Does seagrass influence the behavioural and physiological response to flow in juvenile snapper (*Pagrus auratus*)?

A thesis

submitted in partial fulfilment

of the requirements for the degree

of

Masters (Research) in Biological Sciences

at

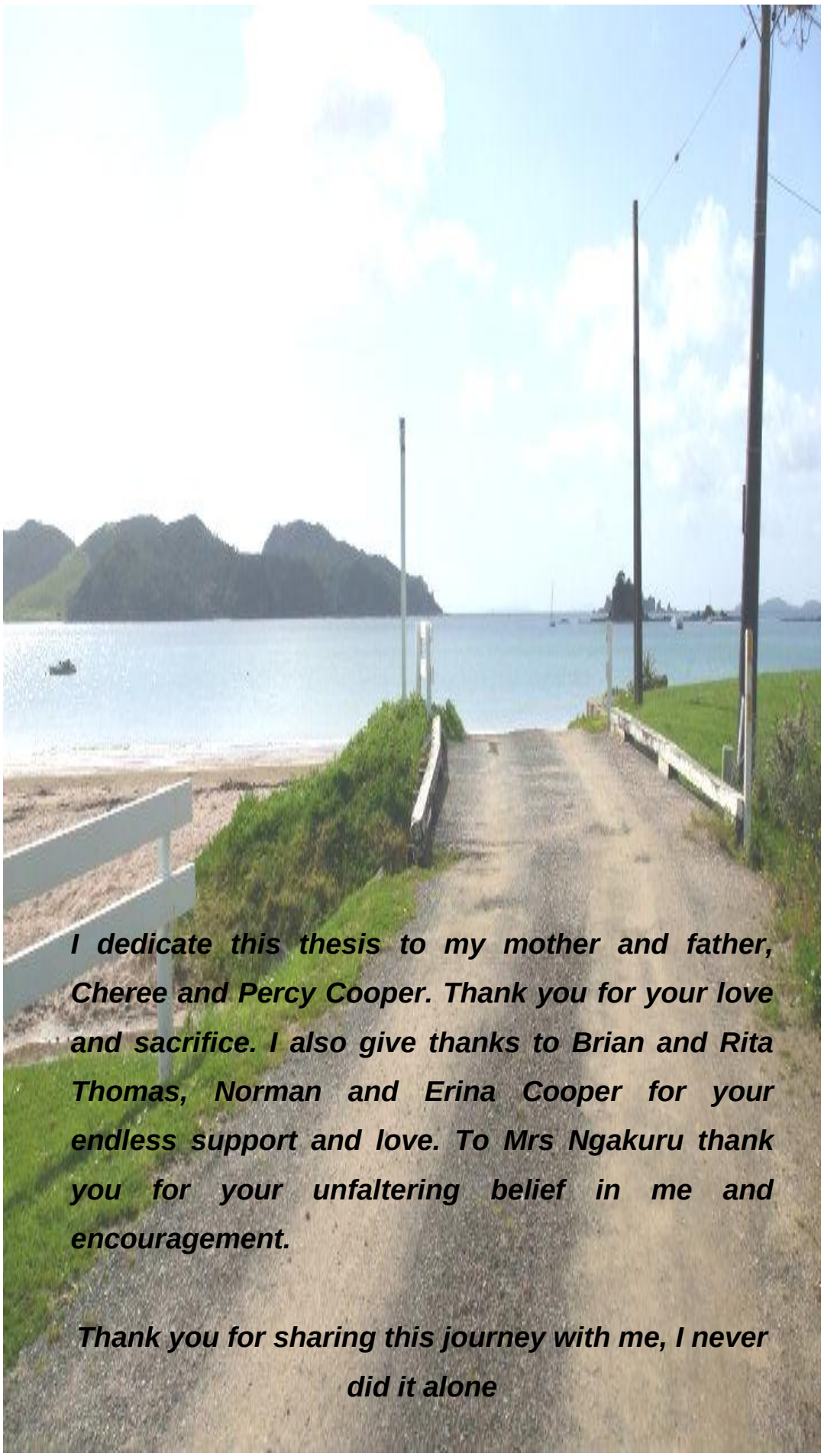
The University of Waikato

by

Jordan Cooper

THE UNIVERSITY OF WAIKATO
Te Whare Wānanga o Waikato

2015



I dedicate this thesis to my mother and father, Cheree and Percy Cooper. Thank you for your love and sacrifice. I also give thanks to Brian and Rita Thomas, Norman and Erina Cooper for your endless support and love. To Mrs Ngakuru thank you for your unfaltering belief in me and encouragement.

Thank you for sharing this journey with me, I never did it alone

Abstract

Many juvenile fish species are associated with structural habitats, potentially benefiting them from reduced predation and competition as well as enhanced feeding opportunities. It is also possible that structural habitats may provide a refuge from flow. Research on juvenile snapper in New Zealand has largely focused on their habitat preference. Juvenile snapper (*Pagrus auratus*) have been observed in close proximity to seagrass (*Zostera muelleri*) in New Zealand estuaries and I tested whether this association offered a refuge from flow. In an annular flume I exposed two cohorts of juvenile snapper 4.1 ± 0.5 cm and 8.9 ± 0.7 cm in length to sequential increases of flow speed (approximately 1 body length per second every 15 minutes). Flow speed increased at 3 cm s^{-1} every 15 minutes for the smaller cohort of juvenile snapper, and 8 cm s^{-1} for the larger cohort of juvenile snapper. Juvenile snapper were exposed to three treatments comprising of; bare, mixed (seagrass, bare and edge habitat) and full seagrass coverage. Fish behaviour was observed and critical swimming speed (Ucrit) estimated (i.e. the flow at which fish can no longer maintain position). Juvenile snapper were exposed to flow speeds that are representative of current flows in New Zealand estuaries and harbours. A startle response was recorded at the end as an indicator of fatigue and from larger juveniles a blood sample was collected via caudal puncture to determine if there were any physiological advantages offered by seagrass, by analysing stress indicators (based on lactate, triglyceride, glucose, haemoglobin and haematocrit).

Velocity profiles indicated that the seagrass treatment and sampling points 2 (seagrass upstream and downstream) and 9 (5 cm into the leading edge of seagrass) from the mixed treatment dampened the flow speed within the annular flume. This result may be responsible for the increased percentage of time spent utilising the edge habitat as flow velocity increased, indicating that juvenile snapper seek refuge from high flows in or on the leading edge of seagrass patches. These results are consistent with an increase in critical swimming speed with increasing seagrass

coverage (smaller juvenile snapper – bare = 19.47, mixed = 21.13, seagrass = 21.66 cm s^{-1}) (larger juvenile snapper – bare = 52.23, mixed = 58.89, seagrass = 60.31 cm s^{-1}). Physiological indicators, triglyceride, yielded significant differences between the bare treatment (1.40 mM) compared to the mixed (1.05 mM) and seagrass (1.01 mM) treatments, suggesting that energy stores were more readily utilised as energy expenditure increased where structural complexity was absent. The bare treatment also produced the highest values for both lactate and glucose, however, results were not significant. Mean cell haemoglobin concentration and total haemoglobin concentration did not yield significant differences between treatments. Whilst producing positive trends, results suggest that the effect of structural complexity was subtle in the annular flume. These findings have important implications for other hypotheses to explain the association between juvenile snapper and seagrass beds.

Acknowledgements

It is with immense gratitude that I acknowledge my supervisors; Associate Professor Conrad Pilditch, Associate Professor Nicholas Ling from the University of Waikato and Dr Darren Parsons from the National Institute of Water and Atmospheric Research (NIWA). Thank you for your patience, support and guidance throughout the duration of my Masters Research. I am grateful for the knowledge and skills they have imparted academically and the numerous opportunities that have developed my appreciation for the field of science. I would like to thank NIWA for contributing to the funds of my Masters research and my tuition fees. This thesis would not have been possible without the support of Plant and Food Research, who supplied the juvenile snapper for this project. Thank you to Warren Fantham for organising the transport of the fish and his continual support with husbandry aspects.

I appreciate all the help that I received from the technicians – Lee Laboyrie, Warrick Powrie, Dudley Bell and Bruce Patty. They were always there to lend a helping hand and I am grateful for their sense of humour, Lee's baking for the lab meetings, Dudley's shooting skills (cheers for the duck Dudley) and Bruce's willingness and enthusiasm to always help with setting up the GoPros and footage analysis.

I would also like to thank the Science and Engineering Maori Advisor, Kevin Eastwood, for his constant encouragement throughout my Masters. One of the highlights during my time here at the University of Waikato was being a part of the Te Huakirangi Maori and Pasifika Science Summer School and being a mentor for younger Maori students and the list goes on, this was all made possible through Kevin. Thank you for providing a support system for Maori students to excel in science and allowing us to hold onto our culture while doing so.

The University of Waikato has taken 5 years of my life and in return has given me; five scholarships, life skills, lifelong friends, two jobs, networking systems, unforgettable experiences and opportunities for progression. I

am grateful for my church family, their support and kindness has been invaluable. I would also like to thank the good people of CORE MMA, for their example that kept me diligent and continually striving for more. I would like to acknowledge all of those who supported and helped me out when important research was stolen – it was your kindness that kept me determined not to give up, but to work even harder. I would like to thank Brydget Tulloch for the opportunity I had to be a demonstrator in the labs, the student recruitment team at University – Alonzo Mason, Cynthia McNabb and Christine Armstrong for the opportunity to work for/alongside them and Community Living Trust for their continual support around my study commitments. What a year it has been!

Finally, I would like to acknowledge my mother and father for everything they have done for me, their sacrifices and constant support has been more than I could have asked for. Thank you to Ashlie and Johnny for your overprotection, our outrageous laughs on the phone and for always being there for me. To my best friend Tui, thank you for helping me with my research – making tinsel seagrass was a new experience for both of us and for keeping me grounded. To the rest of my friends here and abroad thank you for your laughs, belief and sense of humour. To Alicia Catlin, Ashley Webby, Laura Hines, Katie Pepper, Nikki Webb, Alice Wang, Erin Doyle, Katie Davidson and the Tauranga crew, thanks for your support, laughter and mutual understanding of stress and frustration whilst enduring our Masters research together.

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Chapter One

General Introduction

1.1 Structural habitats and their benefits

There is a clear association between structural habitats and juvenile fish species, a phenomenon supported by a number of field and laboratory studies (Francis, 1995; Jenkins & Sutherland, 1997; Jenkins & Wheatley, 1998; Turner *et al.*, 1999; Thrush *et al.*, 2002; Höjesjö *et al.*, 2004; Bloomfield & Gillanders, 2005; Ross *et al.*, 2007; Parsons *et al.*, 2013a). Structured habitats include emergent habitats such as; reef formations, rocky outcrops, vegetation and other physical features that provide some sort of heterogeneity in the environment (Fausch, 1984; Turner*, et al.*, 1999). The hypotheses explaining the relationship between juvenile fish and structured habitats are: 1) refuge and shelter from predation and competition (Heck Jr *et al.*, 2003; Valesini *et al.*, 2004), 2) providing shelter from high flow velocities (Fonseca *et al.*, 1982; Thrush*, et al.*, 2002) and 3) an increase in food supply (Thrush*, et al.*, 2002).

Structural complexity promotes abundance, growth and as a result increases the survival of juvenile fish species (Heck Jr*, et al.*, 2003). An experiment carried out by Wen *et al*., (2013) investigated the habitat preference of juvenile coral trout in the presence of prey. Results revealed that juvenile coral trout preferred structural habitats that offered food and also refuge from predators. Additionally, juvenile reef fish abundances were positively correlated with the level of structural complexity (Zalmon *et al.*, 2010). For example, the average number of individuals per m^2 was highest in habitats with 50 – 100 % structural complexity (Zalmon*, et al.*, 2010). Scharf *et al.* (2006) highlighted the importance of structural habitats on fish survivorship by utilising microhabitats that have a varying degree of structural complexity (Manderson *et al.*, 2000; Ryer *et al.*, 2004). For example, prey mortality of winter flounder, scup, and black sea bass was more than 50 % in unstructured habitats (sand substrate) compared to 20 % mortality in structured habitats (sponge), demonstrating the refuge

structural habitats offer animals (Scharf*, et al.*, 2006). The ecological functioning of juvenile fish species is enhanced by structural complexity, providing refuge from predation and having a positive influence on fish survivorship and abundances. Positioning amongst the structural habitat may also offer further refuge from high flow velocities with energetic savings.

Literature based on structural habitats indicates that the position of fish in relation with the structure may provide energetic benefits (Fausch, 1984; Gerstner, 1998). Fresh water salmonoids have been observed to reside in low velocity flows to reduce energy swimming, but will move into higher flow rates to receive food (Fausch, 1984). Freshwater species maintain optimal positions within streams in order to exploit a food supply and minimise energy costs to retain that position (Fausch, 1984). Salmonoids have been observed to reside in low velocity flows to reduce energy swimming, however are still capable of maximising food supply from higher flow rates (Fausch, 1984). It has also been revealed that structural complexity allows fish to occupy high flow habitats by carrying out flow refuging (Johansen *et al.*, 2008). Flow refuging has been demonstrated in research carried out by Gerstner (1998); where Atlantic cod were shown to position themselves behind a structure when exposed to higher flow speeds, thus, reducing the experienced flow speed. This behaviour is expected to yield energetic savings due to the physiological demands of swimming (Johansen*, et al.*, 2008). Flow refuging also enables slower swimming fish to occupy high flow regimes, expanding their range of habitat and increasing feeding opportunities (Johansen*, et al.*, 2008). It is evident that structural habitats offer significant ecological services for juvenile fish species. The aim of this study is to analyse whether biogenic structures confer advantages for juvenile snapper.

1.2 Study animals

The sparid snapper *(Pagrus auratus)* is one of the most abundant fish species in New Zealand, distributed throughout estuaries and harbours in northern New Zealand (Parsons*, et al.*, 2013a; Parsons *et al.*, 2013b).

Snapper are valued on a commercial, recreational and cultural scale reinforcing the importance of sustainability of this fishery (*Ministry of Primary Industries*, 2014).

Juveniles settle at a length of 20 - 30 mm (Parsons *et al.*, 2009; Parsons, *et al.*, 2013b) and reside in shallow water environments such as estuaries between November and May (Ross, *et al.*, 2007; Usmar, 2009; Parsons, *et al.*, 2013a). Juveniles will then typically migrate into coastal and open waters feeding on invertebrates, echinoderms, polychaete worms, crustaceans and other small fish (Ayling & Cox, 1982; Francis, 2001). Snapper are long lived fish, living up to 60 years of age and ranging between 30 - 90 cm (Francis, 2001). The proposed benefits behind this association are refuge from predation, competition, high flow velocities and an important food supply (Thrush, *et al.*, 2002).

Structural complexity and behaviour of juvenile snapper has been the focal point both in the field and laboratory setting. Habitat structures provide refuge for juvenile snapper and are deemed important, influencing their abundance and distribution (Thrush, *et al.*, 2002; Ross, *et al.*, 2007). One study carried out in Whangapoua harbour revealed high juvenile snapper and spotty (*Notolabrus celidotus*) abundances associated with high and medium seagrass density treatments (Parsons, *et al.*, 2013a). Previous field studies sampled juvenile snapper from the north-eastern coast (Mahurangi Harbour, Whangapoua Harbour and Okakari Point Marine Reserve) of New Zealand at lengths between 12 – 130 mm (fork length) (Ross, *et al.*, 2007; Usmar, 2009; Parsons, *et al.*, 2013a). Therefore, the current study has utilised two cohorts of juvenile snapper distinguished by their size. The smaller juvenile snapper ranged from 30 – 50 mm and the larger cohort of fish ranged between 80 – 120 mm. This study exposed juvenile snapper to three seagrass treatments (bare, mixed (seagrass and bare) and seagrass). These different habitats represent different forms of structural complexity. The bare treatment was selected to represent a habitat with no physical structure that could be compared against the mixed and seagrass treatments where structural complexity was present (Manderson, *et al.*, 2000; Ryer, *et al.*, 2004; Scharf, *et al.*, 2006). The

mixed treatment was representative of a patchy fragmented habitat consisting of two substrates bare and seagrass that have produced three different habitats; seagrass, bare and edge (Gorman *et al.*, 2009; Mills & Berkenbusch, 2009). The edge region is important as it simulates a patchy seagrass habitat that has the capacity to reduce the surrounding flow velocity, differing from a continuous habitat (Fonseca*, et al.*, 1982; Murphey & Fonseca, 1995; Hovel & Lipcius, 2001). Lastly, the seagrass treatment was representative of a continuous seagrass bed employed in previous studies (Heck & Thoman, 1984; Lewis, 1984; Heck *et al.*, 1989). This research will investigate juvenile snapper behaviour as a function of flow speed therefore, solely addressing the flow refuge aspect.

1.3 Seagrass habitats

Seagrass beds provide ecological value to the environment (Hovel & Lipcius, 2001) such as nutrient cycling, trapping sediment and providing complex habitats for marine invertebrates, fish species and shore birds (Turner & Schwarz, 2006; Matheson *et al.*, 2009). Although the distribution of seagrass species *Zostera muelleri* is poorly documented in New Zealand it is widely recognised as intertidal, forming extensive seagrass beds and fringing some sub tidal zones in estuaries (Turner & Schwarz, 2006). The structure of seagrass modifies the surrounding hydrodynamic environment by decreasing the bottom shear stress, affecting the velocity of currents dissipating horizontally and increasing vertically above the seagrass canopy (Gambi *et al.*, 1990; Fonseca & Cahalan, 1992; Worcester, 1995; Heiss *et al.*, 2000; Turner & Schwarz, 2006; Larkum *et al.*, 2007; Matheson*, et al.*, 2009). An experiment carried out by Fonseca *et.al*, (1983), used a salt-water flume to analyse the current flow in and around an artificial model of *Zostera marina*. As flow velocity increased, seagrass blades produced a dense layer that caused water to be directed over and under the canopy, essentially decreasing current velocity within the seagrass (Fonseca*, et al.*, 1982).

Studies have demonstrated that the scale of flow reduction increases with seagrass density and although there is an obvious structural comparison

between seagrass and bare habitats there remains a defining difference between continuous and patchy seagrass beds (Fonseca & Cahalan, 1992; Worcester, 1995; Heiss*, et al.*, 2000; Petersen *et al.*, 2004; Bryan *et al.*, 2007). A study carried out by Worcester (1995) found accelerating flows over the surface of continuous seagrass beds, compared to patchy seagrass habitats with surrounding bare substratum that dampened the effect of tidal currents. Most studies have found that seagrass patches reduce the current velocity as currents intrude into the patch producing flow velocities that are significantly less than the ambient flow (Heiss*, et al.*, 2000; Petersen*, et al.*, 2004; Fonseca & Koehl, 2006; Bryan*, et al.*, 2007). For example, Heiss*, et al.* (2000) found that over one tidal cycle the current velocities were substantially less inside the seagrass (*Zostera novaz.elandica*) patch (0.1 – 1.8 cm s^{-1}), compared to the outside flow velocity (1.2 – 4.6 cm s^{-1}). Flow reduction within the seagrass bed can have biological implications such as creating new microhabitats (edge region of the seagrass bed), enhancing food availability and providing a refuge from flow for juvenile fish species (Jowett & Richardson, 1995; Worcester, 1995; Heiss*, et al.*, 2000; Thrush*, et al.*, 2002; Ross*, et al.*, 2007; Johansen*, et al.*, 2008; Parsons*, et al.*, 2013a). To further the understanding of how juvenile snapper may be utilising seagrass beds both behavioural and physiological aspects were investigated.

1.4 Threats to seagrass in New Zealand

The decline of seagrass in New Zealand has been a result of natural and anthropogenic changes (Reed *et al.*, 2004; Matheson*, et al.*, 2009). Threats include: grazing by waterfowl (Dos Santos *et al.*, 2012, 2013), bioturbation, sedimentation, pollution and physical damage (Turner & Schwarz, 2006; Matheson*, et al.*, 2009). The most detrimental causes of seagrass decline rises from anthropogenic perturbations (Turner & Schwarz, 2006). Sedimentation and nutrient loading (Turner & Schwarz, 2006) are of major concerns in New Zealand estuaries (Matheson*, et al.*, 2009) deriving from urban areas and decreasing light availability for seagrass growth (Matheson*, et al.*, 2009). Direct physical disturbances not only remove seagrass beds but also contribute to increased turbidity and

suspended sediment (Matheson*, et al.*, 2009). The impacts of these processes are currently undergoing extensive research and continual monitoring.

Changes in seagrass density can influence the abundance of juvenile fish within the environment (Parsons*, et al.*, 2013a). Areas in New Zealand where there have been substantial decreases in seagrass have seen a decrease in juvenile fish species (Morrison, 2011). For example, in Whangarei harbour the seagrass extent of 12 km^2 was depleted in the 1960's, Tauranga harbour saw a dramatic decrease of 4,437 ha to 2,933 ha of seagrass coverage between 1959 - 1996 (Park & Environment Bay of Plenty, 1999) as well as Manukau and Waitemata harbour experiencing reductions (Reed*, et al.*, 2004; Turner & Schwarz, 2006; Matheson*, et al.*, 2009; Morrison, 2011). Consequently, the effect of seagrass loss in an estuarine system is also going to affect the abundance of larger fish and other animals that are supported by seagrass beds, through a decrease of juvenile fish settlement in coastal environments (Reed*, et al.*, 2004). Therefore, a significant loss of seagrass may impact negatively on ecosystem functioning for juvenile fish species.

1.5 Energy expenditure assessment

1.5.1 Swimming performance

Swimming performance in fish has been of considerable interest from a physiological and ecological perspective. Swimming performance is an important factor for fish as it affects their ability to escape predation, maintain movement within their environment and obtain prey (Plaut, 2001; He *et al.*, 2013). There are three different types of movements that are recognised from swimming behaviour (Hartwell & Otto, 1991). (1) Sustained swimming, which consists of swimming for a long period of time at a maintainable speed that evades muscular fatigue (Hartwell & Otto, 1991). (2) Burst swimming, involves quick motions that can only be carried out for seconds and (3) prolonged swimming, which involves activity that is maintained for minutes to hours. Burst swimming does not facilitate fatigue

but when combined with prolonged swimming, these swimming types can result in muscular fatigue (Hartwell & Otto, 1991).

First formulated by Brett (1964) cited in (Peake, 2008) the critical sustainable swimming speed (Ucrit) is performed when flow speed increases by one body length (B/L) per flow increment and is stopped when the fish can no longer maintain its position (Boyar, 1967; Hartwell & Otto, 1991; Boyd & Parsons, 1998; Plaut, 2001; He*, et al.*, 2013). Ucrit is the most common method applied in order to quantify energy expenditure/aerobic performance and is based on the maximum sustainable swimming speed (Bainbridge, 1958; Boyar, 1967; Webb & Corolla, 1980; Webb *et al.*, 1984; Nelson, 1990; Hartwell & Otto, 1991; Gallaugher *et al.*, 1992; Boyd & Parsons, 1998; Plaut, 2001; Farrell, 2008). Hartwell and Otto (1991) used this method to discover the Ucrit values of four different fish species (*Brevoortia tyrannus*, *Stenodus leucichthys*, *Sprattus sprattus* and *Clupea harengus*), however, unlike this study both time and velocity increments were utilised in the experiment. Both small and larger juvenile snapper were exposed to flow speeds for 15 minutes that increased by one B/L per flow increment. It is expected that if juvenile snapper gain an advantage from seagrass this will result in a higher Ucrit value in the mixed and seagrass treatments, facilitating a more energetic startle response. Additionally, it is expected that Ucrit will increase across smaller to larger juvenile snapper (Swanson *et al.*, 2000; Bellwood & Fisher, 2001; Allen *et al.*, 2006). Ucrit was analysed for conferred advantages across experimental treatments.

1.5.2 Startle response

In the environment, a startle response or “fast start” is a behaviour that is carried out by animals as an escape mechanism from predators or environmental stressors, posing a threat to the animal (Domenici & Blake, 1991; Hale, 1996; Domenici & Blake, 1997). Startle responses have been utilised in the scientific field as an indication of prey-predator avoidance (Katzir & Camhi, 1993) and swimming development (Fuiman *et al.*, 1999). Startle responses are initiated by mauthner cells (M-cells), which extend along the length of the spinal cord (Sillar, 2009a). Due to the rapid

transmission of action potentials down the spinal cord, these nerve impulses can override present motor activities such as swimming (Hale *et al.*, 2002; Korn & Faber, 2005). The startle response typically occurs in two stages for teleost fish (Eaton *et al.*, 1977). The first stage consists of the fish forming a C shape (Eaton*, et al.*, 1977; Eaton *et al.*, 2001). The second stage involves the fish moving in the opposite direction, changing its orientation and accelerating away from the given stimulus (Hale*, et al.*, 2002). However, not all responses are the same and are dependent on the size of the muscle contraction on both sides of the spine and the time between the contraction of the inhibited and excited muscle (Korn & Faber, 2005).

Previous studies have commonly utilised both acoustic and visual stimuli in order to produce a startle response (Webb & Corolla, 1980; Blaxter *et al.*, 1981; Blaxter & Hoss, 1981; Fuiman & Cowan, 2003; Kastelein *et al.*, 2008). Acoustic stimuli usually involves exposing fish to an audible tone that transmits a frequency detected via sensory systems (Fuiman & Cowan, 2003; Kastelein*, et al.*, 2008; Bhandiwad *et al.*, 2013), whereas visual stimuli involves a change of colour (dark-light) that may occur quickly or with distance over time (Fuiman*, et al.*, 1999; Fuiman & Cowan, 2003). Generally acoustic and visual stimuli are utilised separately but can be combined to represent different forms of environmental stimuli (Fuiman & Cowan, 2003). For this research a visual stimulus was employed to replicate a predatory escape response of juvenile snapper, to relate habitat structure to energy expenditure.

Tail frequency (tail beats per second) is one of the kinematic variables measured from startle responses, which has been widely acknowledged and utilised as an indicator of locomotion efficiency (Bainbridge, 1958; Hunter & Zweifel, 1971; Webb*, et al.*, 1984; Katzir & Camhi, 1993; Hale, 1996; Sillar, 2009b). Tail frequency has shown to increase in a linear fashion with flow velocity whilst being proportional to body length (Hunter & Zweifel, 1971; Webb*, et al.*, 1984). Although only the smaller cohort of fish were startled (body length 4.14 ± 0.48 cm) in the current research, it was expected that tail beats would increase with structural complexity as a

refuge would facilitate a more energetic response. Startle responses (tail beats per second) were used as an indicator of energy expenditure for juvenile snapper, in order to evaluate any differences produced across experimental treatments.

1.5.3 Physiological indicators

Stress is an adaptive mechanism that helps the animal maintain homeostasis in response to a stressor (Johnson *et al.*, 1992; Chrousos, 1998). Three responses are typically produced; primary stress response involves the release of catecholamines and corticosteroids (Barton, 2002), secondary responses comprise of changes in metabolism, immunity and blood physiology (Taylor *et al.*, 2012) and tertiary responses consist of long term changes that effect animal performance such as growth or swimming activity (Barton, 2002). Previous studies, have shown that cortisol concentration in snapper can reach levels of 7.51 mM after swimming and in other fishes can take up to 4 hours to reach peak cortisol levels (Barton & Iwama, 1991; Lowe *et al.*, 1993; Vijayan & Moon, 1994), therefore swimming activity can incur a stressful response.

Hormones that are released into the bloodstream can be used as physiological indicators immediately after extensive exercise (Olsen *et al.*, 1992; Barton, 2002; He*, et al.*, 2013). For example, an increase of lactate in blood can be attributed to the movement of lactic acid from muscle tissue that has been exercised, this has also been shown to take place in trout that have endured extensive exercise (Heath & Pritchard, 1962; Driedzic & Kiceniuk, 1976; Turner *et al.*, 1983; Pankhurst & Dedualj, 1994; Padmavathy & Ramanathan, 2010). Triglyceride is a fatty acid produced in the liver that serves as an important energy store for endurance swimming (Weber *et al.*, 2003; Chatelier *et al.*, 2006; Bennett *et al.*, 2007; Magnoni & Weber, 2007). Chatelier*, et al.* (2006) found that alterations in the composition of fatty acids in the diet of sea bass, effected their critical swimming speed. This further highlights the association of swimming performance with physiological demands. Glucose is widely used as an indicator of stress, indirectly effecting reproductive performance, growth

and food intake in fish (Schreck *et al.*, 2001; Barton, 2002; Jentoft *et al.*, 2005; Barreto & Volpato, 2006; Martinez-Porchas *et al.*, 2009; Soengas, 2014). Glucose levels are elevated in the bloodstream, via glucogenesis, as a physiological response to the release of stress hormones, (Martinez-Porchas*, et al.*, 2009; Wu *et al.*, 2015). A study carried out by Kubilay and Ulukoy (2002) showed that glucose levels were highest (58.53 mg/dL) in stressed rainbow trout that were exposed to environmental stressors such as a change in water quality and overcrowding, compared to unstressed fish which produced glucose concentrations of 26.23 mg/dL. Increases in mean cell haemoglobin concentration and total haemoglobin as a result of stress can be an indication of erythrocyte swelling (Roche & Bogé, 1996; Falahatkar *et al.*, 2009), as a result of the physiological state of the fish (Randall, 1984). Consequently, lactate, glucose, triglyceride and haemoglobin will be measured from fish that have exerted energy in the flume, across each experimental treatment to evaluate energy expenditure.

1.6 Objectives

This research was carried out to determine if seagrass offers a refuge from flow in juvenile snapper and to provide an explanation behind field observations. Refuge from high flow velocities is one of the three hypotheses put forward to explain the association between biogenic structures and juvenile fish species.

The objectives of this research were to gain further insight into juvenile snapper behaviour and their habitat preferences when given a choice of a structural habitat. Three treatments were tested to simulate different habitats (bare, mixed and full seagrass coverage). Within the mixed treatment three habitats were created, seagrass, bare and edge which were analysed in the habitat preference test. To investigate whether seagrass offers juvenile snapper a refuge from flow the experiment was conducted in an annular flume, where I was able to control the flow velocity and correlate this to the position of the fish under experimental treatments. If there are any advantages from this association, they should be evident in swimming performance, startle response (tail beats per

second) and physiological parameters that were tested (lactate, glucose, triglyceride, total haemoglobin and mean cell haemoglobin count).

Apriori expectations:

1. Velocity profiles should show that mixed and seagrass treatments dampen flow speed more, compared to the bare treatment in the annular flume, therefore it is expected that juvenile snapper should utilise these habitats as flow speed increases.
2. Swimming performance of both cohorts of juvenile snapper should be enhanced when exposed to mixed and seagrass treatments compared to the bare treatment.
3. The percentage of time smaller juvenile snapper spend utilising the seagrass habitat should increase as the flow velocity increases. In addition, it was expected that as flow velocity increases the vertical position of juvenile snapper should decrease.
4. Startle responses (tail beats per second) produced by smaller juvenile snapper should potentially be higher in the mixed and seagrass treatments as seagrass provides a refuge from flow, enabling a more energetic response.
5. Energy expenditure across treatments should be distinguishable by associated physiological parameters tested (glucose, lactate, triglyceride, total haemoglobin and mean cell haemoglobin count) from larger juvenile snapper. It is expected that juvenile snapper exposed to the bare treatment will produce higher levels of the above parameters compared to the mixed and seagrass treatments.

Chapter Two

Materials and Methodology

2.1 Fish husbandry

Approximately 100 small (4.14 ± 0.48 cm (±SD) n=45) and 70 large (8.87 ± 0.70 cm n=30) juvenile snapper were sourced from Plant and Food Research, Nelson and were housed at the Waikato University Aquatic Research Centre. Both the smaller and larger juvenile snapper were acclimated for 1 month with both experiments taking a further 2 months to complete. Smaller juvenile snapper were obtained on the 24th January 2014 and larger juvenile snapper were collected on the 8th May 2014.

The first cohort of small juvenile snapper was housed in five 80 L glass aquarium tanks. Each tank had two air stones for oxygenation and a filtering system. Aquaria tanks and filtering systems were cleaned and the water was changed weekly to ensure high water quality standards. Fish were fed a staple diet of frozen *Artemia* and mysid shrimp three times a day. Juvenile snapper were exposed to a 12 hour light and dark photoperiod under controlled laboratory conditions. The experiment was conducted in a controlled temperature room at 16.5 – 17.5 ºC and light conditions were consistent throughout the experiment. Only juvenile snapper that were in healthy condition were chosen for experiments.

The second cohort of large juvenile snapper was housed in a 5000 L fibre glass holding tank. Tanks were run on a recirculating seawater system and compressed air provided oxygenation. Seawater was made up using Crystal Sea Marine mix salt (Marine Enterprises International, Baltimore, Maryland, and U.S.A). The holding tanks contained sheltered areas such as: cinder blocks, half pots and plastic vegetation where the animals could take refuge. Recovery tanks operated on a recirculating system consisting of a protein skimmer, bio filter, UV light and activated carbon.

At the completion of both experiments the fish were euthanized following the procedures set out in SOP# 6. Fish were maintained and handled in accordance with the procedures set out in SOP# 7 and disposed of appropriately following the procedures in FC2 laboratory. All fish husbandry and experimental procedures were approved by the University of Waikato animal ethics committee under permit 907.

2.2 Experimental treatments and protocol

2.2.1 Treatments

Three different seagrass treatments were selected - bare (B), mixed (M) and seagrass (S) based on habitats that juvenile snapper are exposed to in the natural environment (Figure 2.1). Within the mixed treatment three habitats were created, seagrass (S), bare (B) and edge (E). The mixed treatment comprised of a half bare and half seagrass configuration in the annular flume. Perforated templates were fused with tinsel (approximately 40 – 60 mm in length and 5 – 10 mm in width), which was shown by Gartner *et al.* (2013) to create structural complexity and simulate vegetation. Each seagrass unit was made up of three to four strands of tinsel to simulate seagrass species *Zostera muelleri,* which have up to three to four leaves per shoot and are up to 40 – 110 mm in length (Turner & Schwarz, 2006; Matheson*, et al.*, 2009). The height of seagrass was comparable with intertidal sized seagrass in the field, however, in sheltered estuaries where sub tidal seagrass exists on offshore islands, leaf length can range from 17 – 47 cm covering areas of up to 0.03 km^2 (Schwartz *et al.*, 2006). Seagrass bed area in the flume was 0.17 m^2 for the seagrass treatment and 0.085 m^2 for the mixed treatment. The shoot density was the equivalent to 1260 m^2 for the seagrass treatment and 630 m^2 for the mixed treatment. In the field seagrass density has been recorded ranging anywhere from 688 - 5365 m^2 around New Zealand (Reed*, et al.*, 2004). A series of experiments were conducted on small and large juvenile snapper in the annular flume at flow speeds between 0 – 64 cm s^{-1}.

2.2.2 Experimental set up

Shading material was used to frame the annular flume and the experimental area was separated from the experimenter to reduce the influence of external disturbances. The flume was filled with salt water to a total depth of 30 cm from the surface of the seagrass templates (including 5 cm over rotating paddles). An YSI EC 300 Conductivity Meter was used to ensure temperature and salinity was kept constant in the aquaria tanks. Following the husbandry procedures from Plant and Food Research, water salinity ranged from 33 – 34.5 ppt and temperature ranged from 17 - 18 ºC. To ensure oxygen levels within the flume were kept at saturation, an air stone was used to oxygenate the water between the 3 - 4 daily trials (see below) and dissolved oxygen was measured before and after each trial with an YSI 55 hand held oxygen meter. Water in the flume was replaced daily.

2.2.3 Experimental protocol

Each juvenile snapper was trialled under a randomly selected treatment (bare, mixed or seagrass). The order of treatments was randomised daily where 3 – 4 trials were conducted. Each treatment was replicated on 15 smaller juvenile snapper and 10 larger juvenile snapper.

Based on the body length of the smaller juvenile snapper, flow speed ranged from 0 – 24 cm s^{-1}, increasing at 3 cm s^{-1} increments (Appendix: A1.1). Flow speeds were chosen based on critical sustained swimming speed (Ucrit) tests, where flow speed increased by one body length (B/L) per flow increment (Brett, 1964; Hammer, 1995; Peake, 2008; He*, et al.*, 2013). Juvenile fish were exposed to each flow speed for 15 minutes (Hartwell & Otto, 1991). This test allowed inferences about the Ucrit for each individual animal to be made. Juvenile snapper were acclimatised in the flume with no flow for 15 minutes. Three time lapse cameras were positioned around the annular flume and set at a 10 second time interval to capture position (grid based system marked at 15 ° increments), height (marked rulers) and habitat choice of the juvenile snapper. Height was measured when juvenile snapper were positioned over the bare templates

from the boundary to the lower edge of the fish, and when positioned over the seagrass, from the surface of the seagrass to the lower edge of the fish. I observed each trial to capture the point at which the fish failed to maintain its position. Two minutes after the flow was stopped a canopy device was released to elicit a startle response, casting a shadow over the entire flume area. At the end of each trial the cameras were remotely switched to video to record the behaviour of the startle response.

The experiment was replicated with a second cohort of larger juvenile snapper, based on the B/L flow speed ranged from 0 – 64 cm s^{-1} and increased at 8 cm s^{-1} increments (Appendix: A1.2). At the end of each trial the juvenile snapper were anesthetised and a blood sample was retrieved via caudal vein puncture, using a 0.5 mL insulin syringe. The needle and syringe dead space was filled with heparin solution and the blood dilution factor was used for later analyses (Appendix: A2). Previous studies have shown that stress related hormones could not be significantly affected by capture related stress (Taylor*, et al.*, 2012) consequently, blood samples were collected quickly. Due to size limitations approximately 100 µL of blood was collected and physiological parameters (glucose, lactate, triglyceride, haematocrit percentage (%) and haemoglobin absorbance) were analysed (Barton, 2002; Falahatkar*, et al.*, 2009; Padmavathy & Ramanathan, 2010).

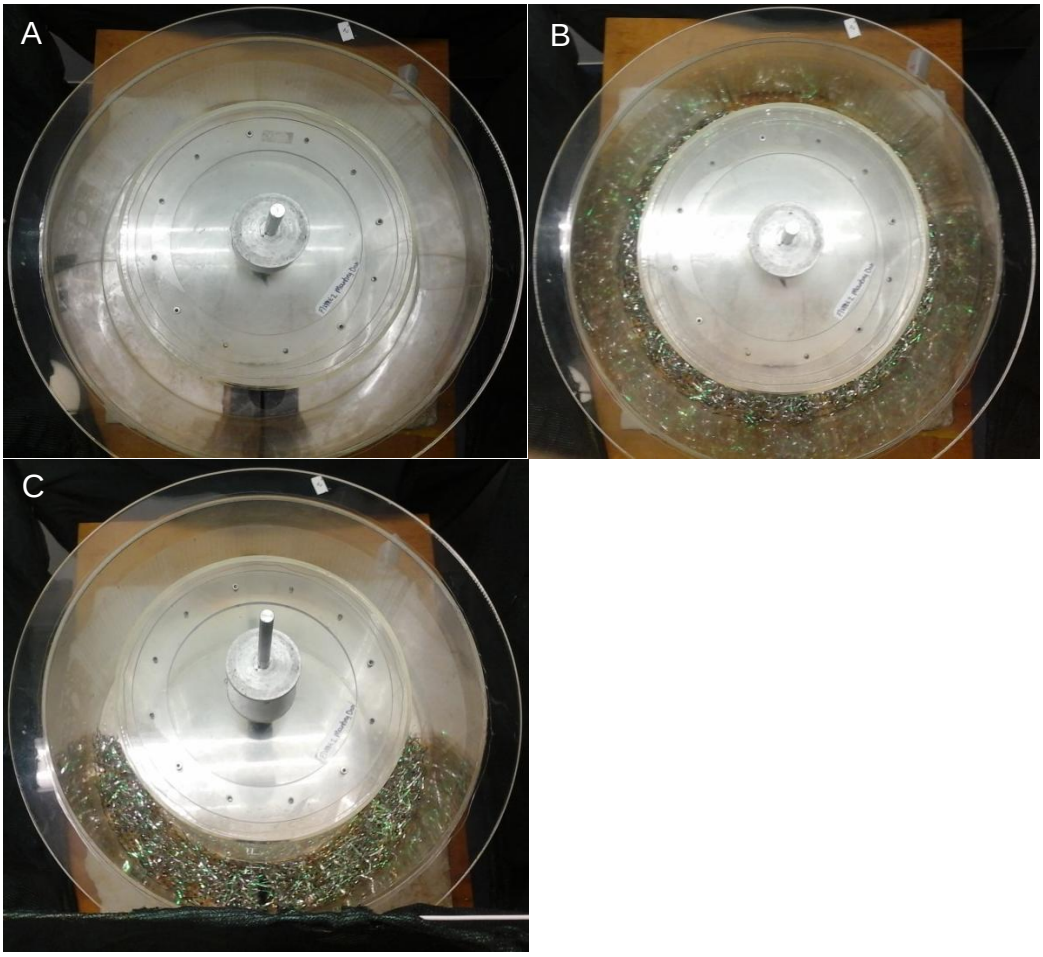

Figure 2.1: Different treatments that were utilised throughout the experiment using bare and seagrass templates. A) Bare, B) Seagrass and C) Mixed

2.3 Laboratory flumes and flow measurements

The annular flume had an outer diameter of 62 cm, inner diameter of 42 cm, channel width of 10 cm, and a bed area of 0.17 m^2 (Jones *et al.*, 2011). Flow was generated in the flume by a computer controlled rotating lid with paddles (Jones*, et al.*, 2011). Initially the flume was calibrated with a downward looking Sontek micro-Acoustic Doppler Velocimeter (ADV) mounted through the base of the flume. Flow measurements were made in a fixed sampling volume 10 cm off the bed for 5 minutes at 0 - 20 rpm, at 2 rpm increments. Averaged across all treatments velocity and rpm were related by: velocity (cm s^{-1}) = 0.455 X rpm / (R^2 = 0.98) from which

rpm values were determined for the experiment. A vertical velocity profile was recorded with the ADV mid-channel, orientated into the oncoming flow (sampling for 4 minutes at 4 Hz at eleven elevations from 3 - 15 cm above the boundary) of the seagrass, bare and mixed treatment to correlate flow velocity with position. The mixed treatment comprised of ten sampling positions that juvenile snapper were observed to occupy across the three habitats (bare, seagrass and edge) (Appendix: A3).

2.4 Laboratory analysis

Blood samples were analysed for glucose, lactate and triglyceride. Glucose was measured on a CareSens N Pop – blood glucose monitoring meter, similarly lactate and triglyceride were measured on an Accutrend Plus - dual monitoring meter. Blood samples were then drawn into 1 – 5 µl micro-capillary tubes (Drummond Scientific Company, USA), sealed with critoseal and centrifuged for 5 minutes at 12,000 rpm. Haematocrit percentage (%) was derived from a haematocrit reader and was used to calculate the total haemoglobin and the mean cell haemoglobin concentration (McHc, g/L) (Dacie & Lewis, 1991).

The remaining blood sample was held on ice before haemoglobin absorbance was measured in the Shimadzu UV spectrophotometer (UV1601). One millilitre of drabkins solution was pipetted into the cuvette and mixed for 1 minute with 5 µL of the blood sample to gain an absorbance reading. Blood samples were diluted 1:200 by placing 5 µl of blood in 1 mL of modified Drabkins solution (1 L of water, 50 mg/L of potassium cyanide, and 200 mg/L of potassium ferricyanide) (Bhutta *et al.*, 2013-2014). Samples were then analysed using a spectrophotometer and a 1 cm path length cuvette. The modified Drabkins solution was used to zero the machine before samples were analysed at a wavelength of 540 nm.

2.5 Data processing and statistical analysis

Three time lapse cameras (GoPro HERO3+) were set at 10 second intervals. Each photograph was used to capture the position, vertical elevation and habitat preference of the smaller juvenile snapper (visual data for larger juvenile snapper was stolen). Juvenile snapper that were observed in the video footage 10 cm upstream and downstream of the mixed treatment were considered as utilising the edge habitat based on flow measurements from this structural habitat. Startle responses were videoed with the GoPro and analysed using Adobe Premier Pro software to evaluate startle movement and the number of tail beats per second produced by the smaller juvenile snapper. Statistical software *Statistica 12* was used to carry out all statistical analyses. Multiple regression analyses were performed to analyse the correlation between the vertical elevation of the juvenile snapper and the flow speed under both bare and full seagrass treatments.

To calculate the critical sustained swimming speed (Ucrit) the following equation (Boyd & Parsons, 1998) was used:

$$Ucrit = (Ui) + ((Uii * (Ti / Tii))$$

Where *Ui* = the highest velocity (cm s^{-1}) reached throughout the trial, *Uii* = velocity increment (3 or 8 cm s^{-1}), *Ti* = time elapsed at fatigue and *Tii* = time interval (15 minutes).

Critical sustainable swimming (Ucrit) values were normalised by individual body length to produce the relative sustainable swimming (RUcrit) values for both cohorts of juvenile snapper. One-way analysis of variance (ANOVA) was carried out for both Ucrit and RUcrit data to test for significance between treatment means. This analysis addresses the objective of whether seagrass offers juvenile snapper a refuge from flow. If a statistically significant result $p < 0.05$ was returned, subsequently a post hoc comparison was carried out to identify which mean contributed to the significant result. Tukey Honest Significant Difference *(HSD)* test was used as a standard post hoc analysis.

One-way analysis of variance (ANOVA) was performed to test whether juvenile snapper preferred a particular habitat within the mixed treatment (bare, seagrass or edge) over a 15 minute interval for the associated flow speed. This analysis was only carried out for the mixed treatment where there was a choice of habitat. If the analysis returned a p value < 0.05 than the percentage of time spent in a particular habitat over the duration of 15 minutes was deemed as significant and a post hoc comparison was performed.

Startle response data was normalised by body length to account for the effect fish size may have on producing tail beats. One-way analysis of variance was carried out to detect any significance between treatment means. If a statistically significant result was returned, subsequently a post hoc comparison was carried out.

The assumptions of homogeneity of variances and normality were tested with Kolmogorov-Smirnov tests on physiological parameters. One-way ANOVA tested for the significance of; glucose, lactate, triglyceride and haemoglobin between treatment means. This analysis focuses on whether seagrass offers any physiological advantage which would be evident in the parameters that were tested. If a statistically significant result $p < 0.05$ was returned, subsequently a post hoc comparison was carried out.

Chapter Three

Results

3.1 Flow mapping

Velocity profiles were performed on bare, seagrass and mixed treatments (10 positions within the mixed treatment) under experimental flow speeds (3, 9, 21, 40 and 64 cm s^{-1}). Four positions in the mixed treatment were; 1 (bare upstream and downstream of the ADV), 2 (seagrass upstream and downstream of the ADV), 9 (flow 5 cm into the leading edge of the seagrass) and 10 (flow 5 cm into the leading edge of the bare templates) were chosen for detailed consideration as they were the main positions occupied by juvenile snapper in the annular flume.

Results were consistent with my expectations which revealed that with increasing height there was an increase in velocity while seagrass was expected to decrease the flow speed (Figure 3.1). For example, in the bare treatment with a flow speed set at 3 cm s^{-1}, flow was measured at 1.50 cm s^{-1} at the boundary and increased to 2.6 cm s^{-1} at 15 cm near the surface of the flume. At approximately 5 cm above the boundary of the annular flume flow speeds were reduced, increased then remained consistent from 8 cm onwards. Flow measurements did not go closer to the bed as measurements could not be made in the seagrass which was approximately 4 – 6 cm. Flow speeds produced by seagrass and sampling points 1, 2 and 9) were reduced compared to bare and the mixed sampling point 10. For instance, the flow speed at 7 cm from the boundary for the bare treatment and mixed sampling point 10 at 64 cm s^{-1} was 68.79 and 70.77 cm s^{-1} respectively, compared to the seagrass treatment under the same settings at 58.21 cm s^{-1}. Variation was also found between the mixed sampling points which altered with the presence and absence of seagrass. Flow speed measured at mixed sampling point 1 (21 cm s^{-1} at a height of 8 cm) was 13.64 cm s^{-1}, compared to mixed sampling point 2 with a flow speed of 10.74 cm s^{-1}.

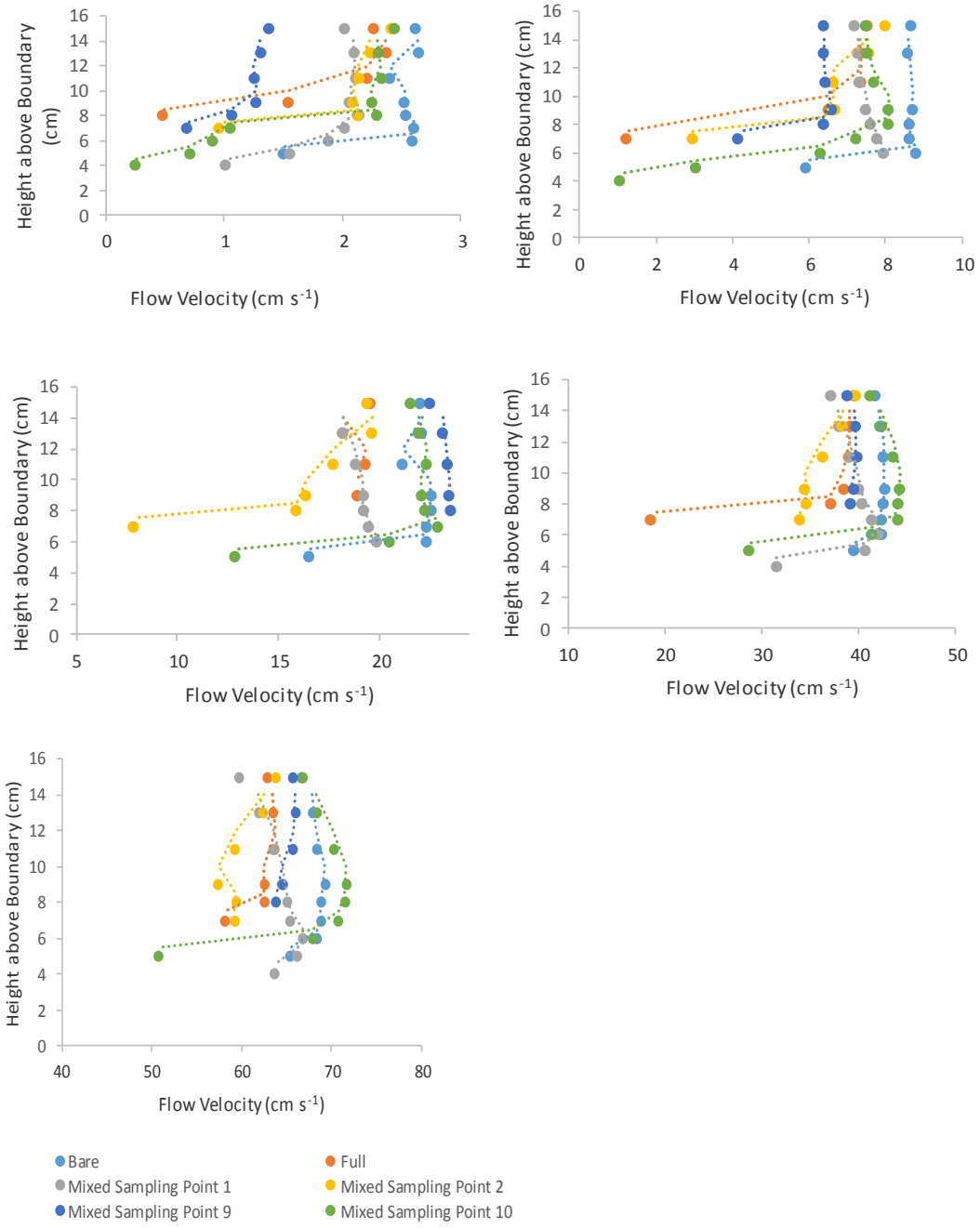

Figure 3.1: Average flow speed as a function of height above the boundary, for five treatment flow speeds (3, 9, 21, 40 and 64 cm s^{-1}) in the seagrass and bare treatments and four positions in the mixed treatment.

3.2 Ucrit small / large fish

Juvenile snapper were exposed to three treatments bare, mixed and seagrass from which the Ucrit was derived. One-way ANOVA tests found that there were no significant differences between the critical sustained swimming speeds for the smaller juvenile snapper (p = 0.55) (Figure 3.2).

Similarly, analyses found that there was no significant difference for Ucrit across bare, mixed or seagrass treatments for the larger fish (one-way ANOVA p = 0.22) (Figure 3.3). However, animals in mixed and seagrass treatments were able to reach a higher critical sustained swimming speed compared to the bare treatment by 6.67 and 8.08 cm s^{-1} respectively. The critical sustained swimming speed was normalised with body length for both cohort of juvenile snapper to produce RUcrit (Figure 3.4 and 3.5). However, results indicated that there was no significant difference between the RUcrit for both cohorts of fish (one-way ANOVA p = 0.55; 0.50).

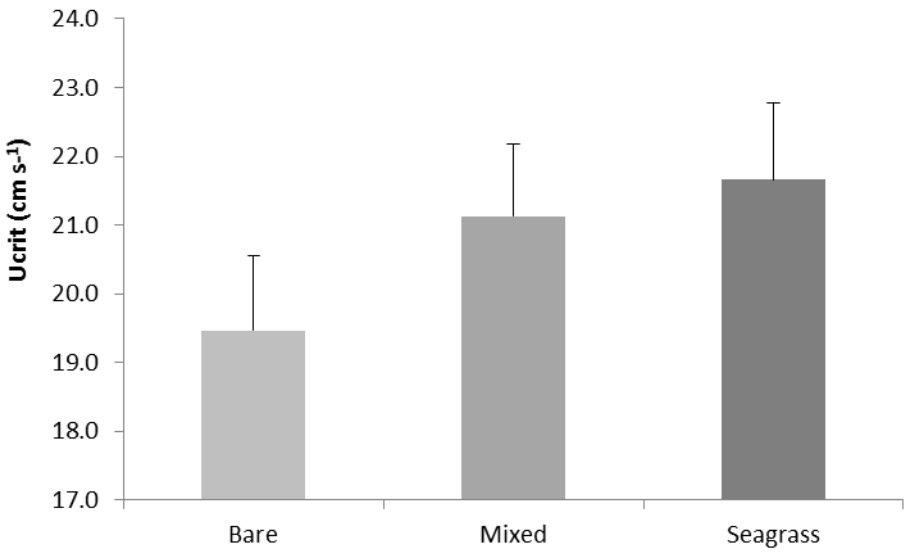

Figure 3.2: Ucrit of smaller juvenile snapper (± 1SE).

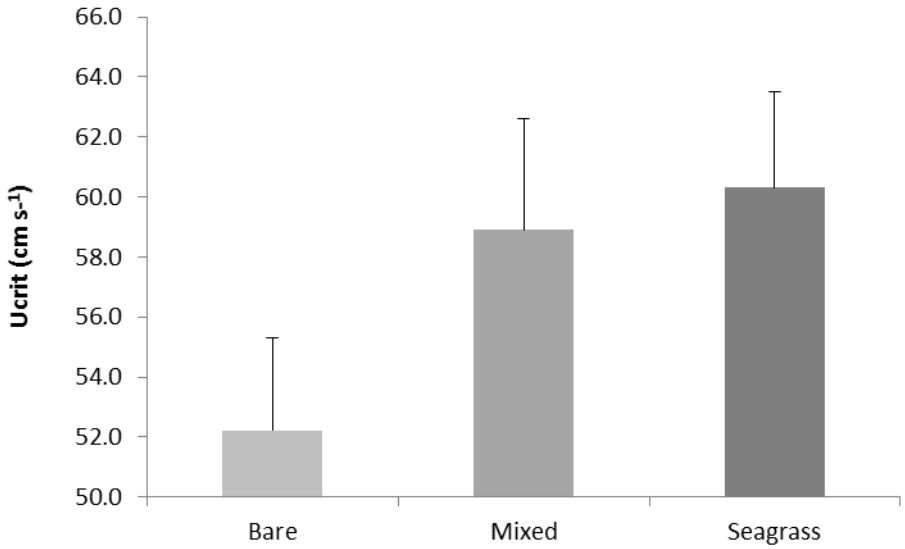

Figure 3.3: Ucrit of larger juvenile snapper (± 1SE).

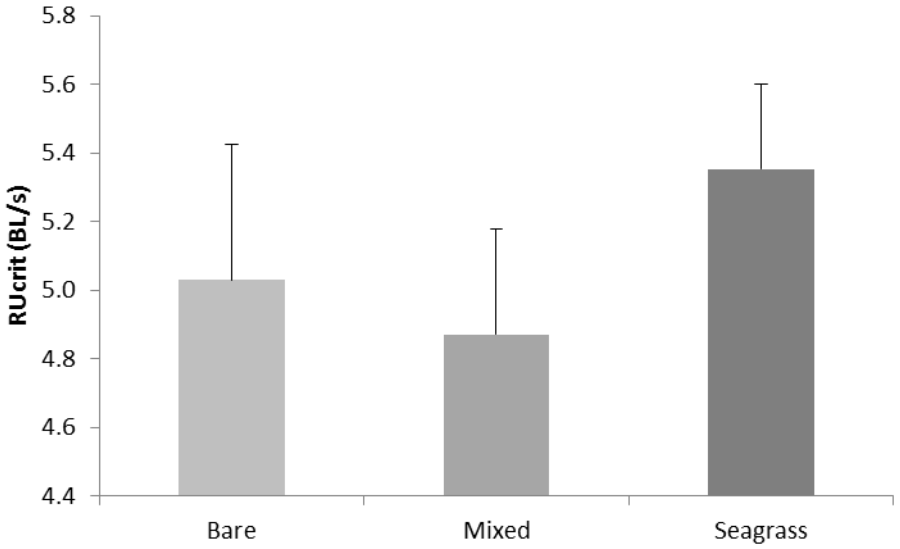

Figure 3.4: RUcrit of smaller juvenile (± 1SE).

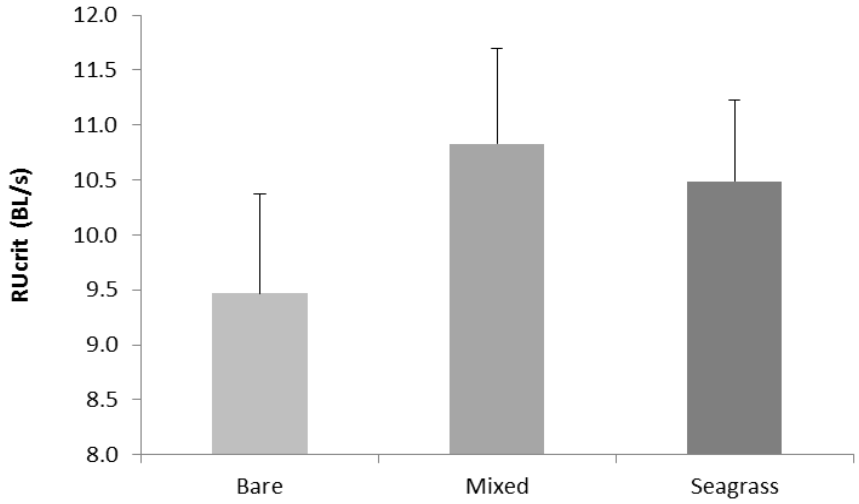

Figure 3.5: RUcrit of larger juvenile snapper (± 1SE).

3.3 Vertical elevation – small fish all treatments

The vertical elevation of juvenile snapper decreased at flow speeds > 18 cm s^{-1} in the bare treatment (y = -0.1834x + 11.14, $p < 0.02$, $r^2 = 0.57$) (Figure 3.6). Likewise the vertical elevation of juvenile snapper in the seagrass treatment also decreased at flow speeds > 6 cm s^{-1}, producing a marginally significant p value (y = -0.1153 + 8.25, $p < 0.06$, $r^2 = 0.46$) (Figure 3.7). ANOVA results indicated that there was a significant difference between the vertical elevation of juvenile snapper and experimental treatments ($p = 0.034$) (treatment means: 8.94 ± 1.95 - bare, 7.48 ± 0.96 - mixed and 7.04 ± 0.75 cm - seagrass). Tukey post-hoc test revealed that the significant difference was between the vertical elevation of bare and seagrass treatments ($p = 0.037$), indicating that juvenile snapper in the seagrass treatment were on average lower in the water column than those in the bare treatment. A one-way ANOVA analysis was performed on each flow speed between treatments but revealed no significant differences ($p > 0.05$). Vertical elevation appears to be lowest in the mixed habitat across higher flow speeds (15 – 24 cm s^{-1}; Figure 3.8), compared to juvenile snapper exposed to the bare treatment (Figure 3.6). One-way ANOVA test revealed no significant difference of vertical

elevation between the three habitat choices in the mixed treatment (p = 0.31).

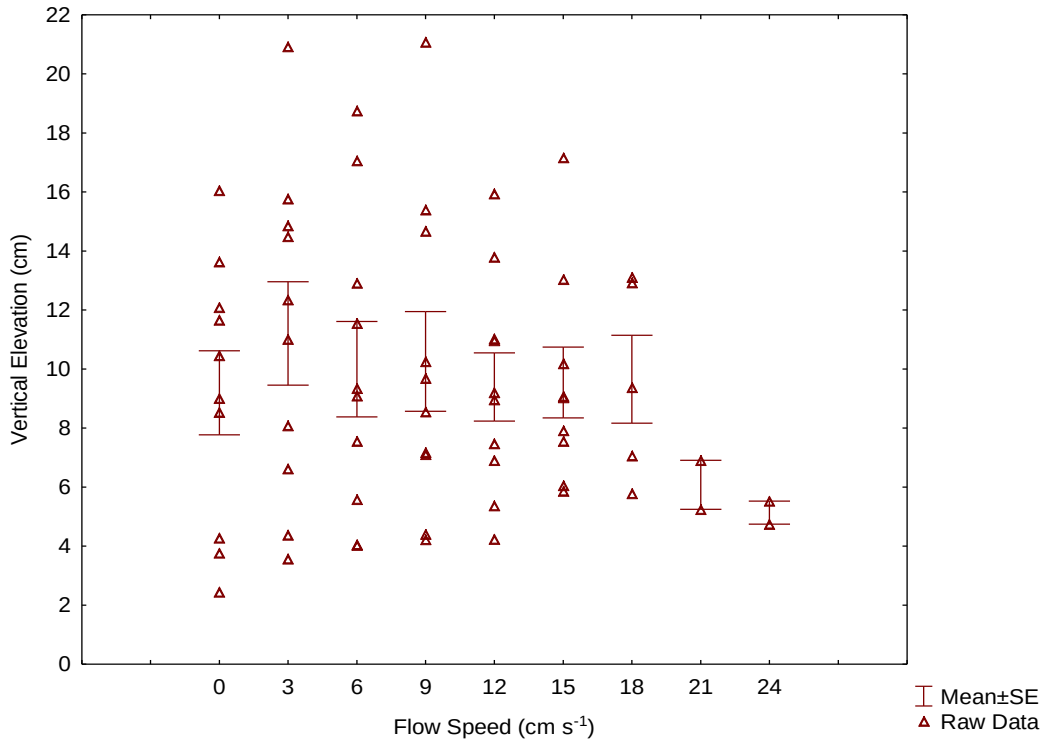

Figure 3.6: Vertical variation of small juvenile snapper exposed to the bare treatment for each flow speed (n=10) (± 1SE).

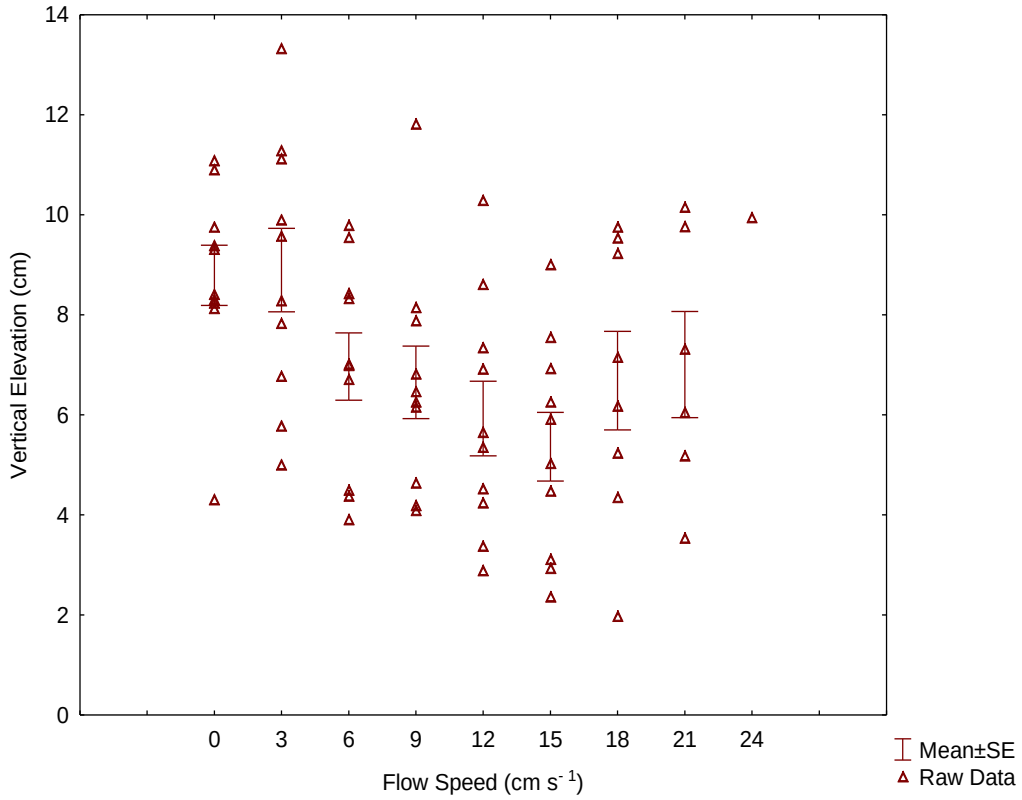

Figure 3.7: Vertical variation of small juvenile snapper exposed to the seagrass treatment for each flow speed (n=10) (± 1SE).

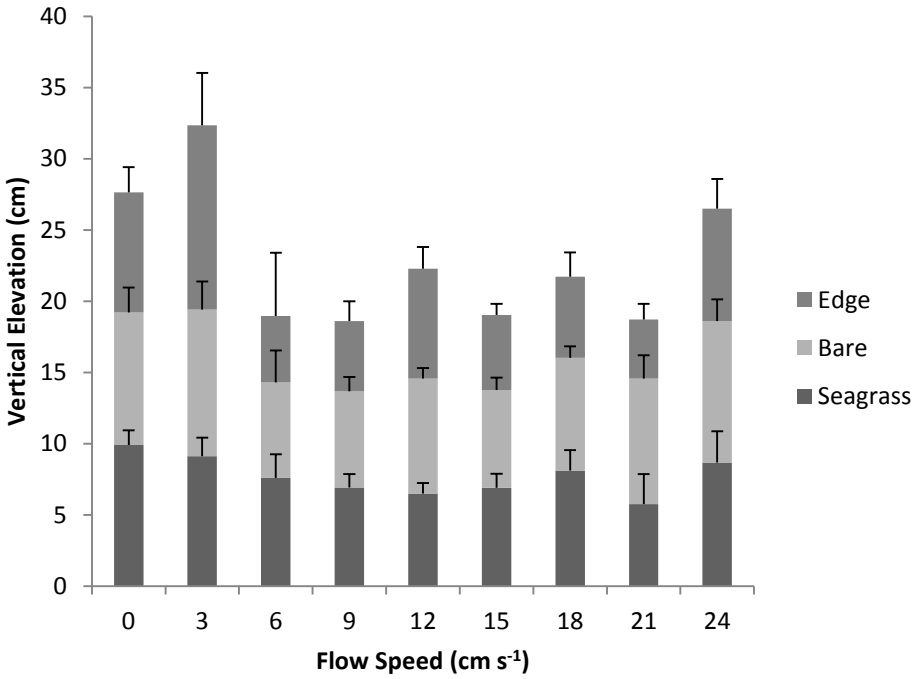

Figure 3.8: Average vertical elevation of juvenile snapper exposed to the mixed treatment for each flow speed. Habitat within the treatment = edge, bare and seagrass (n=10) (± 1SE). Seagrass height decreased progressively with flow speed starting at a height of 6.5 cm at 0 cm s^{-1} to 2.5 cm at 24 cm s^{-1}. A sub – sample population of 10 were analysed out of a total of 15 juvenile snapper.

3.4 Habitat preference – mixed treatment small fish

The mixed treatment produced three habitat choices which were exploited by smaller juvenile snapper (bare, seagrass or edge). Video analysis indicated that juvenile snapper exposed to edge habitats utilised the sheltered zone upstream or downstream of the seagrass template. The percentage of time spent in each treatment varied for each flow speed (Figure 3.9). Comparing the habitat preference across all flow speeds indicated that the percentage of time spent amongst seagrass decreased, (40 to 20 %) conversely, the amount of time spent utilising the edge habitat increased with higher velocities (6 to 14 %). The percentage of time spent in the bare habitat remained relatively constant 50 % for each flow velocity. Smaller juvenile snapper did not occupy every habitat choice for every flow speed (Appendix: A4). Juvenile snapper spent approximately 50 % of the time on bare habitat, showing no changes with flow speed, however, as flow increases > 18 cm s^{-1} there is a shift from seagrass to the edge. This suggests that the edge habitat may be offering more of a refuge from flow than the seagrass habitat. ANOVA analyses found significant differences for the percentage of time spent in each habitat choice across all flow speeds excluding 18 cm s^{-1} (Table 3.1). Tukey post-hoc tests revealed that there was a significant difference between the percentages of time spent in each habitat choice. The percentage of time spent in a habitat was greatly reduced in the edge habitat up to 15 cm s^{-1}, compared to the bare and seagrass treatments (E < B = S, E < S = B ; Table 3.1). However, as flow velocity increased it was

revealed that both seagrass and the edge habitat contrasted with the percentage of time spent in the bare habitat (S = E < B).

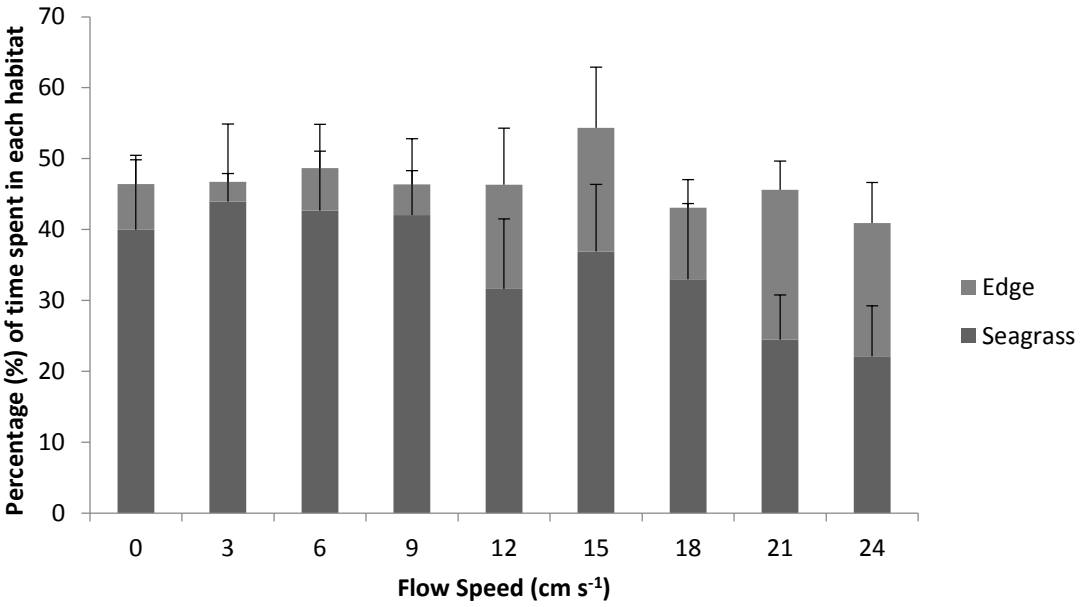

Figure 3.9: Percentage (%) of time spent in each habitat for the mixed treatment for each experimental flow speed. Smaller juvenile snapper were exposed to each flow speed for 15 minutes. (n=10) (1 ± SE).

Table 3.1: Comparison of average percentage (%) of time spent in each habitat (mixed treatment) across experimental flow speeds (cm s^{-1}), showing mean ± standard error, one way ANOVA p value and results of Tukey HSD post-hoc tests (B = bare, S = seagrass and E = edge).

	Treatment Mean ± 1SE				
Flow speed (cm s^{-1})	Bare	Edge	Seagrass	ANOVA *p*	Post-hoc
0	53.58 ± 10.49	6.48 ± 3.58	39.94 ± 10.51	0.002	E < B = S
3	53.26 ± 10.87	2.79 ± 1.23	43.95 ± 10.95	0.001	E < B = S
6	51.33 ± 11.76	6.00 ± 2.52	42.67 ± 12.17	0.007	E < B = S
9	53.64 ± 10.76	4.33 ± 2.05	42.02 ± 10.78	0.001	E < B = S
12	58.34 ± 9.36	10.36 ± 4.43	31.64 ± 9.86	0.001	E < S = B

15	46.00 ± 8.49	11.67 ± 4.07	31.33 ± 9.12	0.012	E < S = B
18	43.81 ± 10.37	9.52 ± 4.74	32.86 ± 12.83	0.069	-
21	55.68 ± 12.99	14.78 ± 3.76	20.87 ± 6.86	0.016	S = E < B
24	57.50 ± 6.59	7.67 ± 1.69	21.49 ± 11.59	0.004	S = E < B

3.5 Startle response - small fish

Startle responses (tail beats/second) produced by the smaller juvenile snapper were normalised with individual fish length, to account for the effect fish size may have on producing tail beats. Video observations showed that all startle responses demonstrated typical curvature movement. It was observed that juvenile snapper exposed to the mixed treatment displayed a decrease in elevation, occupying positions approximately 3.25 cm above the seagrass and 4.63 cm above the bare templates. Juvenile snapper exposed to the bare treatment produced startle responses, where 98 % of those consisted of an elevation decrease in the flume. Juvenile snapper exposed to bare and mixed treatments produced startle responses of 6.17 and 6.60 tail beats/second (Figure 3.10). Conversely, juvenile snapper exposed to seagrass produced an average of 2.70 tail beats per second. A one-way ANOVA test revealed that there was a marginally significant difference between startle responses across all treatments (p = 0.1).

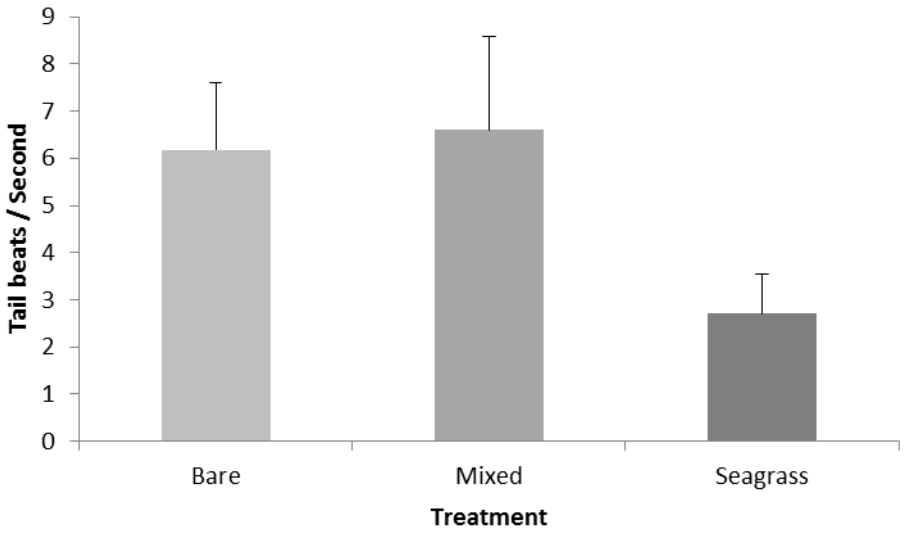

Figure 3.10: Tail beats / second of smaller juvenile snapper that were exposed to each treatment. (± 1SE).

3.6 Physiology - large fish

Physiological parameters (glucose, lactate, triglyceride (mM), total haemoglobin and mean cell haemoglobin concentration (g/L) were used as indicators of energy expenditure for the larger juvenile snapper. Only 24 animals were sampled across the three treatments for triglyceride due to blood volume inconsistencies. ANOVA tests revealed no significant difference between the concentration of glucose or lactate across all experimental treatments ($p > 0.05$; Table 3.2). One-way ANOVA test found a significant difference ($p = 0.01$) between the triglyceride concentration across all treatments. Tukey post-hoc test revealed that there was a significant difference in the triglyceride concentration for fish exposed to the bare treatment than all other treatments. The triglyceride concentration was higher from fish that were exposed to the bare treatment compared to the mixed and seagrass treatment ($p = 0.01$; M = S < B).

A one-way ANOVA test on data revealed no significant difference between the mean cell haemoglobin concentrations across the three experimental treatments ($p > 0.05$; Table 3.2). Similarly, there was no significant difference between the total haemoglobin concentrations across experimental treatments ($p > 0.05$; Table 3.2).

Table 3.2: Treatment means (± 1SE) of blood parameters sampled from larger juvenile snapper, exposed to each treatment flow speed (cm s^{-1}) showing mean ± 1 standard error, one way ANOVA p value and results of Tukey HSD post-hoc tests (B = bare, M = mixed S = seagrass).

	Treatment Mean ± 1SE			ANOVA *p*	Post-hoc
	Bare	Mixed	Seagrass		
Glucose (mM) n=30	5.86 ± 2.56	3.92 ± 1.37	5.03 ± 1.71	0.10	-
Lactate (mM) n=30	1.02 ± 0.49	0.82 ± 0.82	0.84 ± 0.08	0.23	-
Triglyceride (mM) n=24	1.40 ± 0.20	1.05 ± 0.24	1.01 ± 0.25	0.01	M = S < B
Total Haemoglobin (g/L)	66.77 ± 5.07	71.59 ± 6.13	66.68 ± 6.05	0.79	-
Mean Cell Haemoglobin Concentration (McHc) (g/L)	223.61 ± 18.25	211.56 ± 20.73	225.09 ± 23.06	0.88	-

Chapter Four

Discussion

This experiment was implemented in an annular flume within a laboratory setting. The objective of this research was to explore how juvenile snapper utilise their habitat as a function of flow speed and whether this infers any physiological advantages. Three treatments were chosen to simulate different seagrass habitats. The bare treatment represented no seagrass coverage, as a result there was no structural habitat present. The second treatment consisted of half seagrass and half bare to replicate a patchy seagrass habitat, where juvenile snapper could utilise edge positions upstream and downstream of the seagrass. Lastly, full seagrass coverage was chosen to simulate a continuous seagrass habitat. Juvenile snapper behaviour was captured in the annular flume by three surrounding GoPro cameras. Flow speed within the flume was measured using an ADV and was later correlated with the positioning of juvenile snapper.

4.1 Vertical elevation and flow mapping

Based on video footage, velocity profiles were taken of the most common positions that were occupied by juvenile snapper in the annular flume (Figure 4.1). Both seagrass and bare treatments were profiled as continuous treatments and the mixed treatment was manipulated to simulate the range of positions juvenile snapper were observed in. The mixed treatment produced three habitat choices which were exploited by smaller juvenile snapper (bare, seagrass or edge). It appears that although juvenile snapper preferred the edge habitat choice in lower flow speeds < 9 cm s^{-1}, the edge was preferred as flow speed increased as it offered a refuge from higher flow speeds (Johansen *et al.*, 2007; Johansen, *et al.*, 2008). The mixed sampling point 1 (flow was measured amongst bare panels upstream and downstream), sampling point 2, where flow was measured amongst the seagrass (seagrass upstream and downstream) and sampling point 9 (flow was measured 5 cm into the leading edge of

the seagrass) all produced velocity profiles less than the flow speeds produced in the bare treatment. For example, at 24 cm s^{-1} at a height of 7 cm, flow speed was measured at 25.75 cm s^{-1} compared to the mixed sampling point 2, where flow was measured at 16.58 cm s^{-1}, highlighting the dampening effect seagrass has on flow velocity. Although flow was not measured down amongst the seagrass, the dampening effects indicate that flow within the seagrass would be less than the ambient flow and this can be assumed as flow increases vertically above the seagrass treatment (Heiss*, et al.*, 2000; Johansen*, et al.*, 2008).

Consistent with my expectations, it was observed that juvenile snapper exposed to the bare treatment decreased their vertical position as flow speed increased > 18 cm s^{-1} (Fausch & White, 1981; Asaeda *et al.*, 2005; Johansen*, et al.*, 2007). Velocity profiles carried out on the bare treatment showed a decrease in velocity closer to the boundary, followed by an increase that remained uniform 8 cm and above for higher flow speeds. Therefore, juvenile snapper positioned lower to the boundary would have been experiencing lower flows than that higher in the water column of the annular flume (Webb, 1989; Asaeda*, et al.*, 2005). In comparison, juvenile snapper exposed to the seagrass treatment occupied lower depths at flow speeds > 6 cm s^{-1}. Flow regimes in the seagrass treatment showed that seagrass decreased the flow as velocity was less than the experimental flow velocity settings.

There was no significant difference surrounding the vertical elevation of juvenile snapper exposed to the mixed treatment. However, vertical elevation was lowest in the mixed habitat choice and it appears juvenile snapper were exploiting mixed habitats as a refuge from flow. Previous studies implemented in an annular flume, replicating coral habitats also observed similar results from fish (*Halichoeres margari-tacues* and *Chrysiptera brownriggi*) (Johansen*, et al.*, 2008). Utilising habitat structures as a refuge from flow is a common behaviour displayed by fish, as structures have been found to reduce the ambient flow speed by 60 % (Fonseca*, et al.*, 1982; Webb, 1989; Gerstner, 1998; Heiss*, et al.*, 2000; Johansen*, et al.*, 2007; Johansen*, et al.*, 2008). The fragmented effect of

the mixed treatment caused the flow to move over the seagrass canopy and detach from the boundary, creating an active and sheltered zone fish could utilise on the interface of the seagrass and bare templates (Fonseca *et al.*, 1983; Ghisalberti & Nepf, 2002). Fish such as the rainbow trout utilise the lateral line, especially, the two different sectors of the sensory system - canal organs and superficial neuromasts, to accurately measure flow velocity differences (Montgomery *et al.*, 2003). These systems are important as they provide the fish with hydrodynamic information and influence position, as fish tend to sit at a boundary between flow zones rather than directly in the slack water zone (Montgomery*, et al.*, 2003). It was evident that seagrass altered the flow velocity in the annular flume by reducing flow, consequently, providing a sheltered zone for the juvenile snapper, thus, enhancing swimming capabilities.

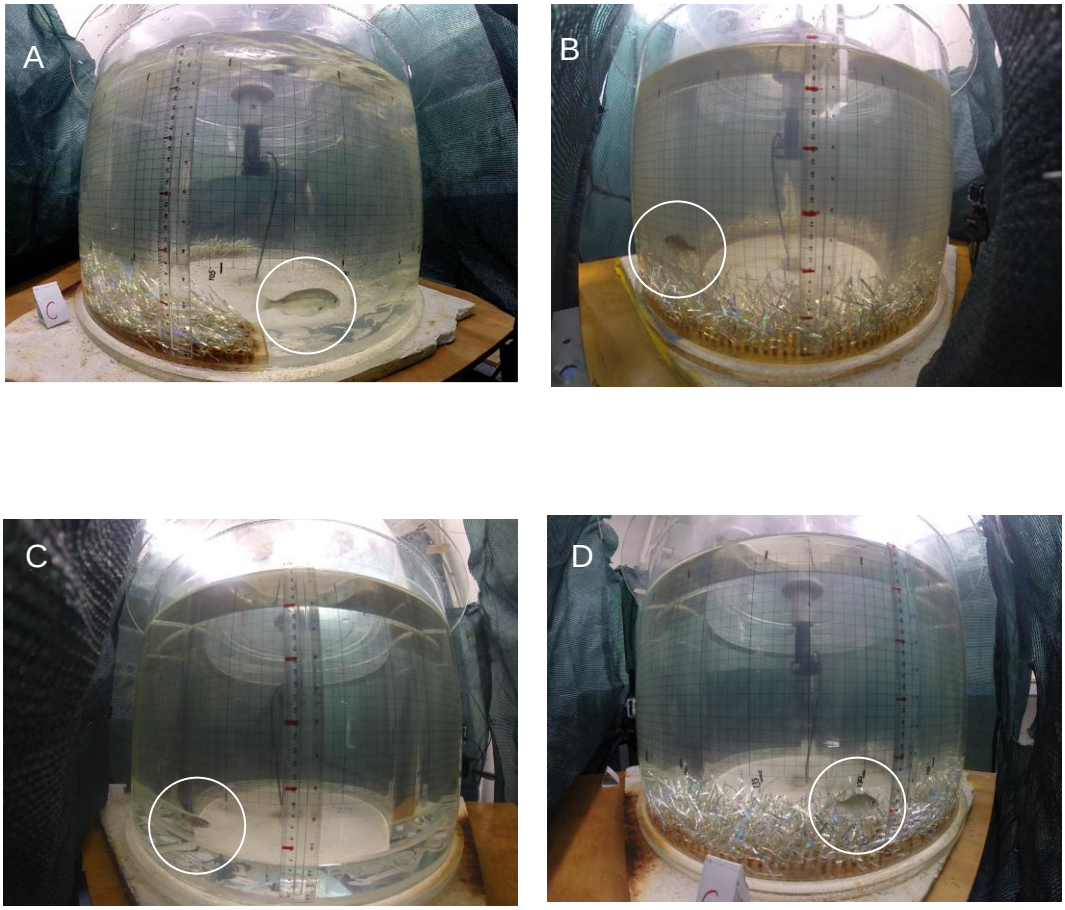

Figure 4.1: The relative height of the seagrass and positions occupied by juvenile vertically and horizontally at differing flows in the three different

treatments. A) Larger juvenile snapper positioned on the edge habitat for the mixed treatment at 64 cm s^{-1} (photo retrieved). B) Smaller juvenile snapper positioned above the seagrass in the seagrass treatment at 9 cm s^{-1}. C) Smaller juvenile snapper positioned above the bare templates at 3 cm s^{-1} and D) Smaller juvenile snapper amongst the seagrass in the mixed treatment at no flow.

4.2 Ucrit small / large fish

Swimming performance is important as it influences activity within the environment such as escaping predators and capturing prey (Plaut, 2001). Importantly, no significant differences in Ucrit/RUcrit (BL/s) were measured for the smaller cohort of juvenile snapper. However, results show that smaller juvenile snapper were able to maintain higher flow speeds with the presence of seagrass, compared to that of the bare treatment. When normalised with body length juvenile snapper maintained highest RUcrit in the seagrass treatment. Similarly, there was no significant difference found in the Ucrit for the larger fish, however, it was evident that Ucrit increased with seagrass coverage, indicating that seagrass provided refuge for juvenile snapper in the annular flume. Studies carried out on coral reef fish found that fish utilising the refuge, were able to swim for considerably longer periods of time as a probable result of energetic savings (Johansen*, et al.*, 2007). Coral reef fish were exposed to speeds of 60 cm s^{-1} similar to flow speeds in this study larger juvenile snapper were exposed to (Johansen*, et al.*, 2007). In addition, the RUcrit of larger juvenile snapper exposed to the mixed and seagrass treatments suggests that the structural presence of seagrass, facilitated juvenile snapper in maintaining their position in higher flow speeds (Johansen*, et al.*, 2007). Asaeda*, et al.* (2005) conducted experiments in the flume, exploring the behaviour of feeding and position as a function of flow speed. Results showed that as flow velocities increased the energy expended increased substantially and prey capture strategies changed in order to minimise energy costs (Asaeda*, et al.*, 2005). The trade-off between feeding and energy costs effected the flow speed that was obtainable, 1-3 B/L being favourable whilst seeking out prey (Asaeda*, et al.*, 2005). However, the current

research did not include the use of prey or predators, which could have influenced the longer period of swimming under seagrass treatments in the annular flume. In the field prey capture and predator avoidance are factors juvenile snapper are exposed to, effecting metabolic costs and ultimately their swimming performance.

Swimming performance increased with size as the larger juvenile snapper produced higher Ucrit values compared to the smaller cohort, similar size dependant results have been revealed in previous studies (Webb*, et al.*, 1984; Swanson*, et al.*, 2000). However, the effect of structural complexity on Ucrit was overall small and these findings have important implications for other hypotheses, to explain the association between juvenile snapper and seagrass beds.

4.3 Habitat preference – small juvenile snapper

In response to environmental changes animals often display behavioural reactions (Beitinger & McCauley, 1990). In order to avoid stressors animals will position themselves in preferred positions, influencing habitat selection. Habitat preference was analysed in the mixed treatment only. Three habitat choices were created from the mixed treatment (seagrass, bare or edge). There was a significant difference between the percentage of time juvenile snapper spent in bare and seagrass habitats, compared to the edge habitat across each flow speed (except 18 cm s^{-1}). However, the percentage of time spent utilising the edge habitat increased with flow, whilst the percentage of time spent in seagrass decreased. This suggests that juvenile snapper may have been seeking refuge on the edges of seagrass as the flow velocity increased. Asaeda*, et al.* (2005) found that fish would actively seek refuge amongst a structural habitat (cavity) in speeds greater than 7 cm s^{-1}, reducing energetic costs after swimming and searching for prey. Seeking refuge on the edge may confer feeding advantages for visually feeding fish in the field and aid in maintaining position (Fausch, 1984; Facey & Grossman, 1992; Hill & Grossman, 1993; Gerstner, 1998; Johansen*, et al.*, 2008; Wen *et al.*, 2013). The edge habitat simulated a patchy seagrass bed comprised of edges that

separated the seagrass from surrounding habitats (Gorman*, et al.*, 2009), compared to the seagrass treatment simulating a continuous seagrass bed (Mills & Berkenbusch, 2009). Edges are dynamic areas in seagrass patches (Fonseca*, et al.*, 1982; Gerstner, 1998; Johansen*, et al.*, 2008) that may offer refuge from flow, being the direct driver of habitat selection in this experiment. The ecological value offered by seagrass may determine habitat selection (Bell & Westoby, 1986) therefore, in the environment other deterring factors may influence habitat preference such as prey availability.

4.4 Startle response

In this experiment the aim was to use startle responses as an indicator of energetic savings, which may be incurred from a structural habitat compared to the absence of one. All fish that were exposed to the bare treatment produced a startle response, whereas fish exposed to the mixed and seagrass treatment produced weak startle responses, where there was no change in direction or acceleration from the canopy device. Startle responses were observed to be directed towards the base of the flume, which could be a result of the direction of the startle response from above the annular flume. It was evident in the video footage that juvenile snapper were swimming in both directions around the flume at lower flow speeds of 0, 3 and 6 cm s^{-1}. Juvenile snapper were also occupying variable vertical heights within the annular flume at low flow speeds. This may be due to the velocity of the flow, where fish will orient and swim against the current in higher flow speeds, but will swim in both directions when flow velocity is low (Boyar, 1967).

It was expected that as structural complexity increased (mixed and seagrass treatment) that the amount of tail beats produced would also increase. Previous trends in results have indicated that juvenile snapper receive a refuge from flow in structural habitats, therefore, it was expected that juvenile snapper would produce more tail beats in the mixed and seagrass treatment. Whereas, the amount of tail beats produced in the bare treatment were expected to be less, as higher flow speeds were expected to tire out the juvenile snapper, generating a lesser response.

Although not statistically significant, results show that startle responses were in fact very similar for both bare and mixed treatments with the least amount of tail beats produced in the seagrass treatment. However, the presence of a structural habitat could have provided juvenile snapper with a refuge, where minimal avoidance was required. Habitat position shows juvenile snapper closer to the seagrass in the mixed treatment but more so for the seagrass treatment. In Domenici and Blake (1997), fish that live amongst complex habitats such as pike and angelfish generally demonstrate a burst speed response to predators/prey, compared to pelagic fish that are more likely to swim for longer and at faster speeds. The energetic requirements are also altered as prey-predator encounters are reduced through the presence of structural complexity (Domenici & Blake, 1997). There is a wide range of literature based on startle performances, expanding to behavioural (prey-predator relationships), physiological and locomotory research (Domenici & Blake, 1991; Katzir & Camhi, 1993; Domenici & Blake, 1997; Hale, 2000; Manderson*, et al.*, 2000; Hale*, et al.*, 2002; Kastelein*, et al.*, 2008; Sillar, 2009b). However, the correlation between startle responses and habitat complexity is still developing in this field.

4.5 Physiology

This experiment focused on aerobic swimming activity supported by red muscle before anaerobic metabolic stores are utilised (Kieffer, 2000). The swimming activity of fish is often characterised as aerobic (sustained swimming) and anaerobic (burst swimming) (Kieffer, 2000). Although not statistically significant, results revealed that highest glucose levels were found in the bare and seagrass treatment followed by mixed. Glucose levels in the bare treatment could have resulted from a short term stress response produced from increased flow in the bare treatment, inhibiting insulin secretion and raising glucose in the blood of fish (Barton, 2002). It is unlikely that blood glucose levels increased in this experiment due to a long term stress response, however, the release of corticosteroids can also increase blood glucose through gluconeogenesis, affecting short term behaviour such as swimming performance (Warren & Jackson, 2008).

Similarly, juvenile snapper exposed to the bare treatment produced the highest lactate levels in the blood. Catecholamine's that are released in response to short term stress can stimulate the process of glycolysis, which consequently produces lactate (Warren & Jackson, 2008). Although not statistically significant an increase of blood lactate may be a result of lactic acid moving from the exercised muscle tissue into the blood stream, where this has also been shown to take place in trout that have endured extensive exercise (Heath & Pritchard, 1962; Driedzic & Kiceniuk, 1976; Turner*, et al.*, 1983; Pankhurst & Dedualj, 1994; Padmavathy & Ramanathan, 2010). Lactate levels suggest that the bare treatment facilitated a stress response as a result of juvenile snapper expending more energy compared to treatments that offered structural complexity.

Triglyceride levels were found to be statistically significant across experimental treatments. Once again juvenile snapper that were exposed to the bare treatment were significantly different compared to that of the mixed and seagrass treatment. Free fatty acids such as triglyceride are synthesised in the liver and are stored in adipose tissue until utilised as an energy source (Scow *et al.*, 1972; Mazeaud *et al.*, 1977; Weber*, et al.*, 2003; Bennett*, et al.*, 2007). Fatty acids such as triglyceride play an important role in swimming performance and overall fitness (Chatelier*, et al.*, 2006; Magnoni & Weber, 2007). White and Fletcher (1986) found a significant decrease in triglyceride levels in fish, in response to starvation, a stressor incurred over 15 days. However, Wang *et al.* (1994) cited in Richards *et al.* (2002), found immediately after exhaustive exercise that rainbow trout also showed decreases in white muscle lipid concentrations. The depletion of these energy stores indicates that rainbow trout were utilising lipids for recovery (Wang*, et al.*, 1994). Therefore, it is uncertain whether higher concentrations of triglyceride in juvenile snapper, was due to energy requirements from exposure to the bare treatment, or, that post exercise recovery was less in the bare treatment. Fish exposed to this treatment did not always reach higher flow speeds, therefore, were not exposed to flow velocities for as long.

Haematological parameters were used as physiological indicators of energy expenditure. Mean cell haemoglobin concentration (MCHC) was not statistically significant and appears to be fairly similar across all treatments. Similar findings were revealed for total haemoglobin across all treatments. It was hypothesised that there would be an increase in MCHC in fish exposed to the bare treatment as a result of erythrocyte swelling (Falahatkar*, et al.*, 2009), however, this was not the case for both parameters and this could be a reflection of the low values produced by the physiological parameters.

Overall the physiological responses to flow were subtle, indicating that the energy expended was not compensated by the structural complexity produced by the seagrass habitat. It also imposes implications for the hypothesis on whether fish gain an energetic advantage from using low flow environments. In the field juvenile fish exposed to denser seagrass beds compared to experimental substrates, maybe receiving more of a refuge and could be utilising more than one type of swimming activity, producing variable physiological results.

4.6 Summary

From this research it can be concluded that seagrass dampened the effect of flow in the mixed and seagrass treatments in the annular flume and under high flow velocities juvenile snapper were seeking refuge. Velocity profiles in the bare treatment showed an increase of velocity with elevation and in some bare configured profiles velocity was more than the experimental speed settings. Swimming performance seemed to be enhanced by structural presence of seagrass in both the mixed and seagrass treatments, compared to the bare treatment for both the smaller and larger cohort of juvenile snapper. The percentage of time spent among the edge habitat within the mixed treatment increased with flow speed, whilst decreasing in the seagrass habitat. The edge habitat appears to be quite an important position for juvenile snapper to gain refuge. The benefits of this region within a seagrass bed could extend beyond this in the natural environment. Interestingly, startle responses produced unexpected results, however, less tail beats produced in the

seagrass treatment may have been a result of the level of avoidance from the stimulus to the seagrass. Although not significant the physiological results were consistent with my expectations, that lactate and glucose yielded highest results in the bare treatment compared to the mixed and seagrass treatment. Triglyceride was significantly higher in the bare treatment compared to the mixed and seagrass treatment, indicating the use of such energy stores at higher flow speeds. The total haemoglobin and MCHC were fairly similar across all treatments and showed no distinguishable results among treatments. Results indicate that structural complexity is important for juvenile snapper as a place of refuge from high flow velocities. However, other determining factors such as food availability and predator avoidance may be more influential in the natural environment. Therefore, seagrass beds pose as an important habitat, whereby a significant loss of seagrass could have negative effects on juvenile snapper that utilise structural habitats in estuaries and harbours in New Zealand.

4.7 Limitations

This is the first time juvenile snapper have been used in an annular flume in a laboratory setting to analyse behaviour and habitat preference of seagrass habitats. Tinsel was used in the flume to mimic the structural complexity of seagrass habitats. To test the reliability of tinsel used as a substitute for seagrass beds in the flume, preliminary trials were conducted and showed juvenile snapper amongst the seagrass utilising the benefits from the seagrass edges. Gartner*, et al.* (2013) demonstrated the use of tinsel to simulate vegetative structural complexity. To avoid familiarity of the placement of the seagrass and bare panels in the mixed treatment, panels were rotated around the flume. Flow speed was the main driver behind habitat preference in this experiment. However, in the natural environment there is more than one limiting factor such as prey, predation and so forth that may influence habitat preference.

The scaling of the seagrass shoot density utilised in the flume compared to seagrass in the field imposes a possible limitation. The seagrass bed area in the flume was 0.17 m^2 for the seagrass treatment and 0.085 m^2 for

the mixed treatment. The shoot density was the equivalent to 1260 m^2 for the seagrass treatment and 630 m^2 for the mixed treatment, allowing fish to move amongst the seagrass habitat. In the field seagrass density has been recorded ranging anywhere from 688 - 5365 m^2, therefore, the flume may have underestimated the reductions in flow speed caused by seagrass in the field (Reed*, et al.*, 2004; Fonseca & Koehl, 2006). Each seagrass unit was made up of three to four strands of tinsel to simulate seagrass species *Zostera muelleri*, which have up to three to four leaves per shoot and are up to 40 – 110 mm in length (Turner & Schwarz, 2006; Matheson*, et al.*, 2009).The length of seagrass (40 – 60 mm in length and 5 – 10 mm in width) used was comparable with intertidal sized seagrass in the field, however, in sheltered estuaries where sub tidal seagrass exists on offshore islands, leaf length can range from 17 – 47 cm covering areas of up to 0.03 km^2 (Schwartz*, et al.*, 2006).

Handling and transportation of juvenile snapper can cause stress, which can affect behaviour and as a result, juvenile snapper were given 15 minutes to acclimate to the annular flume at no flow before the experiment started. To minimise any external disturbances of juvenile snapper behaviour while experiments were in progress, the experimental area was divided and precaution was taken when viewing the trial. Three GoPro cameras were set up around the annular flume, to avoid disturbances of behaviour the camera lights were covered and were operated from outside the experimental area with a GoPro Wi-Fi remote. Instantaneous behavioural sampling was implemented, as every 10 seconds a photo was taken of the flume from three different positions to analyse the percentage of time spent in each habitat for each experimental flow speed. However, the downfall with this method is the positioning between each sampling point is overlooked (Altmann, 1974).

Juvenile snapper were housed in fish tanks that were cleaned regularly to maintain physical condition, to ensure swimming performance was a true representation of critical sustainable swimming speed. However, throughout the duration of the experiment the smaller juvenile snapper contracted a fungal disease that was treated suitably, consequently, none

of these fish were utilised in the experiment and were kept separate from all cohort of fish used. Saturated oxygen (%) levels and salinity were tested to maintain satisfactory levels (80 %, S = 33 – 34.5) before and after each trial to minimise the effect on behaviour and swimming performance.

Colder temperatures can increase muscle aerobic capacity enhancing swimming performance. For this experiment swimming performance was implemented in waters of 16.5 – 17.5 ºC, therefore, Ucrit was limited to this temperature range, as the optimum temperature to reach maximum Ucrit for juvenile snapper was unknown. To calculate the Ucrit it was important to stop the experiment when the fish were no longer able to maintain their position. Therefore, juvenile snapper were stopped consistently when going with the flow of water or displaying quick bursts of swimming which followed the sustainable swimming phase. However, Ucrit across the treatments was non-significant, indicating some juvenile snapper could have been stopped at levels that preceded exhaustion. All juvenile snapper were trialled individually to evaluate performance physiology, however, the way in which the anaerobic metabolism is utilised can differ as fish use different energy stores to derive Ucrit (Nelson, 1990). Therefore, exercise physiology could have been different for fish in the same treatment, but produced similar Ucrit values. It is also important to acknowledge that Ucrit is dependent on a range of external factors such as sex, body length, temperature and light (Hammer, 1995). The Ucrit flow sequence – increasing by one body length per flow increment, may interpret to a similar sequence in a tidal estuary, which fish in the field are known to utilise for feeding opportunities. Fish are known to enter into estuaries on the flood tide and recede on the ebb tide, utilising different phases and experiencing different flow sequences (Swanson*, et al.*, 2000; Eichelsheim, 2012) comparable to that in the annular flume.

The smaller juvenile snapper were approximately 4.14 ± 0.48 cm, therefore, I was unable to extract a sufficient blood sample to test physiological responses. Instead a startle response was implored to analyse tail beats per second as an indicator of energy expended across

experimental treatments. This also meant that smaller and larger juvenile snapper could not be compared physiologically. The startle was elicited from above the annular flume, however, in the environment predatory attacks are typically at the same level or below (Katzir & Camhi, 1993). Control blood samples should have been taken from the larger juvenile snapper and used as a base level for comparison of lactate, glucose and triglyceride across all treatments. Therefore, throughout this study I was only able to suggest that high glucose and significant triglyceride levels were an indication of a short term stress response.

Although limited by time if replication was increased, the variability of the data may have been less and significant changes in swimming performance and positioning may have been observed. The effects of structural complexity imposed on juvenile snapper behaviour and physiological results were subtle. The hypothesis of using structural habitats as a refuge from flow was the only determinant tested in this research. Subsequently, there is a need for other hypotheses to be put forward, as there may be more than just one determining factor that explains the association between seagrass and juvenile snapper, such as food availability and predator avoidance.

4.8 Future research

This research has been a useful preliminary study to demonstrate habitat preference as a function of flow speed and whether it conferred any physiological advantages for juvenile snapper. This was the first time juvenile snapper have been utilised in an annular flume, but has shown that structural complexity, specifically for this research in the form of seagrass, provides a refuge from flow for juvenile snapper.

To improve this study I suggest that future research investigate whether the flow amongst seagrass enhances or reduces food acquisition. I only focused on habitat preference as a function of flow speed, although other factors such as food availability may contribute to habitat preference. This could also lead into investigating whether habitat preference is influenced by prey, as there is generally higher prey abundance associated with

structural habitats compared to bare landscapes (Bloomfield & Gillanders, 2005; Ross*, et al.*, 2007; Wen*, et al.*, 2013). If time permitted I would also increase the number of replicates carried out in the study for both the smaller and larger cohort of juvenile snapper. I would also recommend that future studies carried out based on swimming performance include Ucrit trials at different temperatures, as it was unknown what the optimal temperature was for juvenile snapper to reach their maximum Ucrit. Recovery from exhaustive activity is also of interest as this could influence habitat selection and locomotion throughout the environment. It is currently becoming more acknowledged that juvenile snapper are associated with seagrass and that declines in seagrass are also affecting population numbers of juvenile fish species. It may be of interest to investigate what effect disturbances to habitats that provide a form of structural complexity have on juvenile snapper (Turner*, et al.*, 1999). The scope for this research is not however, limited to just juvenile snapper as the association with structural habitats also extends to other juvenile fish species.

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Appendix

A.1: Swimming performance data

Table A.1. 1: Swimming performance data from the smaller juvenile snapper.

Type	Ui	Uii	Body length	Ti	Tii	(Ui + (Uii *(Ti/Tii)	Ui	Uii	Body length	Ti	Tii	(Ui + (Uii *(Ti/Tii)
Absolute Flow (cm/s)							Relative Flow (BL/s)					
Bare	18	3	4.00	0.56	15	18.11	4.50	0.75	4.00	0.56	15	4.53
Bare	18	3	4.30	1.03	15	18.21	4.19	0.70	4.30	1.03	15	4.23
Bare	15	3	4.40	5.08	15	16.02	3.41	0.68	4.40	5.08	15	3.64
Bare	24	3	3.00	15.00	15	27.00	8.00	1.00	3.00	15.00	15	9.00
Bare	18	3	3.70	6.53	15	19.31	4.86	0.81	3.70	6.53	15	5.22
Bare	12	3	3.70	4.50	15	12.90	3.24	0.81	3.70	4.50	15	3.49
Bare	24	3	3.60	15.00	15	27.00	6.67	0.83	3.60	15.00	15	7.50
Bare	18	3	3.90	3.25	15	18.65	4.62	0.77	3.90	3.25	15	4.78
Bare	24	3	4.10	13.78	15	26.76	5.85	0.73	4.10	13.78	15	6.53
Bare	15	3	3.70	12.85	15	17.57	4.05	0.81	3.70	12.85	15	4.75
Bare	18	3	3.60	2.98	15	18.60	5.00	0.83	3.60	2.98	15	5.17
Bare	18	3	4.50	5.50	15	19.10	4.00	0.67	4.50	5.50	15	4.24
Bare	15	3	4.20	6.42	15	16.28	3.57	0.71	4.20	6.42	15	3.88
Bare	15	3	4.20	12.75	15	17.55	3.57	0.71	4.20	12.75	15	4.18
Bare	18	3	4.40	4.83	15	18.97	4.09	0.68	4.40	4.83	15	4.31
Full	24	3	4.80	15.00	15	27.00	5.00	0.63	4.80	15.00	15	5.63
Full	24	3	4.20	15.00	15	27.00	5.71	0.71	4.20	15.00	15	6.43
Full	18	3	3.40	9.60	15	19.92	5.29	0.88	3.40	9.60	15	5.86
Full	21	3	4.90	3.00	15	21.60	4.29	0.61	4.90	3.00	15	4.41
Full	12	3	3.90	4.88	15	12.98	3.08	0.77	3.90	4.88	15	3.33
Full	24	3	4.30	15.00	15	27.00	5.58	0.70	4.30	15.00	15	6.28
Full	21	3	3.00	0.03	15	21.01	7.00	1.00	3.00	0.03	15	7.00
Full	24	3	4.10	1.07	15	24.21	5.85	0.73	4.10	1.07	15	5.91
Full	21	3	4.20	9.55	15	22.91	5.00	0.71	4.20	9.55	15	5.45
Full	15	3	4.00	12.58	15	17.52	3.75	0.75	4.00	12.58	15	4.38
Full	18	3	3.80	2.73	15	18.55	4.74	0.79	3.80	2.73	15	4.88
Full	21	3	4.40	9.68	15	22.94	4.77	0.68	4.40	9.68	15	5.21
Full	18	3	4.00	5.02	15	19.00	4.50	0.75	4.00	5.02	15	4.75
Full	24	3	4.50	15.00	15	27.00	5.33	0.67	4.50	15.00	15	6.00
Full	15	3	3.40	6.37	15	16.27	4.41	0.88	3.40	6.37	15	4.79
Half	24	3	5.00	10.00	15	26.00	4.80	0.60	5.00	10.00	15	5.20
Half	18	3	4.50	4.50	15	18.90	4.00	0.67	4.50	4.50	15	4.20
Half	24	3	4.10	10.76	15	26.15	5.85	0.73	4.10	10.76	15	6.38
Half	15	3	4.29	3.83	15	15.77	3.50	0.70	4.29	3.83	15	3.68
Half	18	3	4.60	4.73	15	18.95	3.91	0.65	4.60	4.73	15	4.12
Half	18	3	4.20	12.58	15	20.52	4.29	0.71	4.20	12.58	15	4.88
Half	21	3	3.40	8.33	15	22.67	6.18	0.88	3.40	8.33	15	6.67
Half	15	3	4.60	13.58	15	17.72	3.26	0.65	4.60	13.58	15	3.85
Half	18	3	4.60	2.51	15	18.50	3.91	0.65	4.60	2.51	15	4.02
Half	24	3	4.20	15.00	15	27.00	5.71	0.71	4.20	15.00	15	6.43
Half	21	3	4.90	8.90	15	22.78	4.29	0.61	4.90	8.90	15	4.65
Half	24	3	3.70	5.00	15	25.00	6.49	0.81	3.70	5.00	15	6.76
Half	15	3	4.90	6.52	15	16.30	3.06	0.61	4.90	6.52	15	3.33
Half	15	3	4.50	8.05	15	16.61	3.33	0.67	4.50	8.05	15	3.69
Half	18	3	4.30	0.72	15	18.14	4.19	0.70	4.30	0.72	15	4.22
Half	24	3	4.60	15.00	15	27.00	5.22	0.65	4.60	15.00	15	5.87

Table A.1. 2: Swimming performance data from the larger juvenile snapper.

Type	Ui	Uii	Body length	Ti	Tii	(Ui + (Uii *(Ti/Tii)	Ui	Uii	Body length	Ti	Tii	(Ui + (Uii *(Ti/Tii)
Absolute Flow (cm/s)							Relative Flow (BL/s)					
Bare	64	15.00	10.30	8	15	72.00	6.21	15.00	10.30	8	15	14.21
Bare	48	0.77	8.70	8	15	48.41	5.52	0.77	8.70	8	15	5.93
Bare	40	14.00	9.20	8	15	40.80	5.71	14.00	9.20	8	15	13.18
Bare	48	1.50	8.40	8	15	51.21	5.16	1.50	8.40	8	15	5.96
Bare	40	8.07	9.60	8	15	42.18	6.88	8.07	9.60	8	15	11.19
Bare	40	6.00	7.80	8	15	44.14	7.53	6.00	7.80	8	15	10.73
Bare	48	4.00	9.10	8	15	55.11	4.65	4.00	9.10	8	15	6.78
Bare	48	6.67	8.80	8	15	53.62	5.39	6.67	8.80	8	15	8.95
Bare	56	4.75	9.30	8	15	64.00	6.60	4.75	9.30	8	15	9.13
Bare	48	6.02	9.30	8	15	50.79	5.39	6.02	9.30	8	15	8.60
Full	64	4.08	9.30	8	15	67.20	5.13	4.08	9.30	8	15	7.30
Full	56	2.35	7.80	8	15	57.25	7.18	2.35	7.80	8	15	8.43
Full	64	12.78	9.30	8	15	70.82	6.88	12.78	9.30	8	15	13.70
Full	56	11.20	8.40	8	15	61.97	6.67	11.20	8.40	8	15	12.64
Full	32	14.20	8.30	8	15	39.57	3.86	14.20	8.30	8	15	11.43
Full	64	7.77	8.50	8	15	65.29	7.36	7.77	8.50	8	15	11.50
Full	40	13.33	8.60	8	15	48.00	6.21	13.33	8.60	8	15	13.32
Full	56	8.35	8.50	8	15	61.42	3.48	8.35	8.50	8	15	7.93
Full	56	3.35	10.20	8	15	59.56	8.10	3.35	10.20	8	15	9.89
Full	64	2.42	8.70	8	15	72.00	7.44	2.42	8.70	8	15	8.73
Half	64	15.00	10.30	8	15	71.47	4.35	15.00	10.30	8	15	12.35
Half	40	4.37	8.10	8	15	44.30	4.17	4.37	8.10	8	15	6.50
Half	48	10.53	8.90	8	15	50.13	5.27	10.53	8.90	8	15	10.89
Half	64	15.00	9.70	8	15	67.56	5.45	15.00	9.70	8	15	13.45
Half	48	5.23	8.90	8	15	50.53	6.02	5.23	8.90	8	15	8.81
Half	56	3.90	7.60	8	15	60.45	6.59	3.90	7.60	8	15	8.67
Half	64	2.23	9.00	8	15	65.79	5.49	2.23	9.00	8	15	6.68
Half	64	15.00	8.70	8	15	66.33	4.94	15.00	8.70	8	15	12.94
Half	32	10.17	9.20	8	15	34.08	7.37	10.17	9.20	8	15	12.79
Half	64	6.68	7.90	8	15	65.19	7.11	6.68	7.90	8	15	10.67
Half	64	15.00	8.60	8	15	72.00	7.36	15.00	8.60	8	15	15.36

A.2: Physiology data for each treatment

Table A.2.1: Physiology data collected from Juvenile snapper, showing both the raw data and the modified values after including the dilution factor of the Drabkins solution.

Date	Treatment	Volume µl	Blood Dilution Factor	Hb (Abs 540nm)	Glucose (mM)	Haematocrit %	Lactate (mM)	Tryglyceride (mM)	Corrected Value of ABS Hb (540nm)	Corrected Value of Hct (%)	Total Hb (g/L)	Mean Cell Haemoglobin Concentration (McHc g/L)	Glucose (mM)	Lactate (mM)	Tryglyceride (mM)
				Raw Data					Add dilution factor of Heparin	Add dilution factor of Heparin			Add dilution factor of Heparin	Add dilution factor of Heparin	Add dilution factor of Heparin
28/05/2014	Bare	500	1.00	0.157	7.7	27.5	0.8	-	0.158	27.60	46.40	168.11	7.73	0.80	-
4/06/2014	Bare	80	1.02	0.175	5.5	31.9	0.8	1.74	0.179	32.62	52.69	161.54	5.62	0.82	1.78
6/06/2014	Bare	50	1.04	0.189	5	29.5	0.8	1.32	0.196	30.56	57.66	188.65	5.18	0.83	1.37
9/06/2014	Bare	30	1.06	0.203	11	19.5	2.2	-	0.215	20.67	63.36	306.54	11.66	2.33	-
12/06/2014	Bare	100	1.02	0.293	5.75	37.3	1.3	1.31	0.298	37.97	87.83	231.30	5.85	1.32	1.33
16/06/2014	Bare	103	1.02	0.187	4.03	29.4	0.8	-	0.190	29.91	56.03	187.29	4.10	0.81	-
16/06/2014	Bare	100	1.02	0.217	7.4	32.1	0.8	-	0.221	32.68	65.05	199.06	7.53	0.81	-
19/06/2014	Bare	100	1.02	0.237	3	36.4	0.8	1.18	0.241	37.06	71.04	191.72	3.05	0.81	1.20
19/06/2014	Bare	104	1.02	0.23	3.53	22.5	0.8	1.33	0.234	22.89	68.90	301.00	3.59	0.81	1.35
20/06/2014	Bare	95	1.02	0.329	4.2	32.2	0.8	1.33	0.335	32.81	98.71	300.86	4.28	0.82	1.36
6/06/2014	Full	105	1.02	0.295	6.7	32.8	0.8	0.8	0.300	33.36	88.35	264.83	6.81	0.81	0.81
12/06/2014	Full	100	1.02	0.209	5.1	32.5	0.8	0.87	0.213	33.09	62.65	189.36	5.19	0.81	0.89
12/06/2014	Full	30	1.06	0.12	-	21.8	1	1.22	0.127	23.11	37.45	162.09	-	1.06	1.29
13/06/2014	Full	100	1.02	0.195	3.47	33.5	0.8	1.09	0.199	34.10	58.45	171.40	3.53	0.81	1.11
13/06/2014	Full	40	1.05	0.243	1.63	19.4	0.8	-	0.254	20.27	74.77	368.83	1.70	0.84	-
17/06/2014	Full	100	1.02	0.23	4.1	31.9	0.8	0.8	0.234	32.47	68.94	212.30	4.17	0.81	0.81
18/06/2014	Full	120	1.02	0.192	6.77	28.5	0.8	1.01	0.195	28.93	57.38	198.37	6.87	0.81	1.03
23/06/2014	Full	100	1.02	0.173	5.65	32.9	0.8	0.8	0.176	33.49	51.86	154.84	5.75	0.81	0.81
26/06/2014	Full	150	1.01	0.353	4.75	31.5	0.8	0.81	0.357	31.88	105.19	329.98	4.81	0.81	0.82
26/06/2014	Full	100	1.02	0.206	6.35	30.5	0.8	1.49	0.210	31.05	61.75	198.88	6.46	0.81	1.52
4/06/2014	Half	80	1.02	0.397	5.7	30.8	0.8	1.23	0.406	31.49	119.53	379.54	5.83	0.82	1.26
6/06/2014	Half	110	1.02	0.251	3.4	34.1	0.8	1.21	0.255	34.66	75.12	216.74	3.46	0.81	1.23
7/06/2014	Half	40	1.05	0.168	1.6	35.7	0.8	1.44	0.176	37.31	51.69	138.57	1.67	0.84	1.50
7/06/2014	Half	90	1.02	0.214	2.6	34.9	0.8	0.8	0.218	35.60	64.27	180.55	2.65	0.82	0.82
9/06/2014	Half	90	1.02	0.214	3.2	35	0.8	0.8	0.218	35.70	64.27	180.04	3.26	0.82	0.82
16/06/2014	Half	30	1.06	0.135	2.5	31.5	0.8	-	0.143	33.39	42.14	126.20	2.65	0.85	-
17/06/2014	Half	105	1.02	0.264	3.53	30.5	0.8	1.19	0.269	31.02	79.07	254.87	3.59	0.81	1.21
18/06/2014	Half	150	1.01	0.219	3.93	35.4	0.8	1.07	0.222	35.82	65.26	182.16	3.98	0.81	1.08
20/06/2014	Half	100	1.02	0.298	3.53	34.9	0.8	0.94	0.303	35.53	89.33	251.43	3.59	0.81	0.96
20/06/2014	Half	100	1.02	0.24	6	32.7	0.8	0.8	0.244	33.29	71.94	216.11	6.11	0.81	0.81
23/06/2014	Half	120	1.02	0.217	6.2	31.8	0.8	0.8	0.220	32.28	64.86	200.93	6.29	0.81	0.81

A.3: Flow mapping in the annular flume

ADV flow measurements taken at different heights within the annular flume under flow speeds that were utilised in the experiment (see flow mapping methodology).

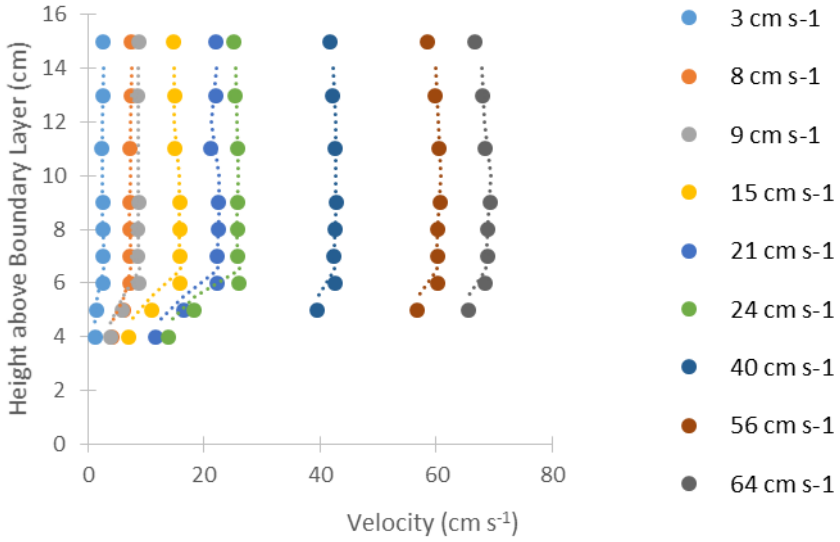


Figure A.3. 1: Flow velocity measurements taken under bare treatment.

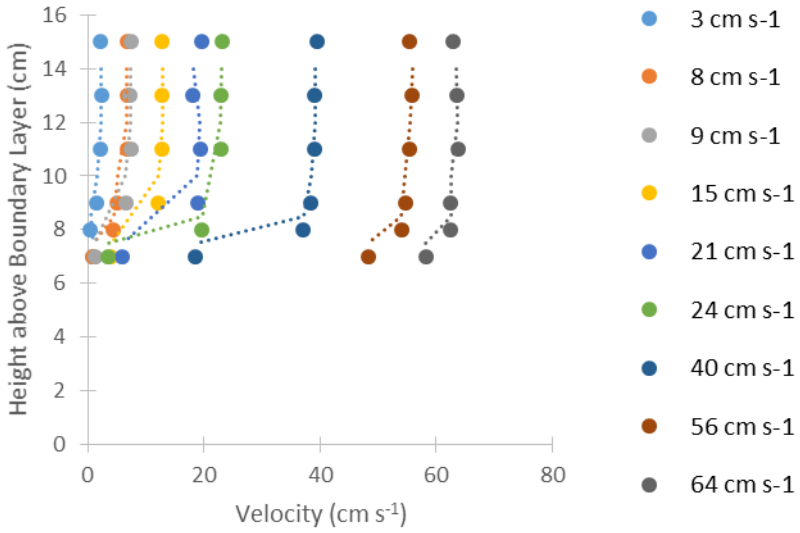


Figure A.3. 2: Flow velocity measurements taken under the seagrass treatment.

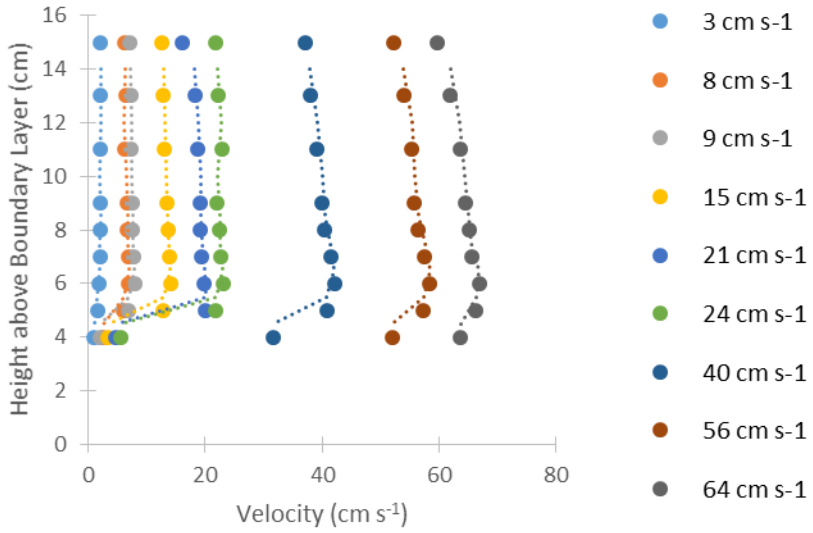


Figure A.3. 3: Mixed sampling point 1 - The ADV position was fixed measuring the flow over bare templates upstream and downstream.

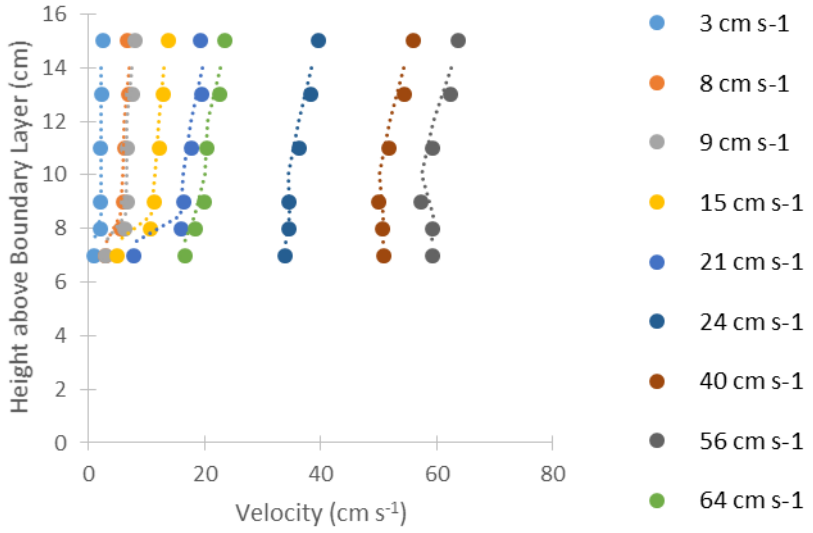


Figure A.3. 4: Mixed sampling point 2 - Flow velocity measurements over seagrass templates upstream and downstream.

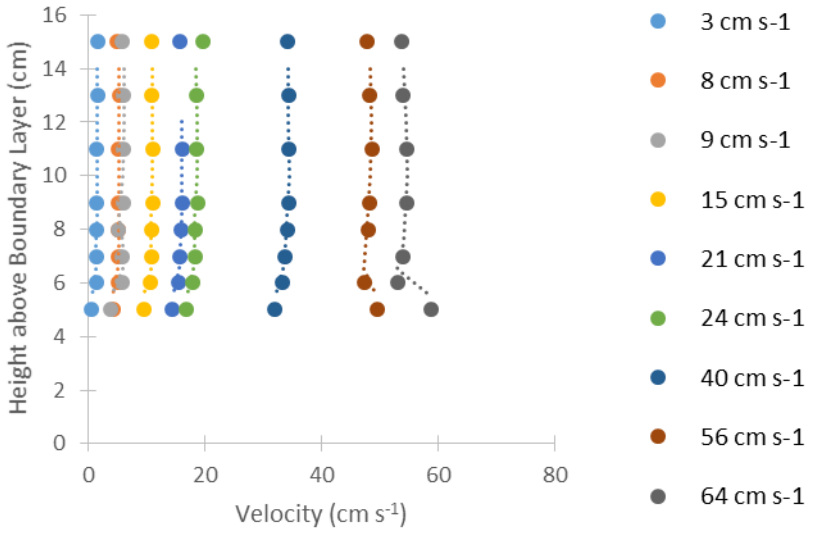


Figure A.3. 5: Mixed sampling point 3 - ADV measurements from flow at 7 cm into the trailing edge of the bare templates upstream and seagrass downstream of the ADV.

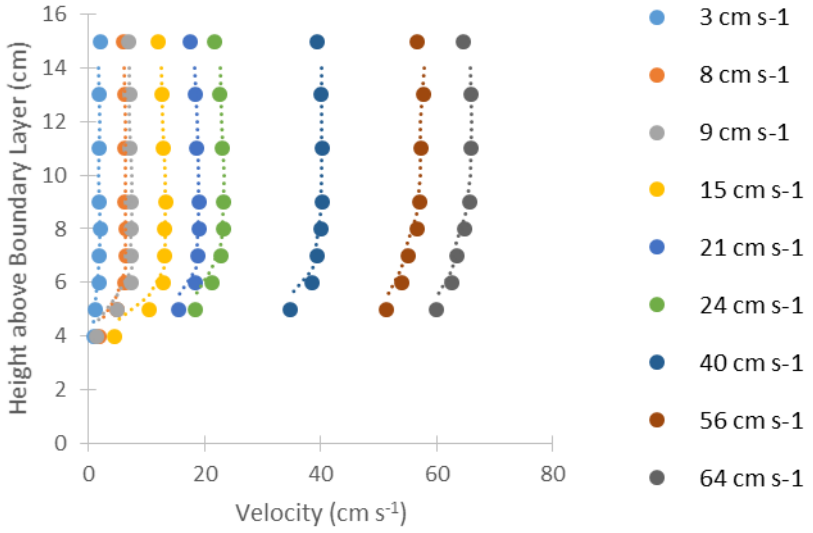


Figure A.3. 6: Mixed sampling point 4 - Flow velocity measurements 10 cm into the trailing edge of the bare templates upstream, 5 cm downstream before seagrass templates.

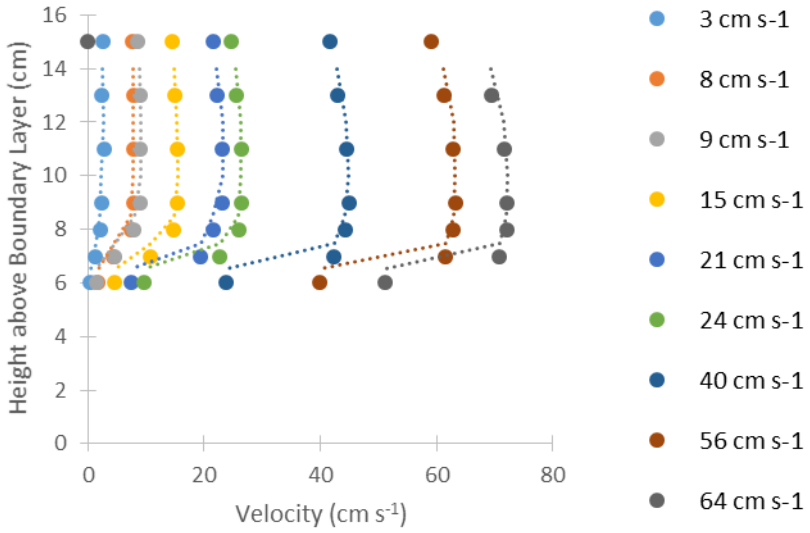


Figure A.3. 7: Mixed sampling point 5 - Flow velocity measurements 7 cm into the seagrass with 5 cm of seagrass downstream before bare templates.

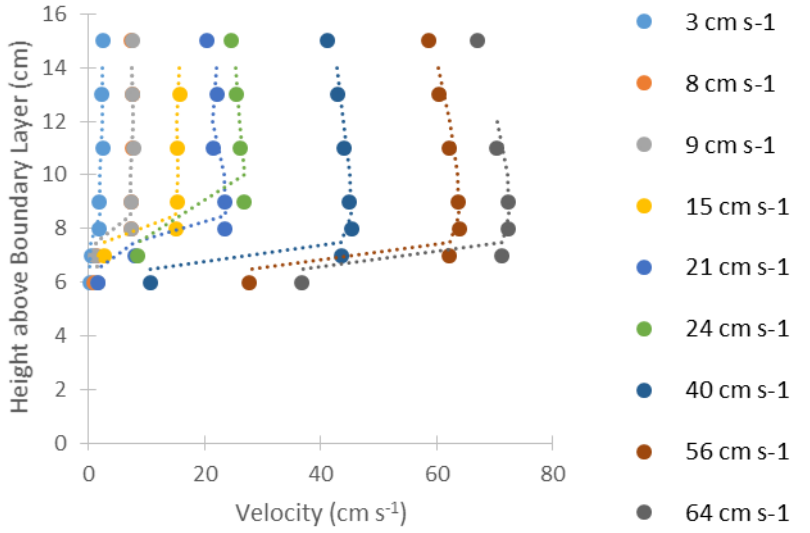


Figure A.3. 8: Mixed sampling point 6 - ADV measurements from flow 7 cm into the seagrass, upstream of the ADV and bare templates downstream of the ADV.

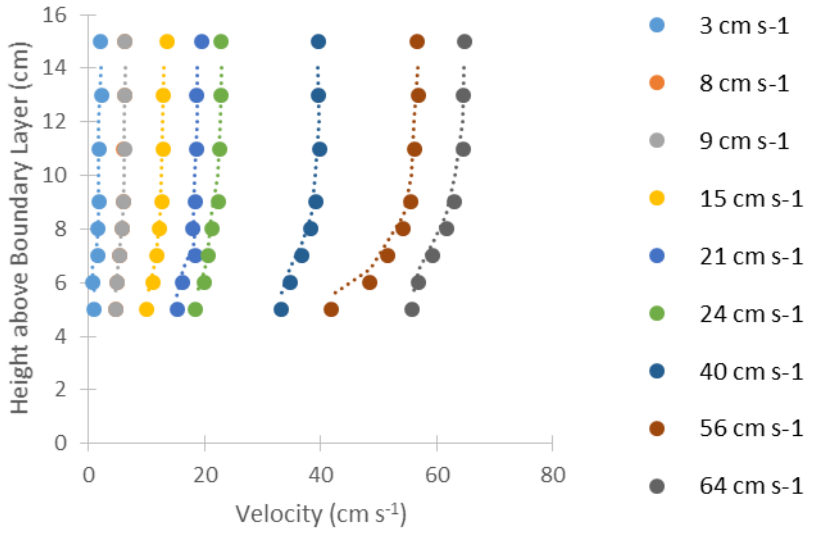


Figure A.3. 9: Mixed sampling point 7 - ADV measurements from flow over the interface of seagrass downstream and bare upstream of the ADV.

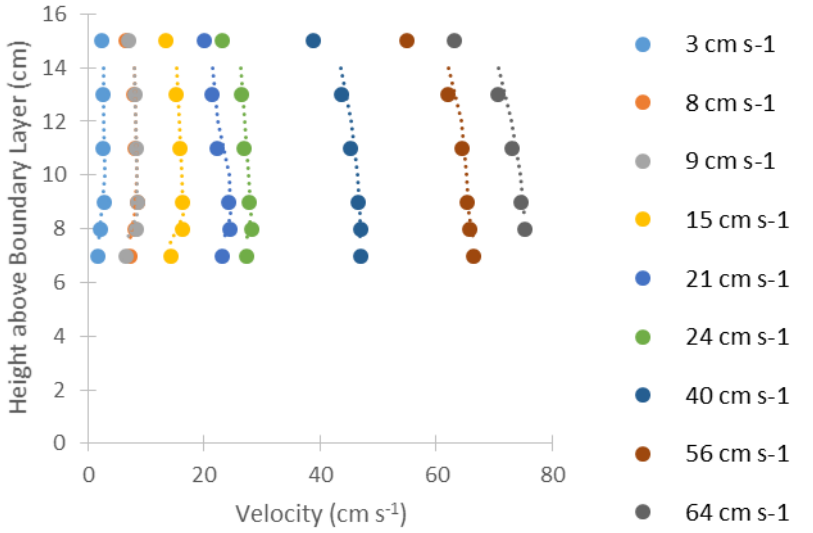


Figure A.3. 10: Mixed sampling point 8 - ADV measurements from flow over the interface of bare downstream and seagrass upstream of the ADV.

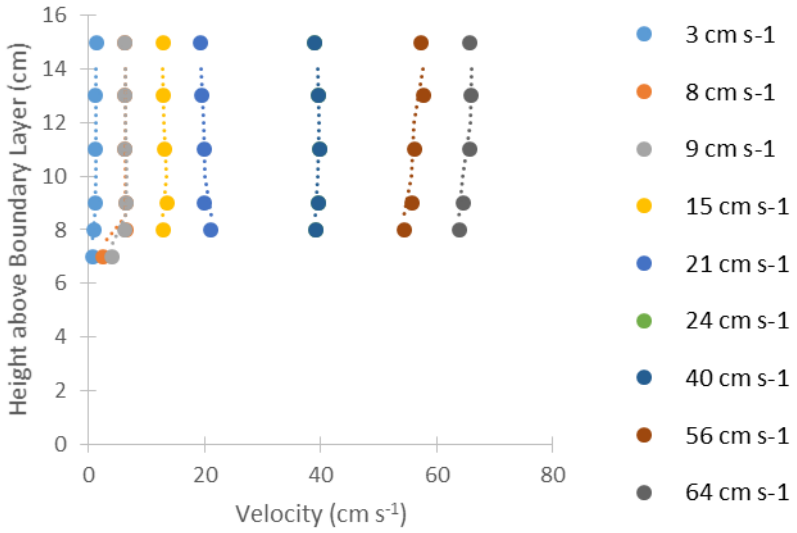


Figure A.3. 11: Mixed sampling point 9 - ADV measurements from flow 5 cm into the leading edge of seagrass downstream and bare templates upstream of the ADV.

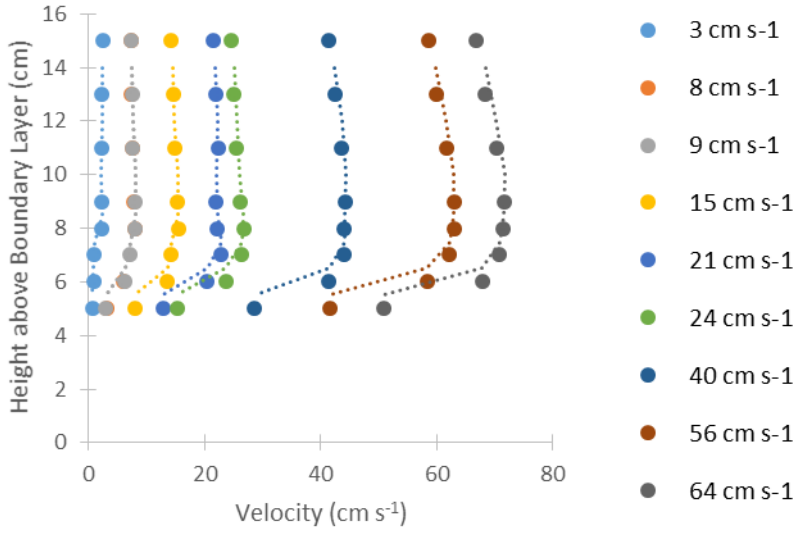
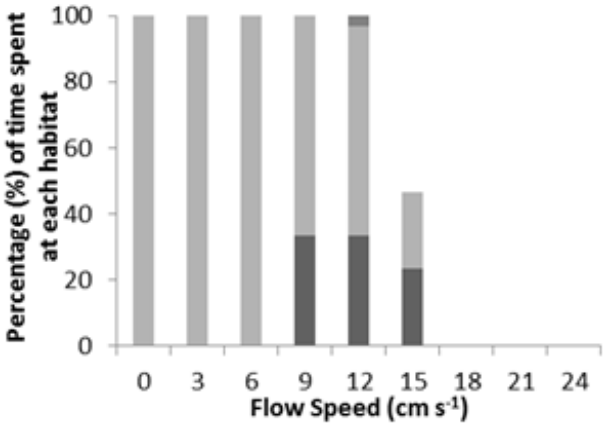
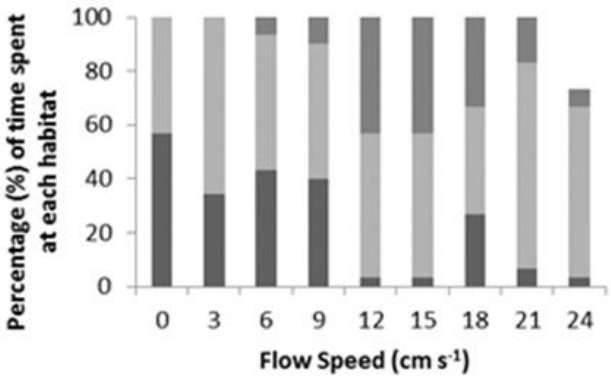
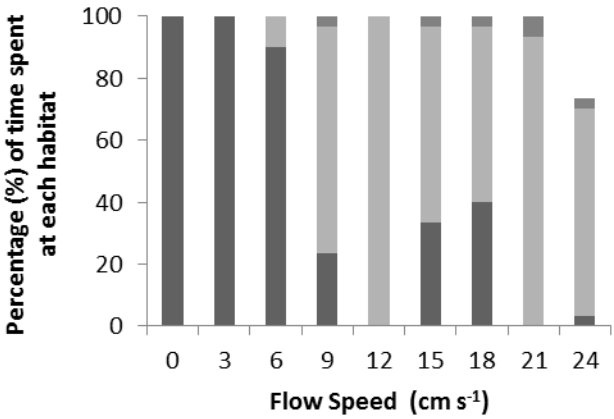


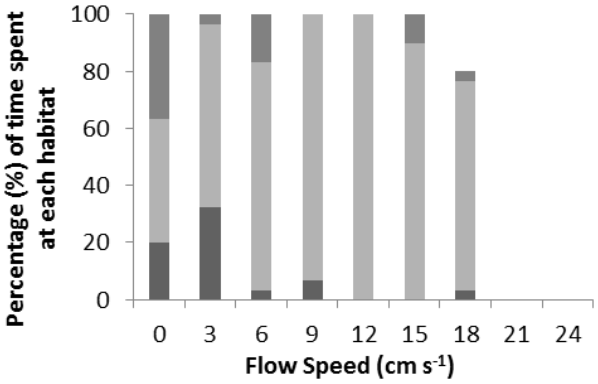
Figure A.3. 12: Mixed sampling point 10 - ADV measurements from flow 5 cm into the leading edge of bare downstream and seagrass upstream.

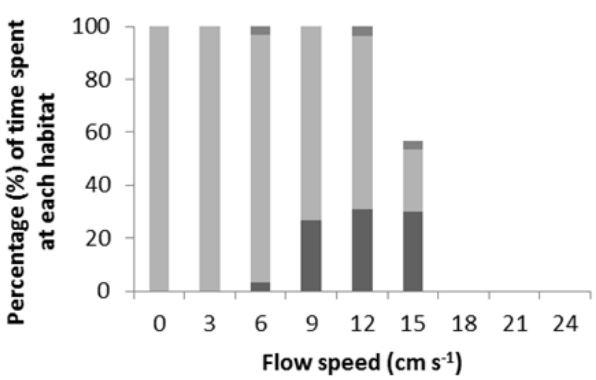
A4: Habitat preference

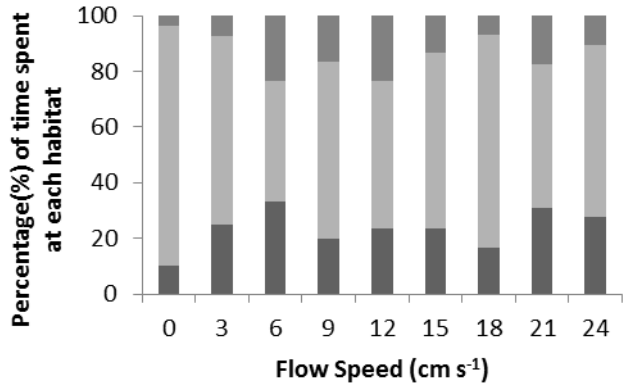


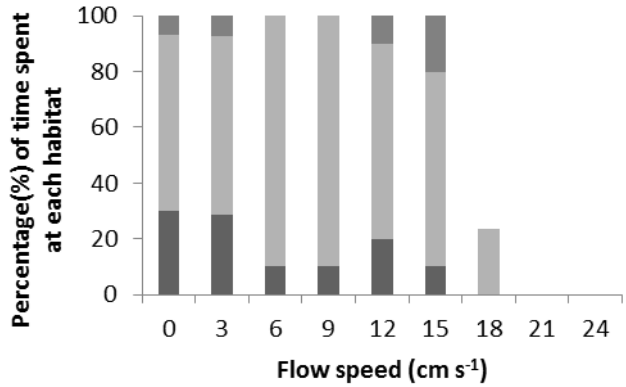





Percentage (%) of time spent at each habitat
100
80
60
40
20
0
0 3 6 9 12 15 18 21 24
Flow Speed (cm s-1)


Percentage (%) of time spent at each habitat
100
80
60
40
20
0
0 3 6 9 12 15 18 21 24
Flow speed (cm s-1)


Percentage(%) of time spent at each habitat
100
80
60
40
20
0
0 3 6 9 12 15 18 21 24
Flow Speed (cm s-1)


Percentage(%) of time spent at each habitat
100
80
60
40
20
0
0 3 6 9 12 15 18 21 24
Flow speed (cm s-1)

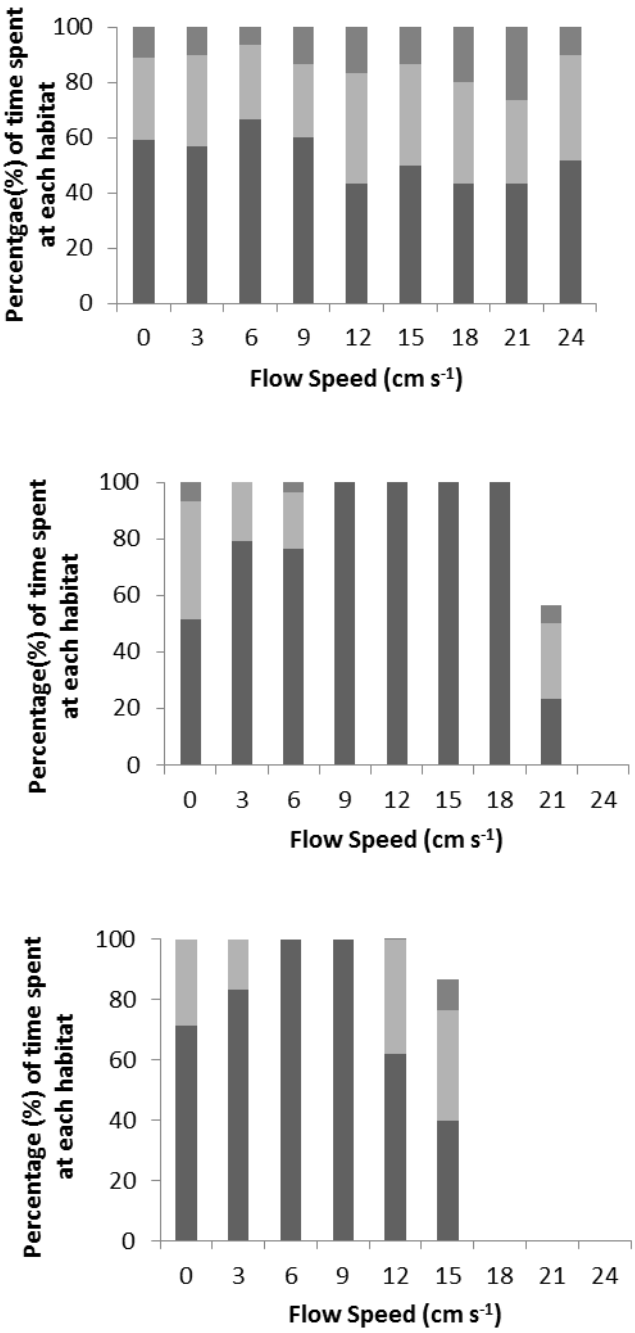


Figure A.4. 1: Percentage (%) of time spent in each treatment for each experimental flow speed. Juvenile snapper were exposed to each flow speed for 15 minutes. (n=10) (Dark grey = Seagrass, light grey = Bare, medium grey = Edge). The maximum flow speed obtained is also shown.