

**Nocturnal patch use by redfinned bullies
(*Gobimorphus huttoni*) in a temperate
stream of southern New Zealand**

Rowan Kenneth Richard Moore

Thesis submitted in partial fulfilment of the requirement for the degree of

Master of Science at the Department of Zoology,

University of Otago, Dunedin, New Zealand

October 2013

Abstract

Understanding how benthic feeding fish track and use patchy resources such as food, is beneficial for conservation and management providing insights into how they perceive and assess their environment. The benthic feeding fish of New Zealand provide ideal study organisms to determine whether fish are selecting patches based on food resources, habitat structure or a combination of both (McDowall, 2010). This thesis aimed to investigate what factors drive nocturnal patch selection by the redfinned bully, in a small temperate stream (Catlins, New Zealand). The descriptive component of this study compared the microhabitat and invertebrate community of nocturnal patches occupied by redfinned bullies to patches sampled at random. It was found that redfinned bullies displayed non-random patch selection, with a preference for patches with cobble substrates and high abundances of invertebrates (particularly chironomids). However, distinguishing whether patch selection by redfinned bullies was driven by the invertebrate community or the substrate was not possible based on the results from the descriptive component of the study. To elucidate what was driving nocturnal patch selection by redfinned bullies an experiment was designed. The experimental component of this study involved a group of twenty stream pools half of which were treated using a cleaning procedure (experimental disturbance) to reduce the abundance of invertebrates and the other half were undisturbed control pools. Pools were monitored over five weeks to observe the response of redfinned bullies to the experimental disturbance (reduced invertebrate abundance), but no distinct response was observed. A lack of response by redfinned bullies suggests a strong affinity to their pool of residence, at least in the short term, despite a low abundance of prey. Home range affinity may have been related to spawning, including activities such as nest guarding, egg laying and fertilisation. If the same experiment were to be repeated outside of the redfinned bully spawning period different patterns of response may have been observed. This study has assisted in understanding aspects of redfinned bully ecology, however further studies, on multiple scales will be required to elucidate the many unknown aspects of redfinned bullies.

Acknowledgements

Firstly I would like to acknowledge all of my excellent field assistants; you were all very helpful and made field work a lot of fun. In particular: Josh Tabak, Peri Subritzky, Sam Van der Horst, Manna Warburton and Thomas Rische. I would like to thank Richard Lean for allowing me to carry out field work on his property.

I would like to say thank you to my excellent supervisor Gerry Closs, for his advice, support and enthusiasm throughout my project. I found Gerry was always willing to help me work through any challenges I had in a manner that gave me a lot of confidence in the work. So thanks Gerry you're a legend!

I would like to thank all of my fellow students at the Zoology department, who were always willing to answer the vast array of questions I posed. In particular: Erin Damsteegt, Nat Jiahui Lim, Katha Lange, Charles Ellen and Katie Blakemore.

I would like to thank all of the Zoology staff, you are a great team, and made study at the Zoology department exciting and enjoyable. In particular: Nicky McHugh, you were such a joy to work alongside, and you run an excellent lab. Kim Garret, you were very helpful whenever I sought your help, and I found the field induction and electrofishing courses you run are excellent. Murray McKenzie, you were always on the go, willing to help out with any task I asked of you, with outstanding results, thanks a lot. Vivienne McNaughton thanks for running such a great store. Ronda Peacock and Wendy Shanks, you are the most lovely and approachable administrative staff anyone could ask for, you have been so helpful and full of good advice thank you.

I would like to say thanks to Gerry's freshwater group, you guys have been really helpful and a pleasure to work with and learn from. In Particular: Lance Dorsey, Peter Jones, Sourav Paul and Aurelien Vivancos.

Finally I would like to thank my lovely family for all their support with my study in Dunedin, you guys are great.

Table of Contents

Abstract	ii
Acknowledgements	iii
Table of Contents	iv
List of Figures	vii
List of Tables	ix
1. General Introduction	1
1.1 Effects of world population growth and consumption rates on freshwater ecosystems	1
1.2 Land use change and its impact on benthic stream environments	2
1.3 Disturbance and its impact on ecosystems	2
1.4 Habitat selection.....	3
1.5 Dynamics of Patchy environments	4
1.6 Stream environments, systems with patchy resource distributions.....	5
1.7 Optimal foraging theory and the role of food subsidies in patch selection of stream fish	5
1.8 Feeding styles of stream fish and behavioural interactions	6
1.9 Habitat selection in benthic stream fish and the potential for study of New Zealands native benthic stream fish.....	7
1.10 The importance of studies on patch use by benthic stream fish incorporating the role of disturbance	8
1.11 Ecological context of study	9
2. Nocturnal patch selection by redfinned bullies	11
2.1 Introduction.....	11
2.2 Methods.....	15
2.2.1 Description of study site.....	15
2.2.2 Methodology for study site	15
2.2.3 Spotlighting.....	15
2.2.4 Invertebrate sampling	16
2.2.5 Microhabitat variables.....	16

2.2.6	Random samples	17
2.2.7	Dietary analysis.....	17
2.2.8	Data analysis.....	18
2.3	Results.....	20
2.3.1	Invertebrate community assemblages and dietary analysis.....	20
2.3.2	Comparison of environmental variables and the invertebrate community between fish and random patches	21
2.3.3	Comparison of environmental variables between patches occupied by male and female fish.....	24
2.4	Discussion	25
2.4.1	Environmental characteristics of patches occupied by redefined bullies	25
2.4.2	Influence of environmental variables on patch selection by redefined bullies.....	25
2.4.3	Effects of invertebrate community on patch selection by redefined bullies.....	27
2.4.4	Breeding habitat requirements affecting patch selection by redefined bullies.....	30
2.4.5	Interspecific interactions affecting patch selection by redefined bullies.	30
2.4.6	Conclusion	31
3.	Effects of experimental disturbance on nocturnal patch selection by redefined bullies	33
3.1	Introduction.....	33
3.2	Methods.....	36
3.2.1	Study site	36
3.2.2	Field methods	36
3.2.3	Spotlighting.....	36
3.2.4	Pre- treatment observational phase	37
3.2.5	Physical habitat measurements	37
3.2.6	Treatment phase	38
3.2.7	Post-treatment observational phase.....	38
3.2.8	Invertebrate sampling	39

3.2.9	Data analysis.....	39
3.3	Results.....	41
3.3.1	Effect of treatment on Invertebrate abundance in control and treatment pools.....	41
3.3.2	Invertebrate species contributions comparison between control and treatment groups.....	42
3.3.3	Abundance of redfinned bullies and other species before and after treatment in control and treatment pools.	44
3.3.4	Interactive effects between fish abundance and invertebrate abundance.....	46
3.3.5	Comparison of environmental variables between control and treatment pools.....	46
3.4	Discussion	47
3.4.1	Interactive effects between invertebrate abundance and redfinned bully abundance.....	47
3.4.2	Effects of disturbance on stream communities	48
3.4.3	Effects of breeding activity on distribution, abundance and patch selection of redfinned bullies.....	49
3.4.4	Substrate driving patch selection by redfinned bullies.....	50
3.4.5	Conclusion	51
4.	General discussion.....	53
4.1.1	Major findings from study.....	53
4.1.2	The importance of multi-scale studies on New Zealand’s freshwater fish	54
4.1.3	Improvements, limitations and recommendations for future study on redfinned bullies	55
4.1.4	Conclusion	57
5.	References.....	59
6.	Appendix	68
6.1	Generalized Linear Model coding (R)	68
6.2	Distance based linear model output	68

List of Figures

Figure 2.1. a) The top five most abundant invertebrate taxa (C = Chironamidae, D = *Deleatidium*, P = *Pyconcentrodes*, O = Oligochaeta, M = *Megaleptoperla*) from fifty surber samples where redfinned bullies were located (grey filled bars) and from fifty randomly taken surber samples (striped bars), values represent mean \pm S.E.M. star symbol denotes a significant difference ($p < 0.05$). **b)** The five most abundant invertebrate taxa (C = Chironamidae, D = *Deleatidium*, E = Elimidae, CH = *Chiltonia*, Z = *Zealandoperla*) found in thirty redfinned bully diet samples (Esophageal, stomach and intestinal content), values represent mean \pm S.E.M. Star symbol denotes a significant difference ($p < 0.05$).....20

Figure 2.2. Distance based linear model, dbRDA ordination plot based on the invertebrate community, using Bray Curtis similarity. Plot displays the relationship between environmental variables and invertebrate abundance among fish patches (green circles) and random patches (blue triangles). Vectors represent environmental variables, they show how each variable is responsible for driving differences between patches, and the length of each vector reflects the amount of variation being explained by that vector. Vector abbreviations: V= Water velocity ms^{-1} , D = Water depth in meters, DST = Dominant substrate type, DNC= distance to nearest cover in meters.....21

Figure 2.3. a) A comparison of the percentage frequency of dominant substrate type between fifty patches where redfinned bullies were located (grey filled bars) and from fifty random patches (striped bars). **b)** Mean abundance of invertebrates across the five substrate types, comparing between fifty patches where redfinned bullies were located (grey filled bars) and fifty randomly sampled patches (striped bars). **c)** A comparison of the percentage frequency for chironomids across the five different substrate types comparing between fifty patches where redfinned bullies were located (grey filled bars) and from fifty random patches (striped bars). CSI = Frequency of chironomids on silt patches, CSA= Frequency of chironomids on sand patches, CG = Frequency of chironomids on gravel patches, CC = Frequency of chironomids on cobble patches, CB = Frequency of chironomids on boulder patches.....23

Figure 3.1. Invertebrate abundance found within stream pools from sampling sessions over the five week monitoring period. **a)** Invertebrate abundance found within treatment pools from four sampling sessions before and following treatment (disturbance). **b)**

Invertebrate abundance found within control pools from three sampling sessions. Values represent mean \pm S.E.M. Different letters denote significant differences ($p < 0.05$).....41

Figure 3.2. **a)** The average number of male fish observed during spotlighting across the ten control and treatment pools over the eleven night observation period. **b)** The average number of female fish across the ten control and treatment pools over the eleven night observation period. **c)** The average number of other fish species and crayfish species across the ten control and treatment pools over the eleven night observation period. Other species included; freshwater crayfish (*Paranephrops zealandicus*), banded Kokopu (*Galaxias fasciatus*), brown trout (*Salmo trutta*), short-finned eel (*Anguilla australisi*) and long- finned eel (*Anguilla dieffenbachii*). Values represent mean \pm S.E.M. Green stars represent disturbance. Blue dashed lines represent control pools and red lines represent treatment pools.....45

Figure 3.3. Scatterplot showing the relationship between mean fish abundance and mean invertebrate abundance. $y = -76.956x + 482.85$, $R^2 = 0.3764$. Data includes averaged invertebrate abundance from four sampling sessions and averaged fish abundance data from each observation night before an invertebrate sampling session took place.....46

List of Tables

Table 2.1. PERMANOVA results based on Euclidian distance, testing for a difference in: a) the biological community assemblages from patches where fish were present and randomly sampled patches, b) the biological community assemblages between patches where male and female fish were found, c) environmental variables between patches where fish were found and randomly sampled patches, d) environmental variables between patches where male fish were located and those where female fish were located. <i>df</i> = degrees of freedom. <i>P</i> values < 0.05 are considered significant.....	22
Table 2.2. A series of Students T-tests, assuming unequal variance comparing environmental characteristics from fish patches and random patches, averaged across the fifty patches in each group. <i>P</i> values < 0.05 are considered significant. V = Velocity, D = Water depth, DST = Dominant substrate type, DNC = Distance to nearest cover.....	24
Table 2.3. A series of students T-tests, assuming unequal variance comparing environmental characteristics from patches where male fish were found and patches where female fish were found. Values are averaged across the twenty one patches where female fish were found and twenty nine patches where male fish were found. <i>P</i> values < 0.05 are considered significant. V = Velocity, D = Water depth, DST = Dominant substrate type, DNC = Distance to nearest cover.....	24
Table 3. 1. One way SIMPER analysis. Table 1 a and b) are assessing which taxa are the most abundant on average in treatment (a) & control (b) pools and what percentage of the biota their abundance is accounting for, prior to disturbance (treatment pools only), one week, three weeks and five weeks after disturbance respectively. Av. Abund = average abundance (based on values in the Bray-curtis similarity matrix and does not represent true abundance estimates), Av. Sim = average similarity, Sim/SD = ratio of average similarity to standard deviation, Contrib% = the percentage each species contributes to dissimilarities, Cum.% = cumulative percent of total dissimilarity.....	42
Table 3.2. A comparison of environmental characteristics of the treatment and control pools averaged across the ten pools in each group. <i>P</i> values < 0.05 are considered significant. V = Velocity, D = Water depth, DST = Dominant substrate type, L = Length, PW =Pool width.....	46

1. General Introduction

1.1 Effects of world population growth and consumption rates on freshwater ecosystems

A six fold increase in the Earth's human population over the past two centuries has increased human dependence on freshwater systems (Radif, 1999). Human population growth has increased pressure on freshwater systems both through consumptive and non-consumptive uses (Radif, 1999). During the 20th century the human population increased fourfold and during the same time period water drawn from freshwater ecosystems increased eightfold (Richter *et al.*, 2003). Recent stress imposed on freshwater systems can be attributed to increased water use for agriculture, industry, recreational activities and human consumption (Dewson *et al.*, 2007; Radif, 1999). Land use change along with an increase in freshwater use has caused degradation of water quality in many of the world's freshwater ecosystems (Dewson *et al.*, 2007; Radif, 1999). Attempts to manage freshwater systems to meet the needs of humans, have resulted in the needs of freshwater species and ecosystems being neglected resulting in major species losses and degradation of many freshwater environments (Richter *et al.*, 2003). Modification and degradation of freshwater ecosystems increases the susceptibility of these systems and their inhabitants to invasion and to disease thus increasing the chances of species being lost or heavily reduced in abundance (Foley *et al.*, 2005). Comparing all ecosystem types, flowing water ecosystems are amongst the most damaged by human activities (Lake, *et al.*, 2007). The world population is expected to continue to grow for several decades (Bongaarts, 2009), therefore it is important effective water management plans are developed to ensure the integrity of freshwater ecosystems, and the wide array of species they support, is not lost (Richter *et al.*, 2003). Management of freshwater ecosystems must also account for the apparent climate change that has altered, and will continue to alter, freshwater ecosystems (Richter *et al.*, 2003).

1.2 Land use change and its impact on benthic stream environments

Stream ecosystems are often heterotrophic, obtaining most of their energy from external sources rather than in-stream production (Clapclott & Barmuta, 2010). In-stream biology and processes are strongly influenced by external patterns of land use (Argentina *et al.*, 2010). Landscape developments and alterations often result in a loss of quality habitat within stream ecosystems; this may alter natural fish movement, behaviour and migration patterns which in turn can reduce species survival (Rashleigh *et al.*, 2004). Small forested headwater streams are highly heterogeneous and many studies have shown land use patterns shape the biological components of small streams which rely on external inputs to provide both structure and energy to the system (Clapclott & Barmuta, 2010). Land use change is considered one of the primary threats to benthic fish species, which are usually the most impacted in degraded systems because stream substrates are usually the first impacted habitat (Midway *et al.*, 2010a). The structure and heterogeneity of benthic stream environments are important components of stream systems, and are highly important for aquatic biota (Argentina *et al.*, 2010). One of the most important components of the benthic stream environment for benthic stream fish is cover, serving a wide range of purposes throughout a fish's lifecycle including a location for spawning, brooding and refuge from predators and disturbance (Midway *et al.*, 2010a). Land use change threatens the wellbeing of benthic stream environments by altering external inputs affecting the structure and biology of the system (Dewson *et al.*, 2007). In New Zealand many streams now drain catchments experiencing rapid land use change due to agriculture, urbanisation and forestry (Winterbourn *et al.*, 1981), therefore they are subject to differing degrees of enrichment and modification threatening the wellbeing of benthic environments and the biota they support (Clapclott & Barmuta, 2010).

1.3 Disturbance and its impact on ecosystems

Disturbance can be defined as the application of potentially lethal forces to a habitat containing a population, community or ecosystem (Lake, 2000). Defining a disturbance should account for the intensity and forms of forces involved, as well as parameters such as frequency, predictability, temporal duration and spatial scale (Lake, 2000). Disturbances play an important role in all environments; by structuring community composition and species richness (Townsend, *et al.*, 1997).

Disturbances can be categorized as one of three types based on their temporal pattern; these are pulses, presses and ramps (Bender, 1984; Lake, 2000). Pulses are short term disturbances with clear temporal boundaries, and include events such as flash floods (Collier & Quinn 2003). Press disturbances have less clear temporal boundaries than pulses, commonly arising abruptly, reaching a specific level that is maintained for a sustained period of time, for example a landslide causing sedimentation of a stream (Lake, 2000). A ramp disturbance is where the strength of the disturbance, increases over time, such as a drought (Angeler & Rodrigo, 2004).

The response of the biological community to a disturbance depends on the strength and scale of the disturbance as well as the resistance and resilience of the community (Detenbeck *et al.*, 1992). The resilience and resistance of a biological community to disturbance is dependent on how adapted the community is to disturbance which is mediated by the variety of available refugia (Detenbeck *et al.*, 1992; Lake, 2000). For example a flash flood in a stream with very little refuge for biological constituents such as an urban channel, could result in a long term recovery time, due to a lack of available colonists caused through a lack of refuge which reduces the resistance and resilience of the biota (Collier & Quinn, 2003).

Human population growth and climate change alter natural ecosystems in various ways, one in particular being alteration of the natural disturbance regime (Lake, 2000). Disturbance events in freshwater environments such as floods, droughts and long term sedimentation occur naturally although they continue to increase in their frequency and intensity as the intensity of climate change and invasive impacts of human colonization continue to increase (Arnell *et al.*, 1996; Rashleigh *et al.*, 2004). Therefore, it is important to understand how species respond to disturbance events to aid in future management and conservation.

1.4 Habitat selection

An animal's habitat is a multidimensional environment that involves several variables and the conditions resulting from their interactions (Madhusudhan & Johnsingh, 1998).

Habitat selection can be defined as, “the process by which individuals choose areas in which they will conduct specific activities (Stamps, 2009).” Habitat selection in an evolutionary sense involves weighing up the costs and benefits associated with each available habitat type (Hutto, 1985). Factors that determine habitat selection are diverse and differ between species and individuals of different ages (Anoop & Hussain, 2004).

Habitats and selection for habitat can occur at different temporal and spatial scales (Elkin & Marshall, 2007; Stamps, 2009). A large scale habitat could be seen as an area that supports long term survival, growth and reproduction of an entire population (Stamps, 2009). A large scale habitat includes the entire area used by each member of a population at each stage of their lifecycle, including dispersal routes between different patches of suitable habitat (Stamps, 2009). An intermediate scale habitat is a habitat chosen by an individual that will support it over a biologically significant proportion of its life time (Stamps, 2009). An example of an intermediate scale habitat is the area selected by Sooty Shearwaters for nesting (small islands in the South Pacific Ocean) (Bragg *et al.*, 2009). The smallest scale habitat selected by an organism can be referred to as its “microhabitat” which is an area where an organism can carry out various life functions including feeding, foraging, spawning and parental care (Stamps, 2009). In mobile organisms microhabitat selection occurs frequently throughout their life time and involves a wide range of habitats (Petty & Grossman, 2010).

1.5 Dynamics of Patchy environments

As a result of landscape heterogeneity the natural environment can be perceived as a mosaic of patches (Pringle *et al.*, 1988). Patches are commonly defined by the homogeneity of internal structure compared to the surrounding environment (Clapclott & Barmuta, 2010). In a stream environment a patch may be homogenous consisting predominantly of one substrate type or alternatively it may be quite heterogeneous consisting of a combination of substrate types (Petty & Grossman, 1996). The natural environment is constantly changing and patches also change in function and size across varying temporal and spatial gradients (Clapclott & Barmuta, 2010). The distribution of physical and biological resources in many ecosystems is patchily distributed both across and within habitats and the distributions of such patches often change on a temporal

basis (Petty & Grossman, 2010). The diversity of physical habitats brings with it diversity in processes that stem from the interactions between patch structure and function (Clapclott & Barmuta, 2010).

1.6 Stream environments, systems with patchy resource distributions

Stream ecosystems are dynamic heterotrophic environments, greatly influenced by external abiotic and biotic factors that shape their internal constituents (Midway *et al.*, 2010b). Temperate streams, such as those here in New Zealand, are often patchy environments where small scale hydrologic variation commonly creates a mosaic of patches with different physical characteristics and biotic assemblages (Petty & Grossman 2010). Streams show high levels of variation in resource availability creating a patchy distribution of physical habitat characteristics and macroinvertebrates across a range of spatial scales (Petty & Grossman, 2007). The stability of patches within a stream is highly dependent on stream flow which may vary across a range of temporal scales (Clapclott & Barmuta, 2010). Macroalgae, periphyton, detritus and invertebrates are often patchily distributed within a stream due to a range of abiotic factors including light, substrate, flow and nutrient regimes (Petty & Grossman, 1996). The patchy distribution of stream organisms has significant effects on the distribution and behaviour of stream foragers such as benthic feeding fish (Petty & Grossman, 2007).

1.7 Optimal foraging theory and the role of food subsidies in patch selection of stream fish

The ability to forage is one of the basic fitness enhancing activities carried out by animals (Stenberg & Persson, 2006). A forager whose resources are patchily distributed is confronted with a set of foraging decisions, including which patches to exploit, when to exploit a specific patch, how long to exploit them, and which of the available foods to consume (Hayslette & Mirarchi, 2002). A theory developed to outline how foragers use patchy resources is the optimal foraging theory, which assumes natural selection promotes behaviour that increases fitness by maximizing foraging efficiency and foraging behaviour that maximizes the long term rate of energy gain (Hayslette & Mirarchi, 2002; Stenberg & Persson, 2006). An optimal forager should remain in a patch until the energetic rewards associated with that patch are equal to the costs (i.e. metabolic,

predatory, energetic and missed opportunity costs) of remaining in the patch (Brown, 1988).

The two main factors affecting feeding patch selection in stream fishes are foraging profitability and the risk of predation (Mcivor & Odum, 1998). The quality of a patch is enhanced when the food return is high and is lowered when there is a high risk of predation on the forager (Holbrook & Schmitt, 1988). A foraging stream fish may trade-off between food abundance and predation risk which commonly results in fish occupying a patch that has a low predation risk but also a diminished food return (Petty & Grossman, 2010). Conflict is created between the risk of predation and food reward; therefore many stream fish develop a foraging tactic that maximizes simultaneous food intake and safety (Holbrook & Schmitt, 1988). Stream fish may develop basic strategies where they will allocate a fixed amount of time to foraging in each available patch regardless of the food density in the patch, or they may do this to estimate the quality of a patch with sample information gained through foraging (Stenberg & Persson, 2006). Sample information gained through prior foraging can maximize food intake by using an assessment strategy allowing a fish to select between patches to find the optimum patch for foraging (Stenberg & Persson, 2006).

1.8 Feeding styles of stream fish and behavioural interactions

The high temporal and spatial variability of resources in stream systems mean stream fish have had to develop certain lifestyles in order to survive in the highly dynamic stream environment (Midway *et al.*, 2010b). Stream fish exhibit two main forms of feeding where a fish will either be a benthic feeder or a drift feeder (Dahl & Greenberg, 1996). Drift feeding fish are fish that feed on drifting invertebrates; this distinct feeding behaviour commonly creates dominance hierarchies between individuals in a stream system (Hansen & Closs, 2005). Benthic feeding fish are bottom dwelling fish that feed predominantly on a range of macroinvertebrates found on and within the substratum (Petty & Grossman, 1996). Unlike drift feeding fish, dominance hierarchies are not often observed in benthic feeding fish communities, but can occur under certain circumstances (Petty & Grossman, 2007). Temporal variability of resources within a stream reach reduces the chances of territorial behaviour being observed in benthic feeding fish

because it places conflicting pressure on the expression of territorial behaviour (Petty & Grossman, 2007). Territorial behaviour in benthic feeding fish is favoured by heterogeneity in the distribution of resources and will persist as long as stable high quality patches are present (Barlow, 1993). Petty and Grossman (2007) found territories were established in populations of mottled sculpins (North American benthic feeding fish) in areas of stream systems where the habitat was stable. If high quality patches occur within a stream system, territorial behaviour should increase an individual's fitness (Petty & Grossman, 2007). However, if patch quality is unpredictable territorial behaviour should reduce fitness (Barlow, 1993). Territorial behaviour in benthic stream fish may be driven by a temporal dimension as seen in drift feeding fish (Hansen & Closs, 2005); for example periods of low rainfall and fine weather may promote stable conditions within a stream reach which in turn will create patch stability potentially promoting territorial behaviour.

1.9 Habitat selection in benthic stream fish and the potential for study of New Zealand's native benthic stream fish

Most studies analysing distribution and habitat selection in relation to patch use and food availability have focused on drift feeding fish, while few studies have examined how benthic stream fish track and use patchy resources such as food (Petty & Grossman, 2010). The effects of prey distribution on patch selection by benthic feeding fish are currently not well understood and this can be attributed to a lack of studies on benthic feeding fish (Petty & Grossman, 1996). Studies of habitat selection in patchy environments suggest that many freshwater fish species can choose patches that maximise energy gain or feeding rates (Clapclott & Barmuta, 2010). The patchy distribution of benthic invertebrates in temperate streams, such as those here in New Zealand would suggest that there would be strong selective pressures for benthic fishes to occupy patches with high prey abundances (Petty & Grossman, 1996). Streams of New Zealand have high heterogeneous resource availability (Winterbourn *et al.*, 1981); therefore they are ideal environments for field tests studying individual and population level habitat selection (Petty & Grossman, 2010).

In New Zealand we have a wide range of native freshwater benthic fish species that are important components of the streams they inhabit (McDowall, 2000). Benthic stream fish of New Zealand, including members of the bully family (Eleotridae) such as the redfinned bully (*Gobiomorphus huttoni*); have been the subject of limited study (McDowall, 2000). It is not currently known how redfinned bullies track and use patchy resources such as food, nor how they respond to disturbance. Fresh water benthic feeding fish are of no real commercial or recreational interest, therefore management and funding towards researching benthic fish is uncommon (Midway *et al.*, 2010b). New Zealand streams have been affected by land use change for decades (Winterbourn *et al.*, 1981) and a growing population and resource consumption means land use will continue to increase in intensity threatening the wellbeing of many stream inhabitants' especially benthic feeding fish (Bongaarts, 2009; Clapclott & Barmuta, 2010). Many of New Zealand's native benthic feeding fish including the redfinned bully are diadromous, traveling between freshwater and the sea as part of their life cycle; this lifecycle increases their susceptibility to being negatively impacted by land use change and development (McDowall, 2010). The susceptibility of benthic feeding fish such as the redfinned bully to impacts of land development and change emphasizes the importance of understanding how these species interact with and respond to changes in their ecosystem, to assist in management and conservation.

1.10 The importance of studies on patch use by benthic stream fish incorporating the role of disturbance

Studying how organisms interact with their environment and with each other is useful as it allows us to tease out the intricate roles of biological and abiotic constituents within an ecosystem that can aid in managing that ecosystem (Clapclott & Barmuta, 2010). Studies combining tests of optimal foraging and patch selection are useful as they can help determine how behavioural decisions of individuals contribute to emergent population level properties, such as population demographics, activity patterns, density distributions and dispersal patterns (Holbrook & Schmitt 1988; Petty & Grossman, 2010). Studying how animals select patches in their natural environment, under stable conditions as well as following disturbance, may provide insights into how animals perceive their environment and assess patch quality. Understanding how animals perceive and assess their

environment can be used to determine habitat quality and allows managers to determine how changes in the environment, such as those caused through disturbance, will affect patch use and selection (Stenberg & Persson, 2006). A realistic representation of how animals select habitats comes from studies that incorporate fitness based criteria (e.g. prey availability) or tests of fitness based theories such as patch use (Petty & Grossman, 2010). Once a basic understanding of the role a study species plays in its ecosystem is determined, it is then important for management and conservation, especially in degraded systems, to see how the study organism responds to disturbance (Lake, 2000; Midway *et al.*, 2010b). Such studies hold great value for resource managers and conservation biologists, which is important in areas where impacts of land use are apparent (Petty & Grossman, 2010; Stenberg & Persson, 2006).

1.11 Ecological context of study

The main species of interest in this study is the redfinned bully, a carnivorous, benthic stream fish, endemic to New Zealand (McEwan & Joy, 2013). Redfinned bullies are one of the most common and widespread freshwater fish species of New Zealand, although they have received very little scientific study (McDowall, 1990). Redfinned bullies are cryptic, nocturnal and diadromous (McEwan & Joy, 2013), inhabiting small, flowing bouldery streams (McDowall, 1964). The wide distribution and high abundance of redfinned bullies makes them an important component of many of New Zealand's coastal streams (McDowall, 1990). The redfinned bully has been considered by many as one of New Zealand's most attractive freshwater fishes and is valued by many people because of its appearance and wide distribution (McDowall, 1990). To date there have been a few studies carried out specifically on redfinned bullies, most of which are from McDowall in years 1962, 1964 and 1965, these studies involved looking at general morphology, life history characteristics, distribution, habitat use and breeding. More recently papers by Jowett and Richardson (1996) and McEwan and Joy (2013) have examined habitat use by redfinned bullies. Many of the techniques used in studies on redfinned bullies are invasive in nature (e.g., using pit tags and electrofishing to analyse habitat selection; McEwan & Joy 2013), potentially affecting how fish behave and, therefore, not giving an accurate representation of redfinned bully habitat selection. Many of the studies on redfinned bullies have focused on diurnal characteristics of redfinned bully habitat use, although

their nocturnal habitat and what drives nocturnal patch selection has not yet been studied. None of the studies on redfinned bullies have looked into how they track and use patchy food resources, nor how they respond to disturbance; therefore, these components of redfinned bully ecology are unknown.

In the latest threat assessment of fresh water fish by Allibone *et al.* (2010) redfinned bullies were listed as a species declining in abundance, emphasising how important it is to gain a better understanding of the ecology of this species to aid management that will help ensure they do not continue to decline into the future. On-going human population growth and land development in New Zealand places pressure on freshwater ecosystems and their inhabitants; therefore, understanding how each species within an ecosystem interacts with the environment and other species will be essential for future management of systems to protect their integrity and inhabitants for future generations (Winterbourn *et al.*, 1981). Degradation of habitat is one of the primary factors threatening declining fish species, and has the greatest impact on benthic and endemic species such as redfinned bullies (Midway *et al.*, 2010a). Studies focusing on patch use and responses to disturbance are useful for management and conservation of declining species in degrading environments (Petty & Grossman, 2010; Stenberg & Persson, 2006). Therefore, this study aimed to improve our knowledge of redfinned bully ecology to enhance future management and conservation, of both redfinned bullies and the ecosystem they belong to.

2. Nocturnal patch selection by redefined bullies

2.1 Introduction

The distribution of physical and biological resources is patchy in many ecosystems, constantly changing across spatial and temporal scales (Petty & Grossman, 2010; Wiens, 1976). Streams in particular have high levels of variability in their biological and physical resource availability, especially in temperate environments (Petty & Grossman, 1996). Stable temperate streams tend to be composed of an array of patches each with differing physical and biological resources, created through small scale variation in water flow (Petty & Grossman, 2007). The spatiotemporal network of patches in stream environments influences organisms in many ways, affecting their distribution, interactions and adaptations (Wiens, 1976).

A forager such as a benthic stream fish inhabiting an environment with patchy resources, is posed with a range of decisions to make, including which patches to inhabit, how long to inhabit each patch and within a patch what invertebrate species to predate on (Hayslette & Mirachi, 2002). A forager's patch selection is determined by the physiological needs of the forager and the biotic interactions with the ecosystem (Zweimuller, 1995).

The quality of a patch is higher when food resources are greater and is lowered when the risk of predation on the forager increases (Holbrook & Schmit 1988). Foragers commonly inhabit patches based on food density; in this case foragers will remain within a patch until foraging costs are equal to total benefits (Hayslette & Mirachi, 2002). The optimal diet of a forager is comprised of food items that do not result in a decrease in the long term rate of energy intake. Therefore, patch selection influenced by food resources is usually driven by a distinct group of foods or prey species that maximise long term energy intake (Hayslette & Mirachi, 2002). Territorial behaviour is promoted in patchy stream environments, influencing patch selection by stream fish. Territorial behaviour in benthic fish is mainly influenced by food, where dominant individuals will occupy high quality patches, and as long as stable high quality food patches are present, the territorial behaviour will continue to persist (Petty & Grossman, 2007). In redefined bullies,

territorial behaviour is commonly seen in male fish during the breeding season, however outside of this period there is little evidence for territorial behaviour (McDowall, 1965a).

The environment within a stream is highly variable, varying in depth, velocity and substrate, even between adjacent patches (Pringle *et al.*, 1988). The large amount of variability within a stream environment often creates a mosaic of patches in the substratum (Petty & Grossman, 1996). Patches in the substratum may be comprised of a single substrate type or a combination of substrate types (Petty & Grossman, 2007). Water velocity strongly influences the distribution of benthic and mobile organisms in a stream environment and has a major influence on the patchiness of the environment (Petty & Grossman, 2007; Pringle *et al.*, 1988). High water velocities caused through rain fall events can reduce the patchiness of a stream, whereas low water velocities and stable stream conditions caused through long periods without rain promote a patchy stream environment (Pringle *et al.*, 1988). High variability in substrate composition, water velocity and depth within the stream environment combined with variation in the external environment, such as differences in canopy cover and nutrient inputs, often creates a patchy distribution of macro-algae, periphyton, detritus and benthic invertebrates (Petty & Grossman, 1996).

Patch selection or use by stream fish is usually driven by biotic or abiotic variables, however, if patches are not selected for their biotic or abiotic factors or a combination of both, other strategies may be used (Petty & Grossman, 2007). Alternative strategies for patch use include devoting a certain amount of time for inhabiting each patch, regardless of food density or quality within the patch, or choosing patches with information gained through foraging (Stenberg & Persson, 2006). Studying how stream fish exploit and select patches in the natural environment can provide valuable information on how fish perceive the environment and assess patch quality (Stenberg & Persson, 2006). Understanding how fish perceive and assess the environment has major benefits for stream management and conservation especially in degraded systems (Allibone *et al.*, 2010; McDowall, 1990).

Studies investigating the effects of invertebrate prey on patch selection by benthic stream fish are not common (Petty & Grossman, 2010). Petty & Grossman (2010) found mottled sculpin, a benthic stream fish from North America, displayed non-random patch use where dominant individuals occupied patches with significantly higher prey densities and renewal rates than patches occupied by subordinates or sampled at random. Mottled sculpin were found to leave patches with low prey densities and occupy patches with significantly higher prey densities (Petty & Grossman, 2010). Mottled sculpins, share many similarities with redfinned bullies in terms of biology, behaviour and environmental preferences, therefore it is likely they will also share similarities in how they select and exploit patches.

The wide distribution of redfinned bullies in New Zealand and their numerical dominance in many streams indicates they are an important component of New Zealand's fresh water river systems (McDowall, 1990). Studies on redfinned bullies are few and many aspects of how they interact with their environment are unknown. Nocturnal patch use by redfinned bullies, looking specifically at the invertebrate community and environmental characteristics of patches occupied by redfinned bullies, has only been covered in one study. Redfinned bullies inhabiting small streams have been shown to selectively feed on certain invertebrate taxa, specifically species belonging to the order Diptera, and show preferences for specific environmental variables (McDowall, 1965b; Jowett & Richardson, 1996). Well defined stable patches with distinct differences in environmental and biological characteristics are common in temperate streams, especially over summer months (Petty & Grossman, 2007). Therefore, it is likely redfinned bullies will have a patchy distribution influenced by either physical or biological characteristics of patches or a combination of both.

Male and female redfinned bullies show differences in habitat selection, specifically preceding or during breeding (McDowall, 1965a). Differences in habitat selection by male and female redfinned bullies have been found to drive differences in diet, although within the same habitat male and female redfinned bully diets are indistinguishable from one another (McDowall, 1965b). Therefore, it is likely patch selection by male and female redfinned bullies may differ.

Breeding activity influences patch selection in benthic stream fish, commonly resulting in a shift from food based patch selection to patch selection based on spawning requirements (Brown, 1988). During the breeding period male redfinned bullies are less mobile and highly territorial, occupying and guarding a nest site. During spawning female redfinned bullies seek out a male occupying a suitable nest site where they deposit their eggs for fertilisation (McDowall, 1965a). Female redfinned bullies are more mobile than males during the breeding period; however, their mobility is reduced by the onset of egg laying (McDowall, 1965a). Therefore, during the breeding period patch selection by redfinned bullies would be expected to be different from outside of the breeding period (McDowall, 1965a).

The aim of this study was to establish an understanding of whether redfinned bullies in a small temperate stream exhibit non-random patch selection, and if so what factors are driving patch selection. Based on existing evidence of patch selection in benthic stream fish and the characteristics of redfinned bullies, it was hypothesised that redfinned bullies would show non-random patch selection, driven by invertebrate abundance and composition.

2.2 Methods

2.2.1 Description of study site

The study site was located on Aurora Creek, a tributary of the Maclennan River, Catlins, New Zealand. Aurora Creek drains a predominantly forested catchment, weaving through native bush and one kilometer of farmland before it enters the Maclennan River. The study site was located on the lower reaches of the Aurora Creek where the stream is partly forested, but predominantly surrounded by pasture grazed by sheep. Aurora Creek and the Maclennan River have gentle gradients and no structural components that may limit redefined bully migration or distribution. The size of the sampling section was approximately 500 meters long and was not set prior to sampling as this was determined once the desired number of fish (fifty fish) had been located. Pre-sampling observations indicated altitude, stream characteristics, and land use between the upper most and lowest reach of the sampling section showed little variation. Within the sampling section the stream was slow flowing, bouldery, no more than one meter deep and two meters wide on average.

2.2.2 Methodology for study site

Field sampling took place over one night and the following day (25th and 26th of May, 2012). Sampling to place during stable weather conditions when the stream exhibited a stable flow rate, a base-flow water level and good water clarity.

2.2.3 Spotlighting

Spotlighting was used to scan the stream at night until fifty undisturbed redefined bullies had been spotted, sexed, measured for length, and their position marked. The position of each undisturbed redefined bully was marked using a weighted fluorescent marker, to ensure accurate sampling of the invertebrate community at each position the following day. Night time spotlighting was used as the method to identify the nocturnal microhabitat of redefined bullies because it is an effective method for surveying small native New Zealand fishes (Hickey & Closs, 2006). A 100 watt spotlight was used to survey the stream. Spotlighting involved scanning the stream bed from bank to bank, walking up stream along the bank to avoid disturbing the stream bed, with one observer and one spotlight operator.

2.2.4 Invertebrate sampling

To determine whether the presence of redfinned bullies was associated with high invertebrate prey abundance, benthic invertebrate communities were sampled. The invertebrate community and physical microhabitat variables within a 25cm x 25cm square area of each patch where a fish had previously been recorded from was collected on the day following fish spotlighting. Invertebrate samples were taken using a Surber Sampler with 500 micron mesh. Taking a Surber sample involved placement of the sampler facing into the current, large stones within the sample area were scrubbed and the substrate was agitated to a depth of approximately ten centimeters thus washing the invertebrates into the sampler. Invertebrate samples were preserved in 70% ethanol and were analysed back in the laboratory. Laboratory analysis of invertebrate samples was carried out using a dissection microscope and involved counting all of the invertebrates and identifying each invertebrate to the lowest taxonomic level possible, using Winterbourne *et al.* (2006). Some taxa could not be identified to genus or species: these included Platyhelminthes (phylum), Oligochaeta (subclass), Ostracoda, Collembola, Isopoda, Cyclopoida (order), Elmidae, Empididae, Hydraenidae, Muscidae, Psychodidae, Ceratopogonidae, Chironomidae (family), Eriopterini (tribe).

2.2.5 Microhabitat variables

To determine whether bullies select specific physical habitat features, a selection of microhabitat variables were measured. Measured physical microhabitat variables within each 25cm x 25cm square patch included, water depth (centimeters), velocity at focal point in meters per second (taken directly above the marker), distance to nearest cover (centimeters) and the dominant substratum composition within the patch. The water depth and distance to nearest cover was measured using a ruler, water velocity was measured using a using a Marsh-McBirney Flo-Mate™ Model 2000 (Marsh-McBirney Inc. Maryland, U.S.A.). Dominant substratum composition within the patch was visually estimated, where a substrate was considered dominant if it made up at least fifty percent of a patch. Dominant substrate was determined using a modified Wentworth scale (<2 mm silt; 2–4 mm sand; 4–64 mm gravel; 64–256 mm cobble; >256 mm boulder; Detritus; other) (Whitehead *et al.*, 2002). Each dominant substrate type was allocated a number (1

= silt, 2 = sand, 3 = gravel, 4 = cobble, 5 = boulder, 6 = detritus, 7 = other) which allowed comparison of the dominant substrate type between patches containing fish and randomly sampled patches (see section 2.2.6). At each marker the stream morphology was defined as either a riffle or pool, where pools were areas of either still or slow flowing water and riffles are areas of turbulent fast flowing water.

2.2.6 Random samples

To determine whether fish were exhibiting non-random patch selection, random patches were sampled in relation to each patch occupied by a fish. Random patches were located 1.5 meters from patches containing fish and were selected using a paired, constrained random sampling design. Locating each random patch involved using a compass heading selected from a random numbers table. This heading was followed to a location 1.5 meters from the focal point (point where a redfinned bully was observed). If the random patch was not underwater, 90° from the original compass bearing was subtracted until an available patch was located. A distance of 1.5 meters was used to separate patches containing fish and randomly sampled patches as this distance prevented patch overlap, and was suitable for the width of the stream. This random sampling procedure was carried out for each fish marked. Macroinvertebrate samples and measured environmental variables recorded from patches occupied by redfinned bullies were compared with samples from randomly sampled patches to determine whether fish were displaying non-random patch selection.

2.2.7 Dietary analysis

Dietary analysis involved capturing thirty redfinned bullies, each taken from within the sampling section. Fish were located by spotlight and collected using a hand net; fish were captured once fifty undisturbed redfinned bullies had been analysed and their position marked. Once captured, fish were immediately euthanized by immersion in a 1mg/l solution of 2-phenoxyethanol. Fish were determined dead after an absence of any movement for at least 5 minutes, including an absence of a response to sharp tap on side of bucket. Fish were preserved in 10% formaldehyde. Laboratory based dietary analysis involved removing the gut (including the oesophagus, stomach and intestines) from each

fish using a scalpel. The gut was cut open and all identifiable invertebrates were counted and identified to the lowest taxonomic level.

2.2.8 Data analysis

To compare the average abundance of the five most abundant invertebrate species between patches where fish were found and randomly sampled patches, two-sample Student's t-tests were used, assuming unequal variance. Environmental characteristics were compared between patches occupied by male fish and female fish as well between patches occupied by fish and random patches. For each environmental variable measured, a two sample Student's t-test, assuming unequal variance, was carried out to test for a significant difference between groups. Student's t-tests, were carried out using Microsoft Excel 2010. To determine whether there was a statically significant difference between diet samples and between the mean abundance of the top five most abundant invertebrate species from diet samples, single factor ANOVA was used. ANOVA was performed using Microsoft Excel 2010. A GLM (Generalized Linear Model) was used to analyse mean abundance of the top five most abundant invertebrate species from diet samples, to determine where a statistically significant difference existed. This model included two factors, species (count data of the top five most abundant invertebrate species from diet samples) and fish (each of the diet samples represented a fish, numbered 1 to thirty), the family of distributions that the data fell into was "quassipoisson", which the model accounted for. The GLM was run in R version 2.15.0 (R Core Development Team, 2006), using the package LME4 (Bates *et al.* 2012) (refer to appendix 6.1 for R code). To determine which invertebrate taxa were primarily responsible for a difference between patches containing fish and random patches, a SIMPER analysis was conducted using PRIMER version 6 (Clarke and Gorley, 2006). Preparation of biological data for SIMPER analysis involved a square root transformation to homogenise variance and reduce the influence of highly abundant species thereby enhancing the influence of less common species. Primer version 6 was used to create a distance based linear model which produced a dbRDA (distance based redundancy analysis) ordination plot; this test models or describes patterns in the biota or biological community using environmental variables (Clarke and Gorley, 2006). Environmental vectors on the dbRDA ordination plot were obtained by calculating the correlation

between patterns on the ordination, between the axes and the underlying environmental variables. When the distance based linear model is run it carries out a marginal test, to test if there is a significant correlation between the biota and each of the environmental variables on their own (Clarke and Gorley, 2006). The selection procedure used for the distance based linear model was step-wise and the selection criterion was AICc (Akaike information criterion). AICc gives the percentage of variation explained by individual axes. The model stops running once a significant difference is reached (Clarke and Gorley, 2006).

PERMANOVA (permutational multivariate anova) was used to test for differences between groupings of biological variables, as well as groupings of environmental variables (Clarke and Gorley, 2006). PERMANOVA tests for a statistically significant difference between groups using a similarity matrix, to do this it creates p values by permuted randomisation of the data (Clarke and Gorley, 2006).

Preparation of biological data for the dbRDA ordination plot and PERMANOVA involved a square root transformation, followed by creation of a similarity matrix which compares each sample to each other sample using the Bray-Curtis similarity index (Clarke and Gorley, 2006). Preparation of environmental data for the dbRDA ordination plot and PERMANOVA involved normalising the data, which is necessary because the environmental variables were measured on different scales. Normalising the data allows each variable to play an equal role by transforming each variable so it has a mean of zero and standard deviation of one (Clarke and Gorley, 2006). Once the data was normalised a similarity matrix using the Euclidian distance was created.

2.3 Results

2.3.1 Invertebrate community assemblages and dietary analysis

The most abundant taxon on average, Chironomidae, was significantly more abundant (df_{98} , $t = 1.99$, $p < 0.01$) in patches where fish were found (Fig. 2.1 a). Patches where redfinned bullies were found (fish patches) averaged 193 chironomids, whereas patches sampled at random (random patches) averaged only 104 chironomids (Fig. 2.1 a). The average abundance of the next four most abundant invertebrate species were not significantly different between fish patches and randomly sampled patches (Fig. 2.1 a).

ANOVA was carried out comparing the abundance of prey taxa between fish diet samples, no significant difference was found (df_{29} , $F = 0.915$, $p > 0.5$). AVOVA was used to compare the abundance of different prey taxa found within diet samples and revealed a significant difference (df_4 , $F = 3.746$, $p < 0.05$). A generalized linear model indicated chironomids were significantly more abundant (GLM: $est \pm S.E.$, 2.0 ± 0.48 , df_{149} , $t = 4.142$, $p < 0.01$) than the other four most abundant taxa in fish diet samples (Fig. 2.1 b).

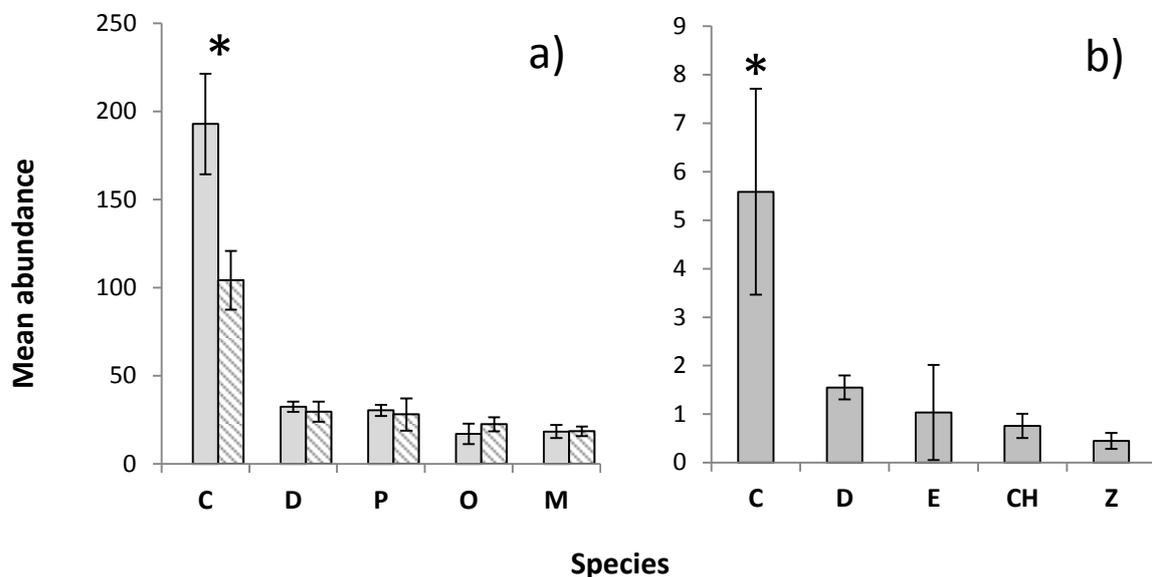


Figure 2.1. a) The top five most abundant invertebrate taxa (C = Chironomidae, D = *Deleatidium*, P = *Pyconcentrodes*, O = *Oligochaeta*, M = *Megaleptoperla*) from fifty surber samples where redfinned bullies were located (grey filled bars) and from fifty randomly taken surber samples (striped bars), values represent mean \pm S.E.M. star symbol denotes a significant difference ($p < 0.05$). **b)** The five most abundant invertebrate taxa (C = Chironomidae, D = *Deleatidium*, E = *Elimidae*, CH = *Chiltonia*, Z = *Zealandoperla*) found in thirty redfinned bully diet samples (Esophageal, stomach and intestinal content), values represent mean \pm S.E.M. Star symbol denotes a significant difference ($p < 0.05$).

Figure 2.2 portrays invertebrate samples from fish patches are tightly clustered and situated on the right hand side of the ordination, whereas invertebrate samples from random patches are more scattered toward the left hand side of the ordination indicating a difference between groups (df_{98} , Pseudo $F = 5.54$, $p < 0.01$) (Table 2.1). Patches containing male fish were not significantly different in their invertebrate community assemblage compared to patches where female fish were found (df_{48} , Pseudo $F = 0.69$, $P > 0.5$) (Table 2.1).

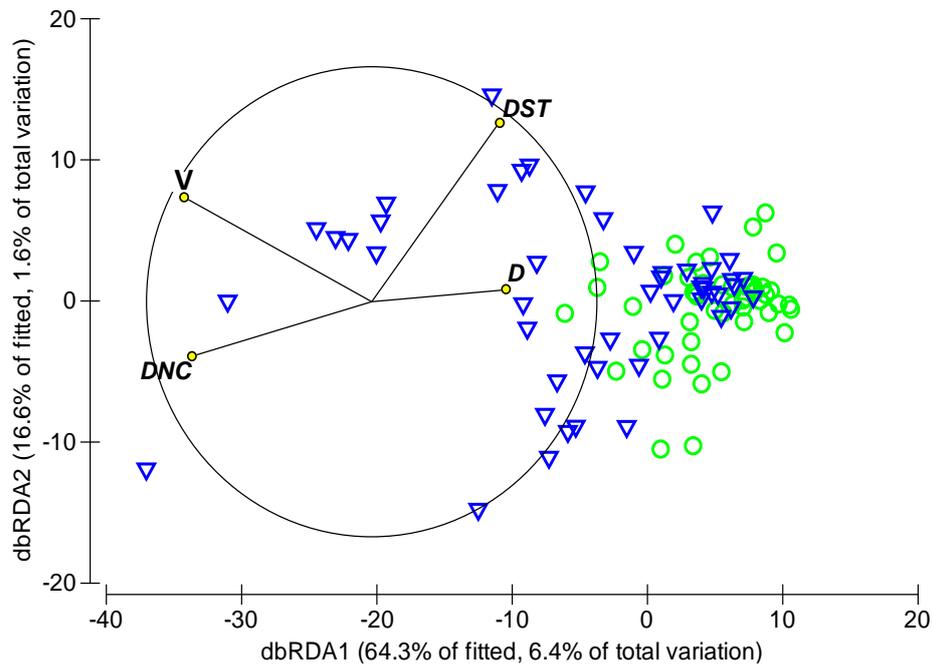


Figure 2.2. Distance based linear model, dbRDA ordination plot based on the invertebrate community, using Bray Curtis similarity. Plot displays the relationship between environmental variables and invertebrate abundance among fish patches (green circles) and random patches (blue triangles). Vectors represent environmental variables, they show how each variable is responsible for driving differences between patches, and the length of each vector reflects the amount of variation being explained by that vector. Vector abbreviations: V= Water velocity ms⁻¹, D = Water depth in meters, DST = Dominant substrate type, DNC= distance to nearest cover in meters.

2.3.2 Comparison of environmental variables and the invertebrate community between fish and random patches

There was a significant difference in environmental variables between patches where fish were found and randomly sampled patches (df_{98} , Pseudo $F = 15.92$, $P < 0.01$) (Table 2.1). Patches containing fish were located in areas with significantly deeper water and significantly slower water velocity than random patches ($p < 0.0001$) (Fig. 2.2, Table 2.2).

Fish patches had significantly closer cover than randomly sampled patches ($p < 0.0001$) (Fig. 2.2, Table 2.2). Fish patches were significantly different in their dominant substrate type compared to random patches, where fish patches were predominantly composed of larger substrate types than random patches ($p < 0.05$) (Fig. 2.3, Table 2.2). The most common dominant substrate type found in both fish patches and random patches was cobble (Fig. 2.3 a). A dominant substrate of cobble was more frequent in patches containing fish (68%) compared to random patches (44%) (Fig. 2.3 a). Dominant substrates of sand, gravel and boulder were present in both random and fish patches, however, were more frequent in random patches (Fig. 2.3 a). None of the fish patches had a dominant substrate of silt, however 6% of random patches had a silt substrate (Fig. 2.3 a).

Marginal tests from the distance based linear model revealed that each of the four environmental variables measured had a significant correlation with the biological data (refer to appendix 6.2 for output), indicating each variable is playing an important role in explaining the variation in the invertebrate community. Student's T-tests revealed there were no significant differences ($p > 0.05$) in mean abundance of invertebrates between fish patches and random patches in each of the four dominant substrate types shared by both groups (Fig. 2.3 b). Chironomids were found on all substrate types except silt and they were most frequently found on a dominant substrate of cobble (Fig. 2.3 c).

Table 2.1. PERMANOVA results based on Euclidian distance, testing for a difference in: **a)** the biological community assemblages from patches where fish were present and randomly sampled patches, **b)** the biological community assemblages between patches where male and female fish were found, **c)** environmental variables between patches where fish were found and randomly sampled patches, **d)** environmental variables between patches where male fish were located and those where female fish were located. *df* = degrees of freedom. *P* values < 0.05 are considered significant.

Factor	<i>df</i>	<i>Pseudo -F</i>	<i>P</i>	Unique perms
a)	1, 98	5.5363	0.001	998
b)	1, 48	0.68647	0.727	998
c)	1, 98	15.919	0.001	999
d)	1, 48	3.2638	0.012	999

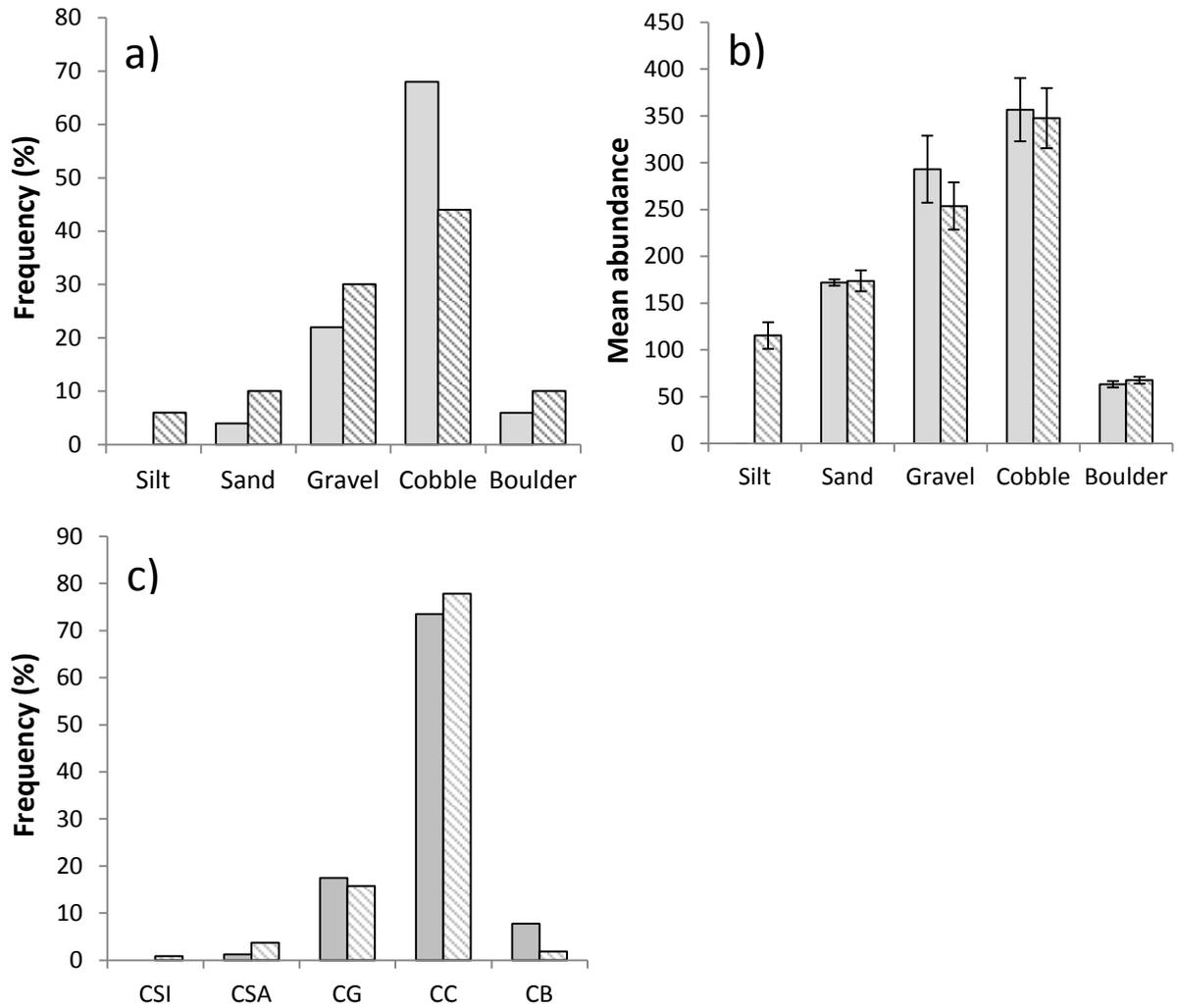


Figure 2.3. a) A comparison of the percentage frequency of dominant substrate type between fifty patches where redfinned bullies were located (grey filled bars) and from fifty random patches (striped bars). **b)** Mean abundance of invertebrates across the five substrate types, comparing between fifty patches where redfinned bullies were located (grey filled bars) and fifty randomly sampled patches (striped bars). **c)** A comparison of the percentage frequency for chironomids across the five different substrate types comparing between fifty patches where redfinned bullies were located (grey filled bars) and from fifty random patches (striped bars). CSI = Frequency of chironomids on silt patches, CSA= Frequency of chironomids on sand patches, CG = Frequency of chironomids on gravel patches, CC = Frequency of chironomids on cobble patches, CB = Frequency of chironomids on boulder patches.

Table 2.2. A series of Students T-tests, assuming unequal variance comparing environmental characteristics from fish patches and random patches, averaged across the fifty patches in each group. *P* values < 0.05 are considered significant. *df* = degrees of freedom, *V* = Velocity, *D* = Water depth, *DST* = Dominant substrate type, *DNC* = Distance to nearest cover.

	D (cm)	V (ms -1)	DST	DNC (cm)
Fish	22.06	0.03	3.76	6.8
± S.E.	(0.94)	(0.006)	(0.09)	(1.34)
Random	15.91	0.11	3.42	13.78
± S.E.	(0.92)	(0.02)	(0.14)	(1.38)
<i>P</i>	0.00001	0.00006	0.046	0.00002
<i>df</i>	98	61	82	67
t-value	4.66	4.32	2.02	4.64

2.3.3 Comparison of environmental variables between patches occupied by male and female fish

Patches containing male fish were significantly different in terms of environmental variables compared to patches containing female fish (*df* 48, Pseudo *F* = 3.26, *P* < 0.05) (Table 2.1). Students T-tests revealed there was no significant difference in dominant substrate type, distance to nearest cover and water velocity between patches occupied by male and female fish (*p* > 0.05) (Table 2.3). However, a Students T-test revealed a significant difference in water depth between patches occupied by male and female fish, on average male fish occupied patches with deeper water than female fish (*p* < 0.01) (Table 2.3).

Table 2.3. A series of students T-tests, assuming unequal variance comparing environmental characteristics from patches where male fish were found and patches where female fish were found. Values are averaged across the twenty one patches where female fish were found and twenty nine patches where male fish were found. *P* values < 0.05 are considered significant. *df* = degrees of freedom, *V* = Velocity, *D* = Water depth, *DST* = Dominant substrate type, *DNC* = Distance to nearest cover.

	D (cm)	V (ms -1)	DST	DNC (cm)
Male	24.31	0.02	3.83	7.48
± S.E.	(1.28)	(0.01)	(0.11)	(0.84)
Female	18.95	0.04	3.67	5.86
± S.E.	(1.12)	(0.01)	(0.14)	(0.81)
<i>P</i>	0.003	0.19	0.38	0.17
<i>df</i>	48	30	41	47
t-value	3.15	1.35	0.88	1.39

2.4 Discussion

This study investigated whether redfinned bullies exhibit non-random, nocturnal patch selection in a small, temperate, forested stream. It was found that redfinned bullies exhibit non-random nocturnal patch selection. Patches occupied by redfinned bullies were significantly different in terms of their environmental and biological parameters when compared to patches sampled at random. These findings raise the question, what is driving the selection of this preferred microhabitat; is it biological factors, environmental factors or a combination of both.

2.4.1 Environmental characteristics of patches occupied by redfinned bullies

Within the range of a stream fish's dispersal abilities and physiological tolerances patch selection is usually determined by a combination of environmental and biological factors (Greenberg, 1991; Leftwich *et al.*, 1997; Zweimuller, 1995). The environment in patches occupied by redfinned bullies consisted of deep water, low water velocities, large amounts of cover and substrates dominated by cobbles. Male and female redfinned bullies inhabited patches that were different in terms of environmental characteristics; this difference was primarily driven by a difference in water depth, where male fish occupied patches with deeper water, lower water velocities and larger substrates on average. Patches available at random covered a greater range of habitats than patches occupied by redfinned bullies. Some randomly sampled patches were very similar to patches occupied by redfinned bullies, but also some very different patches, that were shallow with high water velocities, and fine substrates. Patches occupied by redfinned bullies were all located within pools; no redfinned bullies were spotted in riffles, whereas some random patches were located in riffles. Spotlighting is not very effective for spotting fish in turbulent riffle environments (Hickey & Closs, 2006); however, in our case the riffles within the sampling section were suitable for spotlighting (small and shallow).

2.4.2 Influence of environmental variables on patch selection by redfinned bullies

Each of the measured environmental variables in this study are inter-related, and represent the main components that make up the physical stream environment (Leftwich *et al.*, 1997; Statzner *et al.*, 1988); therefore it is unlikely they independently influence patch selection by benthic stream fish (Greenberg, 1991). Zweimuller (1995) states water

velocity and depth are important factors for determining patch selection in stream fish and states substrate type is a covariate of these two variables. This implies there is a relationship between water depth, water velocity and substrate type, where changes in depth and water velocity will influence substrate type. Redfinned bullies were most frequently found in patches with a dominant substrate of cobble (68 %), more frequently found on cobble substrates than what was available at random (44 %) (Fig. 2.3 a). Cobble substrates were the most frequently occurring dominant substrate type in all sampled patches. A significant difference in all of the measured environmental variables between patches occupied by fish and available at random may be driven by differences in the frequency of cobble substrates between these patches. Cobble patches were commonly located in deeper water, within pools, in areas of low water velocity and provided close cover for fish. Results suggest the “cobble environment” (water depths, velocities and close cover associated with cobble substrates) is a preferred nocturnal patch environment for redfinned bullies in the study site.

Redfinned bullies are nocturnally active; during the day they seek cover, usually under loose aggregations of large stones and boulders (McDowall, 1990). The diurnal retreat of redfinned bullies can be considered an environment dominated by cobbles (Jowett & Richardson, 1996), therefore similarities in substrate type of nocturnal and diurnal retreats, suggests majority of redfinned bullies in the sampling site are not travelling very far from their diurnal retreat to their nocturnal foraging grounds. The reasons behind why fish may not travel far from their diurnal retreat to their nocturnal patch are likely to be related to energy expenditure, where expenditure of higher amounts of energy by travelling further to forage may reduce survival due to increased exposure to predators (Bateson, & Kacelnik, 1998). Patches with a dominant cobble substrate provided immediate cover for redfinned bullies; therefore predator avoidance on a cobble patch would require little effort, thus increasing survival fitness (Bateson, & Kacelnik, 1998). Cover can be considered as an important factor affecting habitat selection by benthic stream fish, serving a number of purposes throughout a fish’s ontogeny, including nesting habitat and predator avoidance (Midway *et al.*, 2010a).

Water velocity and depth play an integral role in determining the physiological and physical limits of stream fish distribution (Zweimuller, 1995). Water velocity is an important component for determining microhabitat use by stream fish, more important for species who inhabit the water column but still important for benthic fish species (Hill & Grossman, 1993). Fish tend to occupy patches with water velocities that allow for maximum energy gain (Hill & Grossman 1993). Water velocity in streams is usually lower closer to the bed, especially in deeper water; therefore many benthic stream fish inhabiting pools tend to be found in areas of low water velocity (Baltz *et al.*, 1982; Stazner *et al.*, 1988). Stream pool environments with slow flowing deep water, such as the preferred microhabitat of redfinned bullies, is an environment where fish use very little energy in navigating or retaining their position on the stream bed (Hill & Grossman, 1993; Stazner *et al.*, 1988). Therefore, patches inhabited by redfinned bullies in our study site would allow fish to function with very little energy use, allowing energy to be invested elsewhere therefore increasing fitness (Bateson, & Kacelnik, 1998).

2.4.3 Effects of invertebrate community on patch selection by redfinned bullies

Invertebrate abundance in patches where redfinned bullies were found was significantly higher than from patches sampled at random (Fig. 2.1 a). Invertebrate abundance was primarily driven by chironomid abundance, with other taxa making only a fairly minor contribution. Chironomids were significantly more abundant in patches containing fish than randomly sampled patches. A likely reason for this difference is due to substrate type, where 68% of patches occupied by redfinned bullies had dominant cobble substrates, compared to random patches 44%. Patches with dominant cobble substrates had the highest abundance of invertebrates in both random and fish containing patches, therefore the difference in the number of cobble patches occupied by fish compared to at random is a likely reason for differences in invertebrate abundance between the two groups. Results suggest chironomids, cobble substrates or a combination of both is driving non-random patch selection by redfinned bullies.

There were no significant differences in invertebrate abundance for each of the different substrate types between patches occupied by fish and random patches (Fig. 2.3 b). This indicates the presence of a fish in a patch is not affecting the invertebrate abundance to

an extent that it is significantly different from a patch composed of the same substrate type sampled at random. During the redfinned bully breeding season mid – July through to December it might be expected that depletion of invertebrates in patches occupied by redfinned bullies would occur, as fish are less mobile (specifically nesting males) and begin to congregate in or around nesting areas (McDowall, 1965a). However, during the sampling period it is likely fish were mobile, moving between patches unrestricted by breeding activity (McDowall, 1965a).

Dietary analysis supports the idea that chironomids may have driven patch selection by redfinned bullies, because chironomids were the most abundant species found in diet samples, significantly more abundant than the other top four most abundant species. McDowall (1965b) also found chironomids were the most abundant species found in the diet samples of 615 redfinned bullies, his results were compared to diet samples from two other streams and similarities in diet between sites justified his diet samples were an accurate representation of a redfinned bully diet. Analysis of redfinned bully diet samples by McDowall (1965b) revealed the average number of invertebrates in gut samples of many fish was low; however, there were numerous fish that had high abundances of chironomid larvae, which indicated selective feeding on chironomids. Variation in the abundance of chironomids between diet samples from my study was high, reflected through large error bars (Fig. 2.1 b). High variation in chironomid abundance between diet samples indicates some individuals are feeding on large numbers of chironomids, which implies selective feeding on chironomids by some of the sampled redfinned bullies is occurring. Selective feeding on chironomids at least by some redfinned bullies in my study site, suggests that chironomids are a valuable food source to redfinned bullies. Variation in the abundance of chironomids between the diet samples could simply be due to variation in chironomid numbers between patches. For example a foraging fish selectively feeds on the most profitable invertebrate species when they are in high abundance, then expands its diet to include less profitable invertebrates when the abundance of more profitable invertebrates is low (Hayslette & Mirachi, 2002).

Variation in the abundance of chironomids between redfinned bully diet samples could be driven by territorial behaviour, whereby dominant individuals occupy the best patches

(those with the optimal fitness return) by pushing out other less dominant individuals (Petty & Grossman, 2010). Presumably dominant individuals would be larger fish; therefore, if this was the case, diet samples of larger fish should contain higher numbers of chironomids. Competition for patches occurs in other benthic stream fish, for example Petty and Grossman (2010) found mottled sculpins competed for patches based on fitness return where the most dominant individuals would occupy the best patches. Therefore, it is plausible competitive interactions between redfinned bullies do occur outside of the nesting period, although further research will be required to determine the extent to which competitive interactions for patches occur in redfinned bullies.

Benthic prey driven distribution of redfinned bullies is likely because redfinned bullies are carnivorous benthic predators preying almost exclusively on stream bed invertebrates (McDowall, 1965b). Redfinned bullies were numerically the most abundant invertebrate predator in the study site; therefore they are likely to have a substantial influence on the benthic invertebrate community (McDowall, 1990). If redfinned bullies were to be removed from the study site, it is likely, that changes in invertebrate abundance and composition would occur, potentially affecting algal grazing and causing a shift in the community structure (Usio & Townsend, 2000). Due to the numerical dominance of redfinned bullies in our study site, and the lack of other invertebrate predators, they have the potential to be a strong interactor with the stream community, and it is common for a strong interactor's distribution to be determined by lower trophic levels such as the invertebrate community (Usio & Townsend, 2000).

Patches occupied by male redfinned bullies were significantly different from patches occupied by females in terms of environmental variables (specifically water depth); however, they were not significantly different in terms of invertebrate abundance. When patches containing redfinned bullies are compared to patches sampled at random there are significantly higher abundances of invertebrates in patches occupied by redfinned bullies, therefore even though there are environmental differences between patches occupied by male and female fish, results suggest both males and females are selecting for patches with high invertebrate abundance. McDowall (1965c) reported outside of the

breeding season (the time in which my sampling took place), no differences in diet between male and female redfinned bullies are known to exist.

2.4.4 Breeding habitat requirements affecting patch selection by redfinned bullies

Potentially, the environmental characteristics required for breeding could explain why redfinned bullies show non-random patch selection. However, it is unlikely breeding activity such as egg laying and fertilisation was taking place at the time of sampling (late April) because redfinned bullies are known to breed during late winter (beginning mid-July), spring and early summer months (McDowall, 1965a). Areas within the sampling section can be considered as ideal breeding habitat for redfinned bullies, “shallow rocky pools where flow is steady but not fast” (McDowall, 1965a). McDowall (1965a) stated that redfinned bullies seek upstream breeding habitat during February, March and April after a post-breeding migration downstream; therefore it is likely when sampling took place fish found within the sampling section had reached a suitable breeding destination. McDowall (1965a) & Hayes *et al.* (1989) reported the environmental change seen when leaving lowland post-breeding habitat and entering upstream breeding habitat are lower water velocities, shallower water depths, more available cover and larger substrate types. Therefore, within the stream reach sampled it is likely the fish prefer to inhabit specific patches within pools, those with large substrates low water velocities and ample cover, because these areas are suitable breeding habitat, which is a likely reason why fish showed non-random patch selection.

McDowall (1965a) found male fish tend to leave the fast water habitats and seek their breeding habitat earlier in the year than females; therefore there are usually distinct differences in the habitat occupied by male and female fish early in the breeding season. Findings from McDowall (1965a) provide a good explanation as to why patches occupied by male fish were different in terms of environmental characteristics compared to female fish, because male fish may be seeking the specific breeding habitat earlier than females.

2.4.5 Interspecific interactions affecting patch selection by redfinned bullies

Potentially predation pressure or interspecific competition could have been driving or influencing non-random patch selection by redfinned bullies. During sampling other

species were observed within the sampled reach; however, their abundances were low and redfinned bullies were numerically the most dominant species. Other species included freshwater crayfish (*Paranephrops zealandicus*), banded Kokopu (*Galaxias fasciatus*), brown trout (*Salmo trutta*), short-finned eel (*Anguilla australisi*) and long-finned eel (*Anguilla dieffenbachii*). The brown trout observed were young of year fish and were predominantly seen in the fast flowing open water, areas not occupied by redfinned bullies, therefore competition or habitat overlap did not appear to be significant. Trout of large size have been reported to feed extensively on bully species in New Zealand (Hobbs, 1940), however trout of a small size and in low abundances are very rarely found to predate on redfinned bullies (McDowall, 1964). The eels observed were in very low abundances and were only seen on a few of the observation nights. Cairns (1942) analysed the stomach content of eight and a half thousand long and short finned eels from rivers throughout New Zealand and found bullies are a component of their diet; however in small rocky streams such as our study site, bullies are rarely found in their diet. Freshwater crayfish were low in abundance, often seen in the same pools night after night sharing pool environments with red-finned bullies. Freshwater crayfish are omnivorous, and their diet is predominantly composed of allochthonous detritus and invertebrates (Usio & Townsend, 2000); therefore it is unlikely there would have been any significant predatory interactions between redfinned bullies and freshwater crayfish. However, competition for invertebrate prey between freshwater crayfish and redfinned bullies may have occurred on a small scale. Banded Kokopu in captivity have been found to predate on redfinned bullies, although in the natural environment this has not yet been observed (McDowall, 1964). Banded Kokopu in the sampling section were small in size and were in very low abundances, therefore any interaction with redfinned bullies is not likely to have had an affect on patch selection. No fish eating birds or mammals were observed in the sampling section, and McDowall (1964) stated that no predators outside of the stream environment are known to predate on redfinned bullies.

2.4.6 Conclusion

In conclusion, my results indicate redfinned bullies display non-random patch selection, with a preference for patches dominated by cobble substrates and high abundances of

invertebrates, specifically chironomids. However, distinguishing what is driving non-random patch selection by redfinned bullies, whether it is invertebrate abundance or substrate type, or a combination of both, is not able to be done based on these results. Therefore, to determine what is driving non-random patch selection by redfinned bullies further experimentation is required.

3. Effects of experimental disturbance on nocturnal patch selection by redfinned bullies

3.1 Introduction

Disturbance plays an integral role in structuring the biological community within streams (Matthaei *et al.*, 1997). Streams in temperate climates are commonly exposed to natural disturbances such as flooding events (Matthaei *et al.*, 2000), although human activity within stream catchments has seen an increase in exposure to anthropogenic disturbance such as sedimentation and chemical pollution (Niemi *et al.*, 1990). Human activity and population growth in the past century has resulted in major changes in the global climate (Lake, 2000; Radif, 1999), which has altered the natural disturbance regime by affecting the intensity and frequency of natural disturbance events (Lake, 2000). The extent to which the biological stream community is affected by disturbance and the rate at which it recovers is usually dependant on how adapted that community is to disturbance (Detenbeck *et al.*, 1992). Recent increases in the intensity and unpredictability of natural and anthropogenic disturbances caused through human activity and population growth (Niemi *et al.*, 1990; Radif, 1999) have resulted in degradation of many stream systems (Lake, 2007). Biological stream communities are commonly well adapted to recover from natural disturbance (Matthaei *et al.*, 1997), although anthropogenic impacts such as chemical pollution can result in extended recovery times and short term loss of non-resilient species, causing shifts in biological relationships and community composition (Niemi *et al.*, 1990).

Natural stream disturbances such as floods can have a major impact on benthic invertebrate communities by drastically reducing their abundance (Matthaei *et al.*, 2000). The rates at which invertebrate communities recover following disturbance depends on the intensity and spatial scale of the disturbance and the resilience and resistance of the invertebrate community which is determined by available refugia (Lake, 2000). Potential refugia from disturbance for stream organisms include lateral stream margins, large substrate particles, zones in the bed where shear stress is always low and the hyporheic zone (Matthaei *et al.*, 2000). Refuges for benthic invertebrates during disturbance events

may increase the resistance and resilience of some species to disturbance, although species traits ultimately determine resilience and resistance to disturbance (Townsend *et al.*, 1997). Stream invertebrate traits that allow for high resilience to disturbance include; small size, high mobility, non-specialist habitat requirements and traits that allow for high resistance to disturbance include clinging ability, streamlined morphology and multiple life stages (Townsend *et al.*, 1997). Invertebrate species that possess a suite of traits that increase their resistance and resilience to disturbance are usually the first species to recolonize an area following disturbance (Death, 1995). However, as succession occurs following disturbance, invertebrate composition changes due to competition, predation and environmental change (Death, 1995; Matthaei *et al.*, 2000), which in turn is likely to affect the abundance, behaviour and distribution of predatory benthic fish (Petty & Grossman, 2007).

Streams are subject to temporal changes in their thermal and chemical regimes as well as their rates of discharge; therefore they are ideal for studying the ecological role of disturbance (Townsend *et al.*, 1997). A lack of study on the recovery of fish and invertebrate communities, and how they interact following disturbance (Dettenbeck *et al.*, 1992), emphasizes the need to gain insights into this area of ecology. Stream fish are known to change their behaviour and intra/ inter specific relationships in response to a change in food supply (Hansen & Closs, 2005; Petty & Grossman, 2007). Stream invertebrates are known to be drastically reduced in abundance following disturbance (Matthaei *et al.*, 2000), therefore it is likely an unknown interactive effect between redefined bullies and invertebrate abundance and composition would occur following disturbance. Increases in the intensity and amount of anthropogenic and natural disturbances occurring throughout the world (Lake, 2000), and with streams being classed among the most susceptible and damaged ecosystems (Lake, 2007), emphasizes why it is important to understand how stream communities respond and recover from disturbance. Understanding how each species within a community responds and recovers from disturbance and how they interact with one another provides insight into the community and the ecosystem itself, thus serving a use for management and conservation of the ecosystem.

The wide distribution and abundance of redfinned bullies throughout New Zealand emphasizes their importance as a component of many of New Zealand's streams (McDowall, 1990). Many of New Zealand's coastal streams are home to redfinned bullies and have been degraded in recent years, primarily due to anthropogenic disturbance (Winterbourn *et al.*, 1981). Recent degradation of many of New Zealand's coastal streams is a likely reason as to why redfinned bullies are declining in abundance (Allibone *et al.*, 2010). There are no published studies investigating how redfinned bullies respond to and recover from disturbance. Understanding how redfinned bullies respond and recover from disturbance taking into account the invertebrate community and any interactive effects that may exist could provide insights into how redfinned bullies will cope with future disturbance and changes in their primary food resource. The declining abundance of Redfinned bullies along with increasing degradation of habitat emphasizes a need to study how redfinned bullies respond and recover from disturbance, to aid in future management and conservation.

The aim of this study was to provide insight into how redfinned bullies respond and recover from a pulse disturbance, specifically looking at the interactive effects between the invertebrate community and redfinned bullies. It was hypothesized that redfinned bully abundance would drop within patches of habitat subjected to a disturbance that resulted in a reduction in invertebrate numbers.

3.2 Methods

3.2.1 Study site

The study site used for this experiment was the same study site on Aurora creek as used in the experiment outlined in chapter one. The stream reach where the experiment took place was approximately six hundred meters long, slightly longer and extending further upstream by approximately one hundred meters than the study reach used for the initial descriptive study. Both qualitative and quantitative data (from chapter 1) indicated the study site was relatively homogenous. Specifically, altitude, stream characteristics, land use and biota between the upper most and lowest reach of the study site showed little variation. The length of the study reach was not set prior to sampling as this was determined once the desired number of pools containing sufficient numbers of redfinned bullies had been located.

3.2.2 Field methods

All field sampling took place during times of stable weather conditions during which the stream exhibited stable flow rates, normal water levels and good water clarity. Three phases were involved in the study, a pre-treatment observational phase (two nights spotlighting), a treatment phase (one day) and a post-treatment observational phase (one night spotlighting immediately after treatment, then two nights spotlighting every week for four weeks post-treatment). The period over which the experiment was conducted began on the 11th of November 2012 and finished on the 12th of December 2012.

3.2.3 Spotlighting

All spotlighting during the entire experiment was carried out one hour after dark onwards of 10pm, to ensure that all of the fish present within each pool had emerged from their daytime retreats (McDowall, 1964). Spotlighting involved observing each pool along the stream reach and was carried out using a 100watt spotlight running on a twelve volt battery. Spotlighting involved scanning the stream bed from bank to bank, walking up stream along the bank to reduce disturbing the stream bed, with one observer and one spot light operator. For each pool spotlighted, the number of fish present was recorded (including both redfinned bullies and any other fish or crustacean species); redfinned bullies sighted had their sex determined and length estimated.

3.2.4 Pre-treatment observational phase

The pre-treatment observational phase involved spotlighting every pool within the stream reach over two nights. This phase was carried out in order to quantify the redefined population within each of the pools along the stream reach. Twenty pools were selected to be included in the experiment based on the number of redefined bullies present in the pools, where pools with a higher number of fish present were selected first. A pool was not selected to be included in the experiment unless it contained at least two redefined bullies over the pre-treatment observational phase. The twenty pools selected to be included in the experiment were allocated a number, ranging from one to twenty in descending order of their position along the reach, moving downstream. Once the pools had been numbered the ten upstream pools were selected as control pools, and the ten pools downstream were selected to be the treatment pools. The reason control and treatment pools were demarcated to upper and lower reaches, rather than being distributed uniformly throughout, was due to the homogeneity of the stream reach. Furthermore, this ensured dislodged debris and invertebrates from the treatment did not enter control pools. Pools were marked with a stake on the immediate stream bank, holding a labelled strip of fluorescent marking tape so they could be easily distinguished and located. Within the sampling section there were ten pools that were not used in the experiment.

3.2.5 Physical habitat measurements

Once the twenty pools that were to be used in the experiment had been selected, the physical habitat in each pool was measured; this took place during the day time hours of the pre-treatment observational phase. Physical habitat measurements included average water velocity (an average of three velocity measurements from the head, tail and deepest point of each pool), measured in meters per second, using a Marsh-McBirney Model 2000 Flo-Mate. Substratum composition was visually estimated (dominant substrate type in the head, tail and deepest point of each pool). A modified Wentworth scale was used to describe and quantify the dominant substrates (<2 mm silt; 2–4 mm sand; 4–64 mm gravel; 64–256 mm cobble; >256 mm boulder; Detritus; other) (Whitehead *et al.*, 2002). Each dominant substrate type was allocated a number (1 = silt, 2

= sand, 3 = gravel, 4 = cobble, 5 = boulder, 6 = detritus, 7 = other) which allowed an average dominant substrate for each pool to be calculated and allowed analysis comparing dominant substrate between control and treatment pools to be completed. Other microhabitat variables measured included; pool length (meters), average pool width (an average of three width measurements one from the head, tail and deepest point of each pool) and average water depth (an average of three depth measurements one from the head, tail and deepest point of each pool). Pool length, width and depth measurements were all obtained using a clear plastic ruler or 50m tape measure.

3.2.6 Treatment phase

The treatment phase commenced on the following day after the second night of pre-treatment observation. To reduce the number of invertebrates present in treatment pools, the substrate in each treatment pool was 'scrubbed clean' using scrubbing brushes and large yard style brushes. Larger substrate (boulders and cobble) was lifted from the stream and cleaned; finer substrate was scrubbed (swept) with a yard brush. Twenty litre buckets filled with water tipped from a height above one meter were used to flush dislodged invertebrates from the treatment pools. The stream's natural flow assisted in washing away the dislodged invertebrates. Control pools also underwent a form of treatment where all of the large stones (those large enough for a redfinned bully to hide beneath) were removed from each pool for a few seconds then returned to their positions on the stream bed; this was to account for the disturbance inflicted on fish in treatment pools created by cleaning the benthos. During the treatment phase we worked our way downstream, to prevent dislodged invertebrates and debris from treatment accumulating in pools already treated. Each pool was separated by a riffle or run spanning at least five to ten meters, therefore it was likely most of the dislodged debris and invertebrates from treatment would not reach downstream pools.

3.2.7 Post-treatment observational phase

The post-treatment observation phase involved two nights spot lighting for fish each of the control and treatment pools every week for four weeks after treatment.

3.2.8 Invertebrate sampling

In each of the treatment and control pools, an invertebrate sample was taken before treatment, after treatment (treatment pools only), two weeks post-treatment, and four weeks post-treatment. Each invertebrate sample involved two components; the first component involved removing the surface invertebrates from three small rocks (cobble size) one from the head, tail and deepest part of each pool. Removal of surface invertebrates involved scrubbing the surface of the selected rock with a scrubbing brush over a 150µm sieve while constantly spraying the scrubbed rock with a squirt bottle to remove any remaining invertebrates. The second component involved collecting three 50ml scoops of finer sediment (included silt, sand and gravel sized particles), from the head, tail and deepest part of each pool. Both components of each invertebrate sample were then placed into a 250ml pottle containing 70% ethanol. Invertebrate samples were taken to the lab where they were analysed by counting all of the invertebrates and identifying each invertebrate species to genus or species level if possible using Winterbourne *et al.* (2006). Invertebrates that were unable to be identified to genus or species level were identified to the lowest possible taxonomic level including: Flatworm (phylum), Oligochaeta (subclass), Ostracoda, Collembola, isopod species, Cyclopoida (order), Elmidae, Empididae, Hydraenidae, Muscidae, Psychodidae, Ceratopogonidae, Chironomidae (family), Eriopterini (tribe).

3.2.9 Data analysis

Mean abundance of invertebrates was pooled for both treatment and control groups for each sampling session over the five week sampling period and plotted on histograms. To determine whether there was a significant difference between the pooled mean invertebrate abundance between sampling sessions for the control and treatment group's, single factor ANOVA was used. ANOVA was performed using Microsoft Excel 2010. If ANOVA indicated a significant difference, a post hoc, Tukey's multiple comparison test was carried out to determine where the differences were occurring (Motulsky, 2007). Tukey's multiple comparison test was carried out using GraphPad Prism version 6. To determine which invertebrate taxa were primarily responsible for a difference between control and treatment pools before treatment occurred, a SIMPER analysis was conducted using PRIMER version 6 (Clarke and Gorley, 2006). SIMPER was also used to

assess which taxa were the most abundant on average in treatment pools following treatment and what percentage of the biota their abundance is accounting for (Clarke and Gorley, 2006). Preparation of biological data for SIMPER analysis involved a square root transformation to homogenise variance and reduce the influence of highly abundant taxa thereby enhancing the influence of less common taxa (Clarke and Gorley, 2006).

Student's t tests, two sample assuming unequal variance, were used to use to test differences between the mean abundance of redfinned bullies and other fish or crustacean species in treatment and control pools before disturbance, over the entire observation period and between observation nights within both treatment and control groups; these tests were performed using Microsoft Excel 2010.

Environmental characteristics were compared between control and treatment pools before treatment occurred. For each environmental variable a Student's t-test, two sample assuming unequal variance, was carried out to test for a significant difference between control and treatment groups. Student's t-tests were carried out using Microsoft Excel 2010.

3.3 Results

3.3.1 Effect of treatment on Invertebrate abundance in control and treatment pools

In treatment pools the mean abundance of invertebrates before treatment was significantly lower (260) than in control pools (453) ($p < 0.05$) (Fig. 3.1 a & b). Mean abundance of invertebrates in treatment pools decreased significantly post-treatment from an average of 260 invertebrates per pool before to 51 post-treatment ($p < 0.01$) (Fig. 3.1 a). The average abundance of invertebrates per treatment pool in week three increased to 123, but was not significantly different from week one before or after treatment ($p > 0.05$) (Fig. 3.1 a). The average abundance of invertebrates in treatment pools increased significantly from 123 in week 3 to 287 in week 5 ($p < 0.05$) (Fig. 3.1 a). There was no significant difference in the mean abundance of invertebrates between week one before treatment and week five after treatment ($p > 0.05$) (Fig. 3.1 a). ANOVA showed there was no significant difference in the mean abundance of invertebrates in control pools over the five week period ($df_2, F = 1.37, p > 0.05$) (Fig. 3.1 b).

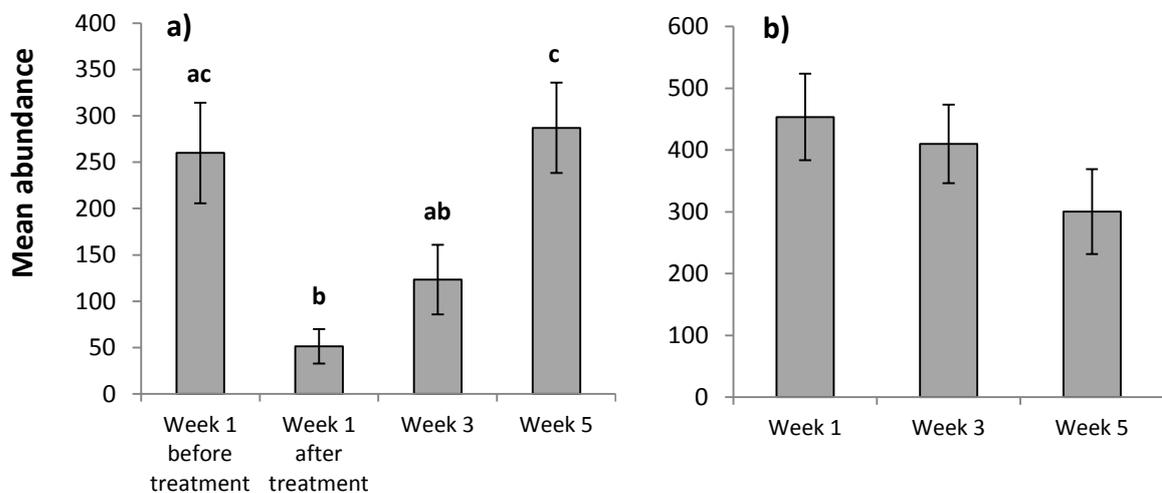


Figure 3.1. Invertebrate abundance found within stream pools from sampling sessions over the five week monitoring period. **a)** Invertebrate abundance found within treatment pools from four sampling sessions before and following treatment (disturbance). **b)** Invertebrate abundance found within control pools from three sampling sessions. Values represent mean \pm S.E.M. Different letters denote significant differences ($p < 0.05$).

3.3.2 Invertebrate species contributions comparison between control and treatment groups

The top three most abundant invertebrate taxa were the same in control and treatment pools prior to disturbance; however they differed in their average abundance. Chironomidae, Oligochaeta and *Deleatidium* were more abundant in control pools than pools allocated for treatment (Table 3.1 a & b). Chironomidae was the most abundant taxa in both control and treatment pools, and was primarily responsible for the observed difference in invertebrate abundance between control and treatment pools prior to disturbance (Fig. 3.1 a & b, Table 3.1 a & b). Together the top three most abundant invertebrate taxa in treatment pools and control pools contributed to 70 and 75% of the invertebrate community respectively (Table 3.1 a & b). Comparison of invertebrate abundances from week one in treatment pools before and after treatment showed post-treatment there was a decrease in the average abundance of the top three most abundant invertebrate taxa and a significant decrease in the abundance of Chironomidae; however, Chironomidae was still the most abundant taxon ($p < 0.05$) (Fig. 3.1 a, Table 3.1 a). Week one after treatment, *Deleatidium* was absent from the three most abundant taxa; instead *Pyconcentrodes* had risen to the top three (Table 3.1 a). On week three in treatment pools, *Deleatidium* returned to the top three most abundant taxa, more abundant than Oligochaeta, however less abundant than the most abundant taxon, Chironomidae (Table 3.1 a). On week five in treatment pools and control pools the top three most abundant taxa were the same as in week one before treatment and the average abundance of invertebrates for both treatment and control pools was not significantly different compared to week one ($p > 0.05$) (Table 3.1 a & b, Fig. 3.1 a & b). In control pools there was no change in the top three most abundant taxa, over the five week period, however abundance did decrease over this time period (Table 3.1 b, Fig. 3.1 b).

Table 3.2. (Following page) One way SIMPER analysis. Table 1 a and b) are assessing which taxa are the most abundant on average in treatment **(a)** & control **(b)** pools and what percentage of the biota their abundance is accounting for, prior to disturbance (treatment pools only), one week, three weeks and five weeks post-disturbance respectively. Av. Abund = average abundance (based on values in the Bray-curtis similarity matrix and does not represent true abundance estimates), Av. Sim = average similarity, Sim/SD = ratio of average similarity to standard deviation, Contrib% = the percentage each species contributes to dissimilarities, Cum.% = cumulative percent of total dissimilarity.

a) Group a): Treatment pools, prior to treatment					
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Chironomidae	13.00	26.73	3.88	46.02	46.02
<i>Deleatidium</i>	3.68	8.55	2.71	14.72	60.73
Oligochaeta	2.83	5.62	3.79	9.67	70.40

Group b): Treatment pools, immediately after treatment					
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Chironomidae	5.49	29.21	2.29	73.76	73.76
Oligochaeta	0.94	3.24	0.66	8.19	81.95
<i>Pyconcentrodes</i>	0.64	3.22	0.68	8.12	90.07

Group c): Treatment pools, three weeks after treatment					
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Chironomidae	8.19	24.81	4.10	45.27	45.27
<i>Deleatidium</i>	2.27	7.79	2.53	14.21	59.49
Oligochaeta	2.21	6.01	1.19	10.96	70.45

Group d): Treatment pools, five weeks after treatment					
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Chironomidae	13.54	25.98	3.18	44.12	44.12
<i>Deleatidium</i>	3.22	6.55	4.84	11.12	55.24
Oligochaeta	3.05	6.37	6.49	10.82	66.05

b) Group a): Control pools, week one time of treatment					
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Chironomidae	18.40	34.97	2.55	54.95	54.95
<i>Deleatidium</i>	4.17	6.64	3.62	10.43	65.38
Oligochaeta	3.37	6.53	2.64	10.26	75.65

Group b): Control pools, three weeks after treatment					
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Chironomidae	17.45	38.13	2.28	65.65	65.65
<i>Deleatidium</i>	2.95	4.74	0.89	8.16	73.81
Oligochaeta	2.52	4.70	1.61	8.09	81.90

Group c): Control pools, five weeks after treatment					
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Chironomidae	14.11	29.79	2.25	55.95	55.95
<i>Deleatidium</i>	2.78	6.71	2.88	12.61	68.56
Oligochaeta	2.77	4.68	0.89	8.79	77.35

3.3.3 Abundance of redfinned bullies and other species before and after treatment in control and treatment pools.

The average number of male redfinned bullies was lower in control pools, but not significantly different to treatment pools over the pre-treatment observation period (df_{14} , $t = 1.63$, $p > 0.05$) (Fig. 3.2 a). Following treatment (disturbance), the average number of male fish in treatment pools showed an initial increase on the first night post-disturbance (night three) followed by a decrease on night four (one week post-disturbance) and another increase to the highest mean abundance of 1.8 fish per pool on night five (one week post-disturbance) (Fig. 3.2 a). After observation night five and for the remainder of the observation period, male fish numbers in treatment pools dropped to an average ranging between 1.1 and 1.2 fish per pool (Fig. 3.2 a). Over the entire eleven night observation period (five weeks) male fish numbers in control pools did not show any noticeable increase or decrease, on average ranging between 1 and 1.3 fish per pool (Fig. 3.2 a). The average abundance of female redfinned bullies was significantly lower in control pools than treatment pools throughout the five week observation period (df_{12} , $t = 7.88$, $p < 0.0001$) (Fig. 3.2 b). In treatment pools the average number of female fish decreased slightly the night immediately after disturbance, followed by an increase to an average of 3.3 fish per pool by observation night five (one week post-disturbance) (Fig. 3.2 b). The average number of female fish in treatment pools decreased to 2.5 fish per pool by night seven (two weeks post-disturbance) then increased to the highest average, observed on night nine (four weeks post-disturbance) of 3.4 fish per pool (Fig. 3.2 b). The observed increase in the average number of female fish per treatment pool over the five week observation period was not significant (df_{11} , $t = 1.38$, $p > 0.05$) (Fig. 3.2 b). Control pools showed a non-significant increase in female fish numbers over the five week observation period, from an average of 1.1 to 1.6 fish per pool (df_{11} , $t = 1.56$, $p > 0.05$) (Fig. 3.2 b).

A total of four other fish species plus crayfish were also observed, but the average number of individuals of other species was low compared to redfinned bullies (Fig. 3.2 a, b & c). In treatment pools, the average abundance of other species showed no major changes before treatment on nights one and two, and after treatment on night three, however on night four (one week post-disturbance) there were no individuals observed in

treatment pools (Fig. 3.2 c). Following night four, the average abundance of other species increased to the greatest mean abundance of 2 individuals per pool on night seven (two weeks post-disturbance), which was followed by a decrease to zero individuals per pool by night eleven (four weeks post-disturbance) (Fig. 3.2 c) In control pools the average abundance of other species showed a slight decrease between nights one and three, and then increased to the highest mean abundance observed on night four (one week post-disturbance) of 2.5 individuals per pool (Fig. 3.2 c). After night four in control pools the average abundance of other species gradually decreased to 1.8 individuals by night eleven (four weeks post-disturbance) (Fig. 3.2 c). No interactive effects were observed between redfinned bullies and other species.

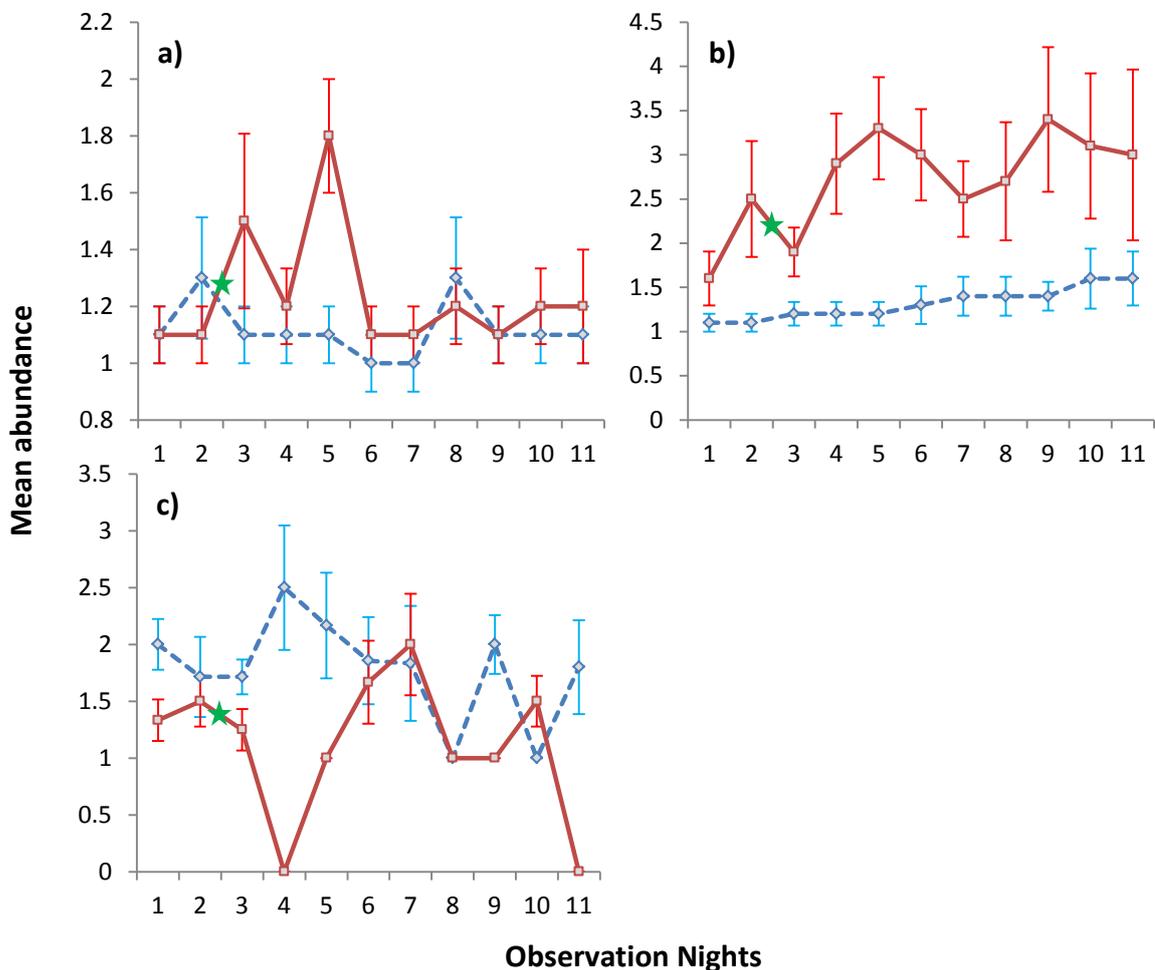


Figure 3.2. **a)** The average number of male fish observed during spotlighting across the ten control and treatment pools over the eleven night observation period. **b)** The average number of female fish across the ten control and treatment pools over the eleven night observation period. **c)** The average number of other fish species and crayfish species across the ten control and treatment pools over the eleven night observation period. Other species included; freshwater crayfish (*Paranephrops zealandicus*), banded Kokopu (*Galaxias fasciatus*), brown trout (*Salmo trutta*), short-finned eel (*Anguilla australis*) and long-finned eel (*Anguilla dieffenbachii*). Values represent mean \pm S.E.M. Green stars represent disturbance. Blue dashed lines represent control pools and red lines represent treatment pools.

3.3.4 Interactive effects between fish abundance and invertebrate abundance

A weak negative correlation ($R^2 = 0.3764$) was found between mean invertebrate abundance and mean fish abundance where an increase in the abundance of fish resulted in a decrease in invertebrate abundance (Figure 3.3).

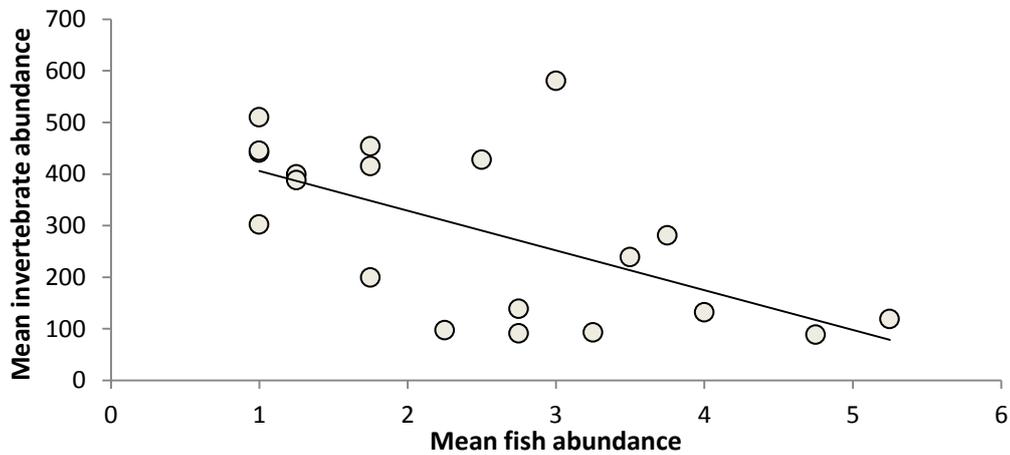


Figure 3.3. Scatterplot showing the relationship between mean fish abundance and mean invertebrate abundance. $y = -76.956x + 482.85$, $R^2 = 0.3764$. Data includes averaged invertebrate abundance from four sampling sessions and averaged fish abundance data from each observation night before an invertebrate sampling session took place.

3.3.5 Comparison of environmental variables between control and treatment pools

Measurements of environmental variables indicated both treatment and control pools were comparable in their environmental characteristics (Table 3.2). No significant differences were found ($p > 0.05$) between control and treatment pools across the range of measured environmental variables (Table 3.2).

Table 3.2. A comparison of environmental characteristics of the treatment and control pools averaged across the ten pools in each group. P values < 0.05 are considered significant. df = degrees of freedom, V = Velocity, D = Water depth, DST = Dominant substrate type, PL = Pool Length, PW = Pool width.

	V (ms -1)	D (cm)	DST	PL (m)	PW (m)
Control	0.02	148.43	3.47	2.4	0.91
± S.E.	(0.004)	(7.67)	(0.21)	(0.19)	(0.08)
Treatment	0.03	147	3.77	2.5	1.11
± S.E.	(0.005)	(16.62)	(0.11)	(0.20)	(0.06)
p	0.25	0.94	0.22	0.71	0.071
df	18	13	14	16	17
t-stat	1.18	0.08	1.28	2.49	2.99

3.4 Discussion

The first study in this project (covered in chapter two) revealed redfinned bullies display non-random patch use, and that patch selection could be driven by prey abundance and/or substrate. The experiment covered in this chapter was designed to determine whether or not invertebrate abundance drives patch selection in redfinned bullies, and how redfinned bullies and the invertebrate community respond to disturbance. Following experimental disturbance redfinned bullies responded with an increase in abundance. In treatment pools post-disturbance the invertebrate community showed a major reduction in abundance and diversity, and then steadily recovered over the five week monitoring period. Changes in the abundance of redfinned bully numbers post-disturbance could be due to an environmental change caused through disturbance or change in the biological community due to disturbance, or a combination of both.

3.4.1 Interactive effects between invertebrate abundance and redfinned bully abundance

The abundance of invertebrates was lower in treatment pools than control pools prior to disturbance and throughout the monitoring period (Fig. 3.1); however, the difference was relatively minor and it was not obvious why there was a difference, as the biological and environmental properties of treatment and control pools were very similar. Comparison between treatment and control pools revealed no differences in dominant invertebrate taxa (chironomids being the most dominant), and there was no significant difference in environmental variables; therefore, redfinned bully abundances and activity would be expected to be similar between the two groups. However, control pools had slightly lower numbers of redfinned bullies than treatment pools prior to disturbance and throughout the monitoring period. Results from chapter two suggest nocturnal patch selection by redfinned bullies may be driven by chironomid abundance therefore, if redfinned bullies were selecting patches based on invertebrate abundance and composition, a decrease in invertebrate abundance, but not composition, in treatment pools would be expected to cause redfinned bullies to leave pools with reduced food availability. However, redfinned bullies were more abundant in treatment pools throughout the monitoring period, and didn't show any sign of leaving after disturbance, even though invertebrate abundance was reduced in treatment pools following disturbance and control pools had a higher

abundance of invertebrates. A negative correlation was found between redfinned bully abundance and invertebrate abundance supporting the idea that invertebrate abundance was not driving patch selection by redfinned bullies during observation period. The fact redfinned bullies did not leave patches of low invertebrate abundance (treatment pools), suggests they were not selecting patches based on invertebrate abundance, at least in the short term; instead it suggests patches are being selected for their habitat structure, substrate type being a likely key variable.

In control pools neither male nor female redfinned bully numbers fluctuated greatly over the five week monitoring period, ranging between one to two male and female fish per pool. In post-disturbance treatment pools female redfinned bully numbers increased and one week post-disturbance, and reached their highest abundance three weeks post-disturbance. Male redfinned bully numbers in treatment pools peaked once one week post-disturbance, then dropped again and plateaued for the remaining observation period. A peak in abundance of both male and female redfinned bullies one week post-disturbance would not be expected if redfinned bullies were selecting pools (patches) based on invertebrate abundance, as invertebrate samples taken the following week revealed invertebrate abundances were below pre disturbance levels. However, it is possible that low food abundance could influence behaviour; the high number of redfinned bullies sighted one week post-disturbance could be due to hunger, as prey-deprived fish may be more active and visible as they seek out food (see Hansen & Closs, 2005).

3.4.2 Effects of disturbance on stream communities

Several factors affect the rate at which a stream community recovers from a pulse disturbance, including disturbance history (Matthaei & Townsend, 2000), the mobility and dispersal ability of stream organisms (Effenberger *et al.*, 2006) as well as the magnitude and spatial scale of the disturbance (Detenbeck *et al.*, 1992). Temperate stream environments, such as my study site, are commonly exposed to rainfall events that cause pulsed disturbances such as floods, therefore their biota are commonly well adapted to disturbance (Effenberger *et al.*, 2006). For example the territorial behaviour and cryptic nature of redfinned bullies are likely to be features that increase their resistance to

disturbance (McDowall, 1990), and may explain why redfinned bully numbers in treatment pools did not decrease post-disturbance. Recovery of an invertebrate community in a small temperate stream following a small scale pulsed disturbance is usually rapid taking approximately three to five weeks (Effenberger *et al.*, 2006; Lake, 2000). Therefore, the four week post-disturbance monitoring period should have been sufficient in capturing any short to medium-term responses by fish to changes in the environmental and biological constituents of treatment pools. Pulsed disturbances, such as flooding, commonly disturb the stream bed and the biota it accommodates (Effenberger *et al.*, 2006), promoting patchy distributions of stream invertebrates (Matthaei & Townsend, 2000) which in turn promotes a patchy distribution of predatory benthic feeding fish if they are selecting patches based on invertebrate abundance (Petty & Grossman, 2010). It is likely redfinned bullies were reluctant to leave pools following disturbance; hence the reduction in invertebrates over the monitoring period could be tolerated. However, presumably if the invertebrate abundance stayed low for an extended period, they would have to leave eventually. This information further emphasizes it is unlikely invertebrate abundance was driving patch selection, where a reduction in invertebrate abundance in treatment pools was not a great enough force to induce fish to leave pools, at least in the short term.

3.4.3 Effects of breeding activity on distribution, abundance and patch selection of redfinned bullies

Potentially the reason redfinned bullies were more abundant in treatment pools than control pools post-disturbance and the ratio of male to female fish was different between treatment and control pools may have been due to breeding activity. Although not reported, within the sampling site many gravid females were observed, as well as males guarding nests, which is a sign that spawning was underway and was not yet completed (McDowall, 1965a). Sampling took place during November and redfinned bullies are known to undertake breeding activity from mid-July through to December in extreme cases, therefore the time of sampling was within the known breeding period of redfinned bullies (McDowall, 1965a). During the breeding period, male redfinned bullies guard a nest site, in which female redfinned bullies will deposit their eggs, resulting in congregations of female fish in pools where available nest sites are located (McDowall,

1965a). Therefore, it is likely treatment pools held a higher number of nest sites than control pools, thus resulting in a higher number of female redfinned bullies in treatment pools over the monitoring period. Increased redfinned bully abundance in a patch during spawning should result in increased predation on benthic invertebrates for food and for protection of deposited eggs from predatory benthic invertebrates (McDowall, 1965b). Therefore, treatment pools having lower abundances of invertebrates than control pools but higher abundances of redfinned bullies before disturbance could be due to a higher number of nesting sites, assuming spawning was underway during the monitoring period. The fact a negative correlation was found between redfinned bully abundance and invertebrate abundance supports the idea spawning was underway and suggests between the first experiment (chapter 2) and the experiment covered in this chapter a change in redfinned bully behaviour may have taken place such as the onset of spawning. Spawning by redfinned bullies requires a specific benthic habitat, comprised of large cobbles with large interstitial spaces, to provide an area for a nest site, where eggs can be easily deposited, fertilised and guarded (McDowall, 1965a). Therefore, during the breeding period fish are selecting patches for the habitat specifically the substrate type as opposed to food, potentially the reason why reduced invertebrate abundance due to experimental disturbance did not reduce the number of redfinned bullies in treatment pools. Redfinned bullies were most likely selecting patches for substrate type assuming spawning was underway during the monitoring period; therefore it is possible that outside of this period patch selection is driven by the invertebrate community, emphasizing a need for experimentation outside of the spawning period.

3.4.4 Substrate driving patch selection by redfinned bullies

The territorial behaviour of redfinned bullies and their cryptic nature reflects the integral role that substrate plays in their lifecycle (McDowall, 1964). Individual redfinned bullies (predominantly males) commonly occupy a territory or a specific area of substrate they defend as their patch (McDowall, 1964). Redfinned bullies rely on substrate for cover, feeding and spawning, which increases resilience to disturbance, predation and competition (McDowall, 1964; McDowall, 1990). The strong connection between redfinned bullies and the substrate emphasizes that if food is not a primary driver of patch selection, it would be expected that substrate would be the primary driver. If

substrate is the primary driver for patch selection it is likely redfinned bullies would be attracted to suitable substrates, and reluctant to leave a suitable patch once located, even if food is depleted for a while.

Treatment pools had reduced invertebrate abundance post-disturbance although redfinned bullies did not leave; instead their numbers increased over the monitoring period. In control pools with higher invertebrate abundances than treatment pools, redfinned bully numbers were lower and did not show a distinct increase over the monitoring period. Results suggest redfinned bullies are selecting patches based on habitat, most likely substrate type, based on results from chapter two. However, if redfinned bullies are selecting patches based on substrate type, it would not be expected that their numbers would increase in treatment pools post-disturbance, as the substrate did not change in composition. However, potentially disturbance enhanced the substrate, by removing deposited fine-sediments (personal observation), thus potentially attracting redfinned bullies to treatment pools. Reduced fine sediment in treatment pools potentially increased the amount of interstitial space available thereby increasing the size and abundance of potential or existing nest sites as well as increasing the amount of available shelter (McEwan & Joy, 2013). Experimentation by Ramezani (2013) revealed fine sediment had a negative correlation with brown trout abundance in two small New Zealand streams, where trout abundance increased in cleaned patches with reduced fine sediment and decreased in patches with an increased fine sediment load. Fine sediment is known to reduce the available habitat for benthic invertebrates as well as reducing the ability of benthic fish to successfully predate on benthic invertebrates that are present beneath or amongst fine sediment (McEwan & Joy, 2013).

3.4.5 Conclusion

In conclusion, this experiment suggests during the spawning period redfinned bullies may be selecting patches for substrate quality over food. Experimental disturbance was effective and the observation period was adequate. However, evidence of spawning activity taking place during the experiment prevents one from assuming that outside of the spawning period patch selection is driven by substrate. Future studies looking to determine what drives patch selection by benthic feeding fish, should be carried out both

during and outside of the breeding period, to gain an idea of the effect spawning has on patch selection.

4. General discussion

4.1.1 *Major findings from study*

Redfinned bullies exhibited non-random patch selection, in a slow flowing semi forested stream (Chapter 2). Habitat patches selected by redfinned bullies were considered non-random because they were significantly different in their biological and environmental properties when compared to patches sampled at random. Redfinned bullies were more frequently found on patches with a dominant cobble substrate than what was available at random. Male redfinned bullies inhabited patches that had significantly deeper water when compared to patches occupied by female redfinned bullies. However, in terms of invertebrate abundance, patches occupied by male and female redfinned bullies were not significantly different. Redfinned bullies occupied patches with a significantly higher abundance of invertebrates than randomly sampled patches. Chironomids were the most abundant invertebrate taxa in both patches containing redfinned bullies and randomly sampled patches, although they were significantly more abundant in patches containing fish. Chironomids were the most abundant invertebrate taxa in redfinned bully diet samples. Results suggest non-random patch selection by redfinned bullies was driven by substrate and/ or food, with no clear indication as to which was the most important.

The experiment covered in chapter three was designed to determine whether nocturnal patch selection by redfinned bullies is driven by invertebrate abundance or substrate type. It was expected that experimental disturbance in pools causing a reduction in invertebrate abundance would result in a reduction in redfinned bully numbers if invertebrate abundance was driving patch selection. However, over the monitoring period post-disturbance, treatment pools with reduced invertebrate abundance actually supported, on average, a higher abundance of redfinned bullies. Chironomids were the most abundant invertebrate taxa in both control and treatment pools throughout the entire study period. These findings suggested that invertebrate abundance was not the primary driver of patch selection; this suggests that substrate seems to be a more important driver, at least in the short term. Post-disturbance a reduction in fine sediment was observed in treatment pools which potentially enhanced the quality of the cobble

substrate and may have influenced patch selection as found by Ramezani (2013). It was observed that gravid females and males guarding nest sites were present in the sampling site, indicating that spawning was underway (see McDowall, 1965a). Spawning activity has a major influence on redfinned bullies affecting patterns of habitat preference, feeding activity, and inter- and intra-specific interactions (McDowall, 1965a). Spawning in redfinned bullies requires a specific benthic habitat for nesting, egg deposition, fertilization and egg guarding (McDowall, 1965a). Therefore, evidence of spawning activity during the experimental period supports the idea that redfinned bullies may have been selecting patches based on substrate as opposed to food. However, it is plausible that outside of the spawning period patch selection by redfinned bullies may be driven by food.

This study highlights the importance of studying fish species at multiple temporal scales because fish behaviour, abundance and distribution is constantly changing with time, influenced by season, environment and age of the individual (McDowall, 1990). This study is useful in providing insights into redfinned bully ecology; specifically into what factors are primarily responsible for driving nocturnal patch selection. Results suggest that if food (invertebrate community) is not a strong driver of patch selection, substrate maybe more important, either as preferred substrate in its own right, or as a cue for the type of habitat that harbors the best food, or potentially a combination of both.

4.1.2 The importance of multi-scale studies on New Zealand's freshwater fish

This study sheds light on some fine scale interactions that occur between redfinned bullies and the ecosystem they exist in, such as fine scale habitat preferences and species interactions. Finer scale studies on stream fish, such as my study, are not common in New Zealand although they are important for management and conservation as they provide insights into the intricate aspects of a species' ecology (McEwan & Joy, 2013) that can be missed or overlooked in larger scale studies. However, larger scale studies are valuable as they take into account spatial variation that is not usually captured in small scale studies (Harrison & Bruna, 1999). Using studies of multiple scales from fine scale through to catchment scale in conjunction with one another is useful when dealing with declining, rare or endemic species, as the distribution and abundance of such species is

commonly sporadic and unpredictable (Lamoreux *et al.*, 2006). New Zealand is a country with a high number of endemic freshwater fish species (86% endemism; Gibbs, 2006). Ecosystems with high numbers of endemic species are commonly favoured sites for study, conservation and management (Lamoreux *et al.*, 2006). However, in New Zealand many of the benthic, endemic, freshwater fish species are not well studied including the redfinned bully (McEwan & Joy, 2013). A lack of study on benthic stream fish of New Zealand can be attributed to several factors, including being nocturnal, cryptic, having complex life histories (McDowall, 1990) and a lack of commercial value (Midway *et al.*, 2010). In the last assessment of New Zealand's native freshwater fish status, it was found that 67% were considered to be threatened or at risk of decline (Allibone *et al.* 2010).

Many of New Zealand's freshwater fish that are under threat and are declining in abundance are benthic species, including the redfinned bully (Allibone *et al.* 2010). Recent declines in New Zealand's native freshwater fish can be attributed to degradation of habitat, increased disturbance and pressure on stream environments caused by human colonization and population growth (McDowall, 1990; Winterbourn *et al.*, 1981). With the current status of New Zealand's freshwater fish community and a growing human population (Bongaarts, 2009), future declines in the distribution and abundance of this fish community are likely without improved conservation and management (Allibone *et al.* 2010). Effective management and conservation of declining freshwater fish species requires a widespread and multi-scale understanding of habitat requirements and biological interactions (McEwan & Joy, 2013). Therefore, given the current status of New Zealand's freshwater fish and ongoing degradation of stream environments, there is a clear need for more studies across various scales to assist in a better understanding of the ecology of New Zealand's freshwater fish, in turn supporting more effective management and conservation.

4.1.3 Improvements, limitations and recommendations for future study on redfinned bullies

One of the issues limiting this study is the time in which each study took place. Habitat use by redfinned bullies may have changed over the six month period between experiments due to factors such as spawning. To overcome temporal differences in fish

behaviour and improve the comparability of findings between experiments, it would be ideal to carry both experiments out at the same time. The reason experiments were not carried out simultaneously was because results from analysis of invertebrate samples from the first experiment outlined in chapter two, were necessary in order to design the second experiment (Chapter 3). Also experiments could not be run simultaneously within the sampling site without disturbing the other.

Although only one stream reach was used in this study, the environmental characteristics (slow flowing, cobble dominated with shallow water) are typical of many small coastal forested streams throughout New Zealand (Winterbourne *et al.*, 1981), therefore my findings are likely to be of relevance for many of New Zealand's streams with similar characteristics. However, it would be useful to compare how patterns of habitat use compare across different streams. This study reflects how benthic fish behaviour may change over a seasonal scale, affected by many factors including disturbance, age, spawning, predation, environment and season (McDowall, 1990; Niemi *et al.*, 1990). Therefore, based on results seen in this study it would be useful for future research to study multiple streams over annual cycles, thus taking into account the effects of spatial and temporal variation, hence supporting more effective management and conservation.

Spotlighting redfinned bullies is an effective and non-invasive technique for observing their nocturnal habitat use (Hickey & Closs, 2006); however, it would be useful for future studies to incorporate additional methods in conjunction with spotlighting to provide a more detailed account of nocturnal patch selection by redfinned bullies. Such methods could include the use of a tagging system and infrared video surveillance. A tagging system that would be effective if used in conjunction with spotlighting is Passive Integrated Transponder (PIT) tags, which have been proven to be effective for locating redfinned bullies both during the day and at night by McEwan and Joy (2013). PIT tagging would complement spotlighting in studies on nocturnal patch selection, because spotlighting does not necessarily ensure all of the fish present in a study reach are located, whereas pit tagging ensures all tagged fish at a location will be located (Gibbons & Andrews, 2004). Infrared motion activated video surveillance has been effectively used in many studies on freshwater fish looking at nocturnal habitat selection, and feeding

regimes (Dou & Tsukamoto, 2003; Tunney & Steingrímsson, 2012). The use of video surveillance would provide a detailed insight into nocturnal patch selection by redfinned bullies that could be used to support information attained via spotlighting and shed light on intra- and inter-specific interactions not observed via spotlighting such as spawning activity or competition for patches.

Questions prompted by my results that would be useful to incorporate into future studies on redfinned bullies include; how does fine sediment affect patch selection? How does invertebrate composition affect patch selection? What roles do intra- and inter-specific interactions play in patch selection? How does fish size affect diet and territorial behaviour? Answering some of the suggested questions may be challenging using solely field based studies; therefore, future studies on redfinned bullies could incorporate laboratory based work in conjunction with field based work. Laboratory based work would reduce the amount of variability encountered in the natural environment, and certain variables of interest could be controlled, such as fine sediment load or invertebrate composition.

4.1.4 Conclusion

This study sheds light on some of the fine scale aspects of redfinned bully ecology, specifically showing nocturnal patch selection in redfinned bullies is non-random. Results suggest patch selection is primarily driven by substrate and food. Results suggest that during the spawning period substrate may be a more important driver of patch selection than food, with fine sediment having a negative influence on patch selection. My results suggest redfinned bullies prefer abundant invertebrate communities and sediment-free cobble dominated substrates, therefore future management should focus on sustaining such environments. The most important factor that needs to be controlled in order to create a healthy benthic stream environment, with abundant invertebrates and sediment free substrates is land use and human activity within stream catchments (Winterbourne *et al.*, 1981). Human activity such as intensive farming and forestry, are two of the greatest contributors to unhealthy benthic stream environments in New Zealand (Winterbourne *et al.*, 1981), therefore effective management of such activities will aid in management, restoration and conservation of benthic stream environments. This study

has revealed some important aspects of redfinned bully ecology, although the understanding of redfinned bully ecology is still poor and many questions remain unanswered. This study along with other studies on redfinned bullies, provide a good base of knowledge and raise many questions that will act in promoting future research into the unknown aspects of this species. Research provides a better understanding of stream fish ecology, which raises awareness thus promoting and improving future management and conservation of stream fish and their environment. Stream environments and their inhabitants are dynamic and complex; therefore future conservation and management of such systems will require a multi-scale understanding of the system and its inhabitants (McDowall, 1990). Knowledge of the ecology of stream systems and their constituents will act as a key component for ensuring a positive future for New Zealand's stream environments and their inhabitants.

5. References

- Allibone, R., David, B., Hitchmough, R., Jellyman, D., Ling, N., Ravenscroft, P. & Waters, J. (2010). Conservation status of New Zealand freshwater fish, 2009. *New Zealand Journal of Marine and Freshwater Research*, 44: 271 - 287.
- Anoop, K.R. & Hussain, S.A. (2004). Factors affecting habitat selection by smooth-coated otters (*Lutra perspicillata*) in Kerala, India. *Journal of Zoology, London*, 263: 417 - 423.
- Argentina, J.E., Freeman M.C. & Freeman B.J. (2010). The response of stream fish to local and reach-scale variation in the occurrence of a benthic aquatic macrophyte. *Journal of Freshwater Biology*, 55: 643 - 653.
- Arnell, R., Bates, B., Land, H., Magnusson, J.J. & Mulholland, P. (1996). Hydrology and freshwater ecology. In: *Climate Change 1995: Impacts, Adaptations, and Mitigation. Scientific-Technical Analysis* (Eds R.T. Watson., M.C. Zinyowera., R.H. Moss & D.J. Dokken), pp. 325 - 364. Cambridge University Press, Cambridge, UK.
- Bates, D., Maechler, B. & Bolker, B. (2012). Package 'lme4': Linear mixed-effects models using S4 classes. [Online: <http://cran.r-project.org/web/packages/lme4/lme4.pdf>]
- Bateson, M., & Kacelnik, A. (1998). Risk-sensitive foraging: Decision making in variable elements. In R. Dukas (Ed.), *Cognitive ecology: The evolutionary ecology of information processing and decision making*, pp. 297 - 341). The University of Chicago Press, Chicago.
- Bender, E. A., Case, T.J. & Gilpin, M.E. (1984). Perturbation experiments in community ecology: theory and practice. *Ecology*, 65: 1 - 13.

- Bongaarts, J. (2009). Human population growth and the demographic transition. *Philosophical Transactions of the Royal Society*, 364: 2985 - 2990.
- Bragg, C., McKechnie, S., Newman, J., Fletcher, D., Moller, H. & Scott, D. (2009). Variation in abundance and harvest of sooty shearwaters (*Puffinus griseus*) by Rakiura Māori on Putauhinu Island, New Zealand. *New Zealand Journal of Zoology*, 36: 275 - 289.
- Brown, J.S. (1988). Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology*, 22: 37 - 47.
- Cairns, D. (1942). Life history of the two species of freshwater eel in New Zealand. II. Food, and interrelationships with trout. *New Zealand journal of science and technology* 23B: 132 - 148.
- Clapcott, J.E. & Barmuta, L.A. (2010). Metabolic patch dynamics in small headwater streams: Exploring spatial and temporal variability in benthic processes. *Freshwater Biology*, 55: 1365 - 2427.
- Clarke, K. R. & Gorley, R. N. (2006). PRIMER v6: User Manual/Tutorial, Plymouth, PRIMER-E Ltd.
- Death, R.G. (1995). Spatial patterns in benthic invertebrate community structure: products of habitat stability or are they habitat specific? *Freshwater Biology*, 33: 455 - 467.
- Detenbeck, N.E., DeVore, P.W., Niemi, G.J. & Lima, A. (1992). Recovery of temperate-stream fish communities from disturbance: a review of case studies and synthesis of theory. *Environmental management*, 16: 33 - 53.

- Dewson, Z.S., James, A.B.W. & Death, R.G. (2007). A review of the consequences of decreased flow for instream habitat and macroinvertebrates. *Journal of the North American Benthological Society*, 26: 401 - 415.
- Dou, S. & Tsukamoto, K. (2003). Observations on the nocturnal activity and feeding behavior of *Anguilla japonica* glass eels under laboratory conditions. *Environmental Biology of Fish*, 67: 389 - 395.
- Effenberger, M., Sailer, G., Townsend, C.R. & Matthaei, C.D. (2006). Local disturbance history and habitat parameters influence the microdistribution of stream invertebrates. *Freshwater Biology*, 51: 312 - 332.
- Elkin, C. E. & Marshall, D. J. (2007). Desperate larvae: the influence of deferred costs and habitat requirements on habitat selection. *Marine Ecology Progress Series*, 335: 143 - 153.
- Foley, J.A., DeFries, J., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, A.J., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005). Global Consequences of Land Use. *Science*, 309: 570 - 574.
- Gibbs, G. (2006). Ghosts of Gondwana. Craig Potton Publishing, Nelson, New Zealand.
- Gibbons, J. W., & K. M. Andrews. (2004). PIT tagging: simple technology at its best. *Bioscience*, 54: 447 - 454.
- Greenberg, L. A. (1991): Habitat use and feeding behavior of thirteen species of benthic stream fishes. *Environmental Biology of Fishes*. 31: 389 - 401.
- Hansen, A. E. & Closs, P. G. (2005). Diel activity and home range size in relation to food supply in a drift-feeding stream fish. *Behavioural Ecology*, 3: 640 - 648.

- Harrison, S. & Bruna, E. (1999). Habitat fragmentation and large-scale conservation: What do we know for sure? *Ecography*, 22: 225 – 32.
- Hayes J.W., Leathwick J.R. & Hanchet S.M. (1989). Fish distribution patterns and their association with environmental factors in the Mokau River catchment, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 23: 171–180.
- Hayslette, S.E. & Mirarchi, R.E. (2002). Foraging-patch use and within-patch diet selectivity in mourning doves, *Zenaida macroura*. *Ecology*, 83: 2637 - 2641.
- Hickey, M.A. & G.P. Closs. (2006). Evaluating the potential of night spotlighting as a method for assessing species composition and brown trout abundance: a comparison with electrofishing in small streams. *Journal of Fish Biology*, 69: 1513 -1523.
- Hill, J. & G. D. Grossman. (1993). An energetic model of microhabitat use for rainbow trout and rosyside dace. *Ecology*, 74: 685 - 698.
- Hobbs, D. F. (1940). Natural reproduction of trout in New Zealand and its relation to density of populations. *New Zealand Marine Department Fish Bulletin*, 8: 1 - 93.
- Holbrook, S.J. & Schmitt, R.J. (1988). The combined effects of predation risk and food reward on patch selection. *Ecology*, 69: 125 - 134.
- Hutto, R.L. (1985). Habitat selection by nonbreeding, migratory land birds. In: Cody, M., ed. *Habitat selection in birds*. New York, NY: *Academic Press*: 455 - 476.
- Jowett, I.G. & Richardson, J. (1996). Distribution and abundance of freshwater fish in New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research*, 30: 239 - 255.

- Lake, P. S. (2000). Disturbance, patchiness and diversity in streams. *Journal of the North American Benthological Society*, 19: 573 - 592.
- Lake, P. S., Bond, N. & Reich, P. (2007). Linking ecological theory with stream restoration. *Freshwater Biology*, 52: 597 - 615.
- Lamoreux, J.F., Morrison, J.C., Ricketts, T.H., Olson, D.M., Dinerstein, E., McKnight, M.W. & Shugart, H.H. (2006). Global tests of biodiversity concordance and the importance of endemism. *Nature*, 440: 212 - 214.
- Leftwich, K.N., Angermeier, P.L. & Dolloff, C.A. (1997). Factors influencing behaviour and transferability of habitat models for a benthic stream fish. *Transactions of the American Fisheries Society*, 126: 725 -734.
- Madhusudan, M.D. & Johnsingh, A. J. T. (1998). Analysis of habitat use using ordination: The Nilgiri tahr in southern India. *Current Science*, 74: 1000 - 1003.
- Matthaei, C., Arbuckle, C. & Townsend, C. (2000). Stable stones as refugia for invertebrates during disturbance in a New Zealand stream. *Journal of the North American Benthological Society*, 19: 82 - 93.
- Matthaei, C., Uehlinger, D. U. & Frutiger, A. (1997). Response of benthic invertebrates to natural versus experimental disturbance in a Swiss prealpine river. *Freshwater Biology*, 37: 61 - 77.
- McDowall, R.M. (1962). A Redescription of the Fresh-water Red-finned Bully *Gobiomorphus huttoni* (Ogilby). *Transactions of the Royal Society of New Zealand, Zoology*, 3: 3 - 15.
- McDowall, R. M. 1964: Studies on the biology of the Red-finned bully *Gobiomorphus huttoni* (Ogilby). Part I - Habitat and species inter-relationships. *Transactions of the Royal Society of New Zealand, Zoology*, 4: 175 - 182.

- McDowall, R.M. (1965a). Studies on the Biology of the Red-finned Bully *Gobiomorphus huttoni* (Ogilby). Part II - Breeding and Life History. *Transactions of the Royal Society of New Zealand, Zoology*, 5: 177 - 196.
- McDowall, R.M. (1965b). Studies on the Biology of the Red-finned Bully *Gobiomorphus huttoni* (Ogilby). Part III - Food Studies. *Transactions of the Royal Society of New Zealand, Zoology*, 5: 234 - 254.
- McDowall, R.M. (1990). *New Zealand Freshwater Fishes: A Natural History and Guide*. Heinemann Reed, Auckland, New Zealand.
- McDowall, R.M. (2000). *The Reed Field Guide To, New Zealand Freshwater Fishes*. Reed Field Guide Series, Reed books, New Zealand.
- McDowall, R.M. (2010). *New Zealand Freshwater Fishes: An Historical and Ecological Biogeography*. Springer 2010. Fish and Fisheries Series.
- McEwan, A.J. & Joy, M.K. (2013). Habitat use of redfin bullies (*Gobiomorphus huttoni*) in a small upland stream in Manawatu, New Zealand. *Environmental Biology of Fishes*, 96: Online early - DOI 10.1007/s10641-013-0131-9.
- McIvor, C.C. & Odum, W. E. (1988). Food, predation risk and microhabitat selection in a marsh fish assemblage. *Ecology*, 69: 1341 - 1351.
- Midway, S. R., Aday, D. D., Kwak, T. J. & Gross, K. (2010a). Cover Preference of the Carolina Madtom (*Noturus furiosus*), an Imperiled, Endemic Southeastern Stream Fish. *Journal of Freshwater Ecology*, 25: 151 - 154.
- Midway, S.R., Kwak, T.J. & Aday, D.D. (2010b). Habitat Suitability of the Carolina Madtom, an Imperiled, Endemic Stream Fish. *Transactions of the American Fisheries Society*, 139: 325 - 338.

- Motulsky, H.J. (2007). Prism 5 Statistics Guide. San Diego, CA: GraphPad Software Incorporated.
- Niemi, G.J., DeVore, P., Detenbeck, N., Taylor, D., J. Yount, D., Lima, A., Pastor, J., & Naiman, R.J. (1990). An overview of case studies on recovery of aquatic systems from disturbance. *Environmental Management*, 14: 571 - 587.
- Petty, J.T. & Grossman, G.D. (1996). Patch selection by mottled sculpin (Pisces: Cottidae) in a southern Appalachian stream. *Freshwater Biology*, 35: 261 - 276.
- Petty, J.T. & Grossman, G.D. (2007). Size-dependent territoriality of mottled sculpin in a southern Appalachian stream. *Transactions of the American Fisheries Society*, 136: 1750 - 1761.
- Petty, J.T. & Grossman, G.D. (2010). Giving-up densities and ideal pre-emptive patch use in a predatory benthic stream fish. *Freshwater Biology*, 55: 780 - 794.
- Pringle, C.M., Naiman, R.J., Bretschko, G., Karr, J.R., Oswood, M.W., Webster, J.R., Welcomme, R.L. & Winterbourn, M.J. (1998). Patch Dynamics in Lotic Systems: The Stream as a Mosaic. *Journal of the North American Benthological Society*, 7: 503 - 524.
- R Core Development Team. (2006). R: a Language and Environment for Statistical Computing. R foundation for Statistical Computing Vienna, Austria.
- Radif, A.A. (1999). Integrated water resources management (IWRM): An approach to face the challenges of the next century and to avert future crises. *Desalination*, 124: 145 - 153.

- Ramezani, J. (2013). Intensive land use effects on fish communities and their invertebrate prey in Otago, New Zealand. University of Otago, Dunedin, New Zealand: PHD thesis.
- Rashleigh, B., Barber, C., Cyterski, M.J., Johnston, J.M., Parmar, R. & Mohamoud, Y. (2004). Population Models for Stream Fish Response to Habitat and Hydrologic Alteration: The CVI Watershed Tool. U.S. Environmental Protection Agency, External Report 600/R-04/190, Athens, Georgia.
- Richter, B.D., Mathews, R., Harrison, D.L. & Wigington, R. (2003). Ecologically sustainable water management: managing river flows for ecological integrity. *Ecological Applications*, 13: 206 - 224.
- Stamps, J. (2009). Habitat selection, pp. 38-44. Em: The Princeton guide to ecology (S.A. Levin, ed.). Princeton University Press, Princeton.
- Statzner, B., Gore, J.A. & Resh, V.H. (1988). Hydraulic stream ecology: observed patterns and potential applications. *Journal of the North American Benthological Society*, 7: 307 - 360.
- Stenberg, M., & Persson, A. (2006). Patch use behaviour in benthic fish depends on their long-term growth prospects. *Oikos*, 112: 332 - 341.
- Townsend, C. R., Scarsbrook, M. R. & Doledec, S. (1997). Quantifying disturbance in streams: alternative measures of disturbance in relation to macroinvertebrate species traits and species richness. *Journal of the North American Benthological Society*, 16: 531 - 544.
- Tunney, T.D. & Steingrímsson, S.O. (2012). Foraging mode variation in three streamdwelling salmonid fishes. *Ecology of Freshwater Fish*, 21, 570 - 580.

- Usio, N. & C. R. Townsend. (2000). Distribution of the New Zealand crayfish *Paranephrops zealandicus* in relation to stream physicochemistry, predatory fish and invertebrate prey. *New Zealand Journal of Marine and Freshwater Science*, 34: 557 - 567.
- Wiens, J. A. (1976). Population responses to patchy environments. *Annual Review of Ecology and Systematics*, 7: 81 - 120.
- Winterbourn, M. J., Rounick, J. S. & Cowie, B. (1981). Are New Zealand stream ecosystems really different? *New Zealand Journal of Marine and Freshwater Research*, 15: 321 - 328.
- Winterbourn, M. J., Gregson, K. L. D. & Dolphin, C. H. (2006). Guide to the Aquatic Insects of New Zealand 4th Edition. Entomological Society of New Zealand.
- Whitehead, A.L., David, B.D. & Closs, G.P. (2002). Ontogenetic shift in nocturnal microhabitat selection by giant kokopu in a New Zealand stream. *Journal of Fish Biology*, 61: 1373 - 1385.
- Zweimuller, I. (1995). Microhabitat use by two small benthic stream fish in a second order stream. *Hydrobiologia*, 303: 125 – 137.

6. Appendix

6.1 Generalized Linear Model coding (R)

glm(formula = Count ~ factor(Species) + factor(Fish), family = quasipoisson)

6.2 Distance based linear model output

Resemblance worksheet

Name: Resem-bio sqrt-Brae curt- inc FR

Data type: Similarity

Selection: All

Transform: Square root

Resemblance: S17 Bray Curtis similarity

Predictor variables worksheet

Name: Normalised env inc FR

Data type: Environmental

Sample selection: All

Variable selection: All

Normalise

Selection criterion: R²

Selection procedure: Specified

VARIABLES

1	Water depth, at focal point (cm)	Trial
2	Water velocity (ms per sec)	Trial
3	Dominant substrate type	Trial
4	Distance to nearest cover (cm)	Trial

Total SS(trace): 1.3519E5

MARGINAL TESTS

Variable	SS(trace)	Pseudo-F	P	Prop.
Water depth, at focal point (cm)	3635.4	2.708	0.005	2.689E-2
Water velocity (ms per sec)	6440	4.9018	0.001	4.7635E-2
Dominant substrate type	4164.6	3.1148	0.003	3.0805E-2
Distance to nearest cover (cm)	5957.3	4.5174	0.001	4.4065E-2

res.df: 98