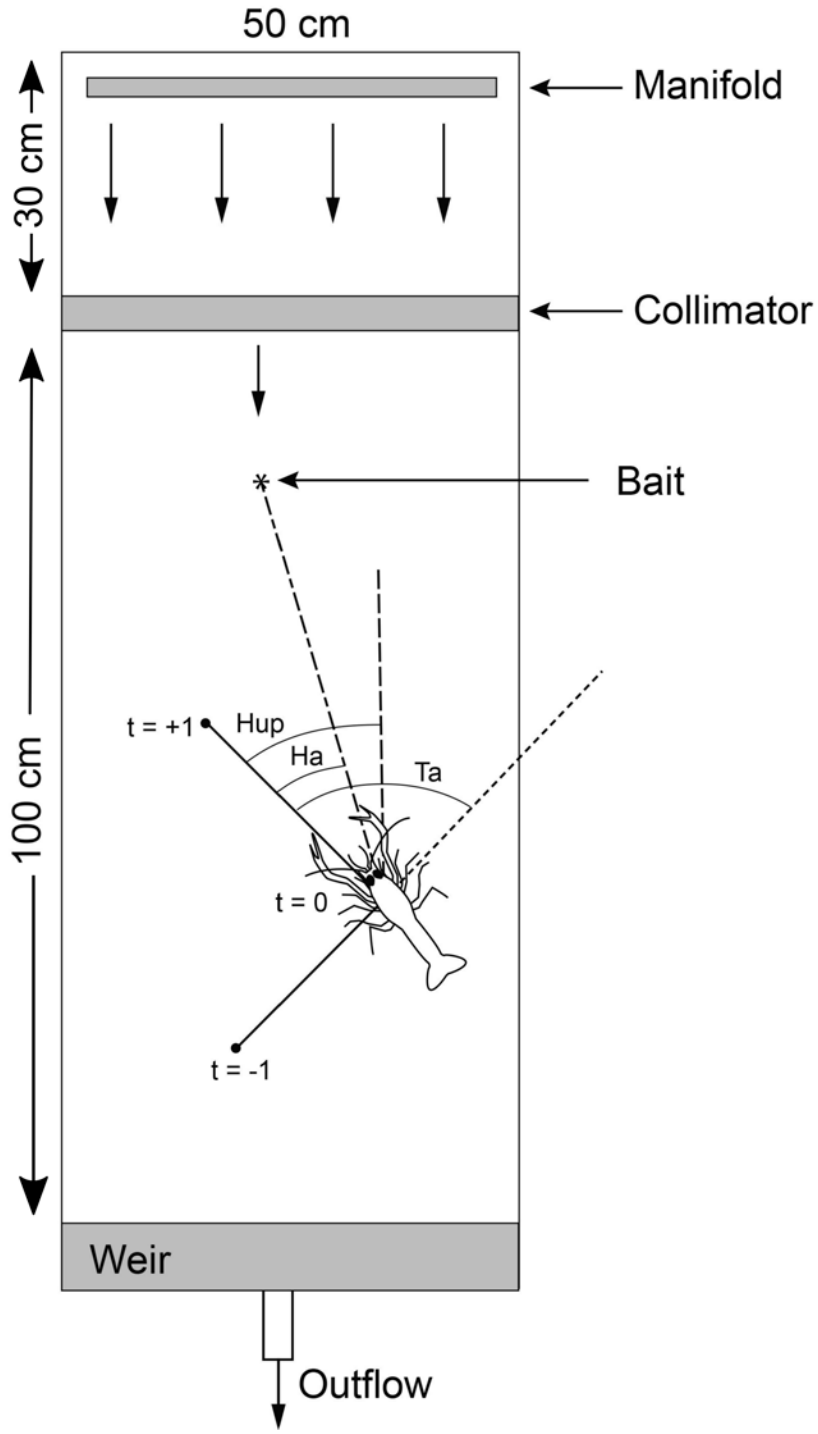

Figure 3.1 Overhead diagram of the experimental behavioural flume showing the five orientation parameters that were measured in this study over three successive positions in video recordings (t= -1, 0, and +1). The short dashed line represents the scampi's projected path (if it had continued in a straight line), from which a turn angle value (Ta) at point t=0 is calculated. Heading angle (Ha) is calculated from the difference of the bearing the scampi is travelling on and the bearing directly to the bait (short/long alternating dashed line). The long-dashed line represents a path that is straight upstream, from which a heading angle relative to upstream (Hup) is calculated.

3.2.3 Flow regimes

The two contrasting water flow regimes, “turbulent” and “laminar” were created in the flume by altering the seawater inflow arrangements. The usages of these terms are not as formal fluid dynamic descriptors, and are used to be able to distinguish clearly between the two flow treatments. Turbulent flow in the flume was generated by passing water entering the flume through only one collimator. Laminar flow was generated by passing the incoming water through two collimators arranged in series. The flow rates of seawater were consistent for both treatments, i.e., 10 l min^{-1}. The varying flow fields were visualised in the flume by releasing food dye from a hypodermic needle at the bait position supplied by a peristaltic pump (Fig. 3.2). In the laminar flow the plume that was released was in a consistent stream and not broken into filaments. In the close-up overhead image of the plume at the point of release (Fig. 3.2A) the small pulses of dye from the peristaltic pump can be seen, and these are also observed in the overhead image of the entire flume photo (Fig. 3.2C) as the stream of dye moves along the flume. In contrast the close up image of dye plume in the turbulent flow (Fig. 3.2B) shows how the eddies and structures in the flow break the dye stream into a number of small filaments that are interspersed with clear water, a pattern that continued to develop across the entire length of the flume (Fig. 3.2D). Flows were tested once per day prior to experiments.

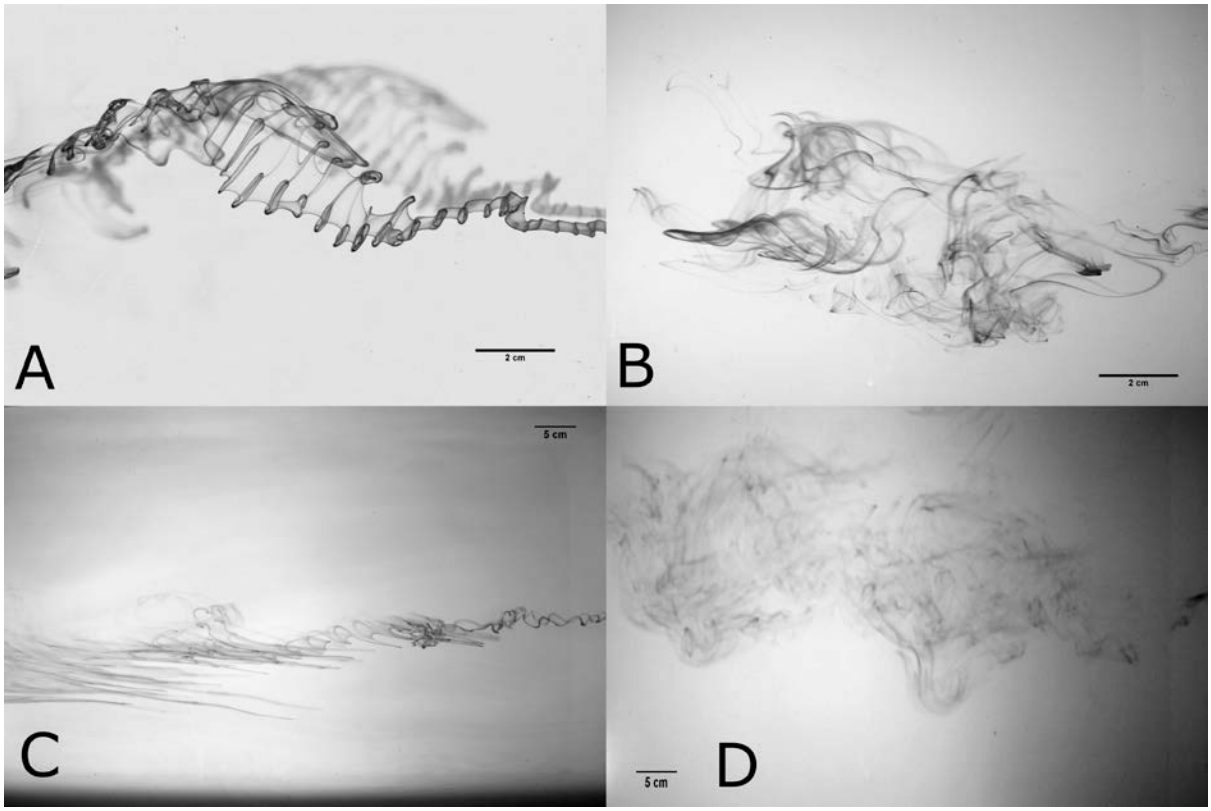

Figure 3.2 Images of the dye tracer plumes generated by food dye released from a hypodermic needle via a peristaltic pump into the water flow in the experimental flume under the two different flow regimes. A: Close up overhead image at the point of release of the dye plume generated in the laminar flow; B: Close up overhead image at the point of release of the dye plume generated in the turbulent flow; C: Overhead image of entire flume showing the structure of the dye plume generated in the laminar flow; D: Overhead image of the entire flume showing the dye plume generated in the turbulent flow.

3.2.4 Behavioural phase analyses

Aspects of chemically-mediated food search behaviour have been categorised into a number of behavioural phases that can be quantified (Lee & Meyers, 1996). These phases of food search behaviour have been adapted and used in scampi (Major, et al., 2017a), and consist of:

1) **Time to detection** - the time taken from when the mesh gate enclosing the scampi is removed until detection of the bait odour by the scampi. Indicated by a marked increase in the movement of appendages that contain the chemosensitive sensilla, including flicking or grooming of the antennae and antennules, beating of mouthparts and digging with, or wiping of dactyls.

2) **Detection period** - the time from the commencement of detection behaviour until the beginning of the search period. The scampi typically continue to display detection behaviour during this period.

3) **Search period** - from when the scampi starts locomotion or orientates into the water current, to the time it arrives at the bait.

4) **Time to reach bait -** time for all of the other behavioural phases combined, i.e., from the time the barrier is lifted to when the scampi reaches the bait.

These phases of behaviour were quantified by assessing the video recording of the bait-seeking behaviour of each scampi.

3.2.5 Tracking analyses

Orientation pathways were digitized using the TrackMate plug-in for ImageJ available in the FIJI package (Schindelin et al., 2012) for those scampi that successfully reached the bait, i.e., 14 scampi for the turbulent mackerel treatment, 12 scampi for both the laminar mackerel and turbulent mussel gonad treatments and 9 scampi for the laminar mussel gonad treatment. Digitizing was undertaken at one frame per second and x and y spatial co-ordinates were obtained for each movement of the scampi. As the scampi can orientate in a range of directions without changing its spatial location a single reference point where the cephalothorax meets the abdomen was used as the spatial reference for digitizing and calculating five orientation parameters (Fig. 3.1). These parameters were adapted from previous research (Moore & Grills, 1999; Moore, et al., 1991b; Wolf et al., 2004) and consisted of:

- **Walking speed** - Distance travelled by the scampi to go from the point in the previous frame to the current point (one second difference between frames).
- **Turn angle** – The difference between the bearing that the scampi walked to get to the current point and the bearing that the scampi turns to move to the next point in the subsequent frame. Hence, low turn angles indicate that the scampi were walking in a straight line.
- **Heading angle** – The angle between a direct bearing to the bait from the scampi's current position and the heading that it is moving in. Hence, higher heading angles indicate that the scampi is orientating further away from the bait.

- **Heading angle upstream** - The angle between a direct bearing upstream from the scampi's current position and the heading that it is moving in. Hence, a heading upstream of zero would indicate rheotaxis and the scampi orientating directly into the current.
- **Tortuosity ratio -** A measure of the directness of the orientation pathway taken by the scampi from the origin to bait destination (Benhamou, 2004), that is calculated by dividing the direct distance from the origin to the bait by the total distance travelled by the scampi. Hence, the closer tortuosity ratio is to 1 the more direct the pathway is.

3.2.6 Statistical analyses

For each combination of baits and flow conditions log–likelihood ratios (G - test) were used to compare the proportion of the scampi successfully reaching the bait. General linear models (GLM) were used to determine the effect of the type of bait, flow regime, size and sex of the scampi on the mean time taken for each phase of chemically-mediated food search behaviour. When the flow regime was observed to have a significant effect on the phases of behaviour post-hoc t-tests with a Holm correction were used to compare effect of the flow regimes within each of the bait treatments. Data for the measures of the time taken to complete each behavioural phase were tested for normality and homoscedasticity using Shapiro's and Levene's tests respectively. When the raw data did not meet these assumptions, it was transformed using either natural logarithm or square-root functions.

For all five of the orientation parameters (walking speed, turn angle, heading angle, heading upstream, tortuosity ratio), a mean value was calculated for each scampi over the duration of the search period when they were actively looking for the bait, and then used in the subsequent statistical analyses (Moore & Grills, 1999). General linear models were then used to compare each of the orientation parameters in relation to the experimental treatments, i.e., type of baits, flow regime, as well as testing for any effect due to size and sex of the scampi. When the GLMs found a significant difference between the flow treatments for an orientation parameter, the means for the laminar and turbulent flow regimes within each of the bait treatments were compared using post-hoc t-tests with a Holm correction for protecting against inflated Type I error rate due to multiple comparisons. General linear models were run using the base R program (R Core Team, 2016), and multiple comparisons using the Multcomp package .

The GLMs for both the phases of chemosensory behaviour and orientation parameters were structured as so: Y = α+$\beta_1 Flow+\beta_2 Sex+\beta_3 Size+\beta_4 Bait$, with flow, sex and bait as fixed variables, while size was included as a continuous variable.

To investigate the relationship between the means and the variances of the different orientation parameters with the distance the scampi were from the bait, the means and variances of each parameter were binned into 5 cm distance intervals from the bait, and then analysed using either linear or 2nd order polynomial regression analyses. The curves and intercepts of the regressions for the two flow regimes were compared for each of the two types of bait using an analysis of covariance (ANCOVA). All means are reported with standard errors (S.E.).

3.3 Results

3.3.1 Success in reaching the baits

Fourteen of the 15 (93%) scampi reached the mackerel bait and 12 of the 15 (80%) scampi reached the mussel bait within the 30 min maximum experimental period in the turbulent flow. Twelve of the 15 scampi (80%) reached the mackerel bait and 9 of the 15 scampi reached the mussel bait (60%) in the laminar flow. The different flow regimes did not alter the success rates for scampi reaching the baits, either overall (G = 5.03, P > 0.05), or for either the mackerel (G = 1.20, P > 0.05) or mussel (G = 1.45, P > 0.05) baits alone.

3.3.2 Behavioural phases

Overall, scampi in the turbulent flow had lower mean search periods (t = 2.02, P = 0.049) and mean total time to bait (t = 2.13, P = 0.039) regardless of the type of bait. Scampi search periods and total time to the mussel bait were both shorter in the turbulent flow compared to the laminar flow (Search period: t = 2.35, P = 0.046, 160.8 ± 32.5 sec versus 318.6 ± 60.3 sec respectively; total time to bait: t = 2.39, P = 0.042, 567.8 ± 93.0 sec versus 1001.0 ± 130.3 sec respectively) (Fig. 3.3). In contrast, no differences were observed in any of the scampi behavioural phases in response to the mackerel bait. Sex and size of the scampi did not significantly affect either search period or total time to bait for either of the baits.

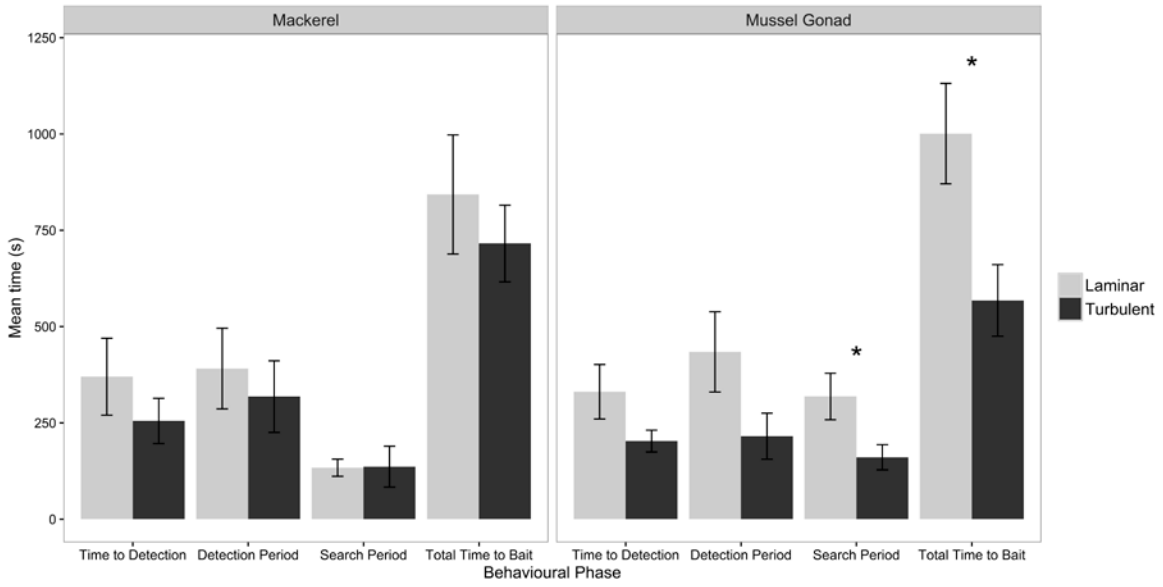

Figure 3.3 The mean (± S.E.) time taken for each of the food search behavioural phases of scampi in response to the mackerel and mussel baits under the laminar and turbulent flow regimes. Asterisk (*) denotes a significant difference ($P < 0.05$) between the mean time taken to complete the behavioural phase between the laminar and turbulent flow regimes. N = 15 for each treatment.

3.3.1 Orientation behaviour

Flow regime was observed to significantly affect the heading angle of the scampi ($t = 2.78$, $P = 0.008$). In the mussel gonad treatment the scampi had a mean heading angle that was 15.2° lower in the turbulent versus the laminar flow ($t = 2.07$, $P = 0.048$). The mackerel treatment also trended in this direction with the scampi having a mean heading angle 14.5° lower when searching in the turbulent flow versus the laminar flow, but this was not significant ($t = 1.83$, $P > 0.05$). No significant differences were observed in the means of the other two spatial orientation parameters (turn angle and heading upstream) due to the two flow or bait treatments (Fig. 3.4). Sex and size of the scampi did not significantly affect any of the orientation parameters.

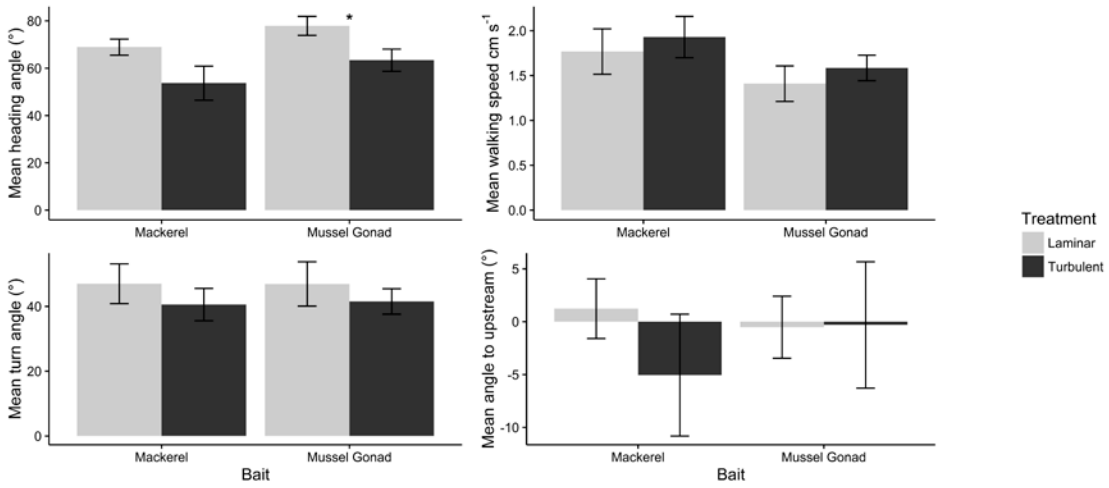

Figure 3.4 The mean (± S.E.) for each of four orientation parameters for the entire tracked path in response to the mackerel and mussel baits under the turbulent and laminar flow regimes. Asterisk (*) denotes a significant difference ($P < 0.05$) between the laminar and turbulent flow regimes within a bait treatment. N = 15 for each treatment.

3.3.2 Tortuosity ratio

Scampi began the search period on average 70.4 ± 2.5 cm from the bait, and travelled 225.7 ± 34.0 cm in search of the bait. Neither the flow regime nor the bait treatment was observed to affect the distance from the bait from where the scampi started their search path. Turbulent flow significantly reduced the tortuosity of the scampi's search paths to baits ($t = 3.04$, $P = 0.004$). The tortuosity ratios of the search path show that the scampi were 24.8% more direct to the mackerel bait ($t = 2.18$, $P = 0.038$) and 52.2% more direct to the mussel bait ($t = 2.10$, $P = 0.045$) in the turbulent flow in comparison with their respective laminar flow results (Fig. 3.5).

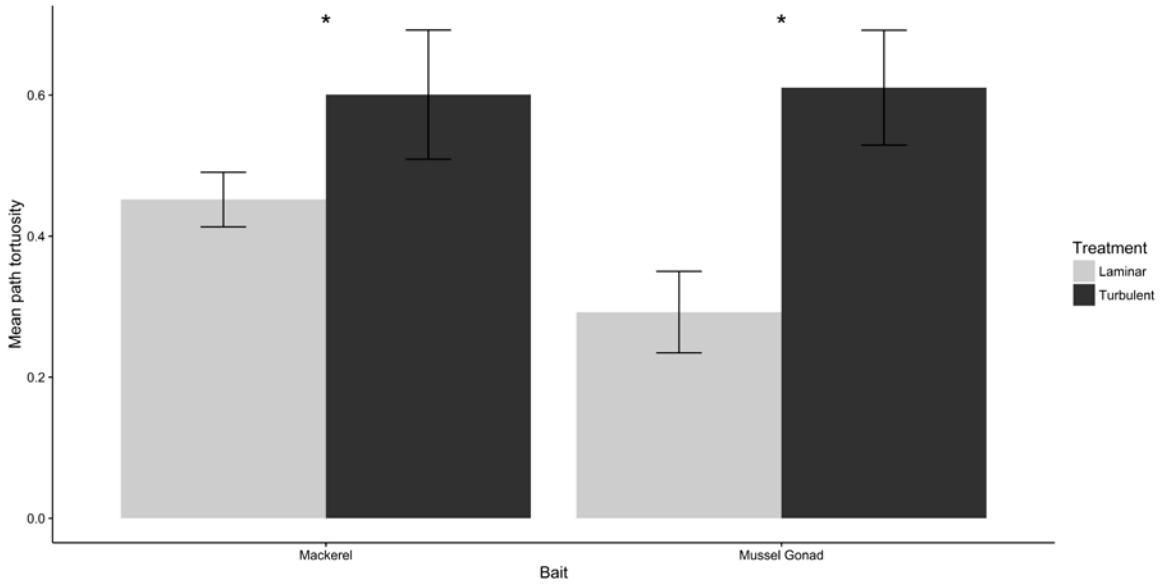

Figure 3.5 The mean (± S.E.) tortuosity ratio of the paths for the scampi in response to the mackerel and mussel gonad baits under the turbulent and laminar flow regimes. The closer the ratio is to 1 the more direct the pathway. Asterisk (*) denotes a significant difference ($P < 0.05$) between the two flow regimes within a bait type. N = 15 for each treatment.

3.3.3 Orientation parameters relative to the distance from the bait

3.3.3.1 Heading angle

Scampi had higher mean heading angles relative to distance when searching for the mackerel bait in the laminar flow regime versus the turbulent flow regime ($F = 6.63$, $P = 0.016$) (Fig. 3.6). For both types of bait and flow regimes the mean heading angle of the scampi tended to start higher at the outset of food search and reached the lowest around 40 - 45 cm from the bait and then tended to increase again in the immediate vicinity of the bait. This trend was not as pronounced for the mussel bait in laminar flow. The variability in the heading angles among individual scampi appeared to alter with distance from the bait for each of the bait and flow combinations (Fig. 3.7). For example, heading angles of scampi were least variable at the outset and conclusion of the food search in response to the mackerel in laminar flow and mussel in turbulent flow. In contrast, the heading angle of scampi was more variable at the conclusion of food search for mackerel in turbulent flow, whereas for scampi searching for mussel in a laminar flow regime there was no pattern to the variability in their heading angles over the duration of their food search.

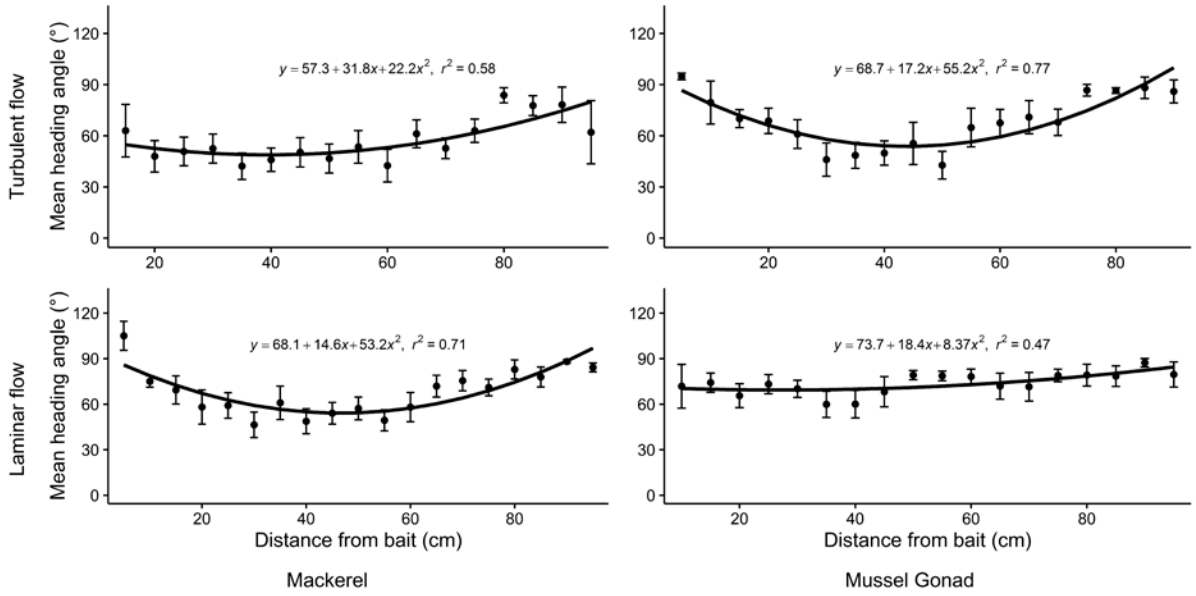

Figure 3.6 Mean (± S.E.) heading angles of the scampi at varying distances from two types of bait (mackerel and mussel) in two flow regimes (turbulent and laminar). All regressions were significant ($P < 0.05$). N = 15 for each treatment.

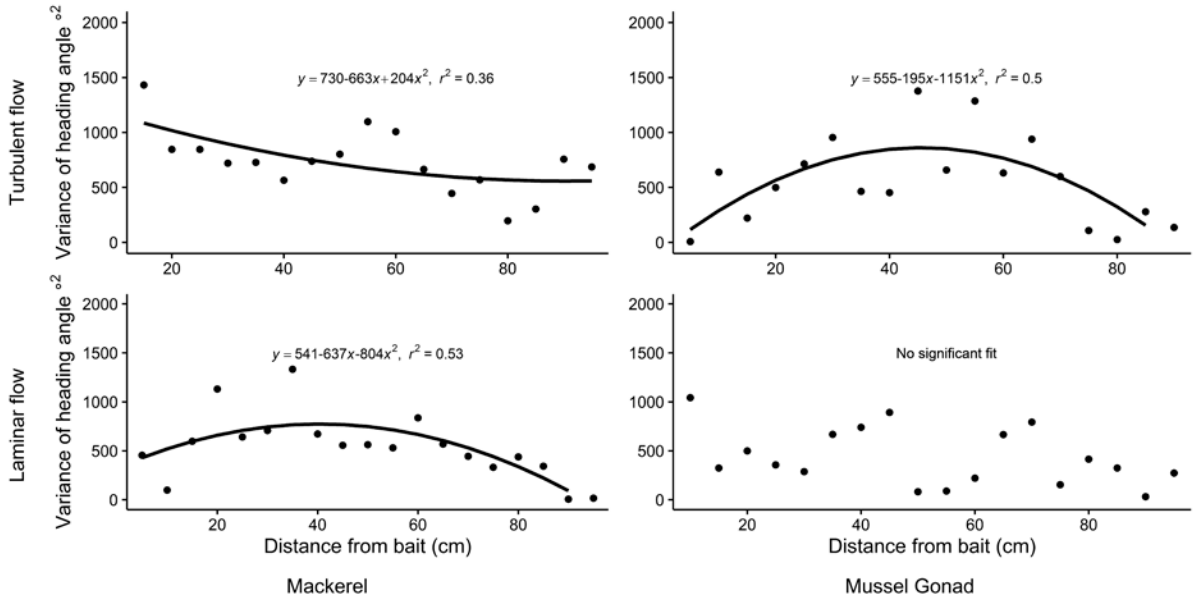

Figure 3.7 Variance of the mean heading angle of the scampi at varying distances from two types of baits (mackerel and mussel gonad) under two flow regimes (turbulent and laminar). All regressions were significant ($P < 0.05$). N = 15 for each treatment.

3.3.3.2 Turn Angles

Overall, the scampi had lower turn angles relative to distance in the turbulent versus laminar flow ($F = 5.34$, $P = 0.028$). For both bait types and flow regimes mean turn angles were higher at the start of

food search, and reached their lowest within 40 – 45 cm of the bait and then tended to increase again in the vicinity of the bait (Fig. 3.8). This increase in mean turn angles closer to the bait was more pronounced when the scampi were responding to the mackerel bait under laminar flow than under turbulent flow (F = 9.94, P = 0.004). The variance of the turn angle had a positive linear relationship to the distance from the bait for the mussel gonad in laminar flow indicating that the turn angle of the scampi was more variable at greater distances from the bait (Fig. 3.9).

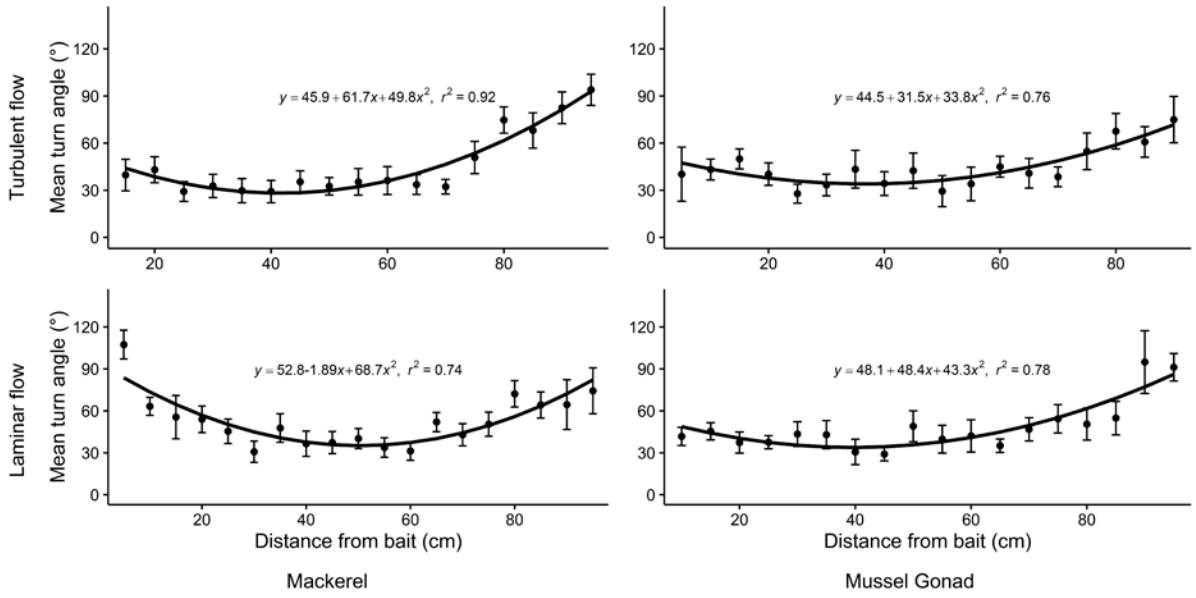

Figure 3.8 Mean (± S.E.) turn angles of the scampi at varying distances from two types of bait (mackerel and mussel gonad) in two flow regimes (turbulent and laminar). All regressions were significant (P < 0.05). N = 15 for each treatment.

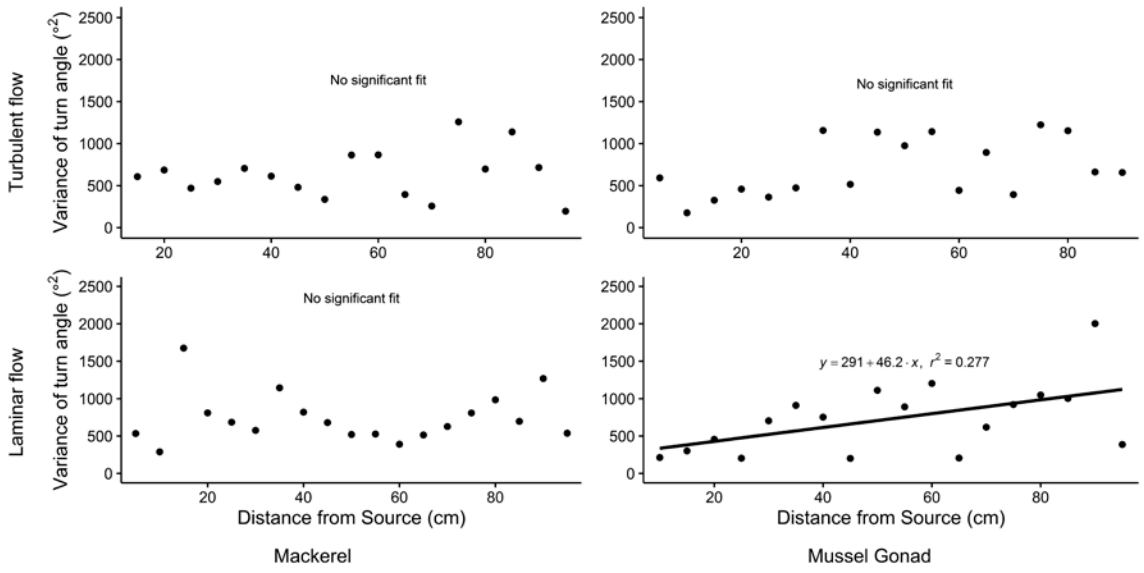

Figure 3.9 Variance of the mean turn angles of the scampi at varying distances from two types of bait (i.e., mackerel and mussel gonad) under two flow regimes (i.e., turbulent and laminar flow). Regressions significant at $P < 0.05$. N = 15 for each treatment.

3.3.3.3 Walking Speed

The mean walking speed of scampi consistently increased as the scampi got closer to the bait for both baits in both flow regimes (Fig. 3.10). However, the increasing walking speed was more pronounced in scampi responding to mackerel bait in a turbulent flow versus those in a laminar flow ($F = 13.15$, $P = 0.001$).

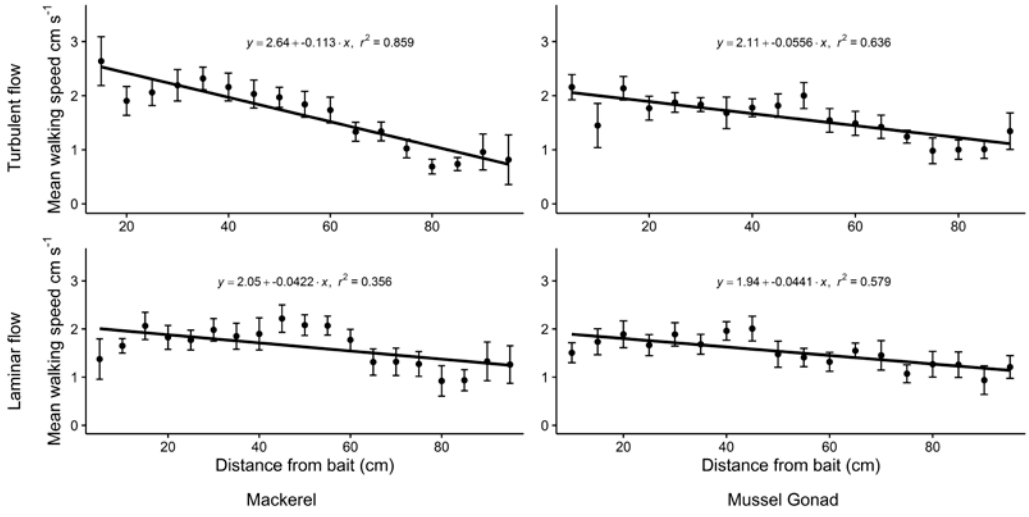

Figure 3.10 Mean (± S.E.) walking speed of the scampi at varying distances from the two types of bait (i.e., mackerel and mussel) in two flow regimes (i.e., turbulent and laminar). All regressions were significant ($P < 0.05$).

3.3.3.4 Heading upstream

The mean heading upstream was not affected by the distance the scampi were from the baits or the different flow regimes (Fig. 3.11). However, the variance of the heading angle upstream tended to increase as the scampi approached the bait (Fig. 3.12) and this was more pronounced for both baits in the turbulent versus the laminar flow (F = 7.17, P = 0.010).

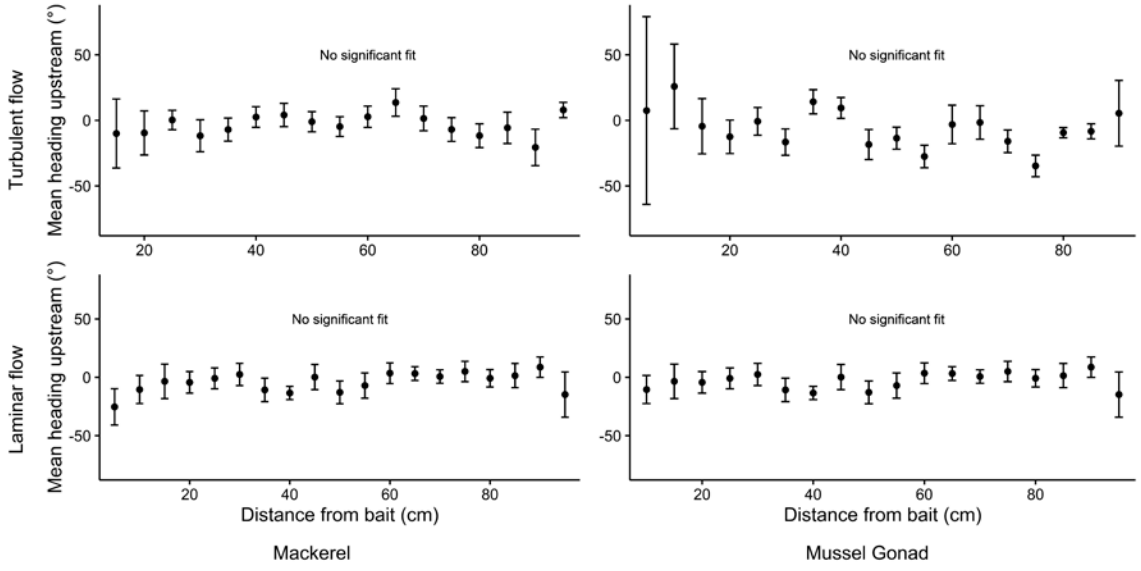

Figure 3.11 Mean (± S.E.) heading upstream of the scampi at varying distances from two types of bait (i.e., mackerel and mussel) under two flow regimes (i.e., turbulent and laminar). None of the relationships were significant at $P < 0.05$. N = 15 for each treatment.

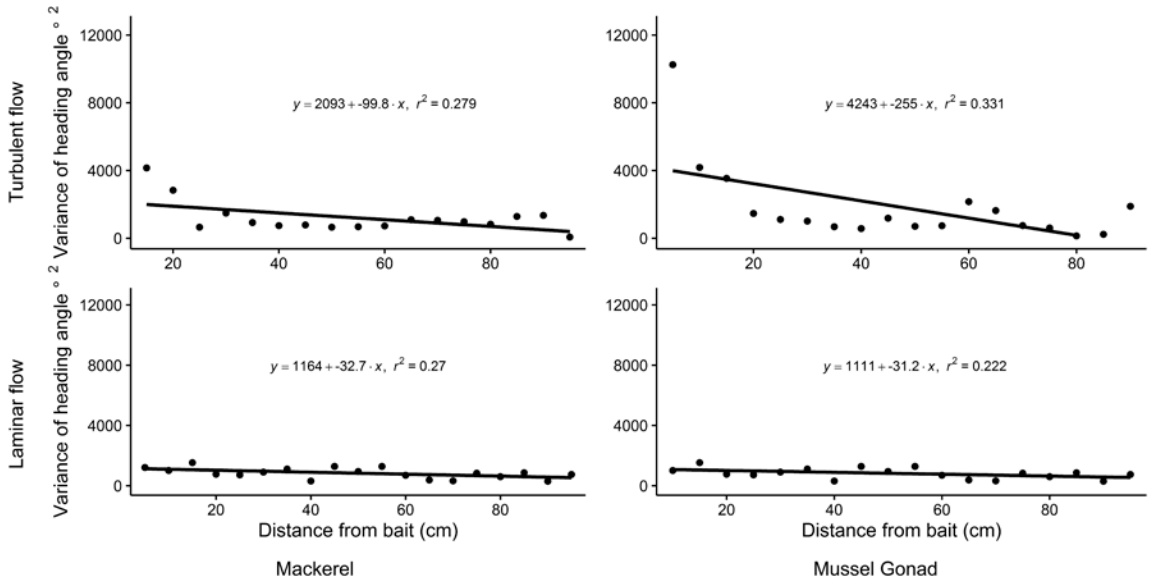

Figure 3.12 Variance of the mean heading upstream of the scampi at varying distances from two types of bait (i.e., mackerel and mussel gonad) under two flow regimes (i.e, turbulent and laminar). All regressions were significant at $P < 0.05$. N = 15 for each treatment.

3.4 Discussion

3.4.1 Success in reaching the baits

The differences in experimental flow regimes (turbulent versus laminar) did not affect the success of the scampi in reaching either of the baits. This is consistent with other studies that have observed variations in search behaviour in lobsters in different flow regimes, but have not observed differences in success rates of lobsters reaching food odour sources (Moore, et al., 2015). This result indicates that the structure of the odour plume in both flow regimes and for both types of bait was suitable for the scampi to reliably track to the odour source.

3.4.2 Search efficiency

Scampi are more efficient at tracking food odours in more turbulent flow conditions. The higher efficiency was achieved by the scampi being more direct to the bait with a mean heading angle that was 14.9° smaller in the turbulent flows than in the laminar flows. This resulted in the scampi travelling between 24.8 – 52.2% less distance when foraging in the turbulent flow, and the scampi reaching the mussel gonad bait 44% faster in the turbulent flow. The dye visualisations in the tank highlight how the turbulent flow broke the plume into a greater number of filaments and dispersed

these filaments across the width of the flume, compared to the single continuous narrow plume with only a small number of large filaments forming under laminar flow conditions. Filaments and microscale eddies in odour plumes create variation in odour concentration which have been highlighted as responsible for improving the efficiency of food search behaviour in a number of other lobster species (Atema, 1996; Kozlowski et al., 2003). High variation in odour signal structure at the height of the antennules is associated with higher foraging speeds and greater success in blue crabs but in rough turbulent flows this signal structure degrades due to increased mixing and results in less directed and slower movements of crabs toward odour sources (Jackson, et al., 2007; Weissburg, et al., 2012; Weissburg & Zimmer-Faust, 1994). In the current study less direct search paths were indicated by greater heading angles, higher turn angles and low tortuosity ratios. Less direct search paths were most commonly observed in laminar flow conditions. These results suggest that scampi are tuned to detect and respond to odour plumes with more complex structure that is typical of more turbulent water flow conditions.

The flow regime was observed to have more of an effect on the scampi searching for the mussel baits than the mackerel bait, with marked differences observed in search periods, heading angles and turn angles between the flow regimes. These differences between the two baits are most likely due to differences in the mix and concentrations of the attractant chemicals released from the two baits (Zimmer & Butman, 2000). Higher concentrations of chemical odours that elicit a strong food search behaviour will generate larger odour concentration gradients within odour plumes, especially across odour filaments and eddies which have been associated with facilitating the orientation response in lobsters (Atema 1996; Moore and Grills 1999; Kozlowski et al. 2003). Mussel gonad is known to be highly attractive to many crustaceans due to the high rate of release of amino acids, especially glycine (Carr, et al., 1996; Williams, et al., 2005), which is known to stimulate food search behaviour in many crustaceans (Carr, et al., 1996; Williams, et al., 2005). Furthermore, the 5 g of mussel gonad was cut from several whole mussels for the experiments whereas only a single piece of mackerel tissue of the equivalent mass (5 g) was used. Consequently, the higher surface area to volume ratio of the experimental mussel bait would have further promoted the release of attractive chemicals into the resulting plume (Westerberg & Westerberg, 2011).

Walking speed is a temporal orientation parameter that has been observed to be an indicator of lobsters coming into contact with an odour filament and moving towards the source (Kozlowski, et al., 2003). The current study did not observe a difference in mean walking speed due to the two flow regimes. However, when the walking speed was compared in relation to distance from the bait, the scampi had a larger increase in the walking speed as they approached the mackerel bait in the turbulent versus the laminar flow. This result is in contrast from previous studies that have observed lobsters to slow down as they approach the source of the odour (Moore, et al., 1991b). Walking speeds of crustaceans are affected by the spatial arrangement of the odour signals (Wolf, et al., 2004) as the faster the crustacean progresses along the odour plume, the more regularly odorant filaments are encountered (Page, et al., 2011a). This result suggests that scampi were encountering more odour filaments as they approached the bait and sped up as a result during their approach.

3.4.3 Orientation strategies

Changes in the orientation parameters of scampi relative to their distance from the odour source is an indication of the orientation strategies that are being utilised, and changes in these parameters have been previously been used to identify when freshwater crayfish were altering their orientation strategies (Kraus-Epley et al., 2015; Moore, et al., 2015; Wolf, et al., 2004). The results of this study suggest that the scampi were progressing up the plume as they encountered filaments of high concentration chemicals, a form of odour-gated rheotaxis, which uses chemical and rheotaxic information similar to other crustacean species (Kraus-Epley, et al., 2015; Weissburg & Zimmer-Faust, 1994). As both the turn and heading angles of the scampi initially decreased and then increased again as the scampi approached the baits, the results suggest that the scampi are using other sensors to spatially sense the plume and guide the rheotaxis (Vasey, et al., 2015; Zimmer-Faust et al., 1995). This is because the variabilities in turn and heading angles may be caused by encountering longer periods of odour intermittency further from the source, which makes spatial localisation more difficult (Page, et al., 2011b). As this pattern is consistent in both flow regimes and for both baits, it suggests that the scampi are likely to be utilising the same orientation strategy in both flow regimes. Consequently, in the turbulent flow the scampi were typically more accurate in determining their pathway once they were closer to the bait. This improved accuracy in turbulent flow may be due to the turbulence reducing the boundary layer and improving the performance of less sensitive secondary chemosensors located around the mouthparts and on the legs (Moore, et al.,

1991b). These secondary chemosensors are also known to play an important role in the final stages of localising baits in the American lobster (*Homarus americanus*) (Moore, et al., 1991b) and in the blue crab (Jackson, et al., 2007; Keller, et al., 2001).

3.4.4 Implications

In the deep sea benthic environment where scampi dwell the hydrodynamics can change markedly when the sheer stress from tidal currents generates turbulence and alters current speeds (Kawanisi & Yokosi, 1994; Nimmo Smith, et al., 1999; Wagner et al., 2007). The results of this study suggest that scampi are tuned to search for food more efficiently during periods of higher turbulence and hence this may help to explain the association of the timing of emergence and feeding activity in scampi with periods of higher current flow (Bell, et al., 2008; Tuck, et al., 2015).

Deep sea lobsters use burrows as their primary defence to avoid predators. Emergence patterns of Norway lobster on the continental shelf peak during periods low light to avoid visual predators (Sbragaglia, et al., 2015). However, at the depths scampi live, there is limited light and tidal cycles may be the only zeitgeber present (Wagner, et al., 2007). Ling (*Genypterus blacodes*), are one of the primary predators of scampi, and scampi are often in the gut content of ling caught between 382 – 428 m (Dunn, et al., 2010). Therefore, if scampi are tuned to emerge from their burrows due to tidal changes, then the adaption of foraging more efficiently in these turbulent conditions would reduce the time they are out of their burrows and available to predators. Consequently, a fishery using bait to attract scampi into pots should be targeting scampi during periods of higher tidal flows.

3.4.5 Conclusion

Chemosensory food searching in scampi is more efficient in turbulent flow as a result of adopting more direct search paths. This improved food-finding accuracy suggests that scampi are using spatial information within the plume and utilising the secondary chemoreceptors on their walking legs and mouthparts, the performance of which is improved in turbulent flow conditions. In the wild, scampi display a pattern of emergent foraging behaviour associated with periods of stronger tidal flow. By having their chemosensory system and behaviour tuned to turbulent flow, scampi would be more efficient foragers when they are out of their burrow, enabling them to avoid predators. Therefore, these results have the potential to assist with improving the effectiveness of a developing pot fishery for scampi by targeting them during periods of higher tidal flow. The results of this study highlight that

any laboratory analysis of the food search behaviour of scampi needs to be done in turbulent conditions. Consequently, a binary-choice flume that is in development in order to efficiently compare the attractiveness of a range of baits to scampi will need to have the same turbulent flow regime as identified in this research.

Chapter Four:

Laboratory comparison of potential baits for potting New Zealand scampi

4.1 Introduction

Many marine capture fisheries are at a critical juncture where they are trying to balance the environmental effects of fishing operations with the generation of high quality seafood, employment and economic activity (Suuronen, et al., 2012). One such fishery is for New Zealand scampi (*Metanephrops challengeri*), which are deep-sea lobsters that live between 200 – 600 m on muddy areas of the continental slope around New Zealand (Bell, et al., 2013). Trawling for scampi damages the sea floor, produces high levels of bycatch and uses large quantities of fuel (Anderson, 2012; Cryer, et al., 2002). This has led to the proposed development of a potting fishery for scampi, which would replicate the northern hemisphere pot fishery for the ecologically similar Norway lobster (*Nephrops norvegicus*) (Major, et al., 2017b). Potting for scampi has the potential to lessen the environmental impact and improve the fuel efficiency of the fishery (Leocádio, et al., 2012; Major, et al., 2017b; Suuronen, et al., 2012). However, for a scampi potting fishery to be viable it requires baits that are effective at attracting scampi into pots, while also being cost effective and preferably derived from a sustainable source (Miller, 1990).

In lobster and other crustacean pot fisheries, forage fish species (i.e., herring, anchovies or sardines) or fish that are suitable for human consumption, especially oily fish such as mackerel, are primarily used as bait (Chanes-Miranda & Viana, 2000; Dellinger, et al., 2016; Ungfors, et al., 2013). This puts additional pressure on often depleted populations of these forage fish (Essington et al., 2015), requires a large amount of fuel to catch them (Driscoll & Tyedmers, 2010), and is a significant expense for fishers (Chanes-Miranda & Viana, 2000). These issues are exacerbated as large amounts of bait are often required. Estimates of the ratio of bait to catch varies between fisheries with estimates from 1.1 kg of bait to 1 kg of Norway lobsters (Ungfors, et al., 2013) to 1.9 kg of bait to 1 kg of catch for the American lobster (*Homarus americanus*) fishery in Nova Scotia (Harnish & Willison, 2009). It has been estimated that 304,000 t of fish bait is used for catching the 160,000 t of American lobsters landed every year on the northeastern seaboard of North America (FAO, 2016). To alleviate

the pressure on sources of bait and to increase the economic effectiveness of pot fisheries, there has been increasing research into alternative baits, including artificial baits made from fisheries bycatch (de Rozarieux, 2014), by-products (Chanes-Miranda & Viana, 2000; Dale, et al., 2007; Daniel & Bayer, 1989) and synthetic materials (Dellinger, et al., 2016; Mackie, et al., 1980; Montemayor, et al., 2002). However, artificial baits remain to be widely adopted in any commercial fishery, primarily due to the generalisation that "the best artificial bait is no better attractant than a good natural bait" (Miller, 1990). However, with the growing pressures on forage fish and the price of bait increasing (de Rozarieux, 2014), studies are re-evaluating the use of more sustainable and cost effective artificial baits (Dellinger, et al., 2016). To develop effective artificial baits, such as for potting scampi, chemoattraction and the chemically-mediated food search behaviour of the target species need to be understood (Løkkeborg & Johannessen, 1992). Chemoattraction consists of a number of key components; 1) the composition of the attractant chemicals in the bait (Carr, 1978; Carr & Derby, 1986; Mackie & Shelton, 1972), 2) the rate of release of the attractant chemicals from the bait (Keller & Weissburg, 2004; Zimmer, et al., 1999), 3) local hydrodynamics that transport the chemicals to the target animal in the form of an odour plume (Atema, 1996; Kozlowski, et al., 2003; Major & Jeffs, 2017), 4) sensor morphology and the behaviour of the target animal, enabling them to sense and then track the odour plume back to its source (Moore, et al., 1991a; Moore & Crimaldi, 2004).

The two key components of chemoattraction that can be controlled in the development of an artificial bait are; 1) the component attractant chemicals, and 2) the rate of release of the attractant chemicals (Løkkeborg, 1991). Earlier research focused primarily on the identification of the attractant chemicals in bait through the use of fractionation techniques (Derby, 1984; Mackie & Shelton, 1972). However, the results of these studies highlighted that no single compound was responsible for eliciting food search behaviour in lobster species, with chemical mixes simulating natural baits consistently found to be the most effective (Mackie & Shelton, 1972). The release rate of attractant chemicals from an artificial bait can be controlled by the type of binders used to hold an artificial bait together (Daniel & Bayer, 1989; Løkkeborg, 1991). Release rates that closely mimic the natural prey of the target species have observed to be the most attractive (Mackie, et al., 1980; Zimmer, et al., 1999). Despite the use of binders in a number of artificial baits, the effect of changing the rate of release of the chemicals from artificial baits on their attractiveness has received little research attention for commercial species. Laboratory studies of the release rates of attractive odour chemicals from natural

and artificial baits have primarily focused on changes in chemical release over 24 hours (Daniel & Bayer, 1987; Løkkeborg, 1990), and on changes in attractiveness due to the aging of natural baits (Løkkeborg & Johannessen, 1992).

In field experiments the most successful artificial baits have involved setting natural bait materials, primarily from fisheries and aquaculture by-products, with suitable binders (Chanes-Miranda & Viana, 2000; Dale, et al., 2007; Daniel & Bayer, 1989; Vazquez-Archdale & Kawamura, 2011). By doing so these baits either create a bait from products that would otherwise be thrown away, or extend the use of the natural source material by diluting the raw material and prolonging the release of the attractant chemicals. An example of this is the eel and whelk fishery on the east coast of the United States of America, where the overfished Atlantic horseshoe crab and their eggs are the preferred bait (Wakefield, 2013). While a replacement for the attractive proteins in the horseshoe crab eggs could not be synthesised (Ferrari & Targett, 2003), researchers generated equivalent catches using artificial bait containing an eighth of a horseshoe crab, versus the half of a whole crab traditionally used for baiting each pot (Wakefield, 2013).

Experiments with bait materials are usually conducted in operating fisheries comparing catch rates (Vazquez-Archdale et al., 2008). However, as there is currently no operational potting fishery for scampi, laboratory behavioural assays using y-maze or binary choice flumes are an alternative optimal method to investigate chemoattraction behaviour to the presentation of different experimental baits (Jutfelt et al., 2016). This research approach has been successfully used for a number of crustacean and fish species, including for successfully identifying attractive compounds of aquaculture feeds (Nunes, et al., 2006). However, determining the strength of behavioural responses of crustacean subjects to a range of experimental chemical attractants in the laboratory can be challenging (Ryan, et al., 2014). One solution is the application of analytical methods that are commonly used in medical and social sciences, such as survival regression analyses and proportional hazard models, which have increased discriminatory power when applied to foraging behaviour (Gols et al., 2005). The increasing application of these techniques in studies of animal sensory behaviour has the potential to enhance our understanding of foraging in a number of species (Tenhumberg et al., 2001).

The development of effective potting methods for scampi provides an opportunity to investigate the potential for sustainable baits utilising aquaculture meals or fisheries discards. This study aims to firstly, identify the most attractive natural bait material for scampi from a group of six candidates, including bycatch and aquaculture meal products, by assessing the behavioural responses of scampi to the baits in a binary-choice flume. The corresponding chemically-mediated food search behaviour of the scampi in the flume was compared to the rate of release of soluble amino acids from the baits. Secondly, the study investigates the potential to reduce the amount of natural bait material by using the flume to experimentally assess scampi responses to incorporating reduced proportions of the most effective natural bait into an alginate binder.

4.2 Methods

4.2.1 Experimental animals

The scampi used in the experiments were obtained from a depth of 300 m on the Chatham Rise on the southeast coast of the South Island of New Zealand (42°S, 176°E) in March 2016 using a short duration, 2 hour bottom trawl at slow speed of 2.8 km h^{-1}. Scampi that were in good condition upon landing were transferred into on-board aquaria with seawater held at their ambient temperature at point of capture (10-12°C). The scampi were transported to the laboratory at the Cawthron Aquaculture Park in Nelson, New Zealand, where they were held in a recirculating aquaculture system at 12°C with a salinity of 36 ppt. The scampi were held in individual enclosures in plastic tanks under red light (λ > 600 nm) for a minimum of one week and a maximum of 13 weeks prior to commencing experiments. During acclimatisation to the system scampi were fed squid mantle tissue (*Nototodarus sloanii*) every 3 days. Prior to their use in a behavioural assay, food was withheld from scampi for 7 days to ensure they were responsive to food odour cues (Major & Jeffs, 2017).

4.2.2 Behavioural assay

Pairwise choice experiments, between a bait and inert control treatment, were conducted using a 1.5 × 0.5 × 0.3 m (L× W × D) flume that was separated into a choice arena adjacent to the outflow from the flume and preceded by two 0.5 x 0.25 m (L × W) channels (Fig. 4.1). The flume was supplied with 10 µm and activated carbon filtered seawater at 10.5°C, pumped into the flume intake manifold at 6 l min^{-1}. The flume was designed to facilitate pairwise choice experiments with the scampi able to freely choose between water flowing past the two respective bait treatments held in the two different

channels. Dye tests using food dye, were used to ensure that the odour plumes created from the bait treatments were parallel down each channel and into the choice arena, and were consistent throughout the experiment and the velocity was the same down each channel. The flow regime of the flume was set up in a turbulent manner, which was observed to facilitate the efficient food search behaviour for scampi (Major & Jeffs, 2017).

Prior to each experiment, a scampi was placed into the back of the choice arena immediately adjacent to the outflow and allowed to acclimate for at least 30 min. The scampi was then gently herded to the starting point in the centre of the choice arena immediately in front of the outflow at the rear of the tank and a thin gauge PVC coated wire-mesh gate was used to ensure the scampi did not move into the channels as the experiment was being set up. A 5 g piece of defrosted bait material was then placed in a mesh bait bag, and suspended in one of the channels 2 cm above the tank floor, whilst in the other channel; an identical bait bag containing a 5 g piece of glass was suspended as a control. The bait channel was chosen randomly by a coin toss. Once the bait was in position, the wire gate was carefully removed to minimise any disruption of the odour plume or scampi and the experiment was allowed to run for 30 min. At the start of each day the flow within the flume was visualised with dye to ensure it was consistent. The setup and the experiments were conducted under infrared light and filmed from an overhead position using a Brinno TLC 200 Pro time-lapse camera in ASAP mode. The flume was completely emptied and thoroughly cleaned using ethanol between experiments.

The baits used in the experiments were polychaete meal (made from *Nereis virens, Nereis diversicolor* and potato starch by ProChaete Innovations Limited, UK) set in alginate (5% alginate, 83% water, 12% polychaete meal), javelinfish (*Lepidorhynchus denticulatus*), dark banded rattail (*Coelorinchus maurofasciatus*), and pilchards (*Sardinia neopilchardus). In addition,* two pilchard-alginate baits were made by combining pilchard tissue at either 1% (5% alginate, 1% pilchard tissue and 94% water) or 10% (5% alginate, 10% pilchard tissue and 85% water) by wet weight into the same bait. Pilchard tissue was filleted from a defrosted whole fish and then blended to a paste before being incorporated into the alginate and water mixture. The alginate baits were then placed into 5 ml moulds and sprayed with a 10% calcium chloride solution to promote setting of the alginate binder. In addition to the baits outlined above, squid mantle (*Nototodarus sloanii)*, which was provided as an

effective feed for the scampi prior to experimentation, was used as a positive control for comparative purposes.

Scampi that were not active during the 30 min acclimation period in the flume arena were excluded from their use in further experimentation. Of the 147 scampi that were used in the experiment, 42 (29%) were not active. The number of inactive scampi in this experiment is consistent with studies of other lobster species (Moore, et al., 1991b; Ryan, et al., 2014). A mix of captive male and female scampi were used in the experiments, however, a limited supply of scampi made maintaining a 50:50 sex ratio for the experiment difficult and therefore a total of 35 females and 80 males were used. No gravid females were used and any scampi that had recently moulted were excluded from experiments. The orbital carapace length (OCL) the scampi was measured (mm) after each experiment, and no scampi were subjected to repeated experiments.

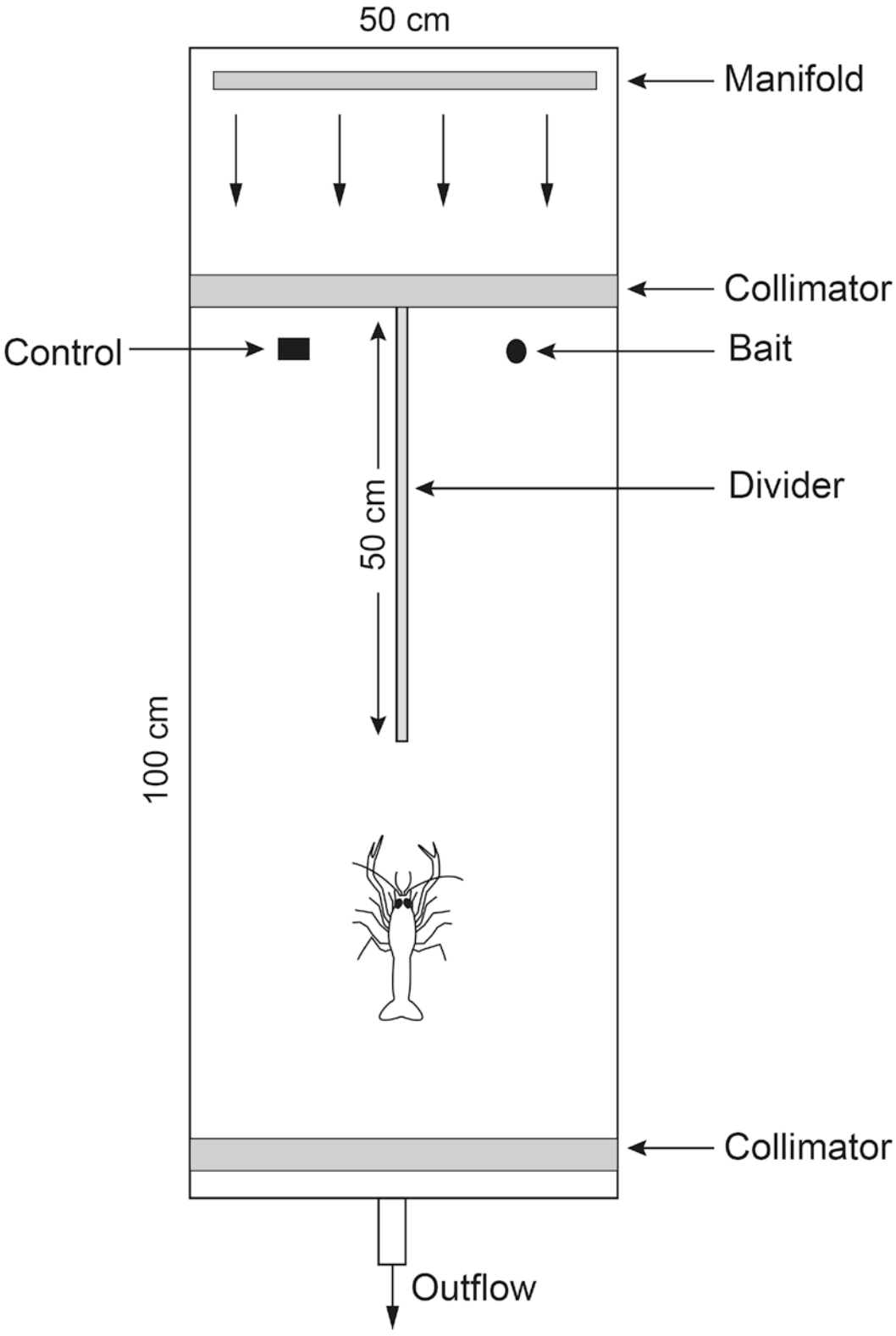

Figure 4.1 Diagram of the experimental behavioural chamber used to record the chemically-mediated food search behaviour of *Metanephrops challengeri*. Experiments were run in the dark and were filmed from an overhead video recorder under infrared lighting. Bait and control channels were chosen randomly.

4.2.3 Video and behavioural analysis

The 30 min videos of the experiments were analysed by replaying them and quantifying the:

- Time for the scampi to reach the bait starting from when the wire gate was raised.
- Time the scampi spent in the bait channel
- Time scampi spent interacting with the bait bag
- Time spent in the control channel
- Time spent interacting with the control bait bag
- First channel entered
- If the scampi reached the bait

4.2.4 Ninhydrin analysis

The total free amino acids released from the bait during the 30 min experiment were analysed using a fluorometric ninhydrin assay (Jones et al., 2002; Warren, 2017). Three 5 g replicates of bait for each treatment were prepared in an identical manner as for the behavioural assays. The leaching of amino acids was simulated by placing each piece of bait into a 400 ml vessel of freshwater which was mounted on an orbital shaker rotating at 40 rpm, a similar rate to water flow in an aquaculture facilities (Williams, et al., 2005). A 25 ml sample of the water was taken as soon as the bait was placed into the water (0 min), then again at intervals of 1, 5 10, 15, 20, 25 and 30 min. All water samples were taken from the top of the water level, to avoid collecting any solid material in the samples. The water samples were then frozen until analysis. Three technical replicates of each sample were plated at random onto a 96-well plate alongside a set of serially diluted standards made from glycine (Sigma-Aldrich), analysed with a ninhydrin assay, and read with a fluorometric plate-reader (Perkin-Elmer Enspire). Results were assessed against the glycine standard curve, reported as free amino acid equivalents of µM l^{-1} of glycine, which were adjusted for the water loss owing to the serial sampling.

4.2.5 Statistical analyses

Firstly, the descriptive details (sex and size) of the scampi were compared across the six bait treatments and positive control to check for possible experimental bias. The number of active scampi and the number of females to males for each of the bait treatments were compared using Fisher's exact tests. The mean size of the scampi for each bait treatment was compared using a one-way

ANOVA, followed by a post-hoc Tukey test with a Benjamini–Hochberg correction for multiple comparisons.

The temporal variables (time to bait, time in bait channel, time at bait bag) where analysed using general linear mixed models (Bates et al., 2015) incorporating the bait, sex, size, bait channel as variables, whilst the number corresponding to the individual scampi was included as a random factor. Student's t-tests were used within each bait treatment to compare the mean time the scampi spent in the bait channel versus their time spent in the control channel. Normality and heteroscedasticity of the data were tested using Shapiro's and Levene's tests respectively, and square root transformations were applied if the data violated these assumptions.

Binary data, which included the first channel the scampi entered and if the scampi reached the bait, were analysed using mixed effects logistic regression models with a binomial distribution and incorporating the same factors as the temporal variables (Jaeger, 2008). The outputs of these models are in log-odds (logit) and are used to observe if the different baits increased the probability of the scampi reaching the bait or entering the bait channel first. Additionally, the time that the scampi spent in the bait channel of the tank was transformed into a proportion and then analysed using similar logit-linked mixed models including the individual scampi as a random effect in the model (Bolker et al., 2009; Jutfelt, et al., 2016).

The time to bait and number of scampi that reached the bait were used in a time-to-event regression analysis using a Cox's proportional hazard model built using the 'survival' package in R (Therneau, 2015). Proportional hazard models are a type of survival analysis that relates several risk factors to the survival time, generating a chance per-unit of time called the hazard rate. In traditional survival analyses this is a modelled estimate of the risk of failure, however, in this case the risk of success was modelled, i.e., the probability of the scampi reaching the bait (Tenhumberg, et al., 2001). The model combined the number of scampi that reached the bait and the time taken to generate hazard ratios that were then used to compare among the baits. The model included bait, sex, size and bait channel as factors in the analysis, the data was censored by the end of the experiment (1800 sec) if the scampi did not reach the bait.

For the regression analyses each of the factors (bait, sex, size and bait channel) were analysed by likelihood ratio tests of nested models. When a factor was considered to significantly affect the

measured variable, then pairwise comparisons between groups within the factor were made using post-hoc Tukey's tests with Benjamini–Hochberg corrections for multiple comparisons to control for the false discovery rate (McDonald, 2014).

Whenever post-hoc comparisons using t-tests were undertaken, a Dunnett's test (Dunnett, 1955), comparing all of the bait treatments to the positive squid control was also conducted. This allowed for comparisons to be made against a food item that the scampi were well conditioned to and therefore could help to determine if they were less or more attractive to a bait than this positive control.

The results of the ninhydrin assays were analysed using a one-way ANOVA comparing the differences in the cumulative concentrations of free amino acids that were released by the baits at each of the different time points. The rate of release was then compared by creating linear models of the change in free amino acids concentrations over time for each of the baits and compared using a multiple linear regression.

4.3 Results

4.3.1 Details of scampi

Of the 147 scampi in the experiment, 42 were not active, leading to data from 105 scampi being used in the subsequent statistical analyses (71.4%). The numbers of active scampi were 15 out of 20 for the pilchard, 15 out of 20 for the javelinfish, 15 out of 20 for the rattail, 15 out of 28 for the polychaete meal, 15 out of 15 for the 1% pilchard-alginate bait, 15 out of 17 for the 10% pilchard-alginate bait and 15 out of 27 for the squid control. Bait type was not observed to significantly affect the amount of inactive scampi ($P = 0.11$). The ratio of male to female scampi was not significantly different for the different bait treatments ($P = 0.70$). However, the size of the scampi was observed to significantly differ between the baits ($F = 3.22$, $P = 0.017$). The scampi used in both the 1% (53.8 ± 1.0 mm) and 10% (49.6 ± 0.8 mm) pilchard-alginate bait treatments were significantly larger than all of the other bait treatments, additionally the scampi used in the pilchard (44.7 ± 1.4 mm) and polychaete meal (43.1 ± 1.8 mm) treatments were significantly larger than the scampi used in the squid (37.2 ± 1.8 mm) treatment.

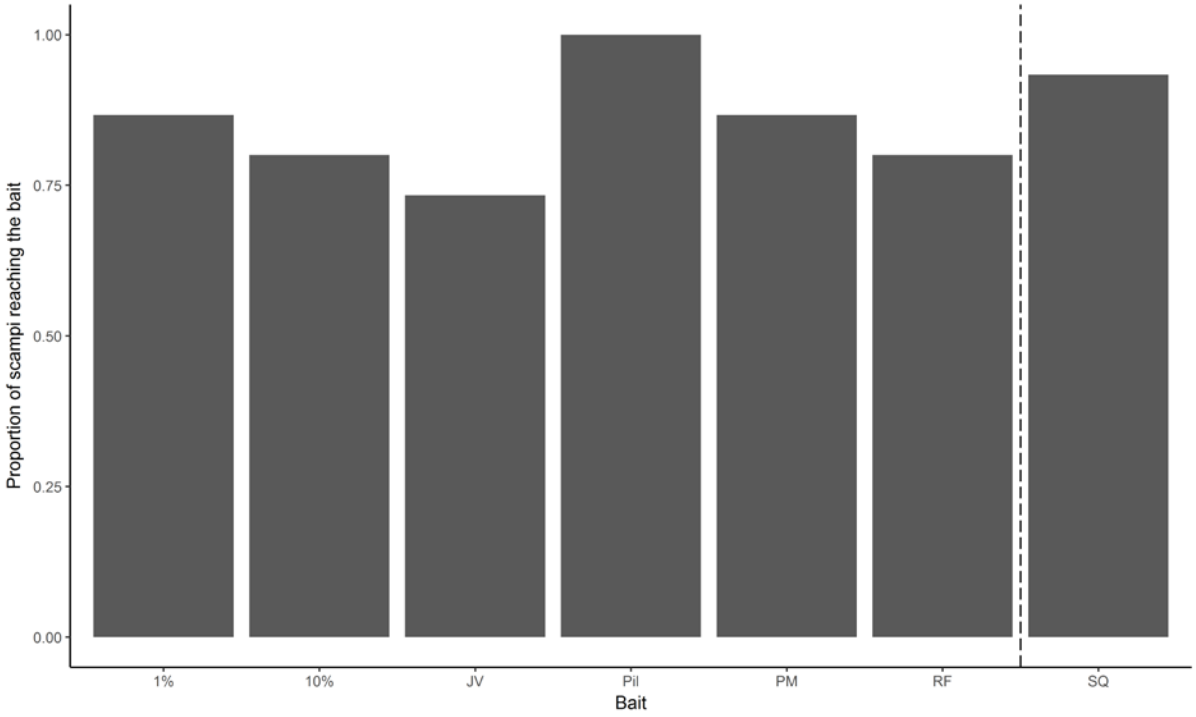

Figure 4.2 The proportion of scampi that reached each bait. JV = Javelinfish, Pil = Pilchard, PM = Polychaete meal, RF = Rattail, 1% = 1% Pilchard–alginate bait, 10% = 10% Pilchard-alginate bait, SQ = Squid. N = 15 for each treatment.

4.3.2 Reaching bait

The majority (84.4%) of the active scampi tested reached the bait treatments during the 30 min experiment. Pilchard (100%) had the highest proportion of scampi reaching the bait, while javelinfish (73.3%) had the lowest (Fig 4.2). The type of bait did not significantly affect the probability of the scampi reaching the bait during the 30 min experiment (χ^2 = 6.72, *P* = 0.24). Scampi were equally as likely to reach the squid as any of the bait treatments (SQ-1%, z = 0.07, *P* = 0.95; SQ-10% 0.6, *P* = 0.95; SQ-JV, z = 1.2, *P* = 0.95; SQ-Pil, z = 0.006, *P* = 0.95; SQ-PM, z = 0.4, *P* = *0*.95; SQ-RF, z = 0.9, *P* = 0.95).

4.3.3 First channel entered

Regardless, of bait treatment the majority (69.3%) of scampi entered the bait channel first during the 30 min experiment. Polychaete meal (86.7%) resulted in the highest percentages of scampi entering the bait channel first and rattail (46.7%) had the lowest. However, there were no differences among the bait treatments in the probabilities that the scampi would enter the bait channel first (χ^2 = 6.73, *P* =

0.24). The only difference observed between a bait candidate and the squid was that the scampi were more likely to enter the bait channel in response to the squid than the rattail (z = 2.66, P = 0.046).

4.3.4 Time to bait

The mean time to bait for the scampi for the six candidate baits was shortest in response to the pilchard bait (217.5 ± 38.0 sec) and longest in response to the javelinfish bait (679.3 ± 159.2 sec) (Fig. 4.3). The type of bait affected the time taken by scampi to reach the bait (χ^2 = 12.54, P = 0.03) with scampi arriving at the pilchard bait earlier on average when compared to those responding to javelinfish (z = 3.25, P = 0.03) and rattail baits (z = 2.92, P = 0.02). The sex and size of the scampi did not affect the time it took for the scampi to reach the bait (sex: t = 1.72, P = 0.09; size: t = 0.23, P = 0.82). When comparing the bait candidates to the positive control, the scampi reached the squid significantly faster than the javelinfish (z = 2.75, P = 0.04).

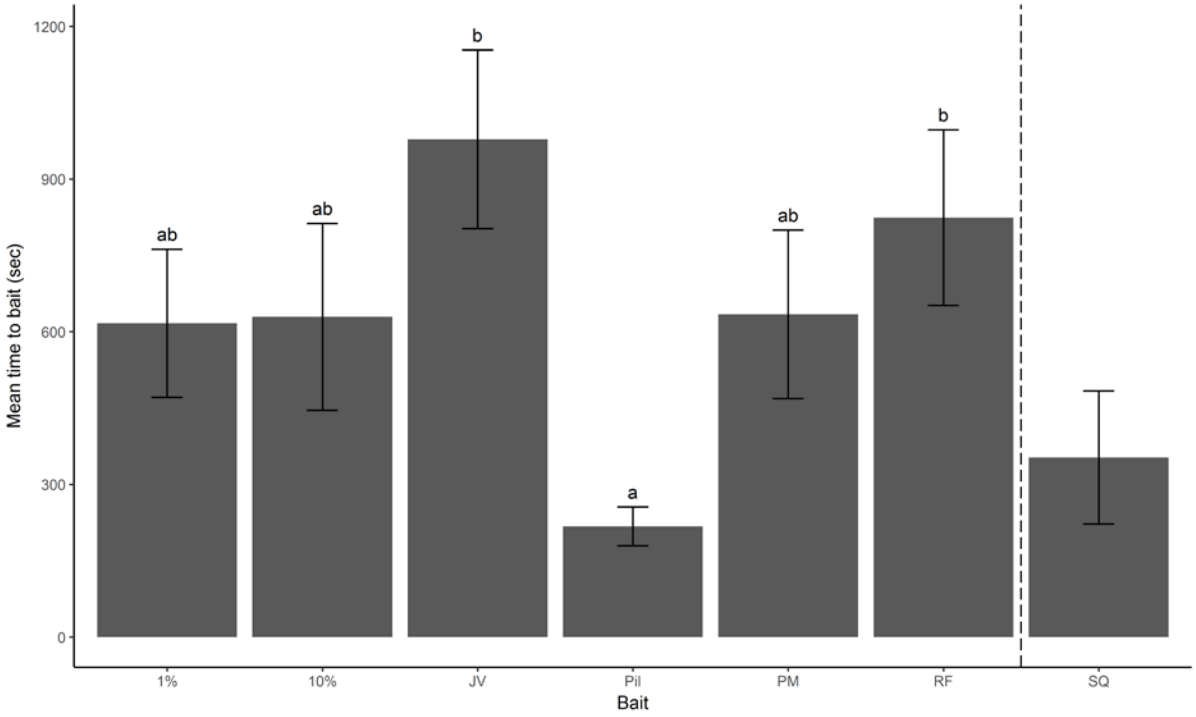

Figure 4.3. The mean time taken by scampi to reach the six different bait candidates and the positive squid control in an experimental binary choice chamber (± standard error). JV = Javelinfish, Pil = Pilchard, PM = Polychaete meal, RF = Rattail, 1% = 1% Pilchard–alginate bait, 10% = 10% Pilchard-alginate bait, SQ = Squid. Different letters between pairs of means indicates they are significantly different (Tukey HSD, P < 0.05). N = 15 for each treatment.

4.3.5 Time in bait channel & time at bait bag

The type of bait significantly affected the amount of time the scampi spent in the bait channel (χ^2 = 10.02, *P* = 0.04). The scampi spent the most amount of time in the bait channel in response to the 10% pilchard-alginate bait (770 ± 203.5 sec) and the least amount of time in response to the javelinfish (444.0 ± 141.0 sec). However, the mean amount of time spent by scampi in the bait channel was only higher than the time spent in the corresponding control channel for the pilchard bait (*t* = 2.08, *P* = 0.047) and the 1% pilchard-alginate bait (*t* = 2.37, *P* = 0.03) (Fig. 4.4). When comparing the baits to the positive control, the scampi spent significantly longer in the bait channel versus the javelinfish (*z* = 2.63, *P* = 0.03) and rattail treatments (*z* = 2.63, *P* = 0.03).

The type of bait significantly affected the mean time the scampi spent interacting with the bait bag (χ^2 = 20.41, *P* < 0.01) (Fig. 4.5). The scampi spent the most amount of time interacting with the 10% pilchard-alginate bait (599.7± 170.8 sec), which was significantly higher than for javelinfish (*t* = 3.21, *P* = 0.010), polychaete meal (t = 3.91, *P* = 0.001) and rattail baits (*t* = 3.93, *P* = 0.001). The scampi spent significantly longer at the bait bag in response to the squid than the javelinfish (*z* = 2.75, *P* = 0.012), polychaete meal (*z* = 3.32, *P* = 0.003), and rattail (z = 3.54, *P* = 0.002).

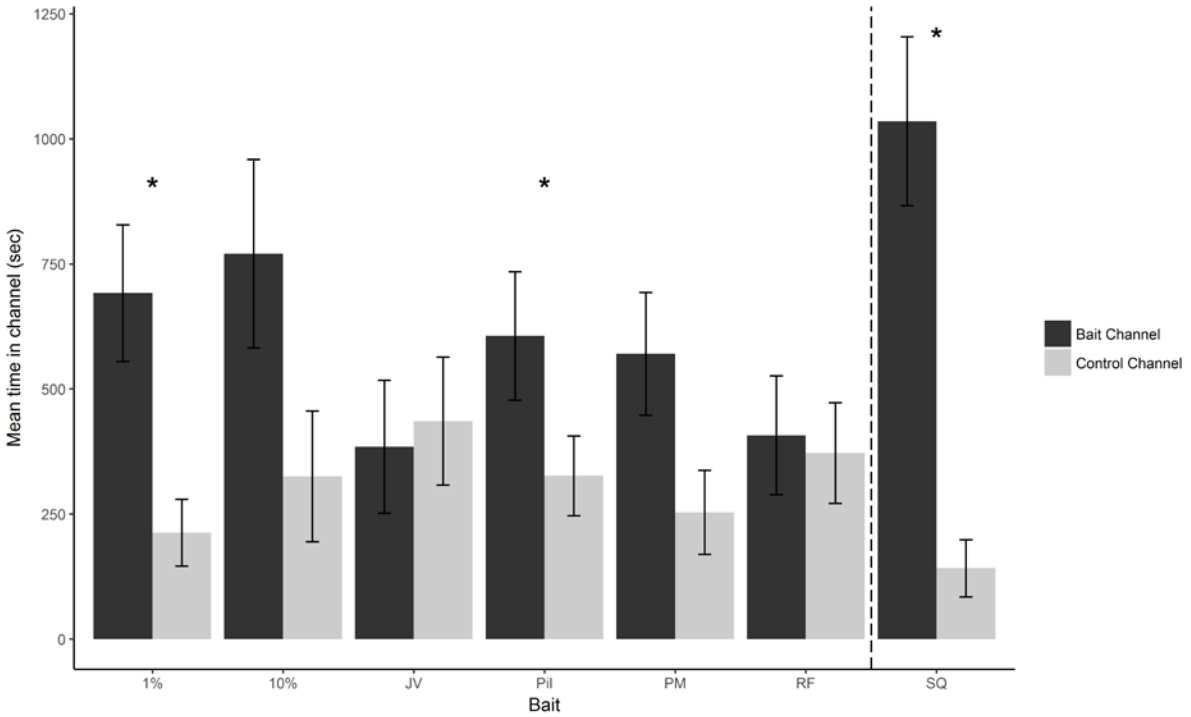

Figure 4.4 The mean time (sec ± SE) the scampi spent in the bait channel versus corresponding control channel of the flume in response to the different bait treatments and the positive control. Abbreviations are as follows: JV = Javelinfish; Pil = Pilchard; PM = Polychaete meal; RF = Rattail; 1% = 1% Pilchard–alginate bait; 10% = 10% Pilchard-alginate bait, SQ= squid. Asterisk (*) indicates a significant difference between the mean time spent in the bait channel versus the control channel for individual bait treatment (Student's t-test, $P < 0.05$). N = 15 for each treatment.

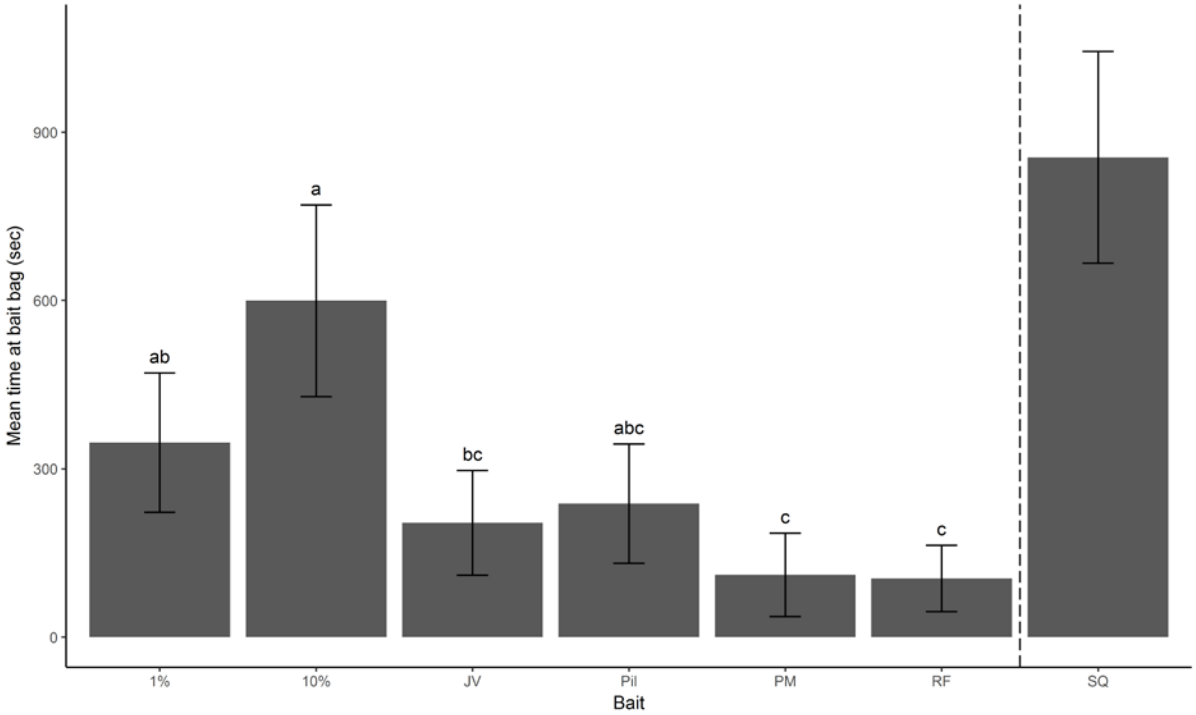

Figure 4.5 The mean time (sec ± SE) spent by scampi interacting with the bait bag in response to the different bait treatments. Abbreviations are as follows: JV = Javelinfish; Pil = Pilchard; PM = Polychaete meal; RF = Rattail; 1% = 1% Pilchard–alginate bait; 10% = 10% Pilchard-alginate bait, SQ = Squid. Different letters indicate significant differences between pairs of means (Tukey HSD, $P < 0.05$). N = 15 for each treatment.

4.3.6 Time-to-event analysis

Survival analysis curves show that scampi had the lowest median time to bait (time at which 50% of scampi had reached the bait) in response to the pilchard bait (182 sec) and highest in response to the javelinfish bait (1165 sec) (Fig. 4.6). Bait was observed to significantly affect the formation of the Kaplan-Meier curves ($\chi^2 = 13.5$, $P = 0.019$). Indicating that the scampi were more likely to reach the pilchard bait than either the javelinfish ($z = 3.35$, $P < 0.001$) or rattail ($z = 3.03$, $P = 0.001$) within the 1800 sec experiment.

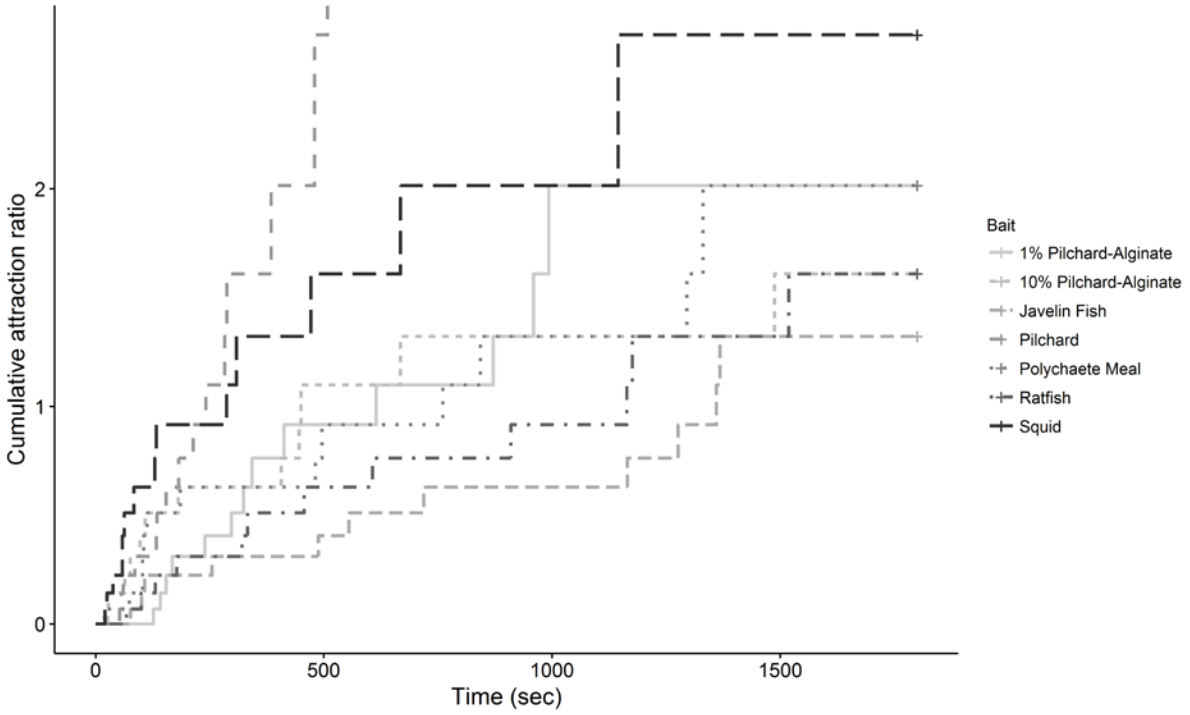

Figure 4.6 Cumulative event plot of the number of active scampi reaching the different bait candidates during the experimental duration (i.e., 1800 sec). N = 15 for each treatment.

4.3.7 Ninhydrin results

The candidate baits and the positive control released free amino acids in significantly different cumulative amounts for each of the seven sampling events over 30 min experiment (Fig. 4.7, Table 4.1). At the conclusion of the experiment, the polychaete meal had released the greatest amount of free amino acids at an overall rate of 11.18 µM sec^{-1}, while the squid released the smallest amount at a rate of 1.06 µM s^{-1}. Pairwise comparisons of linear models of the amino acid release rates for each of the baits found that they were all significantly different (Table 4.2) with the relative rates of amino acid released by the candidate baits remained largely consistent over the course of the 30 min experiment (Fig. 4.7).

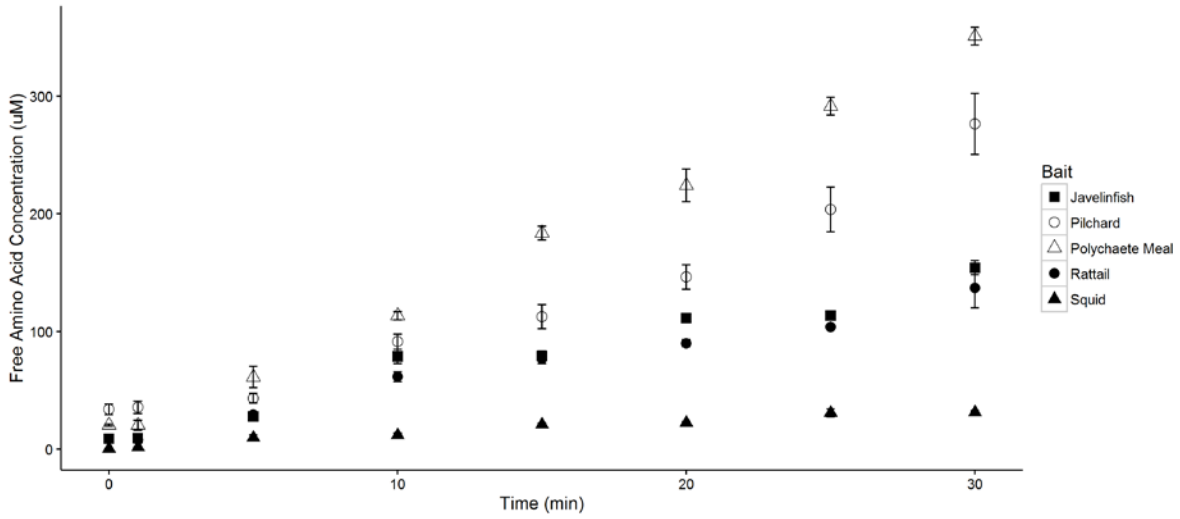

Figure 4.7 The cumulative amount of free amino acids released at five min intervals by the candidate baits and positive squid control over the course of the 30 min experiment. N = 3 for each treatment.

Table 4.1 The results of statistical comparisons of the cumulative concentrations of free amino acids (µM) released by each of the baits over the 30 min experiment. Different letters indicate significantly different means among the five baits for each five minute event, i.e., within rows (Tukey HSD, $P < 0.05$). N = 3 for each treatment.

Sample event	Javelinfish	Pilchard	Polychaete meal	Rattail	Squid
0 min	8.9 ± 0.8^{b}	33.8 ± 4.5^{d}	20.4 ± 0.9^{c}	8.4 ± 1.1^{ab}	0.3 ± 0.3^{a}
1 min	9.3 ± 0.6^{ef}	35.5 ± 5.3^{g}	20.2 ± 4.2^{f}	7.9 ± 0.9^{e}	1.6 ± 0.3^{e}
5 min	27.7 ± 1.7^{hi}	43.3 ± 4.1^{ij}	61.1 ± 9.1^{j}	29.4 ± 2.3^{i}	9.7 ± 2.4^{h}
10 min	78.8 ± 6.1^{lm}	91.3 ± 6.5^{m}	113.4 ± 3.4^{n}	61.5 ± 4.1^{l}	11.8 ± 4.2^{k}
15 min	79.2 ± 4.2^{p}	112.5 ± 10.2^{q}	183.7 ± 5.9^{d}	77.1 ± 4.5^{p}	20.8 ± 1.3^{o}
20 min	111.4 ± 3.9^{s}	146.2 ± 10.5^{t}	224.2 ± 13.9^{u}	90.0 ± 3.2^{s}	22.3 ± 1.3^{r}
25 min	113.5 ± 2.1^{w}	203.7 ± 18.9^{x}	291.5 ± 7.6^{y}	103.7 ± 2.5^{w}	30.8 ± 3.2^{v}
30 min	154.1 ± 6.0^{aa}	276.4 ± 26.1^{bb}	351.0 ± 7.5^{cc}	136.9 ± 16.8^{aa}	31.4 ± 1.3^{z}

Table 4.2 Comparsions of the slope of the release rate of free amino acids from the baits over the 30 min experiment. P-values generated by a post-hoc pairwise tests of the linear models. Abbreviations are as follows: JV = Javelinfish; Pil = Pilchard; PM = Polychaete meal; RF = Rattail; SQ =Squid. N = 3 for each treatment.

	Estimate	Std. Error	t value	P-Value
PIL - JV	45.2	7.3	6.15	< 0.001
PM - JV	85.1	7.3	11.59	< 0.001
RF - JV	-8.8	7.3	-1.20	0.75
SQ - JV	-56.0	7.4	-7.59	< 0.001
PM - PIL	39.9	7.3	5.47	< 0.001
RF - PIL	-54.0	7.3	-7.41	< 0.001
SQ - PIL	-101.1	7.3	-13.82	< 0.001
RF - PM	-93.9	7.3	-12.88	< 0.001
SQ - PM	-141.0	7.3	-19.27	< 0.001
SQ - RF	-47.1	7.3	-6.44	< 0.001

4.4 Discussion

Among the six baits tested, the pilchard and the pilchard-alginate baits were identified as the most attractive to the scampi and have the most potential as bait for developing a scampi potting fishery. For all behavioural measures, the scampi consistently responded positively to these pilchard baits, although these responses were not different from the squid positive control. The manner in which the scampi responded to the baits provides insights into how scampi search for food, and the characteristics of the bait that stimulate foraging behaviour. Furthermore, the results from the alginate bound baits indicate the potential for the development and use of artificial baits.

4.4.1 Quantifying behaviour

Knowledge of the food search behaviour of a target species is critical for enabling the efficient identification of effective species specific baits (Løkkeborg, et al., 2014). The three key phases of food search behaviour that enable capture of target species are; 1) detection of the odour, 2) tracking the

odour plume, and 3) initiation of feeding (Løkkeborg, et al., 2014). In a potting fishery, these phases are important, as they are required for the animal to locate the baited pot (Thomsen et al., 2010), entice the animal into the pot (Watson & Jury, 2013), and help retain the animal inside the pot (Jury et al., 2001). A key factor in all of these behavioural phases is the strength of the motivation of the animal to feed versus the perceived risk of predation (Zimmer-Faust, 1987). In decapod crustaceans it has been suggested that this risk assessment is determined by the 'quality' of the odorant chemicals present in the plume, and this can be positively or negatively affected by previous experiences with food items (Derby, 2000; Steullet, et al., 2002). Internal factors, such a starvation state, size and age of the animal, will also greatly influence the expression of food search behaviours (Moir & Weissburg, 2009). Previous studies have been unable to consistently distinguish between the behavioural responses of scampi to baits, possibly as a result of the poor discriminatory ability of the methods used (Major & Jeffs, 2017; Major, et al., 2017b).

Consequently, one of the first steps for this study was to develop a flume methodology to more effectively quantify and compare baits. The binary choice flume used in this study was capable of distinguishing baits that elicited weaker food attraction behavioural responses in scampi. For both javelinfish and rattail the scampi consistently took longer time to reach the baits, spent less time at the bait bags, spent a similar amount of time in the control channel versus the bait channel, and generated lower bait attraction ratios as calculated by the Cox proportional hazard models. In contrast, the pilchard baits had the lowest times to bait, were identified as being more attractive by the Cox proportional hazard models, and spent longer in the bait channels compared to other baits. While in these channels the scampi were strongly expressing proximate feeding behaviours, such as digging and probing with the walking legs trying to search for the bait within their reach (pers. obs.). These behaviours have previously been observed to dominate the orientation by scampi once they are within 40 cm of the bait (Major & Jeffs, 2017), similar to the length of the channel. This suggests that the characteristics of the pilchard baits were eliciting different behaviours compared to the other baits

4.4.2 Bait characteristics

Despite their high level of attractiveness to scampi, the pilchard bait did not have the highest release rate of amino acids. This suggests that the scampi were more attracted to the chemical profile of the

odour plume released from the pilchard baits rather than the overall concentration of the chemicals in the odour plume. Furthermore, as no differences were observed between the 1 and 10% pilchard baits and the intact pilchard tissue, this also suggests that the profile of the odorant chemicals is more important than the amount of odorant chemicals that are released. This is consistent with results of studies of the leaching rates of aquaculture feeds on the behaviour of ornate spiny lobsters (*Panulirus ornatus*) (Williams, et al., 2005) and the response of American lobsters to a range of herring meals (Daniel & Bayer, 1989). Feeding preferences of both these lobster species was observed to be strongly linked to the leaching rates of specific highly attractive combinations of free amino acids and soluble proteins. For example, lobsters preferred natural mussel product over aquaculture feeds because of the higher concentration of glycine and other soluble nitrogenous compounds, such as peptides, that were released from the mussel (Williams, et al., 2005). Although amino acids are the most commonly identified odour chemicals that leach from food, it is possible that other chemical compounds that were not assayed, such as lipid, were also leaching and contributing to the observed behavioural responses of the scampi. However, it is likely that the leaching of free amino acids from baits would also serve as a general indicator of the overall amount of soluble odorant chemicals that are leaching out of the baits.

Polychaete meal and the two discarded bycatch fish species, the rattail and javelinfish, were used as bait treatments in this study as potential alternatives to traditional forage fish baits. All three of these items have been identified as dietary items in other *Metanephrops* species (Choi, et al., 2008; Cristo & Cartes, 1998; Wassenberg & Hill, 1989). Discarded fish species have been suggested to supplement the diets of benthic crustaceans and other scavengers (Bergmann et al., 2002b; Saila et al., 2002; Wassenberg & Hill, 1989). Additionally, as javelinfish and rattails account for up to 60% of the estimated 1430 t of all bycatch discarded from the combined New Zealand trawl fisheries in 2005-06 (Anderson, 2012), it is likely that scampi in their natural habitat could have access to these fish at times. It is surprising that the odour profile of the pilchard, is more attractive than the types of food items they are more likely to encounter and consume in the natural environment, such as benthic polychaete worms (Choi, et al., 2008; Sahlmann, et al., 2011). This could be due to the heat treatment used for processing the polychaete meal which is known to denature attractive compounds in preparing other animals meals for aquaculture applications (Daniel & Bayer, 1989), and may have reduced the attractiveness of the polychaete meal to the scampi. If scampi are feeding on fisheries

discards, then they may be more attracted to the decomposing tissue than the fresh tissue presented in our experiment. Strong attraction to decomposing tissues releasing cadaverine and putriscene as attractants has been determined in other benthic decapod species (Mendoza, et al., 1997; Montemayor, et al., 2002).These results suggest that more in-depth chemical analyses are required to identify the combination of odour chemicals from the most attractive baits that are most attractive to scampi.

The scampi spent longer in the respective bait channels versus the control channels only in response to the pilchard and 1% pilchard baits, and spent significantly longer at the 1% and 10% pilchard-alginate bait bags than a number of the other bait types. In crustaceans the initiation of feeding is controlled by the distributed sensory system, that is present all across the body, but primarily in dense tufts on the mandibles and walking legs (Derby & Atema, 1982). The chemosensory neurons of the distributed sensory system are tuned to different chemicals at higher concentrations than the sensors used to detect and track plumes (Garm, et al., 2005). Therefore, this suggests that the chemical profile of the odour plume was more likely to trigger these behaviours than the other baits.

4.4.3 Potential for an artificial bait

The results suggest that there is the potential to create artificial baits, which incorporate diluted amounts of effective natural bait material, potentially reducing the amount of fish tissue used as bait in a potting fishery for scampi. Studies have observed the chemosensory systems of crustaceans to be very sensitive, and can detect and respond to attractant chemicals at low concentrations (Zimmer-Faust, 1991). Additionally, once concentrations are over a specific threshold, any increase in concentration will not increase the behavioural response of the crustacean to the plume (Page, et al., 2011a). Other experimental artificial baits have incorporated natural products at percentages ranging from 30% fish product (Vazquez-Archdale & Kawamura, 2011) to 85% fish product (Chanes-Miranda & Viana, 2000). These studies have also used a range of binders, including starches (Chanes-Miranda & Viana, 2000; Vazquez-Archdale & Kawamura, 2011), gelatine (Dale, et al., 2007; Nunes, et al., 2006), alginate (Wakefield, 2013), and guar gum (Løkkeborg, 1991), all of which affect the rate of release of the chemoattractants from the baits, and have been observed to affect both the catch rates and bait loss (Løkkeborg, 1991). Increasing the strength of the binder will slow down the rates of release of the attractant chemicals and may in some instances reduce the catch rates of artificial baits

(Dale, et al., 2007). Therefore, there is a need to match the longevity of artificial baits to the soak time of the pots, while still maintaining the release of sufficient odour chemicals to attract animals into the pots. Future development of artificial baits for scampi should focus on experimenting with binder strength and how this affects the release rates of attractants and bait longevity.

4.4.4 Conclusion

In conclusion, scampi displayed the highest levels of attraction to the pilchard and pilchard-alginate baits. Interestingly neither of these baits had the highest release rate of free amino acids, which suggests that an attractive profile of odour chemicals is more important than just high concentrations of soluble odour chemicals. Baits made with common fisheries discard species or the polychaete meal, were less attractive to scampi and not considered viable as potential bait. However, the scampi were strongly attracted to alginate baits incorporating 1% and 10% pilchard, suggesting that artificially bound baits using natural marine tissues could be suitable baits, however, additional research is required on the longevity of their effectiveness before being used in developing a potting fishery for scampi. The results of the study highlight the need for field testing of the baits to observe their effect on catch rates of both scampi and bycatch species.

Chapter Five:

Factors affecting bycatch in a developing New Zealand scampi potting fishery

5.1 Introduction

5.1.1 Bycatch in potting fisheries

Bycatch is the unintentional capture of non-target species during fishing. It is caused by low selectivity in fishing gear and represents a challenge to fishers and fishery managers around the globe (Suuronen, et al., 2012). Around 8% of global fisheries catch is considered to be bycatch and is mostly discarded back into the ocean (Kelleher, 2005). Bycatch increases the amount of effort required to catch and process the target species, and has been linked to population declines in a number of seabird and marine mammal species (Abraham & Thompson, 2011). Crustacean trawl fisheries typically have high bycatch rates per kilogramme of the target species landed (Broadhurst et al., 2006; Catchpole, et al., 2008; Suuronen, et al., 2012). For example, tropical shrimp trawling has the highest discard rate among fisheries, contributing to 27% of estimated global fishery discards (Kelleher, 2005).

Pots (also known as traps or creels) are widely used for catching crab, lobster and some shrimp species (Miller, 1990). Pots tend to be more selective and produce less bycatch and benthic habitat disturbance than trawling methods and have been highlighted as a low impact and fuel efficient fishing method (Broadhurst et al., 2007; Eno et al., 2001; Suuronen, et al., 2012). For these reasons potting methods are frequently used as a more sustainable alternative to trawl fisheries for Norway lobster, *Nephrops norvegicus*, and spot prawns, *Pandalus platyceros* (Favaro et al., 2010; Leocádio, et al., 2012). Pots are primarily limited to areas where trawler access is restricted due to the seafloor rugosity or legislation (Ungfors, et al., 2013). However, pots can be economically advantageous as they require less fuel to fish and pot-caught animals often attract a premium price due to their superior size and condition (Leocádio, et al., 2012; Morello, et al., 2009; Ungfors, et al., 2013). Large numbers of pots are typically required to be deployed in a developed fishery, and consequently even low bycatch rates in pots can result in significant impacts on the local ecology. For example, in the British Columbian pot fishery for spot prawns, the rockfish, *Sebastes* spp., is a common bycatch species

which is also vulnerable to overfishing. As 3.4 million pots are lifted each year during the eight-week season, even though bycatch rates are low, the large number of pot lifts has contributed to the declining populations of rockfish, leading to the development of bycatch reduction devices (Favaro et al., 2013; Favaro, et al., 2010).

Pot bycatch is determined by the selectivity of the pot and is affected by features such as the pot size and shape (Butcher et al., 2012), the size of the mesh (Vazquez-Archdale et al., 2006), number and position of entrances (Morello, et al., 2009; Vazquez-Archdale, et al., 2006; Vazquez-Archdale et al., 2007) and the number and size of escape windows (Arana et al., 2011; Boutson et al., 2009; Harada et al., 2007). Bycatch in pots typically consists of undesirable species and target species that are undersized or gravid (carrying eggs) which are discarded; or non-target fisheries species which are still collected and sold, such as European brown crab, *Cancer pagurus*, in some Norway lobster fisheries (Leland et al., 2013; Ungfors, et al., 2013). Moreover, bycatch species are a nuisance as they take up valuable space, damage and consume the bait, and can impede the target species from entering the pot, ultimately reducing the number and value of the target species that are caught (Adey, 2007).

Bycatch in pot fisheries can be reduced by the inclusion of bycatch reduction devices (Favaro, et al., 2013), by increasing the mesh size in the body of the pot or escape windows (Groeneveld et al., 2005; Ovegård et al., 2011) and the inclusion of escape windows (Arana, et al., 2011). In fisheries where there is a minimum size of capture for the target species, regulations can mandate the inclusion, size and location of escape windows (Treble et al., 1998). Different construction materials for pots can also exclude some species. For example, steel entrance rings are promoted as being able to exclude crabs from pots targeting Norway lobster (Carapax, 2015). Bycatch in pots can also be reduced by how the pots are deployed, such as, the use of floating pots to target demersal cod can virtually eliminate the bycatch of benthic-dwelling red king crab (Furevik et al., 2008).

Baits are an integral part of any crustacean potting fishery and fishers strive to use baits that specifically attract target species as they can greatly influence the catch rates (Miller, 1990). Bycatch species are typically generalist scavengers (Moore & Howarth, 1996), and bycatch rates in commercial potting fisheries are generally not affected by bait choice (Favaro et al., 2010). However, benthic scavengers of European fishery discards show clear preferences among echinoderm, mollusc

and crustacean baits, and are universally attracted to fish baits (Bergmann, et al., 2002b; Groenewold & Fonds, 2000). One scavenger frequently attracted to baits are sea lice (Order: Isopoda), which can consume the bait, reducing the effectiveness of the pot for catching the targeted species (Miller, 1990; Morello, et al., 2009). To reduce the impact of sea lice and other scavengers, as well as target species, on the longevity of bait, plastic bait containers (also known as snifters) are used to protect the bait in many pot fisheries. However, sea lice can sometimes pass through the holes or meshes in the bait container, and consume the bait. Consequently, there is the potential to minimise bycatch by optimising the choice of baits and the bait containers to ensure the pots can fish as efficiently as possible.

5.1.2 Scampi pot fishery

New Zealand scampi (*Metanephrops challengeri*) are a highly valuable lobster species which are widely distributed on the continental shelf of New Zealand in depths of 250-550 m (Tuck, et al., 2015). Scampi are fished in waters of around 300 m depth by bottom trawling with triple rigged otter trawls. The scampi trawl fishery has the highest discard rate among deep-water fisheries in New Zealand, discarding on average 4.2 kg of bycatch for every 1 kg of scampi caught (Anderson, 2012). Potting has been suggested as an alternative and more sustainable method for harvesting this species (MBIE, 2014). Potting is widely used for harvesting Norway lobster in Europe, a species sharing many biological and ecological similarities with *Metanephrops* species (Bell, et al., 2013; Ungfors, et al., 2013).

Previous attempts to catch NZ scampi in European-style pots resulted in a large bycatch of hagfish, *Eptatretus cirrhatus,* and sea lice (Martin Cryer, pers. comm. 2015). Hagfish secrete a large volume of mucous when entrapped which can make pots difficult to handle, reduce the ability of the pot to continue fishing and potentially suffocate any scampi inside the pots, as occurs in the white-spotted conger eel, *Conger myriaster,* fishery in Japan (Harada, et al., 2007). Furthermore, there is a small hagfish fishery operating in New Zealand and concerns over the state of the stock of this species has led to recent recommendations for tighter control on the numbers of smaller hagfish being caught (Ministry for Primary Industries, 2014). For these reasons, reducing the amount of hagfish bycatch is one of the biggest concerns for a developing scampi potting fishery.

5.1.3 Aim and objectives

The aim of this study was to identify the factors which influence the bycatch of non-target species in pots targeting scampi. The factors that were considered to influence bycatch were; bait species, pot design, pot soak time, deployment event, individual string on which any pot is deployed, and effectiveness of the design of the bait containers as assessed by the presence of sea lice in the container. The study investigated these factors at two well-known fishing sites for scampi to ensure the results are not location specific. The results of this study will be used to guide the future design of scampi-specific baits and pots for a developing potting fishery targeting scampi.

5.2 Methods

5.2.1 Fishing experiments

Four different pot designs that are widely used in the Northern Hemisphere for catching Norway lobster were experimentally deployed at two study sites in New Zealand waters that are well-known fishing grounds for scampi (Fig. 5.1). Three different bait species were used in the pots (barracouta, *Thyrsites atun*; mackerel, *Scomber australasicus*; and New Zealand arrow squid, *Nototodarus sloanii*). At the first study site on the Chatham Rise (42-43°S, 176-177°E), a total of 279 pot lifts were undertaken by deploying a total of nine strings of pots over three separate deployment events from the fishing vessel *Sea Hawke II* during 26 November – 12 December 2014. Each deployment event consisted of three 500 m long strings of pots each made of a line with an anchor at each end and carrying 30 pots consisting of 10 each of three different designs, Pot 1, Pot 2 and Pot 3 (Fig. 5.2). The 30 pot attachment points were evenly spaced (roughly 17 m) along each string and the pots of the three different designs randomly allocated to each attachment point and connected to the string with a 1.8 m bridle. Additional pots were added to the end of each string to account for losses if they occurred; this led to a total of 94 × Pot 1, 94 × Pot 2 and 91 × Pot 3 pots being deployed and retrieved over the course of the sampling. Five randomly selected pots from each design were baited with 120 g of mackerel and five were baited with 120 g of squid. The bait was cut from frozen on board the boat and placed into the bait containers, as the pots were being deployed. Overall, 47 Pot 1, 47 Pot 2 and 46 Pot 3 pots were deployed with squid baits and 47 Pot 1, 47 Pot 2 and 45 Pot 3 pots were deployed with mackerel bait. Two varieties of bait containers, Artel bait container (A) and Carapax bait container (B) (Fig. 5.3), were used due to the different designs of the pots. All pots were weighted with a 1 kg steel bar to ensure they landed on the seafloor upright and in the correct orientation to catch

scampi. The time of deployment for the Chatham Rise pot strings varied between 01:00 and 03:00 hrs New Zealand Standard Time (NZST).

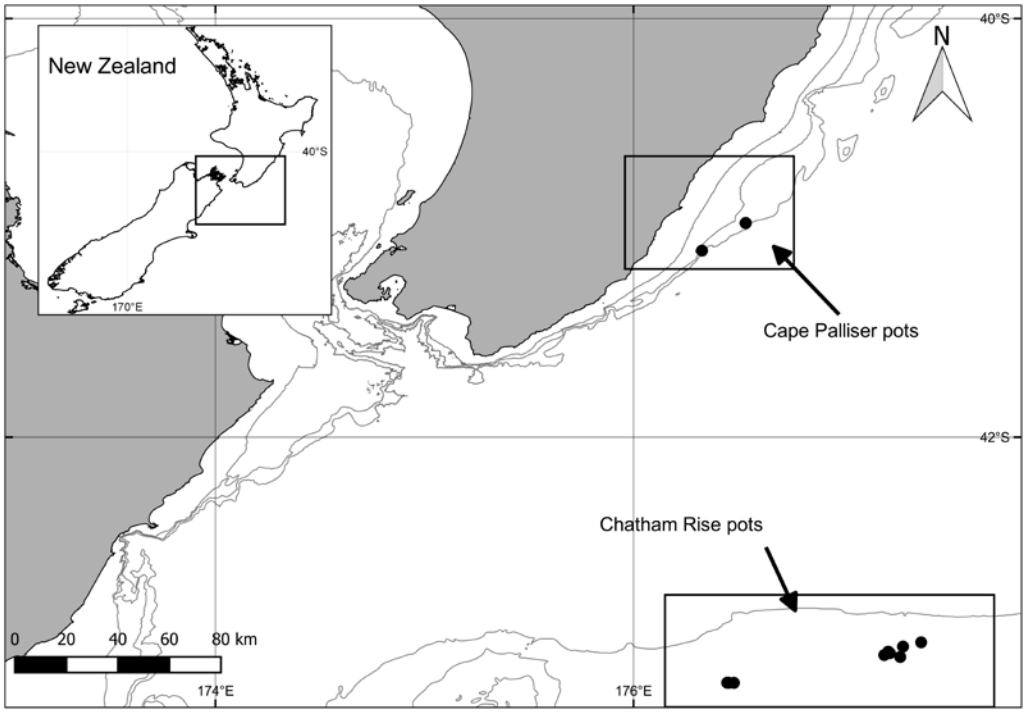

Figure 5.1 Map showing the location of the two study sites, the Chatham Rise and Cape Palliser, on the east coast of New Zealand. Black dots show the location of an individual string of pots that was deployed during the study.

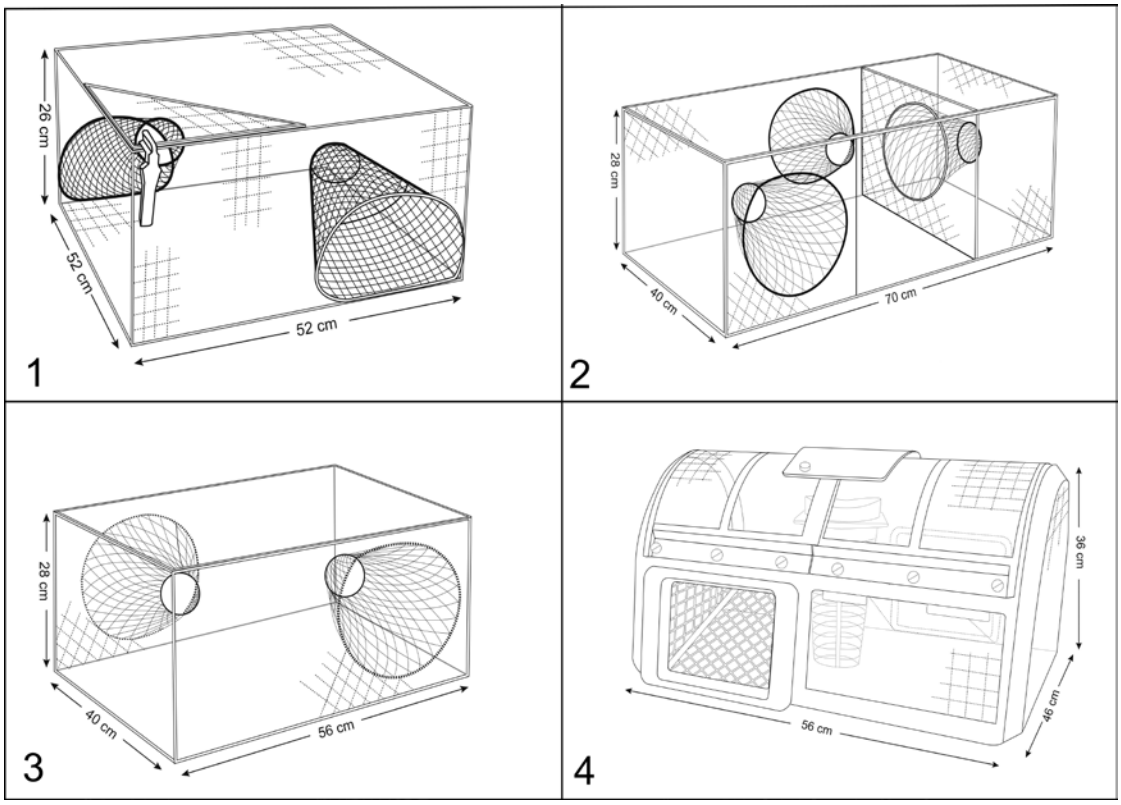

Figure 5.2 The four pot designs that were used in the study. 1: Pot 1; 2: Pot 2; 3; Pot 3; 4: Pot 4. Dimensions and additional details of the pots are present in Table 5.1.

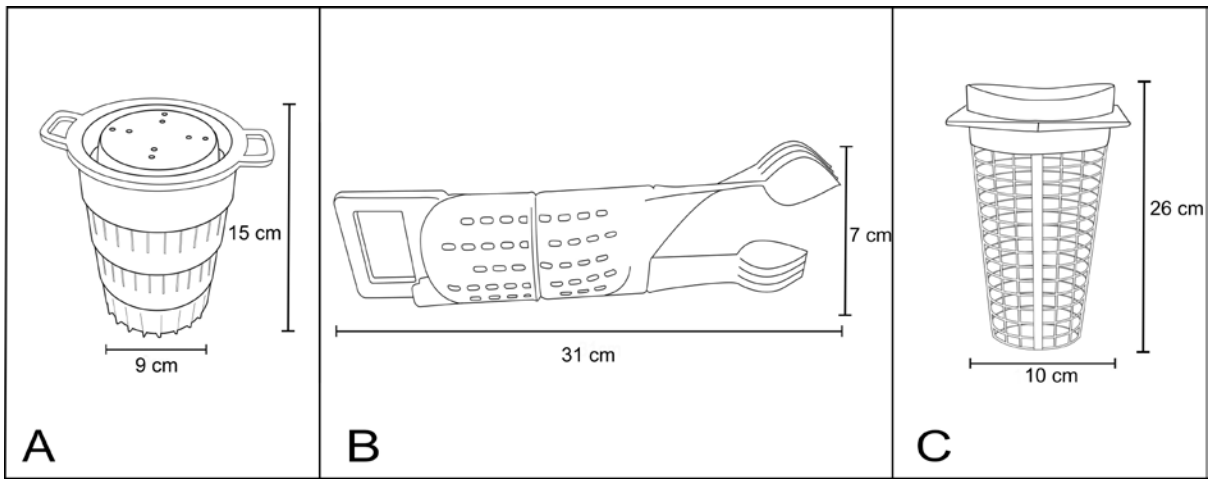

Figure 5.3 The three different bait container types that were used in the varying pot designs. A - Artel bait container used in Pot 1; B: Carapax bait container used in Pot 2 and Pot 3; C - Fluted bait container built into Pot 4.

The second study site was off Cape Palliser (40-41°S, 175-176°E) where a total of 91 pot lifts were undertaken by deploying four different pot designs (Pot 1, 2, 3 & 4) in three deployment events during 16 – 23 April 2015 from the fishing vessel *Te Kahurangi* (Table 5.1). Each deployment event consisted of a single 500 m string of pots carrying 30 pots with a representative mix of the four pot designs. Pots of the four different designs were randomly distributed along the 30 pot attachment points which were evenly spaced along each string. Each pot was attached to the string with a 1.8 m long bridle. Seven Pot 1, Pot 2 and Pot 3 and between 9 and 10 Pot 4 pots were on each string, resulting in a total of 21 × Pot 1, 21 × Pot 2, 21 × Pot 3 and 28 × Pot 4 being deployed and retrieved at this site. Half of the pots of each design were randomly selected and baited with 120 g of barracouta and the other half were baited with 120 g of squid with all bait being placed in bait containers, three varieties of containers were used due to the constraints of the different designs of the pots . Overall, a total of 11 Pot 1, 11 Pot 2, 10 Pot 3 and 14 Pot 4 pots were deployed with squid bait and 10 Pot 1, 10 Pot 2, 11 Pot 3 and 14 Pot 4 pots were deployed with barracouta bait. All pots were weighted with a 1 kg steel bar as per the deployment of pots at the Chatham Rise and the time of deployment for strings of pots varied between 13:00 – 21:00 hrs NZST.

Table 5.1 Specifications of the four pot designs that were experimentally compared for bycatch whilst fishing for scampi.

Pot name and design	Company and country of origin	Dimensions L x W x H (cm)	Frame	Mesh covering	Entrance	Bait Container
1 – regular box shaped creel.	Carapax, Sweden	52 x 52 x 26	6 mm plastic coated steel wire	22 mm mesh polyethylene netting,	2 entrances with 7.5 cm plastic eyes and ramp	Artel bait container – with 1 mm wide slots (Fig 5.3 B)
2 – rectangular creel with parlour	Carapax, Sweden	70 x 40 x 28	6 mm plastic coated steel wire	22 mm mesh polyethylene netting	2 entrances 7 cm plastic coated steel eyes, netting entrance	Carapax bait container – with 2 mm wide slots (Fig 5.3 A)
3 – standard creel	Carapax, Sweden	56 x 40 x 28	6 mm plastic coated steel wire	22 mm mesh polyethylene netting	2 entrances 7 cm plastic eyes, netting entrance	Carapax bait container – with X mm wide slots (Fig 5.3 A)
4- UK Pot-Domed plastic pot	Polypot, United Kingdom	56 x 46 x 36	10 mm steel frame	Moulded polyethylene, 14 mm mesh	2 entrances nylon with 9 cm nylon eyes and a nylon ramp	Fluted bait tube built into pot – with 6 -10 mm wide mesh (Fig 5.3 C)

The deployment of each string of pots had a target soak time of 18 h, at which time the strings were retrieved using a hydraulic line hauler. Once on board the vessel, each pot was emptied and the bycatch species were identified to species where possible and counted. When sea lice were present in the bait containers they were in large numbers making it difficult to count them, as a result only the presence of sea lice within the bait containers was recorded for each pot to determine the effectiveness of the bait container designs in protecting the bait. In addition, at Cape Palliser it was also recorded if the bait container was empty. Photographs were taken of species that could not be identified at sea and were later identified using an identification guide (Tracey et al., 2011). Due to commercial sensitivity the catch of scampi in the experimental pot deployments has not been reported here.

5.2.2 Data analyses

The data from the two sampling sites were analysed separately due to differences in location, season, baits and number of pot designs used at each of the sites. For each sampling site the bycatch species was analysed using log-linked generalised linear models (GLM) to compare the effect of the experimental factors (bait species, pot design, string number, deployment date, soak time (as continuous), presence of sea lice, presence of remaining bait (Cape Palliser only) and the interaction of bait species and pot design). Models were firstly constructed for the catches of the total bycatch (i.e., counts of all captured taxa) and secondly for three broad groupings of bycatch taxa; hagfish, other fish species, and invertebrates (Zeileis et al., 2008). The analyses proceeded by identifying the correct distribution (negative binomial or Poisson) for each of the bycatch groups by creating models with both distributions and comparing them using a likelihood-ratio test (Jackman, 2015). The bycatch of other fish species (i.e., not including hagfish) on both the Chatham Rise and Cape Palliser, as well as the invertebrate bycatch at Cape Palliser were found to have a Poisson distribution, while all other bycatch taxa groupings and total bycatch had a negative-binomial distribution.

The full models incorporating all of the factors were tested using alias methods to identify factors that were causing multicollinearity (Chambers & Freeny, 1992), this led to soak time, deployment event and the interaction of bait species and pot design being removed from the Chatham Rise models, and soak time, deployment event, and the interaction of bait species and pot design being removed from the Cape Palliser models. Deployment event was considered to be a potentially important factor, and

was included in the analysis by creating a separate model in which deployment event replaced string as a factor.

To test the significance of each of the factors, reduced models were created and then compared to the full model using a likelihood-ratio test, where a significant result indicated that the inclusion of the predictor factor in the full model leads to a significantly better fit of the model to the data (Quinn & Keough., 2002). When a categorical factor was observed to be a significant predictor variable by the likelihood ratio tests, multiple comparisons were made using Tukey methods ($\alpha = 0.05$) to determine the differences in mean catches within the category (Hothorn, et al., 2008). The log odds ratios and 95% confidence intervals (CI) from the multiple comparisons were then transformed and used to assess the strength of the differences within the categorical factor that significantly affected the bycatch group (Carruthers et al., 2009; Watson et al., 2005).

Contingency tables with a chi-square test were used to compare the number of zero bycatch events and catch events of five or higher bycatch individuals for each of the different pot types as these events are an important indicator of the selectivity of the pots. Contingency tables were also used to compare the presence of sea lice in relation to the three bait container designs.

5.3 Results

5.3.1 Bycatch composition

Overall, 370 pot lifts were undertaken on the Chatham Rise and Cape Palliser, resulting in the sampling of 19 different bycatch species (Table 2), with a mean total catch (±S.E.) of 1.3 ± 0.1 bycatch individuals per pot on the Chatham Rise and 3.2 ± 0.5 at Cape Palliser. Regardless of pot design, 32% of the 370 pot lifts were retrieved empty of bycatch. Hagfish were the most common bycatch species, comprising 43% of the catch on the Chatham Rise and 84% of the catch at Cape Palliser, whereas invertebrate species comprised 33% and 10%, and other fish species (i.e., excluding hagfish) comprised 24% and 5%, of the catch on the Chatham Rise and Cape Palliser respectively. Only three of the bycatch taxa caught were unique to one or other of the two sampling sites. Armoured flathead (*Hoplichthys haswelli*) and sea-urchins (class: Echinoidea) were only caught on the Chatham Rise, and the draughtsboard shark (*Cephaloscyllium isabellum*) was only caught at Cape Palliser.

Table 5.2 Taxonomic groups and species identified at the Chatham Rise (CR) and Cape Palliser (CP) sites.

Group	Common name	Scientific name	CR	CP
Invertebrates				
	Hermit crab	*Diacanthurus rubricatus*	✓	✓
	Starfish	*Psilaster acuminatus*	✓	✓
	Garrick's masking crab	*Leptomithrax garricki*	✓	✓
	Frilled crab	*Trichopeltarion fantasticum*	✓	✓
	Other crabs	*Order: Decapoda*	✓	✓
	Squat lobster	*Munida spp.*	✓	✓
	Whelk	*Penion chathamensis*	✓	
	Knobbled whelk	*Austrofusus glans*	✓	✓
	Nudibranch	*Doriopsilla sp.*	✓	✓
	Sea Urchins	Class: Echinoidea	✓	
Hagfish				
	Hagfish	*Eptatretus cirrhatus*	✓	✓
Other -Fish				
	Ling	*Genypterus blacodes*	✓	✓
	Sea gurnard perch	*Helicolenus percoides*	✓	✓
	Red cod	*Pseudophycis bachus*	✓	✓
	Armoured flathead	*Hoplichthys haswelli*	✓	
	Conger eel	*Conger verreauxi*	✓	✓
	Draughtsboard shark	*Cephaloscyllium isabellum*		✓
Sea Lice				
	Isopods	Order: Isopoda	✓	✓

5.3.2 Bait

The three types of bait used in the study did not significantly affect the quantity or composition of bycatch in the scampi pots (Fig. 5.4). The only broad taxa group to be significantly affected by the bait species was the invertebrate bycatch on the Chatham Rise (χ^2 = 3.9, P = 0 .048). On average mackerel bait tended to catch 1.5 times the number of invertebrate bycatch than squid bait (95% CI:

1.2 - 1.8 times), however, this was not significant (P = 0.067). For the other bycatch groups on the Chatham Rise there was no difference in the total bycatch (χ^2 = 3.2, P = 0.074), hagfish (χ^2 = 1.4, P = 0.24) or other fish bycatch (χ^2 = -0.08, P= 0.78) taken in pots for mackerel versus squid bait. Similar results were observed at the Cape Palliser site for barracouta versus squid bait, i.e., total bycatch (χ^2 = 0.44, P = 0.5), hagfish (χ^2 = 0.2, P = 0.66), other fish (χ^2 = -2.9, P = 0.089) and invertebrate bycatch (χ^2 = -1.3, P = 0.25).

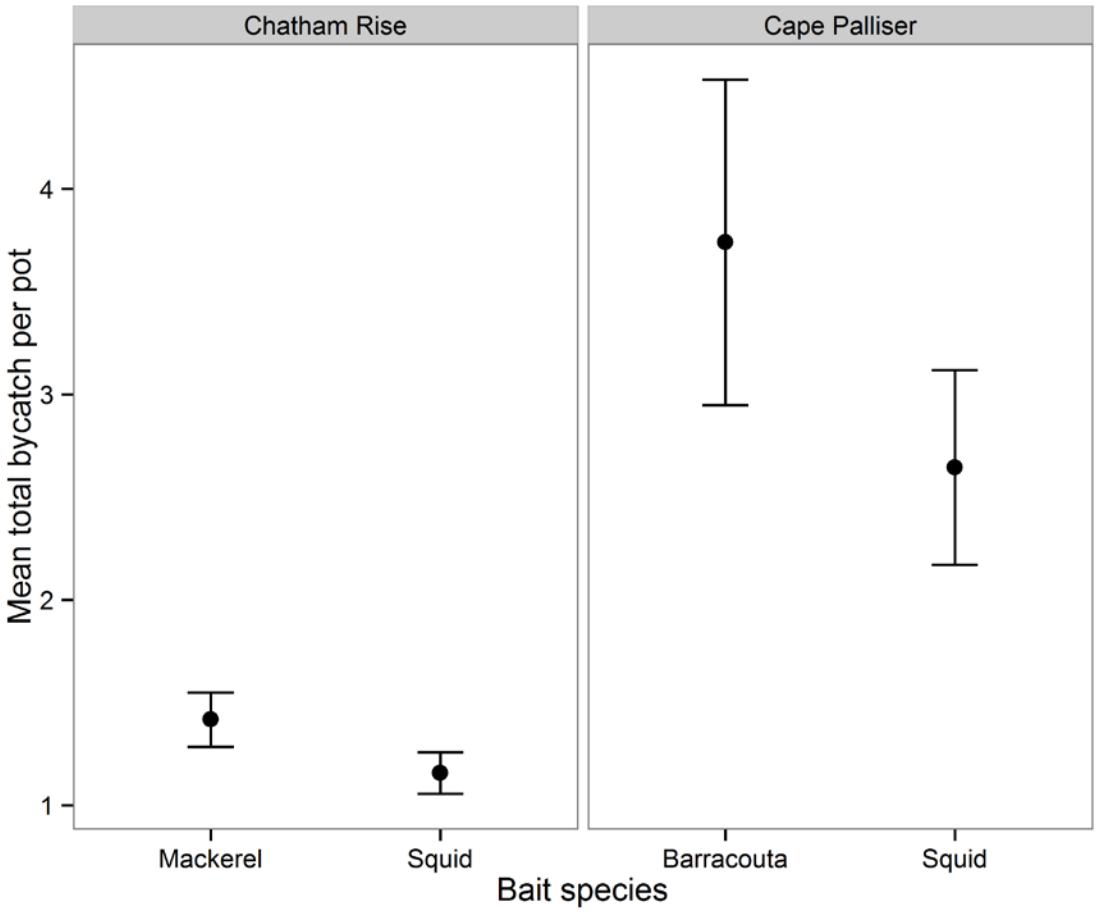

Figure 5.4 Mean total bycatch per pot ± S.E. for the three different bait species used in experimental scampi pots at two sampling sites. Sample sizes for each treatment are: Chatham Rise: Mackerel N = 139; Squid N = 140. Cape Palliser: Barracouta N= 45; Squid N = 46.

5.3.3 Pot design

For both sampling sites pot design significantly influenced total bycatch (Chatham Rise: χ^2 = 12.1, P = 0.002; Cape Palliser: χ^2 = 41.5, P < 0.001) and hagfish bycatch (Chatham Rise: χ^2 = 17.4, P < 0.001; Cape Palliser: χ^2 = 37.8, P < 0.001) in pots (Fig. 5.5). Only at the Chatham Rise did pot design have a

significant effect on the amounts of other fish bycatch (χ^2 = 10.9, P = 0.004) and invertebrate bycatch (χ^2 = -11.27, P = 0.004) in pots.

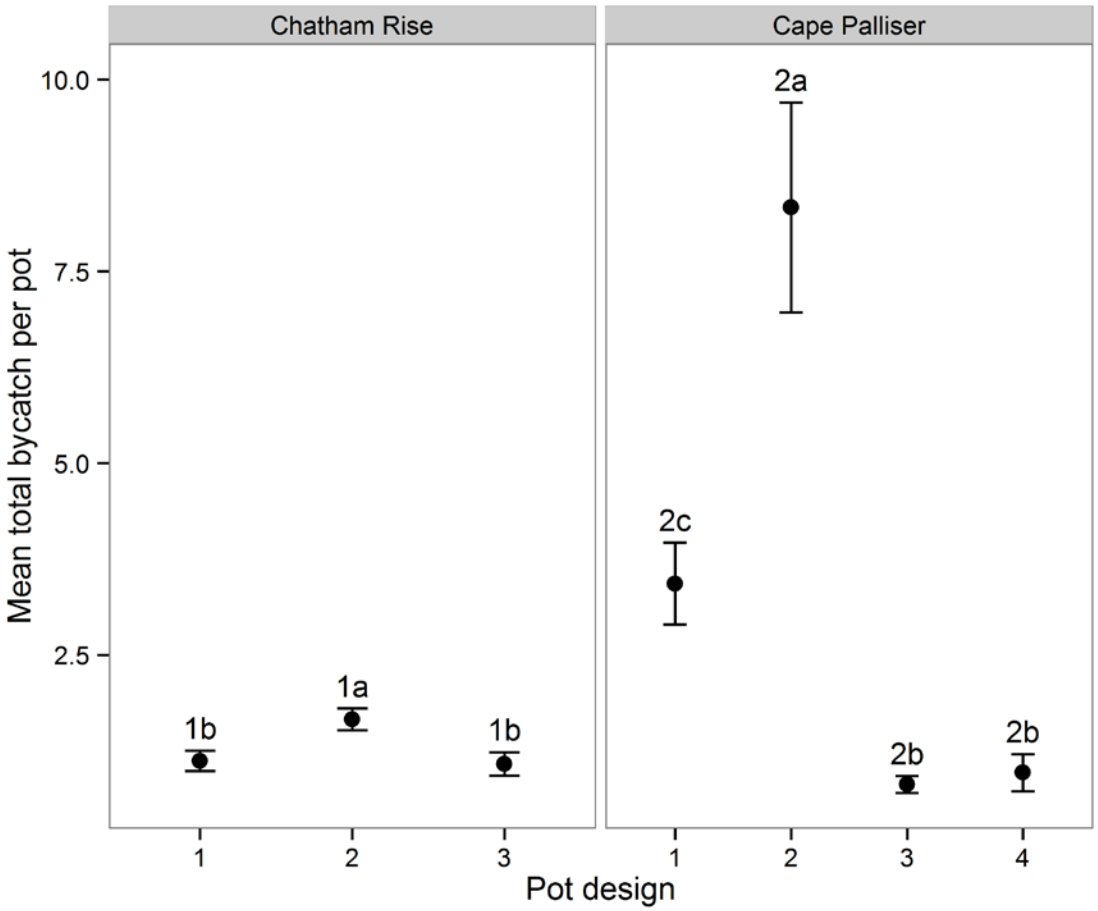

Figure 5.5 Mean total number of bycatch per pot ± S.E. for the different pot designs used on the Chatham Rise and Cape Palliser. Means with different letters within each site (1 for Chatham Rise and 2 for Cape Palliser) indicate significant differences (Tukey HSD, P < 0.05). Sample sizes for each treatment are Chatham Rise: Pot 1 N = 94, Pot 2 N =94 and Pot 3 N = 91. Cape Palliser: Pot 1 N = 21, Pot 2 N = 21, Pot 3 N = 21 and Pot 4 N =28.

On the Chatham Rise, Pot 2 caught significantly more total and hagfish bycatch than Pot 1 and Pot 3, and significantly more other fish bycatch than Pot 1, with the size of these differences ranging from 1.5 times higher for the total bycatch and 1.8 – 2.3 times higher for the hagfish and other fish bycatch (Table 5.3). There were no significant differences in the mean bycatch for any of the taxonomic

groupings between Pot 1 and Pot 3. At Cape Palliser, Pot 2 caught more total and hagfish bycatch than Pot 1, Pot 3 and Pot 4. Similarly, Pot 1 caught more total and hagfish bycatch than Pot 3 and Pot 4, while Pot 3 and Pot 4 were not significantly different from each other for any of the bycatch groups. These differences varied between 2.2 – 9.0 times higher for the total bycatch and 11.3 – 58.3 times higher for the hagfish bycatch (Table 5.3). Although pot design was a significant factor in the bycatch of invertebrates on Cape Palliser, multiple comparisons could not identify any differences between the individual pot designs.

On the Chatham Rise of the 279 pot lifts 35% were retrieved empty and 4% caught five or more individual bycatch items (Fig. 5.6). In total 21% of Pot 2 were retrieved empty, compared to 40% and 41% of Pot 1 and Pot 3 respectively, which was significantly different ($\chi^2 = 23.1$, $P < 0.001$). In contrast, 4% of Pot 1, 2% of Pot 2 and 5% of Pot 3 caught five or more bycatch individuals, this was not significantly different ($\chi^2 = 3.5$, $P = 0.174$). In comparison, on Cape Palliser of the 91 pot lifts 28% were retrieved empty and 20% caught five or more individual bycatch items (Fig. 5.7). In total 51% of Pot 4 were retrieved empty, while 10%, 20% and 24% of Pot 1, Pot 2 and Pot 3 respectively were empty, which was significantly different ($\chi^2 = 11.4$, $P = 0.009$). Whereas, 20% of Pot 1, 50% of Pot 2 and 0% of Pot 3 and Pot 4 had catches of five or more bycatch individuals, this was significantly different among the pot designs ($\chi^2 = 41.2$, $P < 0.001$).

Table 5.3 Comparisons of the different pot designs and deployment events that were significantly different by multiple comparisons (α =0.05).

Comparison	Bycatch group	Odds ratio size difference	95% CI	P (Tukey HSD)
Chatham Rise pot designs				
Pot 2 - Pot 1	Total bycatch	1.5	1.1 - 2.3	< 0.01
	Hagfish	1.8	1.2 - 3.0	< 0.01
	Fish	2.3	1.2 - 4.5	< 0.05
Pot 2 - Pot 3	Total bycatch	1.5	1.1 - 2.3	< 0.01
	Hagfish	2.3	1.5 - 4.0	< 0.01
Cape Palliser pot designs				
Pot 1 - Pot 3	Total bycatch	4.5	1.8 - 9.9	< 0.01
	Hagfish	4.8	1.2 - 12.5	< 0.01
Pot 1 - Pot 4	Total bycatch	4.0	1.5 - 10.4	< 0.01
	Hagfish	22.4	4.8 - 105.2	<0.01
Pot 2 -Pot 1	Total bycatch	2.2	1.2 - 4.3	< 0.01
	Hagfish	2.4	1.2 - 4.8	< 0.01
Pot 2 - Pot 3	Total bycatch	10.1	4.3 - 22.1	< 0.01
	Hagfish	11.3	45.1 - 22.8	< 0.01
Pot 2 - Pot 4	Total bycatch	9.0	3.4 - 21.0	< 0.01
	Hagfish	53.1	12.3 - 229.1	< 0.01
Chatham Rise deployment events				
Deployment 2 - Deployment 1	Total bycatch	1.5	1.5 - 2.2	< 0.05
	Hagfish	2.4	1.5 - 4.3	< 0.01
Deployment 2 - Deployment 3	Hagfish	2.1	1.2 - 3.6	< 0.01
Deployment 3 - Deployment 1	Fish	1.8	1.0 - 3.4	< 0.05
Deployment 3 - Deployment 2	Fish	2.5	1.2 - 4.8	< 0.05

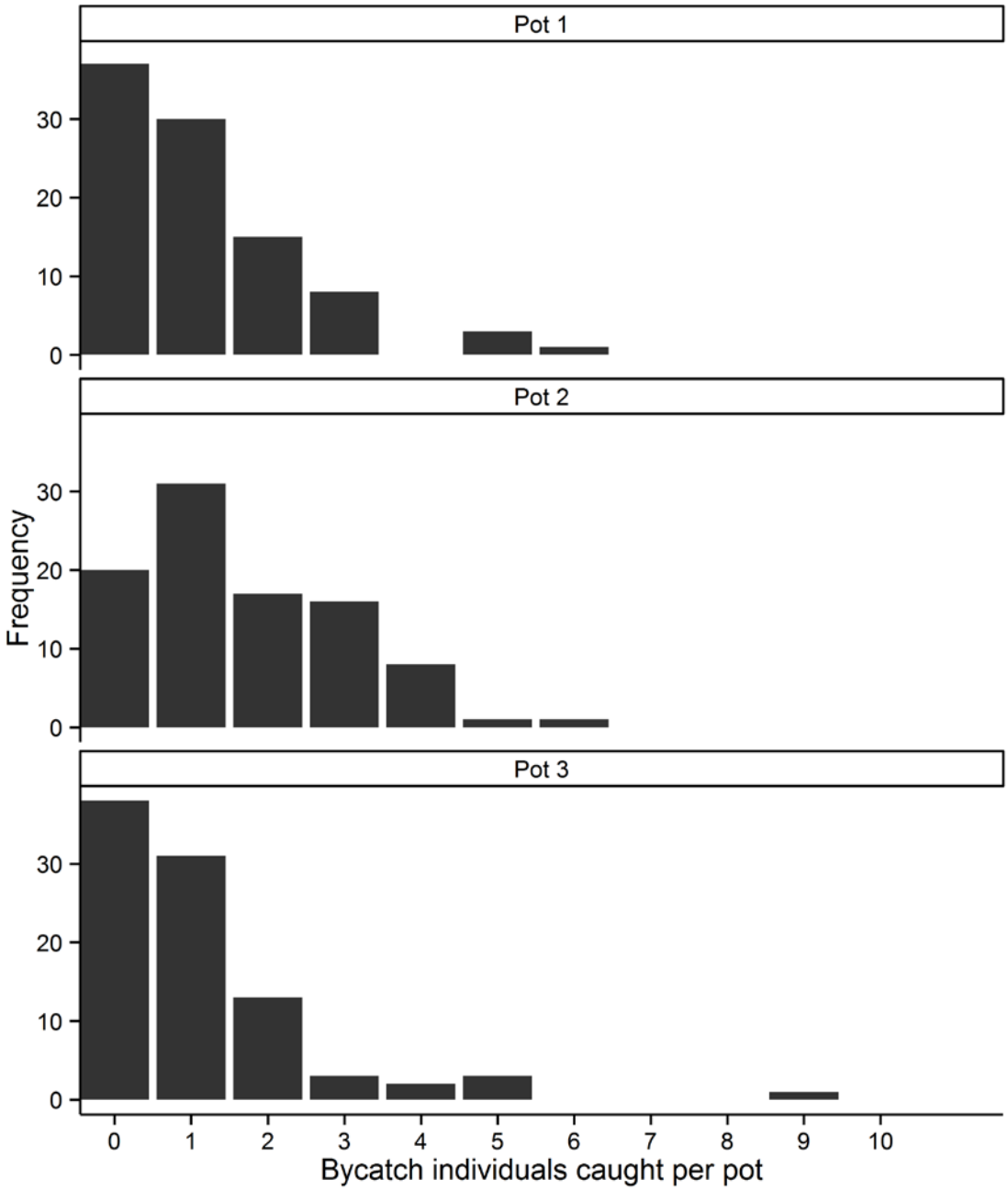

Figure 5.6 Frequency plots of the number of bycatch individuals caught per pot for the three different pot designs fished on the Chatham Rise. Sample sizes for each treatment are Pot 1: N = 94, Pot 2: N = 94 and Pot 3: N = 91.

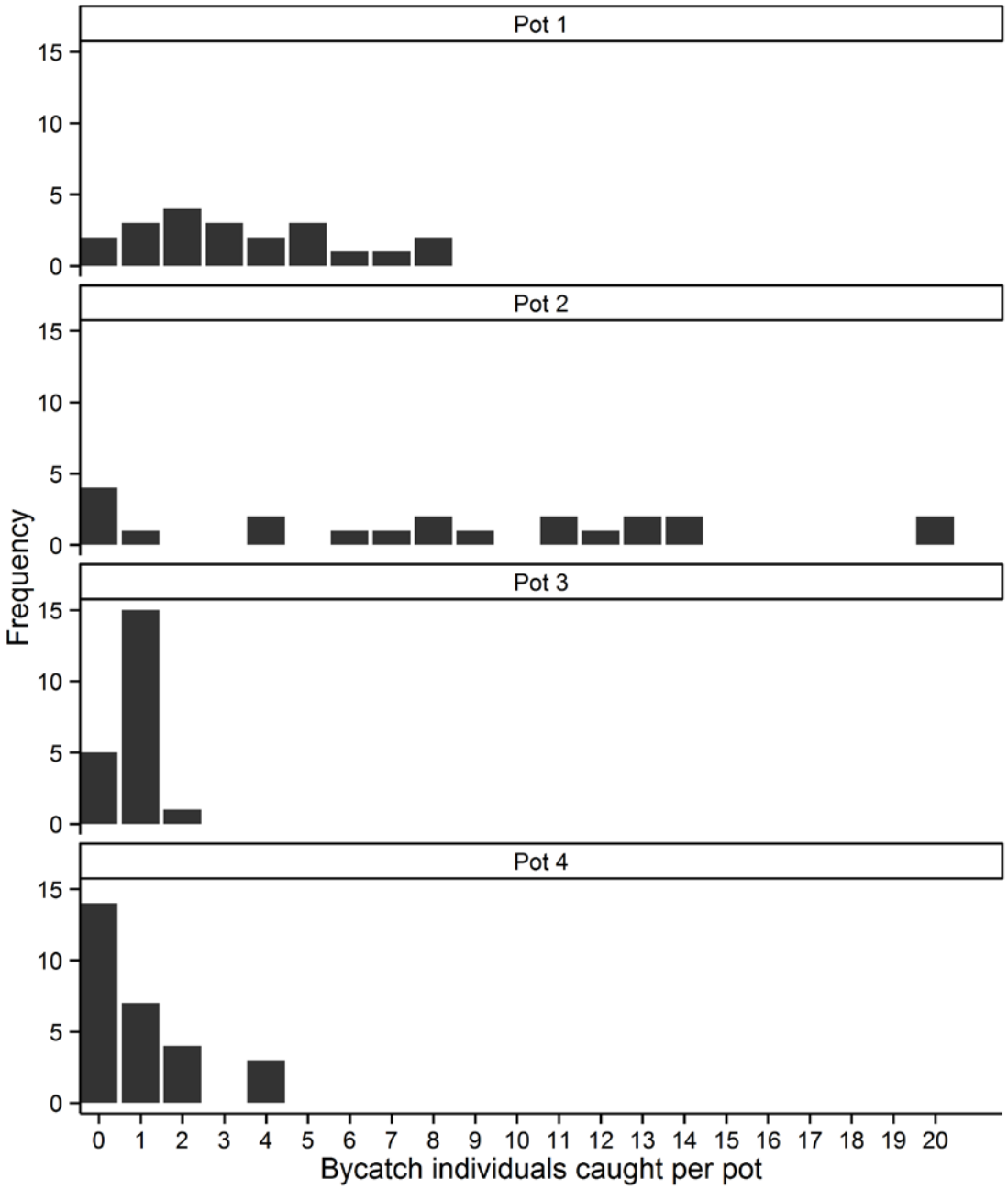

Figure 5.7 Frequency plots of the number of bycatch individuals caught per pot for the four different pot designs fished on Cape Palliser. Pot 1: N = 21, Pot 2: N = 21, Pot 3: N = 21 and Pot 4: N =28.

5.3.4 Effects of location

The separate strings were a significant predictor of the total, hagfish and other fish bycatch in pots on the Chatham Rise (total: $\chi^2 = 31.2$, $P < 0.001$, hagfish: $\chi^2 = 54.1$, $P < 0.001$, other fish $\chi^2 = 23.8$, $P = 0.002$) and a predictor of invertebrate catch on Cape Palliser ($\chi^2 = 20.6$, $P = 0.002$). On the Chatham Rise, Strings 3, 4, 5 and 7 caught significantly more total bycatch than String 1 (Fig. 5.8). Hagfish bycatch was highest for String 4 and 5 which caught significantly more than Strings 1, 6, 8 and 9.

Lastly, multiple comparisons could not detect any differences among the strings for other fish bycatch, despite overall differences being detected among strings. At Cape Palliser String 2 and 3 both caught significantly more invertebrate bycatch than String 1 (String 2: $P < 0.001$; String 3: $P < 0.001$). Some of these significant differences occurred within the same deployment events. Such as, during the first deployment event on the Chatham Rise, String 3 caught significantly more total bycatch than String 1, and in the second deployment event, String 4 and 5 caught significantly more hagfish bycatch than String 6 (Table 5.3).

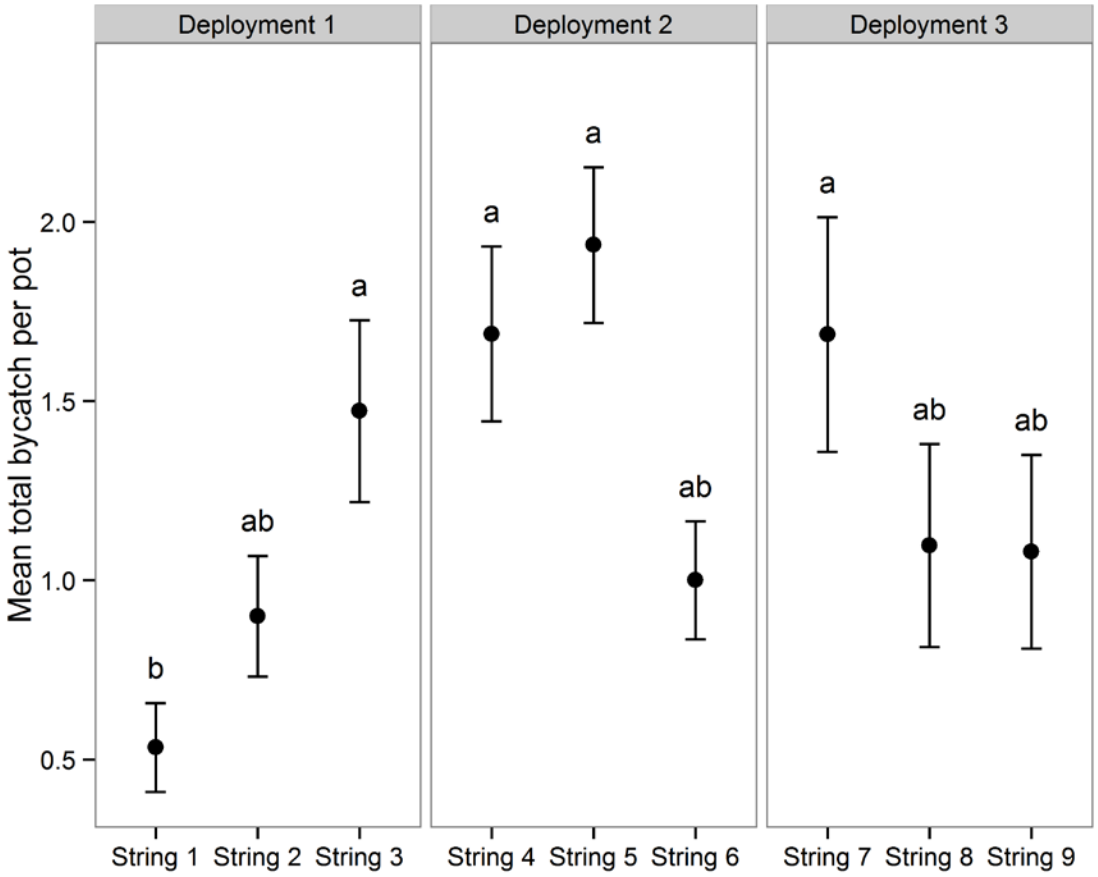

Figure 5.8 The mean total bycatch per pot of the different strings for three deployment events on the Chatham Rise. The means for strings with different letters indicate significant differences across all three deployments (Tukey HSD, $P < 0.05$). Sample sizes (N) for each string are: 1 = 30, 2 = 30, 3 = 36, 4 =32, 5 = 31, 6 = 29, 7=35, 8 =31, 9 = 25.

When the bycatch from deployment events was analysed separately, it showed that the deployment event significantly influenced the total bycatch ($\chi^2 = 8.4$, $P = 0.015$), hagfish ($\chi^2 = 18.5$, $P < 0.001$) and other fish bycatch ($\chi^2 = 12.6$, $P = 0.002$) on the Chatham Rise. The second deployment event caught

more total and more hagfish bycatch than the first deployment event, and more hagfish bycatch than the third deployment event, while deployment event 3 caught more fish bycatch than both deployment events 1 and 2 (Table 5.3). The invertebrate bycatch was not significantly affected by the different deployment events.

5.3.5 Bait containers

The key measure of the performance of the three different bait containers was the presence of sea lice in each pot and the presence of residual bait. Overall, for all pot lifts at both sites, sea lice were present in 12% of the Artel bait containers (Pot 1), 41% of the Carapax bait containers (Pots 2 & 3), and in 100% of the Polypot bait containers (Pot 4). The presence of sea lice was observed to be significantly different due to the bait container design on both the Chatham Rise and Cape Palliser (CR: $\chi^2 = 26.0$, $P < 0.001$; CP: $\chi^2 = 41.0$, $P < 0.001$). However, the presence of sea lice was not considered to be a significant predictor for any of the bycatch on either the Chatham Rise or Cape Palliser.

Only on Cape Palliser was a record kept of the presence of residual bait in the bait containers. Residual bait was present in 100% of the Artel bait containers, 95% of the Carapax bait containers and 1% of the Polypot bait containers. When incorporated into the model the presence of residual bait was found to be a significant factor for the catch of hagfish at Cape Palliser, associated with 6.8 times (95% CI: 1.6 – 30.9) greater hagfish bycatch by compared to those pots with no residual bait.

5.4 Discussion

5.4.1 Bycatch composition

A wide range of bycatch species were captured in the experimental pots at both the Chatham Rise and Cape Palliser sampling sites. Only three bycatch species were unique to either of the two sites, suggesting the habitat was broadly similar at the two sites. Hagfish was the predominant bycatch species at both sites (61% of overall bycatch in pots) whereas it makes up only a small proportion (0.2%) of the bycatch in trawls for scampi fishery observed over 20 years (Anderson, 2012). In the pots, other fish species comprised 15% of the bycatch, while fish species and arrow squid account for 78% of the total bycatch in the scampi trawl fishery. The fish species caught as bycatch in the trawl nets were primarily non-commercial rattail species (Family: Macrouridae) (29%) and commercially fished species such as sea perch (8%), ling (7%) and hoki, *Macruronus novaezelandiae* (6%). The

only commercially fished species that were caught in the pots were small sea perch (9%), red cod (3%) and ling (2%) taken in all pot hauls respectively. Rattails, which were the most caught fish group by the trawls, were absent from the pot bycatch, even though smaller individuals would be able to fit in the pots. This is likely to be due to behavioural differences in these species making them less likely to enter pots or that hagfish arrive at the baits earlier than the rattails and exclude other species. Previous studies have suggested hagfish feeding behaviour restricts access to carrion and actively discourages the activity of other scavenging species (Catchpole et al., 2006a). However, the pots (23%) caught a higher proportion of invertebrate bycatch species than the trawl nets (5%) (Anderson, 2012). This is consistent with other pot fisheries targeting both crustaceans and fish (Moffett et al., 2012; Zhou & Shirley, 1997). For example, the 11 most abundant bycatch species by weight in pots used for the spot prawn fishery of British Columbia are crustaceans (Favaro, et al., 2010). Pots targeting Norway lobster in both the UK and Sweden report similar levels of fish (around 10%) bycatch to the experimental pots in this study and also caught much lower levels of fish bycatch than corresponding trawl fishing (36 – 55%). However, the levels of invertebrate bycatch in the European pot fishery for Norway lobster (52%) was similar to that of the trawl fishery (60%) (Adey, 2007; Bergmann et al., 2002a; Jansson, 2008).

5.4.2 Effect of pots

Pot design was found to significantly influence total bycatch and hagfish bycatch at both sampling sites, and the bycatch of other fish only on the Chatham Rise. The four pot designs that were tested in the experiment all had two funnel shaped entrances in similar positions on the pot and no escape windows. Design differences among the pots amounted to differences in mesh sizes, some construction materials, volume of the pots and the size of the pot entrances. Pots 1, 2 & 3 all had 22 mm mesh netting and 70 -75 mm entrance, while Pot 4 had 14 mm moulded plastic mesh (hard plastic) and a 90 mm entrance. On the Chatham Rise only two bycatch species were not caught by all three pot designs, these were sea-urchins and the armoured flathead, however, both of these were only caught in low numbers (2 and 1 respectively). On Cape Palliser squat lobsters and hermit crabs, ling, starfish, red cod and a draughtsboard shark were only caught in one of the pot designs. However, all but the draughtsboard shark were also caught in the other pots on the Chatham Rise, implying that all of the bycatch species were able to be caught in all four of the pot designs.

Over both sites Pot 2 caught between 1.5 - 10.1 times more total bycatch and 1.8 – 53.1 times more hagfish bycatch than the other pots. The design of Pot 2 differed from the other pots as it incorporated a parlour, a secondary chamber within the pot with its own internal entrance. The parlour is designed to separate the caught animals from the bait and make it more difficult for the caught animals to escape. Parlour pots have been found to have significantly better catch rates for European brown crabs, and European clawed lobsters, *Homarus gammarus*, than traditional single chambered pots, with the majority of lobsters being caught in the parlour section (Lovewell et al., 1988). However, in the present study the parlour feature may have been an extra obstacle within the pot which significantly increased the hagfish and other fish bycatch. For example, sea perch on the Chatham Rise were also more commonly caught in Pot 2 than in the other pots. Among the other pots, Pot 1 caught more total bycatch and hagfish bycatch than Pots 3 and 4 on Cape Palliser. The primary differences among these pots were that the Pot 1 was box-shaped and Pot 3 and 4 were both rectangular in shape, while Pot 4 also had smaller mesh and larger entrances. These shape differences may affect the amount of bycatch that can enter the pot, and the larger entrances of Pot 4 could have made it easier for the bycatch species to escape, even though it had the smallest mesh. Pot shape has been observed to affect the catch per unit effort of snow crabs and the associated bycatch in pots (Hebert et al., 2001), with rectangular pots recommended instead of square pots for this reason. Interestingly, Pot 3 and Pot 4 were the two pots which had the largest and the smallest total pot volumes, 58.2 l and 80.9 l respectively. Previous studies have suggested that pot volume has an impact on the catchability of some species (Boutillier & Sloan, 1987), however, the results from this study do not indicate that volume affects the rates of capture of bycatch species.

The bycatch of hagfish could be a significant issue for a developing scampi potting fishery as it is in other potting fisheries around the globe (Catchpole, et al., 2006a; Harada, et al., 2007). This is due to the prodigious mucous secreted by hagfish when they are captured, which has been observed to disturb sediments and cover associated equipment and bait (Martini, 1998), and discourages other scavenging species from the area (Catchpole, et al., 2006a). As a result, any pot which contains hagfish is unlikely to be as efficient at catching scampi compared to a pot without hagfish. This problem has been solved in the Japanese white-spotted-conger eel fishery, where hagfish landings were greatly reduced by increasing the size of escape windows in pots to greater than 13 mm

(Harada, et al., 2007). Therefore, there is the potential to reduce the bycatch of hagfish by incorporating escape windows into future pot designs used for targeting scampi.

5.4.3 Effect of location

The amount of hagfish bycatch and the amount and composition of the total bycatch caught in the pots were observed to vary within and between deployments and among the individual strings at both of the sites. Bycatch that was caught in every string included, crab species, hagfish and sea lice, while red cod and whelks were present in all but one of the pot strings on the Chatham Rise. However, starfish, nudibranchs, armoured flathead, sea urchins and conger eels were not caught in all deployment events. The results of the current study are consistent with previous potting trials targeting Norway lobster, which found that the composition and biomass of bycatch species, varied considerably among strings and within locations at different sites (Adey, 2007; Adey et al., 2008; Bergmann, et al., 2002b). This is in contrast with the bycatch caught in trawl fisheries for Norway lobster and scampi which is consistent within a specific site, but varies among fishing grounds, such as between the Chatham Rise and Auckland Islands or the North and South Clyde sea (Anderson, 2012; Bergmann, et al., 2002a). These results suggest that on the smallest scale sampled (string) some of the bycatch species are patchily distributed in the benthic environment, but over a larger scale of deployment event and site (Chatham Rise vs Cape Palliser) all of the bycatch species are encompassed. The catch rates of benthic scavengers in pots is related to the surrounding area of bait odour attraction for the pot and the background densities of the scavengers (Groenewold & Fonds, 2000). In a study of scavenger behaviour in the southern North Sea, the area of attraction of the pots was observed to be up to 1200 m^2 for gadoid fish (cods and hakes) and 284 m^2 for swimming crabs (Groenewold & Fonds, 2000). Similarly, hagfish are very mobile scavengers with sophisticated olfactory sensors (Martini, 1998) and have been estimated to travel over 600 m to reach whale falls (Smith & Baco, 2003). For this reason it may be difficult to operate pots for scampi and completely avoid the bycatch of some scavengers that appear to have large olfactory sensing and feeding ranges.

Trawling for scampi currently occurs in both of the study sites where the pots were experimentally deployed. The pots in this experiment were placed in areas on the edges of trawling grounds in locations were the fishers would have liked to have been able to trawl but could not due to the

rugosity of the sea floor. Therefore, they are both suitable areas where a pot fishery could potentially be developed.

5.4.4 Bait

The only bycatch group observed to be significantly affected by the bait species were the invertebrates on the Chatham Rise site, with the mackerel bait catching 1.5 times more invertebrates than the squid bait. This result is similar to previous studies which observed that most scavengers will readily consume fish baits (Bergmann, et al., 2002b; Groenewold & Fonds, 2000). In contrast, bycatch rates in the Canadian commercial spot prawn fishery did not differ between formulated fish pellets or tuna-based cat food when used as baits in pots (Favaro, et al., 2010). As the bait experiments were done within each string of pots there is the possibility that different bait odours from adjacent pots may have mixed with one another as the current transported the odour through the water column potentially resulting in similar catch rates between the two different baits. However, as the pots were typically submerged over the entire tidal cycle, and were well spaced apart both from each other, this should not have greatly affected the odour plumes from each pot. Furthermore, the deployment of baits within each line of pots was randomised so that if any effect of bait odour mixing occurred it would be included in the overall assessment of experimental variability.

5.4.5 Bait containers

The presence of sea lice was found to be different among the bait container designs at both sites. On the Chatham Rise the Carapax bait containers had more sea lice, and on Cape Palliser the inbuilt flute bait container in the Polypot had lice present in every pot, a much higher incidence than the other two bait container designs. The Polypot bait containers had plastic mesh ranging from 6 - 10 mm, whereas the Artel and Carapax bait containers had 1 and 3 mm slots respectively. This meant that the sea lice could easily reach the bait in the Polypot bait container, and could only reach the bait in the Artel and Carapax bait containers if the lice were very small, or if the containers were incorrectly closed.

The presence of lice did not appear to directly affect the quantity of any of the three categories of bycatch that were landed. However, on Cape Palliser the presence of residual bait in pots was associated with a 6.5 times higher bycatch of hagfish than those with empty bait containers. As both bycatch and the target species caught in the pot will attempt to leave once the bait supply is

extinguished (Tallack, 2007), the higher proportions of remaining baits in the Artel bait containers, may then have led to the increased catches of hagfish and total bycatch in Pot 1.

5.5 Conclusion

The quantities and composition of the bycatch caught in four designs of European pots at two offshore sites was influenced by a combination of the pot design, the bait used and the location of pot deployment. The dominant bycatch species was hagfish, a species which also creates additional problems for fishers because of its ability to release prodigious quantities of sticky mucous into pots. The inclusion of a parlour section in one of the pot designs (Pot 2) greatly increased the bycatch of hagfish compared with any of the other three pot designs. Furthermore, differences in the bycatch of hagfish among pots imply that hagfish bycatch may be reduced by including escape windows into any future pot design. Hagfish bycatch varied at both the string and deployment scale on the Chatham Rise, suggesting spatial variability in hagfish abundance. Therefore, it may be possible to reduce hagfish bycatch by restricting pot fishing to those areas with low catches of hagfish. Mackerel baits caught marginally more invertebrate bycatch on the Chatham Rise than the squid bait, but overall the bait selection does not appear to be an important consideration for reducing bycatch. Accordingly, further research should focus on developing pots that enable hagfish and other fish species to escape from pots whilst retaining scampi and identifying locations where hagfish bycatch can be minimised.

Compared to the bycatch in the trawl fishery for scampi the pots caught a lower proportion of fish species and higher percentages of hagfish and invertebrate bycatch. Together these results suggest that a potting fishery, using careful pot design and spatially-targeted fishing, has the potential to reduce bycatch in the scampi fishery, and potentially many other crustacean fisheries that are currently fished with bottom trawling methods.

Chapter Six:

General discussion

6.1 Introduction

Prior to this research, no previously published studies had reported laboratory investigations of any aspect of the behaviour or ecology of New Zealand scampi. The only other formally published studies on scampi have focused on larval development (Wear, 1976), evolutionary characteristics (Jenkins, 1972), genetic variations in populations (Smith, 1999), and patterns of emergence from burrows (Tuck, et al., 2015). The majority of our knowledge of the natural ecology of the species comes from changes in catchability from trawling and investigations focused on stock assessment of the species for commercial fisheries that are updated regularly for the different scampi fisheries areas around New Zealand (e.g. Cryer, et al., 2005; Cryer, et al., 2001; Cryer, et al., 2004; Tuck, 2014).

The overall aim of this current research was to identify baits to be used in developing a potting fishery as a potential alternative to the environmentally damaging trawling fishery for New Zealand scampi. Previous studies of the food search behaviour in benthic decapod crustaceans has found it is highly motivated and facilitated by food odours, although the pattern of chemically-mediated food search behaviour appears to vary among individual species (Derby, et al., 2001; Moore, et al., 1991b; Zhou & Rebach, 1999). A seven point framework was set out for the identification of chemoattractants and feeding stimulants for the use in penaeid shrimp aquaculture (Lee & Meyers, 1996). Using this framework the current research focused on the three main research steps for a crustacean displaying attraction, 1) identifying the specific behaviours the crustacean demonstrates in response to chemoattractants; 2) undertaking experiments to investigate food search behaviour by using hydrodynamic regimes in the laboratory that mimic natural conditions, and 3) use of y-maze or choice flumes to quantify the attraction of the crustacean to specific items releasing chemical odours. Therefore, the starting point for this research was to use a simple flow-through tank to closely examine and describe the chemically-mediated food search behaviour among captive scampi responding to different types of baits.

6.2 Chemosensory behaviour of New Zealand scampi

6.2.1 Behavioural phases

The study successfully described the chemically-mediated food search behaviour of scampi and separated this behaviour into a number of different phases based on the apparent use of different chemosensory appendages by the scampi. High levels of variability in the phases of food search behaviour, especially for the search phase, were observed among individual scampi and among different natural marine baits. The behavioural assays demonstrated that a taxonomically diverse range of baits consistently elicit strong food search behaviours in scampi, suggesting that they are generalist or opportunistic feeders. A generalist diet would allow scampi to spend less time out of their burrows and travel shorter distances to find food items when searching for food with the potential benefit of reducing exposure to mobile predators.

6.2.2 Influence of hydrodynamics on food search behaviour

One of the key aspects determining the success of crustaceans in tracking odour plumes back to their source (i.e. bait) is how the local hydrodynamics structure the plumes. Consequently, it was hypothesised that the high level of variation in scampi search behaviour using the experimental tank used for the research presented in Chapter 2 was due to the hydrodynamics of the tank generating odour plumes that the scampi had some difficulty tracking. Therefore, an investigation into the influence of hydrodynamics on scampi food search behaviour was undertaken. The orientation pathways of the lobsters were quantified with image-tracking methods in conjunction with previously used quantification of phases of food search behaviour to identify differences in the behaviour of the scampi. These results showed that scampi were more efficient at searching for food in turbulent versus laminar water flow, as a result of taking more direct paths to the odour source. The improved accuracy of this food search behaviour in turbulent conditions suggests that scampi are using spatial information derived from sensing the odour plume in more turbulent conditions to improve the efficiency of their orientation to the odour source.

6.2.3 Binary-choice flume experiments

To improve the ability to discriminate the relative attractiveness of a variety of potential baits for scampi a binary-choice behavioural flume was used, with the hydrodynamic regime in the flume based on the results of the research conducted in Chapter 3. One of the advantages of using a

binary-choice flume is the ability to undertake experimental runs more efficiently, which in turn allows for more bait candidates to be evaluated and a larger suite of statistical analyses to be applied to the responses of the animals. The binary-choice flume demonstrated that scampi showed the highest levels of attraction to the pilchard and bound pilchard-alginate baits, compared to the flesh of two discarded fish species and polychaete meal. In so doing, the research highlighted the effectiveness of the use of binary-choice flumes to investigate the foraging behaviour and the relative responses to different baits in larger decapod crustaceans.

6.2.4 Contribution to the understanding of the feeding ecology of New Zealand scampi

How lobsters respond to different food items is based on a perceived quality of the food, and can be influenced by previous experiences. Lobsters can learn as to whether an odour will result in a potential meal, or whether they should avoid specific odours. This is followed by an internal risk-assessment (Moir & Weissburg, 2009), which compares the potential risk of starving with the risk of being predated upon, and is used to decide whether or not the lobster should commence foraging (Derby, 2000). Therefore, the research can assess how the scampi were responding to different food items, and then draw conclusions based on whether these food items comprise part of the natural diet of scampi, or if the scampi consider them to be high quality.

The simple flow-through tank deployed for experiments in Chapter 2 was unable to identify any consistent differences among a selection of 4 different baits. However, the binary-choice flume used in Chapter 4 allowed a distinguishing of differences in the food search behaviour of scampi responding to 6 different baits. This difference between these methodologies was most likely due to the less turbulent hydrodynamics generated by the experimental tank used in the experiment for the research presented Chapter 2. The research presented in Chapter 3 clearly demonstrated that greater turbulence in the flume could improve the efficiency of the search behaviour of scampi. One of the conclusions of the research presented in Chapter 2 was that scampi were generalist feeders, and may be feeding on fish species frequently discarded from trawlers. The most common discard species from New Zealand trawl fishers are the javelinfish and rattails, and these were both tested as baits in the research presented in Chapter 4. However, due to the low level of attraction of scampi to both of these discard fish species, neither were considered to be a potentially suitable bait for scampi, and

suggesting that these discard species may not be a common part of their natural as was previously concluded.

The strong attraction behaviour that scampi demonstrated toward the odour from pilchards may be due to similarities of the odour profile of pilchards to preferred natural food items in the diet of scampi. Aquaculture diet development studies have shown that dietary sources of lipids, such as would be amply available from consuming pilchard, are critically important in lobsters in supporting fundamental physiological processes and somatic growth (Powell & Eriksson, 2013). In the benthic environment that scampi live lipids and oils may be a limited resource and therefore the scampi could be more highly attracted to them as they are perceived as a higher quality food and so are prepared to take higher risks to acquire them.

The results of the research presented in Chapter 3 highlight that scampi are more efficient foragers in turbulent conditions which may provide some insight into their natural ecology and their emergence behaviour. New Zealand scampi, like Norway lobster, spend the majority of their time within their burrows and only emerge to forage and search for food and mates (Chapman & Howard, 1979; Cryer, et al., 2001). A number of studies have linked the catch rates of Norway lobster (Bell, et al., 2008) and the emergence behaviour of scampi (Tuck, 2015) to periods of tidal flow. The results of the current study indicate that scampi chemosensory systems are tuned to determining the source of odour plumes in turbulent hydrodynamic conditions, and since turbulence near the seafloor in the deep sea is driven by changes in the tidal flow (Nimmo Smith, et al., 1999), it seems more likely that scampi would be emergent and searching for food under these conditions. Therefore, the effectiveness of a developing pot fishery for scampi could potentially be improved by targeting the deployment of scampi pots to the seafloor during periods of higher tidal flow.

6.3 Application to a potting fishery

6.3.1 Bait items identified in the behavioural studies

A key aim of this research was to identify potentially effective baits for a developing a potting fishery for New Zealand scampi. Over the course of the three laboratory flume experiments scampi were presented with tissues from nine different species (mackerel, squid, polychaete meal, porcelain crab, pilchard, mussel gonad, javelinfish and rattail). In these studies, pilchard was identified as the most attractive bait candidate for potting scampi. This is consistent with a number of fisheries for other

lobster species, where oily fish, such as sardines and mackerel, are widely used as baits in pots (de Rozarieux, 2014; Ungfors, et al., 2013). The weaker food search behaviour elicited for baits made from finfish species commonly discarded from New Zealand fisheries (i.e., rattail and javelinfish) and baits made with aquaculture meal (i.e., polychaete meal) indicated that these should not be considered as viable bait options. In contrast, discard species have frequently been found to be useful as baits in some other decapod fisheries (de Rozarieux 2014).

Previous studies have shown that the characteristics of a bait that influence how attractive it is include the profile of odour chemicals produced by the bait, the relative concentrations of these chemicals in the profile, and the release rate of the attractant chemicals from the bait (reviewed in Zimmer & Butman, 2000). In this current study, candidate baits which released the highest amount of free amino acids (e.g., polychaete meal) were not as attractive to the scampi as baits with lower rates of amino acid release. This suggests the odour profile of candidate baits plays a potentially more important role in the different relative strength of food search behaviour elicited in scampi. Identifying the chemical odour profile involved in eliciting a strong food search behaviour in scampi could be the target for future research that could help with a more rapid evaluation of other potential baits, or combinations of baits.

The scampi were observed to be significantly faster to reach the pilchard bait than either of the discard baits during the binary-choice experiments. Few previously published studies have reported the progression of laboratory bait studies into the field situation. A study of an artificial bait versus a conventional bait for European lobsters found no difference between them in laboratory experiments, but conventional baits proved superior in a subsequent field experiment (Mackie, et al., 1980). It was concluded that the lobster interactions with the conventional bait may have increased the effectiveness of its odour plume to attract other lobsters, while the inability for the lobsters to feed on the artificial bait may have encouraged them to escape. More accessible artificial baits have subsequently proven to be as effective for lobsters and crabs as forage fish baits (Dellinger, et al., 2016). This is an encouraging result for future field experiments of the effective baits identified in the laboratory research once effective scampi pot designs are available. Such field experiments should include comparisons of baits with lower levels of attraction as determined in the laboratory research

presented in this thesis, to validate if the laboratory methods were effective at identifying potential baits.

6.3.2 Potential for the development of artificial bait

This current study found that baits made from lesser amounts of natural bait material and bound with alginate would elicit food search behaviour in scampi that was similar or better than for a range of natural baits. For example, stronger food search behaviours were elicited by scampi in response to alginate baits made with small amounts of pilchard (i.e., 1 and 10% by weight) compared to a bait made with polychaete meal. Furthermore, the scampi were responding to alginate baits made with either 1% or 10% pilchard concentrations at similar levels to the 100% pilchard tissue, suggesting that artificial baits could significantly reduce the amount of fish material required for baits to catch scampi. These results also suggest there is good potential for the use of artificial baits in developing a potting fishery for New Zealand scampi. However, further research is required into the longevity of artificial baits in terms of their ability to continue to attract scampi to a pot over the entire period that a pot is deployed to the seabed.

6.3.3 Potential for a potting fishery for New Zealand scampi

A model created for how baited traps fish (Königson et al., 2015), highlights the factors that affect the effectiveness of pots, primarily, the distribution of the animals around the pots and the efficiency of the pots to capture them (Fig. 6.3). This model can be illustrated as a triangle, with the width of each section indicating the potential number of scampi that each step interacts with. As we progress through the model, the widths of each section decreases as the inefficiencies of each step in the model reduce the number of scampi that can finally be caught.

Firstly, distribution of scampi in the fishery area affects the maximum number of scampi which can interact with the pots. The distribution of New Zealand scampi has been studied through the analyses of catch rates from commercial fishing operations and from photographic surveys, which has allowed densities of scampi to be estimated at between 0.02 – 0.1 m^{-2} (Tuck, 2010). Additionally, the distribution and abundance of scampi may be greatly influenced by the suitability of benthic sediments in which they can burrow, as has been found for Norway lobster (Lauria et al., 2015).

Secondly, pot efficiency is influenced by the effectiveness of the bait, the biology and behaviour of the animals and the design of the pots. The effectiveness of the bait is primarily related to the area of

effect of the baits, which includes the area over which feeding attractants from the bait are present in concentrations above the response threshold of the scampi. Chapter 4 highlighted that over a short (1 m) flume scampi will respond to 1 and 10% concentrations of pilchards at a similar rate to whole pilchards. While this is a rough estimation of dilution it does suggest that scampi will respond to low concentrations of this bait. The next step is to identify how the odour plume from these baits disperses at depth and the explicit thresholds of response of the scampi to these bait plumes. From this research the area of effect of the baits can be estimated.

Biological and behavioural factors that affect the catchability of a species include, feeding motivation, and the ability of the scampi to detect, locate, and consume the bait. Chapters 2 and 3 both investigated aspects of these in flume studies. Chapter 2 observed how scampi responded to a range of baits and investigated if size, sex and starvation period affected the response to the baits. While starvation period was observed to significantly affect the responses of scampi to the baits, however, it is unknown how well this behavioural response of scampi in the unnatural conditions of the flume is consistent with the behavioural response of scampi searching for the same bait in natural habitat. In the field, catch rates of lobsters in pots are an indication of their motivation to feed and the factors that affect this motivation. In other lobsters in other pot fisheries have observed that catch rates of females vary due to reproductive cycles and larger, male animals are the most likely to be caught (Leocádio, et al., 2012; Miller, 1990; Pickering et al., 2010). These results suggest that large males are the most motivated to feed or the most effective foragers. Additionally, Chapter 3 highlights that scampi are more effective at detecting and locating bait in turbulent conditions. This result indicates that pots targeting scampi should be fished over multiple tidal cycles to ensure that they are fishing during periods of greater tidal flow when they are more likely to be effective for capturing scampi.

Lastly, the design of the pot can influence the percentage of target animals that enter and are retained in the pots. The rates for lobsters approaching pots and then entering have been observed to be as low as 4% for American lobsters, and the likelihood of a lobster escaping a pot decreases the longer they feed on the bait within the pot (Jury, et al., 2001). Pot design can also reduce the capture of bycatch species that can take up space or scare off the target species, reducing CPUE. In Chapter 5 the results showed that the design of the pots affected the amount of hagfish bycatch caught, a

species that may affect the amount of scampi caught in a pot. Therefore, pot design aimed at reducing the bycatch of hagfish is critical to the success of a potting fishery targeting scampi.

To develop a successful potting fishery for scampi a fuller understanding of key factors is required, including the distribution of scampi, the area of effectiveness of the bait and periods of high scampi activity. The potting fishery will need to be targeting areas with high natural densities of scampi. Research correlating scampi distribution with seafloor hardness or seafloor features that are associated with higher densities of scampi would potential increase the efficiency of identifying high density scampi habitat for targeting a potting fishery. Baits that are used in a trap fishery will need to have an area of effect large enough to be effective in areas of high density of scampi. The use of formulated baits to extend the area of effect of baits and their period of effectiveness is also indicated as a future area of useful research by the results of this study. The pots will need to be fished during periods of activity of the scampi in relation to tidal, diel and potentially moult and reproductive cycles. Finally, the pots that are used in the fishery need to be efficient at catching scampi while also allowing the primary bycatch of hagfish to escape and not interact with the scampi catch.

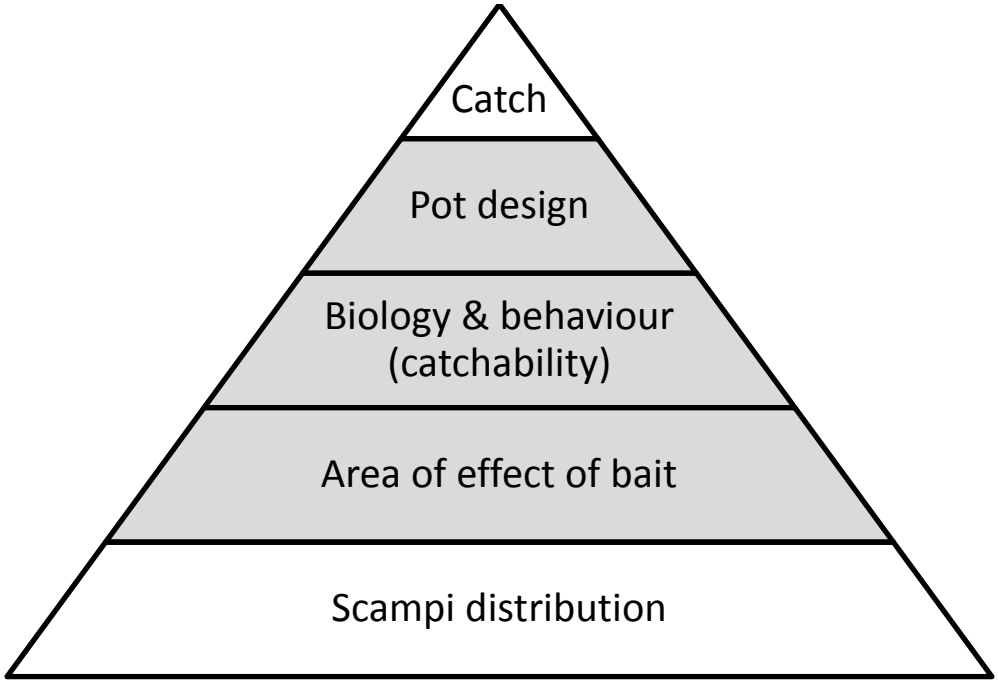

Figure 6.1 Model of the factors effecting the effectiveness of baited traps, firstly the distribution of scampi and secondly the factors affecting the efficiency of the pots (highlighted in grey). The narrowing of each section throughout the model indicates the reduction in the number of scampi each step interacts with due to inefficiencies in the previous step. Adapted from Königson et al. (2015).

6.4 Contribution to the knowledge of chemically-mediated food search behaviour in decapods

This current study has largely focused on the observable behavioural responses of scampi to chemical cues to quantify their attraction to the different baits. The results of this current study also contribute to our greater understanding of how decapod crustaceans search for food through the examination of food search behaviour in a different genus (i.e., *Metanephrops*) to the model species which have been the focus of prior published research, i.e., *Homarus*, *Panulirus*, *Callinectes*, *Procambarus* and *Orconectes*. Differences in the food search behaviour of scampi versus these model species may potentially provide some insights into their ecological niche and evolutionary history. For example, antennular flagellum length in palinurid lobsters varies greatly among genera and species. The variations in flagellum length affect the amount of water the lobster can sample with every flick of their antennules and is thought to be directly related to the different foraging strategies of each of the species (Goldman & Patek, 2002).

Spatial and temporal analyses have been used to assess the foraging strategies for a range of model decapod crustaceans (Moore, et al., 1991a; Moore & Grills, 1999; Reeder & Ache, 1980; Weissburg & Zimmer-Faust, 1994). The current research is the first study to use these methods to analyse the foraging behaviour of a member of the *Metanephrops* or *Nephrops* genera. The results from the current study suggest that scampi are using spatial information interpreted from the complex odour plume generated in turbulent hydrodynamic conditions to orientate toward the source of the odour plume. The patterns of behaviour expressed by scampi whilst food searching are quite similar to those previously described for *Homarus* species and the freshwater crayfish *Procambarus* and *Orconectes*, but are quite different to those described for *Callinectes* and *Panulirus*. Of the model species, *Panulirus* has been suggested to have the most direct search pathways (Reeder & Ache, 1980). In contrast the search pathways of *Callinectes* changes depending on the structure of the odour plume. *Callinectes* display very direct pathways in response to continuous odour plumes, and as the plume starts to meander or break up then the pathways become more indirect as the crabs cast from side to side of the plume in an effort to locate plume boundaries on which to orientate

(Page, et al., 2011b; Weissburg & Zimmer-Faust, 1994). In contrast, the orientation pathways of *Homarus* and scampi change as they get closer to the odour source and is characterised by increasing heading and turn angles close to the odour source, 22 cm for *Homarus* and 45 cm for scampi. In experiments where chemosensory sensilla are ablated (removed) it has been observed that the orientation pathways of crustacean species is altered (Reeder & Ache, 1980). This suggests that the differences in the orientation pathways observed among species may be directly related to differences in the structure and use of the chemosensory organs among different species.

Panulirus have been observed to use both the aesthetascs and bimodal sensilla located on their antennules to search for food. When both lateral antennules are completely ablated, they cannot locate food odours (Steullet, et al., 2001). In contrast, *Callinectes* use chemoreceptors on both their walking legs and antennules to track odours. Without their antennular chemoreceptors, *Callinectes* were unable to progress upstream along a plume, and without the sensilla on their walking legs *Callinectes* could not maintain contact with the odour plume as it narrowed and consequently had a higher frequency of course corrections (Keller, et al., 2003). The antennules of *Homarus* species have been observed to be similarly important, as the removal of theses sensilla greatly reduces their ability to locate food (Devine & Atema, 1982). However, the walking legs of *Homarus* have also been identified as being critical to localising odour sources, and when the walking legs are ablated the lobsters will walk over food items without picking them up (Derby & Atema, 1982). It seems likely that as *Homarus* gets closer to food items they switch from using their antennules to detect food items and begin using their walking legs to search for the nearby food items (Moore, et al., 1991b). The results of the current research suggest scampi are showing similar behaviour and are probably using the chemosensors on their walking legs for localising odour sources. During the current research scampi appeared to switch to this local food search behaviour at around 45 cm away from the source of the bait, double the distance of *Homarus*. This may be a function of differences in the morphology of these sensors, or the type of food items that these species are seeking.

This current research has developed and proved the effectiveness of a new laboratory method (i.e., the binary-choice flume) to compare chemoattraction behaviour of benthic decapod crustaceans to a range of intact natural bait tissue. The advantages of this methodology include firstly, that it presents the animals with an odour plume that is likely to be more consistent with what they would encounter in

their natural environment. Secondly, that it provides simple objective measurements for researchers, enabling large numbers of animals to be analysed quickly. For future studies using similar binary-choice flume methodologies, the first step is to identify a hydrodynamic environment in which the target species can reliably search for food. This information can then be used to guide the set-up of an appropriate hydrodynamic regime for the binary-choice flume where bait candidates can be presented versus a control.

The remaining aspects of chemosensory behaviour to be investigated in scampi are related to the structure and function of the chemosensory receptors that the scampi are using to track the odour plumes. Scanning electron microscopy of the aesthetascs and bimodal sensilla of scampi would show the structure of these organs and allow for a closer comparison with the model species. Following this, ablation experiments would help to confirm which sets of sensors the scampi are using to track the odorant chemicals. In terms of practical application of these behaviours to development of an efficient potting fishery, investigations into the distance that scampi can detect the chemicals from the bait are needed because any increase in the spatial range of baits attracting scampi to pots has the potential to greatly improve catch efficiency.

6.5 General conclusions

The research presented in this thesis investigates the chemosensory behaviour of scampi with the aim of using this knowledge to assist with identifying effective baits that could be used for the development of a scampi potting fishery. The research developed a novel and efficient binary-choice flume methodology to quantify and compare the attractiveness of baits to mobile benthic crustaceans. In this study pilchard was identified as the leading candidate bait for use in the development of a potting fishery targeting scampi. The identification of pilchard as a leading bait contender involved initially testing other methods for behavioural assay that were less effective in distinguishing differences in attractiveness among a group of candidate baits for scampi. However, the application of these initial methods was helpful to characterise the influence of environmental conditions on the food search behaviour in scampi. The advances in the understanding of scampi behaviour made by this research highlight that New Zealand scampi are likely to feed on a wide range of food items, and should have improved food search behaviour during periods of higher tidal flow associated with greater turbulence near the seafloor. The results of this research may also be useful for application to

the 18 other *Metanephrops* species around the globe which share similar ecology, and which could also have the potential for the introduction of potting methods for harvesting. Additionally, further research into the practical applications of artificial baits, such as how to increase their longevity while maintaining sufficient chemical release rates and investigations into the effective distance for attracting scampi into pots are recommended.

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