Links between personality and individual niche in the freshwater fish *Gobiomorphus cotidianus*

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Abstract

All individuals within a population are unique. Individual variation in behaviour – or animal personality – occurs consistently throughout the animal kingdom. Understanding how individuals vary in their behaviour is imperative in fully deducing the impact that animal personalities can have at the population or even ecosystem level. Resource use has also been shown to consistently differ between individuals in a population, and can have effects on the strength and variety of interactions an animal has within its ecosystem. At present, there has been very little research on how the personality of an animal affects individual resource use, especially the comparison between behavioural variation and diet in a natural setting. The aim of this research was to investigate individual behavioural variation and resource use in a New Zealand freshwater fish (common bully, *Gobiomorphus cotidianus*), and understand how these individual parameters may affect both each other and an individual fish’s fitness. The individual behavioural variation of common bullies was examined through repeated assays of boldness, aggression and exploration in 93 fish. The habitat use, diet and growth of individuals were also repeatedly measured in pond mesocosms that mimicked the bullies’ natural ecosystem. Behavioural types, in particular individual boldness, were found to be moderately to strongly repeatable through time. There were also significant correlations between all behavioural types, where bolder fish were consistently more aggressive and more exploratory, establishing the existence of a proactive/reactive behavioural syndrome. 50% of the total dietary niche width of the population was accounted for by individual specialisation, while habitat use was found to be only weakly repeatable. It was found that behaviour was correlated with individual resource use in fish that had their personality analysed prior to their resource use, where more exploratory, less bold fish ate larger prey in shallower habitats. In contrast, correlations in fish that had their behaviour assayed after placement in mesocosms were non-significant. There were also no significant correlations between an individual’s growth, and its behaviour or resource use, though there was a near-significant tendency for more proactive fish to have slower growth rates. Overall, the discovery of this behavioural syndrome and resource specialisation is important as it highlights the uniqueness in how each individual reacts to different situations and how these could then feed through to alter predator-prey interactions. This could then affect abundances of species at trophic levels with which they are connected, and potentially the functioning and services an ecosystem provides. Ultimately, this study advances our understanding of the individualities of the behaviour and niche within this species, and gives insight into the possible mechanisms for effects that animal personalities can have on ecosystems.
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Chapter One

General Introduction
1. Individual variation in populations

Scientists have long recognised that natural populations are composed of individuals that are phenotypically varied (Van Valen 1965, Huss et al. 2008, Bolnick et al. 2011). This individual variation can play an influential role in shaping species' dynamics, offering the cornerstone for survival in a changing environment, and ultimately providing the basis for natural selection (Bassar et al. 2010, Bolnick et al. 2011). An individual animal may therefore differ significantly from conspecifics in the population in order to increase its fitness and survival (Biro et al. 2003b). These variations may also be consistent in individuals over time (Dingemanse et al. 2012). Consequently, a population is likely not merely a group of animals that vary around a mean ecological parameter (Mittelbach et al. 2014), whether that parameter is a food source, a body shape, or behaviour, but rather a heterogeneous group of animals that are consistently, individually different (Bolnick. et al. 2003, Luttbeg and Sih 2010, Bolnick et al. 2011, Zhao et al. 2016).

Whilst phenotypic variation between conspecifics has been an important focus in evolutionary concepts since its recognition by Darwin (Bolnick et al. 2011), variation at the individual level has often been ignored in ecological disciplines. Prior to the last decade, research has frequently focussed on species-level dynamics, with individual variation being taken simply as random deviation around a mean and not of consequence (Sih et al. 2012, Wolf and Weissing 2012, Mittelbach et al. 2014). This has resulted in many ecosystem models assuming that all members of a population are essentially interchangeable (Bolnick. et al. 2003), which may mask potentially important individual-level variation that could modify ecosystem dynamics to a considerable extent (Mittelbach et al. 2014). From a growing body of work, it has become increasingly clear that populations are in fact composed of individuals that show repeated variation in multiple behavioural and ecological dimensions (Bolnick. et al. 2003, Biro and Stamps 2008). This has been consistently demonstrated across a multitude of taxa and we must therefore appreciate that this variation can affect the variety and strength of ecological interactions and scale up to alter population dynamics and food web ecology (Wolf and Weissing 2012). Despite these possible consequences, our understanding of how individual differences affect species’ ecology remains limited, including links between multiple individual aspects and their potential to affect an individual’s growth, survival and reproduction. Ultimately, a more comprehensive framework of the relative importance and effect of individual variation on an ecosystem is needed to truly understand the ecosystem’s functioning.
Analysing individual variation in ecology is currently at the forefront of much ecological study. From the long-standing knowledge of individual differences in sexes and age class (Polis 1984, Shine 1989) to phenotypic variation in parameters such as morphology (Bourke et al. 1997, Kern et al. 2016), resource use (Ingram et al. 2011), behaviour (Wilson et al. 1993), resistance to pathogens (Johnson et al. 2009) and the ability to tolerate differing abiotic factors (Mathot and Dingemanse 2015), it is clear that there is consistent variation at the individual level. However, what is unclear is how these differences in an individual’s morphology, resource use, behaviour and other variables might interact and play a role in shaping an individual’s ecology, and how this may affect the population, community or entire ecosystem.

To fully understand population or ecosystem dynamics we must take into account variation at the individual level, otherwise we may miss alternative strategies or mask important variation in the ecological aspects of an animal (Wolf and Weissing 2012). Biological trade-offs are likely an important factor as to why an animal may display consistent variation in certain ecological parameters (Mittelbach et al. 2014), therefore individuals may differ in aspects of their ecology and prioritise certain energy or reproductive gains or losses with certain risks. These alternative ecological options would mean an individual interacts in different ways with different parts of its ecosystem (Bolnick et al. 2011), whether that is conspecifics in the population, prey, predators or its environment. Thus, these individual differences have the potential to affect all aspects of an ecosystem, and could alter food web interactions, food availability or ecosystem processes (Bolnick et al. 2011, Wolf and Weissing 2012).

There are major gaps in our understanding of how different aspects of the individual may be linked. Parameters such as an individual’s behaviour, diet, or morphology may influence each other (Ingram et al. 2011, Dwyer et al. 2014) and result in suites of trait correlations should this variation be consistent. For example, an animal that utilises a food source that has larger food items may also have a larger mouth in order to successfully consume this resource (Frederick et al. 2000). Or an animal that is more aggressive may also be larger (Molina-Borja et al. 1998). There are numerous studies of how individual variation in morphological parameters are associated with ecological characteristics (Bourke et al. 1997, Dwyer et al. 2014, Kern et al. 2016). However, there is practically no research on the potential link between the resource use and behaviour of an individual.
How an individual utilises resources, such as food sources or habitats, within its ecosystem will ultimately have an effect on different aspects of the food web within which it interacts (Bolnick et al. 2011, Laskowski and Bell 2013). This resource utilisation may be related to how an individual behaves, with certain behavioural characteristics relating to an individual’s ability to exploit certain prey, access particular areas or interact with conspecifics (Kalinkat 2014, Modlmeier et al. 2015). These predator-prey interactions are the central component of food webs. Therefore, studying individual variation and the links between different parameters is imperative in order to fully understand the ecology of a species and deduce how it interacts within its food web.

The ecological significance of individual variation has received little attention (Mittelbach et al. 2014). While it is known that many species vary individually in aspects such as their diet, behaviour and morphology, the role this variation may play in shaping an ecosystem is poorly understood (Bolnick et al. 2011). Ultimately, a more comprehensive understanding of the relative importance and effect an individual exerts on its ecosystem is needed to truly understand an ecosystem’s functioning. If individual level parameters are ignored we could miss important variation that might alter individual fitness or survival, and that could affect population dynamics to ecological level consequences, such as driving or altering food web ecology through different biological interactions (Modlmeier et al. 2015). For example, both the individual feeding morphology of the freshwater fish alewives (*Alosa pseudoharengus*) and the duration spent in certain habitats strongly influenced the community structure of zooplankton (Post et al. 2008), which suggests multiple facets of an individual’s ecology can have cascading effects to other trophic levels within an ecosystem. Niche partitioning can result from consistent inter-individual differences in the ecology a population, which again may force changes to community structure and ecosystem connections (Tinker et al. 2012, Brandl and Bellwood 2013). Investigating these individual traits could show potential resilience or vulnerabilities to a changing ecosystem, which may be important for survival during environmental change (Sih et al. 2011).

2. Drivers of individual variation
Whilst the proximate causes of individual variation are likely numerous and are yet to be fully deduced, the ultimate reasons for individuals to have consistently varied phenotypes are more intuitive. For a phenotype to persist in a population, it must provide some benefit to either survival or reproduction (Bergmüller and Taborsky 2010, Tinker et al. 2012).
Therefore, how an individual varies in the population, whether it is morphologically, through its diet or how it reacts to a changing environment, should be advantageous to that individual’s fitness. Differences in individual parameters such as diet, behaviour or habitat may be linked to competition (Svanbäck and Bolnick 2007, Huss et al. 2008). In order to aid its fitness an animal might utilise specific resources that others in the population do not, so as to both avoid depleted resources and gain access to more or better food, habitats or mates in the process. Bergmüller and Taborsky (2010) hypothesise that competition and the social niche within which an individual is a part of can drive specialisation in both behavioural variables and interactions with conspecifics, which in turn can result in individuals utilising different resources throughout the population. Therefore competition could mediate certain behavioural traits of an animal, such as its activity levels or exploratory tendencies (Han et al. 2016). Competition could also result in diet specialisations within a population, where certain individuals prefer to consistently utilise particular food sources or habitat types within the ecological niche of the population, so as to avoid competition (Laskowski and Bell 2013).

Trade-offs causing specialisation in individual parameters are a common concept in animal foraging and reproduction literature, and have been frequently documented (Damsgird and Dill 1998). They typically arise when an individual will search for food or mates at the heightened expense of using more energy, or being more conspicuous to predators, and have been shown to cause intra-specific variation in different areas such as food preference, behaviour and habitat use (Biro and Stamps 2008). It has therefore been hypothesised that, because of these trade-offs, the consistent individual differences seen in various aspects of an animal’s ecology can be favoured when those traits enhance growth, fecundity or survival (Biro and Stamps 2008, Bremer Hansen et al. 2009). Some individuals therefore may find it better to stay in one particular habitat, utilising resources immediately available to them and making themselves less conspicuous to predators (Bell and Sih 2007). In contrast, other members of the population may have more exploratory or active tendencies, and therefore may be able to access better resources or avoid competition; however, this could come at the cost of an increased risk of predation (Thomson et al. 2012). These trade-offs between energy gain, loss and predation risk may lead to variation in individual parameters such as behaviour and resource use and could potentially result in suites of correlated qualities an individual is likely to possess (Smith and Blumstein 2008). These correlations are a further potential link in uncovering how consistent individual variation arises in a population, as some members may be better
suited to accessing particular resource types due to other individual parameters such as morphology or behaviour (Luttbeg and Sih 2010).

If individual behaviour and resource use variation are correlated, this may reflect underlying variation in physiological or metabolic traits (Dwyer et al. 2014, Mathot and Dingemanse 2015). The need for a certain amount of energy in order to sustain a metabolic rate may cause individuals to utilise certain resource types and, in turn, the metabolism of an animal could affect the behaviours they exhibit, such as activity levels or exploratory tendencies (Han et al. 2016).

3. Individual behaviour and animal personalities

Inter-individual variability within a population can be seen in an animal’s morphology, genetics and other parameters such as resistance to pathogens (Wolf and Weissing 2012). Animal personality research has also unravelled this uniqueness in many species, showing that individual animals often display their own set of behavioural characteristics that are different from conspecifics (Sih and Del Giudice 2012). Individual behavioural variation can be defined as consistent differences in the behavioural traits of members of a population (Mittelbach et al. 2014). It takes into account the fact that an animal population cannot be defined simply by a mean behavioural type with variation around it, but rather by a collection of varied behavioural traits that are repeatable by that individual over time (Roche et al. 2016). These repeatable behavioural traits may also consistently correlate to form behavioural syndromes or personalities (Stamps and Biro 2016).

Research into variation in individual animal behaviour is a rapidly growing topic in ecology. In the last two decades, there has been a shift from the traditional population level study of animal behaviour to a focus on how individuals may influence populations through their behaviour (Sneddon 2003, Sih et al. 2004, Kalinkat 2014, Mittelbach et al. 2014). Ignoring these consistent differences in inter-individual behaviour and assuming all members of a population can be characterised by mean behaviours have been shown to mask important individual level variation (Mittelbach et al. 2014). In reality, particular individuals may display certain repeatable behaviours that are distinct from others in the population, which could scale up to influence other population and ecosystem dynamics (Dingemanse and Reale 2005, Biro and Stamps 2008).
Individual behaviour was initially studied in the 1970s to 1990s. This was the first research to highlight the potential importance of the individual level of behaviour within a population (Huntingford 1976, Huntingford 1982, Wilson et al. 1993). These studies found that there are indeed individual differences in behaviour and that these differences can play a role in altering conspecific interactions. Since then, a plethora of studies have attempted to measure the personalities of animals, resulting in frameworks and methods for studying certain behaviours (Bell 2007, Carter et al. 2013, Cleasby et al. 2015). Activity, boldness, aggression and exploration are the most common behavioural traits studied, although this “categorisation” of behaviours has received some criticism (Conrad et al. 2011). Because behaviour can vary both between and within individuals, and it is known that behavioural types are not necessarily fixed, some scientists have contended that a “continuum” should be used in identifying animal personalities (Wilson et al. 1993, Sih et al. 2012, Adriaenssens and Johnsson 2013). Use of these “categories” versus a “continuum” of behaviour simply comes down to the way behaviour is measured and the interpretation of results. For example, instead of saying one fish is bold and another is timid, a spectrum analysis would say “one fish is bolder than another” and therefore would not interfere with the way in which the assays are carried out.

4. The relationship between individual behaviour and resource use
In a population, each individual will have unique interactions with the ecosystem within which it resides (Cachera et al. 2017). No two individuals will utilise the exact same resources, which can lead to specialisation in aspects of the niche such as diet and habitat (Stamps et al. 2012) and these can have consequences for the species’ role in the food web (Bolnick et al. 2011). While individual resource use and niche specialisation has been documented across an array of animals (Dall et al. 2012, Hill et al. 2015, Robertson et al. 2015), present research does not entirely appreciate how individuals can vary in numerous ecological dimensions, and how these facets may interplay to influence each other. For an animal to utilise certain resources, it may also need to display certain behaviours, therefore it could be deduced that aspects of an individual’s behaviour and resource use are related (Bergvall et al. 2011). Despite this, very few studies have explicitly studied either the link between individual behaviour and resource use or the role of these aspects of individuality on fitness.

Variation in diet and behaviour of the same individuals may not have been studied previously, as it is reasonably difficult to accurately measure behaviour in a setting where
an animal is still able to access its natural diet over a long period of time. A way to combat this is to assay the behavioural parameters of an animal before or after it undergoes diet evaluation. It is important that these diet choices are measured in a reasonably natural setting with realistic diversity of food sources and habitats, to ensure that our understanding of how behaviour and resource use are linked is applicable to the species’ natural ecology.

Few studies have looked directly at individual behavioural parameters and resource use using the same individuals. A study on fallow deer (Dama dama) looked at the relationships between deer personality and foraging decisions, with boldness being related to food choice (Bergvall et al. 2011), and a study on mud crabs (Panopeus herbstii) found that feeding rate was influenced by individual activity levels (Toscano and Griffen 2014). However, research on field crickets (Gryllus bimaculatus) found that cricket personality was not related to different decisions in macronutrient uptake (Han et al. 2016). These studies evidently highlight both the important link between individual behavioural variation and the individual niche, and the lack of understanding surrounding these potentially important, co-varying parameters.

5. Study Species – Gobiomorphus cotidianus

Freshwater fish have become model organisms for studying individual behaviour (Conrad et al. 2011, Mittelbach et al. 2014), and the relevant literature contains methodology that is geared toward understanding how fish vary in their behavioural types. Gobiomorphus cotidianus, or the common bully, is an abundant, small native fish that is found throughout New Zealand in slow-flowing rivers, lakes and wetlands (Hammond-Tooke et al. 2012). Common bullies feed mainly on benthic invertebrates and zooplankton in the littoral zone of lakes and are themselves important prey for introduced fish species such as salmonid fishes and perch, as well as New Zealand short-finned and longfin eels (Anguilla australis and Anguilla dieffenbachi). Common bullies are mostly solitary, and males become territorial during the breeding season (Stephens 1982, Hammond-Tooke et al. 2012). Freshwater fish have been consistently used as a model organism in studies of individual behaviour (Conrad et al. 2011, Mittelbach et al. 2014, Budaev et al. 2015), and the local abundance of G. cotidianus and their applicability to native New Zealand freshwater conservation makes them an ideal species to use in this research. Individual behavioural variation of common bullies has been observed once before with some success (Hammond-Tooke et al. 2012), finding a significant correlation between activity and
aggression. However, individual diet and habitat use has not been studied in depth in common bullies, and the link between individual behaviour and resource use specialisation is yet to be examined in this species.

6. Aims and Hypotheses
The overall aim of my MSc thesis was to investigate individual variation in the behaviour and resource use of *G. cotidianus* and to deduce how these individual parameters may influence each other. It was hypothesised that individuals would display repeatable behavioural types, and that these behavioural types would consistently correlate to form behavioural syndromes (Chapter 2), as has been found in a previous study on *G. cotidianus* (Hammond-Tooke et al. 2012) and in many other freshwater fish species (Budaev et al. 2015). It was also hypothesised that there would be individual niche specialisation, and that individual resource use will be related to behavioural types or behavioural syndromes (Chapter 3). A secondary aim of this study was to determine how aspects of an individual’s behaviour and ecology might influence that individual’s fitness (Chapter 3). Multiple studies have researched the fitness consequences of individual behaviour (Smith and Blumstein 2008) with varying outcomes as to which behavioural types provide fitness advantages or disadvantages (Cutts et al. 2001, Sinn et al. 2006, Adriaenssens and Johnsson 2010, Careau and Garland 2012, Colchester and Harrison 2016, Kern et al. 2016).

For this study multiple behaviours of individual common bullies were repeatedly assessed, and these same fish had their individual niche use and growth analysed through repeated sampling over a two-month period. The resource use (habitat and diet) of individual fish was analysed in semi-natural mesocosms over this time, where fish had access to food resources and habitats that mimicked the lake from which the common bullies were sourced. The individual behaviour and resource use of 77 fish could then be accurately deduced. This project was the first to examine the relationship between behaviour and resource use in the same individuals, where fish had access to resources comparable to their natural ecosystem.
Chapter Two

Individual variation in the behaviour of

*Gobiomorphus cotidianus*
2.1 Introduction

Every member of a population is unique (Bolnick et al. 2011). Populations are made up of phenotypically varied individuals, and these individual differences are fundamental to evolutionary processes, as they provide the basis for variation that selection acts upon (Sih et al. 2004, Dingemanse and Reale 2005, van Oers and Mueller 2010, Wolf and Weissing 2012). We know that animals vary individually in aspects such as their genetics, morphology, resource use, immunity, physiology and behaviour (Van Valen 1965, Dall et al. 2012, Wolf and Weissing 2012); however, the ways in which these individual characteristics influence one another remains understudied (Wolf and Weissing 2012, Mittelbach et al. 2014). It is becoming apparent that studying animals at the individual level can uncover important, influential variation and that many generalist populations are actually composed of individual specialists that utilise subsets of the population’s niche (Bolnick et al. 2003).

2.1.1 Animal personalities

Animal personalities are widespread across the animal kingdom (Brown et al. 2005, Wolf and Weissing 2012). These personalities are defined as individual behavioural traits that are consistent and stable across different contexts and over time (Wilson et al. 1993). It is now evident that populations of animals cannot generally be classified as having mean behaviours with random variation around this mean, but that this biological variation is actually of direct importance to a species’ ecology (Cleasby and Nakagawa 2011). Individual animal behaviours have recurrently been found to be highly stable, where they seem to be relatively consistent across time and different behaviours can be correlated across contexts and situations (Biro and Stamps 2008, Wolf and Weissing 2012). From hermit crabs (Pagurus bernhardus) showing repetition in multiple behavioural traits (Mowles et al. 2012), to consistent variation in individual chimpanzee (Pan troglodytes) behaviour (Massen et al. 2013), we now know that a plethora of animals display diversity in individual behaviour, and that personalities are not limited to humans.

At the turn of the millennium interest in individual behaviour has come with the development of new terminology, methods and statistical frameworks in which animal personalities can be studied. Individual behavioural traits have been termed, among others, behavioural temperaments, behavioural types, and coping styles (Carter et al. 2013, Toscano and Griffen 2014). These behavioural types are not necessarily fixed (Adriaenssens and Johnsson 2013) and their extent may vary within individuals as well as
between them. “Behavioural syndromes” and “animal personalities” go one step further, to describe correlations between behavioural types, or suites of linked behaviours (Dingemanse et al. 2012, Mowles et al. 2012). This concept has taken hold in animal behaviour research, and behavioural syndromes have been found across multiple phyla (Brown et al. 2005, Sinn et al. 2006, David et al. 2011, Massen et al. 2013). The term “behavioural syndrome” is generally used when an animal consistently displays the same set of multiple behavioural types, with the most common being recorded as the “proactive/reactive” behavioural syndrome. This usually contains suites of boldness, aggressiveness, high activity and exploratory tendencies, and seems to be an applicable concept across a wide range of species (Dingemanse et al. 2007, Dochtermann and Jenkins 2007).

Methods for analysing individual animal behaviour have been developed to accommodate this rapidly expanding research area. Therefore behaviour can be measured using a consistent set of behavioural assays that can be repeated both between individuals in a population and across multiple taxa, which provides a reliable outline for quantifying animal personalities (Dingemanse et al. 2010, Carter et al. 2013). It also allows the study of plasticity and an individual’s variation in a certain behaviour, as well as behavioural types (Dingemanse et al. 2010). The main behavioural traits that have generally been studied are measures of activity, boldness, exploration, and aggression (Conrad et al. 2011). Freshwater fish have become model organisms for studying individual behaviour (Budaev et al. 2015), and can be analysed using robust methodology that is geared toward understanding how fish vary in their behavioural types.

2.1.2 The causes and consequences of animal personalities

Individual variation in behaviour can alter an animal’s interactions with other members of its population, species within the wider community, and its abiotic environment. (Smith and Blumstein 2008, Sih et al. 2012, Wolf and Weissing 2012). Behavioural differences are often connected to life history strategies. Certain behaviours can be linked directly to mortality/fecundity; they may result in an individual using certain habitats, and with that comes exposure to different resources, predators, competitors or parasites. Behavioural variation has also been correlated with alternative pace-of-life syndromes (Tuomainen and Candolin 2011, Zhao et al. 2016). If an animal behaving in a certain way can improve its fitness and survival this may consequently feed back to promote this individual behavioural variation (Smith and Blumstein 2008). Other potential causes of the presence
or absence of behavioural syndromes in a population that have been hypothesised are changes to the environment such as the arrival of seasonal predators or a depletion of energy sources which may force an animal to vary its behaviour (Pruitt et al. 2012, Rupia et al. 2016). Abiotic alterations in the environment have also been shown to coincide with changes to an animal’s behaviour, perhaps to better cope with the new conditions (Dwyer et al. 2014).

It has also been proposed that metabolism may be linked to individual behavioural types and the consistency of syndromes throughout a population (Biro and Stamps 2010, Careau and Garland 2012, Toscano and Monaco 2015). An animal with a faster metabolism could expend more energy therefore most likely resulting in a more active individual, which may coincide with other behaviours such as being more exploratory or bold. This could then link back in to resource consumption, as an individual that expends more energy would require higher or more energy rich food intake, therefore resulting in the need to forage or hunt more effectively. For example, in small mud crabs (Penopeus herbstii) it was found that individual activity level significantly affected the rate of food consumption, with more active individuals eating more food, which suggests a link between metabolism and individual activity levels (Toscano and Griffen 2014).

The role of individual behaviour in ecosystem dynamics and its importance in a larger community sense is understudied (Wolf and Weissing 2012). Life history traits, such as survival and fecundity, are crucial elements of an individual’s fitness, and differences in fitness due to these variations in behaviour can affect the demographics, density and productivity of populations (Biro et al. 2003a, Bassar et al. 2010). Understanding the links between behavioural syndromes and other individual parameters will help us understand how behaviour may play a role in shaping an individual and a population (Bergmüller and Taborsky 2010). Deducing how an animal’s behaviour may affect its inter- and intra-specific interactions also shows us that different behavioural types can affect food web links. We therefore need to understand personalities to figure out how behavioural variation may alter food webs or population resilience.

2.1.3 Parasitism, body size and individual behaviour

Multiple characteristics, such as body size and parasitism, may be drivers of individual differences in behaviour within a population (Coats et al. 2010, Poulin 2013, Dwyer et al. 2014). In order for a parasite to survive and complete its lifecycle, it must be transmitted
from one host to the next (Brown 1999, Day 2001). Most importantly, transmission relies on an interaction between the parasitised animal and its next host and this may occur frequently, or might be more rare (Cézilly et al. 2010). In order to ensure its successful reproduction and survival, a parasite may enhance its chances of successful transmission, and it has become widely accepted that a way this may occur is through behavioural manipulation (Moore 2002, Poulin 2010). Manipulation of host behaviour by parasites has evolved to enhance the probability that a parasite is transmitted, which should result in successful reproduction and lifecycle completion, and ultimately leads to the survival of the parasite species (Moore 2002, Thomas et al. 2005). Parasite load may influence the personality of an individual in order to increase its chances of transmission, or it may hinder an animal’s ability to perform behaviours through decreased fitness, and is thus an important factor to consider when studying the individual behavioural variation of a species.

The size of an individual may also affect its behaviour. The pace-of-life hypothesis predicts animals with higher boldness, exploratory and activity tendencies should be larger-bodied and have a higher growth rate (Réale et al. 2010b) and size and growth rate have been related to behavioural types such as aggression and exploration (Le Galliard et al. 2013, Dwyer et al. 2014, Thomas et al. 2016). Therefore, understanding how body size may play a role in predicting the behaviour of individuals is important in order to fully grasp why certain individuals may display consistencies in behavioural syndromes.

2.1.4 Gobiomorphus cotidianus

Freshwater fish have become model organisms for studying individual behavioural and resource use ecology. *Gobiomorphus cotidianus*, the common bully, is a small, abundant freshwater fish native to New Zealand (Stephens 1982). They are found throughout New Zealand in slow-flowing rivers, lakes and wetlands and feed mainly on benthic invertebrates and zooplankton (Hammond-Tooke et al. 2012). Common bullies are generally solitary however males often display territoriality during the mating season (Rowe et al. 2001). This species is not sexually dimorphic, and fish above 40mm are at least one year old and large enough to be mature (Stephens 1982, Rowe et al. 2001). Common bullies were chosen as the study species for my thesis as it could act as an appropriate model organism for studying facets of individual behavioural variation. A prior study of this species found consistent behavioural types and a behavioural syndrome, as well as an interaction between parasite load and aggression (Hammond-Tooke et al. 2012).
Therefore, some processes for studying the personality of this species have already been validated. Similar goboid freshwater fish species have also been studied for their individual behaviour (Dwyer et al. 2014, Kalb et al. 2016).

2.1.5 Aims and hypotheses

The overall aim of this study was to investigate the individual behavioural variation of the native New Zealand freshwater fish *G. cotidianus*, to identify behavioural syndromes present within the population. This chapter examined the behaviours aggression, boldness and exploration in individual *G. cotidianus* through repeated assays over periods of four weeks. The second aim was to understand how two biological factors, parasitism and fish size, could affect the personality of common bullies. In total, the behaviour of 93 fish was examined and any repeatability and correlations between behavioural parameters were assessed to understand how common bullies vary individually in their behaviour. It was hypothesised that common bullies would show repeatable, consistent individual variation in their behaviour, and that these behavioural types would correlate with each other to form behavioural syndromes. Based on a previous study examining personality in *G. cotidianus* (Hammond-Tooke et al. 2012), it was predicted that:

1) More aggressive individuals were more likely to be bolder and more exploratory, and vice versa, as these behavioural traits would likely complement each other to provide advantages in resource utilisation or predator avoidance, respectively.

2) The increased conspicuousness of bolder/exploratory/aggressive individuals may lead to higher chances of predation and therefore parasite transmission, and aggression and parasite load were found to positively correlate in a previous study (Hammond-Tooke et al. 2012). The pace-of-life hypothesis also predicts larger bullies to have more proactive personalities as bolder, more exploratory fish should be able to grow faster (Le Galliard et al. 2013). Therefore, parasites and total length of fish would correlate with the personalities of *G. cotidianus*, with more proactive behavioural syndromes coinciding with both a higher parasite load and larger-bodied animals.
2.2 Materials and Methods

2.2.1 Field sampling

Lake Waihola (46°02’S 170°05’E) is a relatively small (5.5 km²), shallow (average depth of approximately 1 m) lake 30 km south of Dunedin in Otago, New Zealand. It forms part of a wetland complex that includes Lake Waipori and the Waipori and Taieri Rivers. Lake Waihola is influenced by tides as it is only 0.5 m above sea level despite being ca. 10 km from the mouth of the Taieri River, and saltwater intrusion is rare (Schallenberg et al. 2003). Lake Waihola was selected as the sampling site as it is an important ecosystem for both native and exotic wetland plants, fish, birds and invertebrates, is easily accessible, and is known to have a large population of common bullies (*Gobiomorphus cotidianus*).

There were two fish collection rounds in order to analyse fish behaviour before and after having their resource use examined in the mesocosm portion of the study (Chapter 3). The first round of fish trapping occurred during late spring on the 4th, 5th, 6th, 9th and 10th of November 2015. During mid to high tide, a row boat was used to set Gee minnow traps (6.35 mm square mesh with 25 mm openings at each end) at various locations in the North-East and Eastern parts of the lake. These areas were chosen for their accessibility and their diversity in benthic and shoreline environments. Traps were haphazardly placed throughout the sampling areas, covering a variety of substratum and shoreline characteristics (reeds, shrubs/trees, logs, grass, rocks). Traps were collected the following day at mid/high tide, and were not left for longer than 24 hours to minimise stress to fish.

When the traps were collected, all fish were identified, counted and recorded. Common bullies that were at least 4 cm in total length were placed in 2 L plastic containers, with cool source water replaced every hour and no more than four fish per container. Any other fish species were released where they were caught. Once all traps were checked and fish were collected they were transferred to aquaria in the Zoology Department, and trapping was repeated until 80 bullies were collected. All methods involving animals were approved by the University of Otago Animal Ethics Committee (protocol 85-15).

2.2.2 Fish maintenance

Fish were individually tagged using visual-implant elastomer, which has been successfully used in common bullies previously (Goldsmith et al. 2003) (Northwest Marine Company, WA, USA). Elastomer tags were chosen as the identification method as they are bright and
can be administered on the dorsal side of the fish, which enables individuals to be easily identified from above. This was necessary as fish would later need to be individually identified from a distance for the mesocosm portion of the study. Four colours of elastomer (yellow, pink, orange, and blue) were used in conjunction with four tag placement areas on the dorsal side of the fish. Each bully was assigned a unique elastomer tag combination with coloured tags in one or two dorsal locations. To administer the elastomer tags, a fish was held gently and securely in one hand. The needle of a syringe containing the elastomer was inserted under the scales and skin at one of the four body positions. It was inserted at a flat angle so as not to push too deeply into the tissue and so that the elastomer would be visible. A small amount of elastomer was then carefully injected into the tissue just under the skin whilst the needle was being pulled out. The fish was then placed in a 2 L container containing cool water to recover for at least five minutes, and monitored for any adverse effects to the tagging procedure.

Eight 40 L glass aquaria were filled with freshwater one week before trapping began. Each contained a bubbler, a sponge filter and a 10-cm long section of PVC pipe for refugia. The aquaria were in a climate-controlled animal containment room, at a temperature of 18°C during the day and 16°C at night, which closely mimicked average field temperatures during spring/summer, and a light regime of 12 h light/dark with 1-hour dawn and dusk periods at 7am and 7pm. Prior to being placed in glass aquaria, fish underwent salt water baths in order to treat any potential infections. Ten fish at a time were bathed in salt water for two minutes, to rid them of ectoparasites and fungi. Ten fish were then placed in each tank, grouped with fish of similar size so as to minimise aggression and risk of cannibalism. Fish were left to acclimatise for 24 hours before any feeding took place. Fish and aquaria were checked every day and any fish death, potential illness, cleanliness of aquaria and any issues with equipment were recorded and measures to correct any problems were taken. Fish were fed with frozen bloodworms (Chironomus midge larvae) (Hollywood Fish Farm, Auckland, New Zealand) every second day (approximately six grams per aquaria). Initially they had been fed bloodworms and frozen *Daphnia* (Hollywood Fish Farm, Auckland, New Zealand) on alternating feeding days to ensure the fish experienced a more natural mix of diet types. It became obvious, however, that fish would not eat the *Daphnia*, so it was decided that fish would receive only bloodworms whilst in aquaria. Fish were left to feed for five minutes and any uneaten food and waste were removed both after this time and daily using a fine net and a siphon. Twice a week,
one third of the water in the tanks was replaced and any algal and waste build-up on the tanks was wiped clean.

Thirteen days after the last fish were trapped and brought to the tanks, a parasite or fungal outbreak occurred. Affected fish were put into isolated tanks immediately that contained one-sixth salt water to five-sixths fresh water and five drops of methylene blue. The salt-water was gradually increased throughout the next day to one-third. Fish presenting advanced symptoms were placed in another tank containing one-third salt water and two-thirds freshwater and ten drops of methylene blue to intensely treat them. All equipment was then disinfected using Halamid Universal Disinfectant (Vet Hygiene Solutions Ltd., Auckland, NZ) and tanks were refilled with one-third salt water to two-thirds freshwater, which was slowly phased to freshwater only over the subsequent weeks. Fish were left in these treatments for three days. After this, any fish that were not displaying symptoms of the infection were transferred back to their tanks. Treatment continued until all fish were either deemed healthy, or had died.

Another problem that arose whilst housing the fish was cannibalism, which was both witnessed and was deemed the cause for the disappearance of some fish. Cannibalism was likely caused by aggression or territoriality. If a fish was seen being attacked by another or showed signs of damage (damaged/missing fins, body scarring), they were placed in a fish larvae net to recover away from potential attackers. In total, 36 of the 120 fish died either due to the fungal infection or cannibalism.

2.2.3 Behavioural trials

There were two sessions of behavioural trials. The first behavioural trials were carried out prior to the mesocosm study on the first 80 fish caught (“session one”). The second session was carried out after the mesocosm study on the 40 fish that were caught in February (“session two”). Fish were left to acclimatise for two weeks after capture before behavioural assays began. Behavioural trials took place from the 17th of November 2015 to the 8th of February 2016. Every bully was individually assayed four times for each of the four behavioural traits, however the first round of trials was discounted as it occurred before the fungal outbreak. The following non-invasive trials are well established in the animal behaviour literature (Gosling and John 1999, Dingemanse et al. 2010, Stamps and Groothuis 2010), including studies on G. cotidianus (Hammond-Tooke et al. 2012), and were refined using an earlier pilot study. There were two assays for boldness, one assay
for exploratory behaviour, and one for aggression. All assays were recorded using a GoPro Hero digital camera (GoPro Inc, San Mateo, California, U.S.) and were not viewed in real time to minimise disturbance to the fish during trials.

Prior to each trial, the focal fish was removed from its tank and allowed to acclimatise in an opaque 10-L container for 30 minutes. There was at least an hour between each trial, and all assays were completed within a 48-hour period for each fish. Each fish from both sessions were then tested again approximately 14 and 28 days after the first assays,

**Boldness 1**

The first boldness assay measured the latency time for a fish to emerge from cover (a PVC half-pipe) after a simulated “lunge” predator disturbance (a dark ruler with a cover over the end moving toward but not making contact with the fish, the lunge was performed by the same experimenter for every assay). The refuge was placed in the container 10 minutes before the beginning of this assay to allow the fish to acclimatise to it and be made aware of it. The disturbance took place when the fish was not in the refuge. Once the video was recording, the “lunge” took place and the fish was left for seven minutes, which provided sufficient time for the fish to enter the refuge (two minutes) and exit it (five minutes) should it display those behaviours.

Each video was played back to record each behavioural measure. The time from when the fish entered the refuge to when its head (the tip of the snout to the eyes) emerged from the edge of the refuge was recorded as the latency to emerge from cover after a predator attack. If the fish did not enter the refuge in the first two minutes, its latency was recorded as 0 seconds. Each individual was given a maximum of five minutes to emerge. If the fish did not exit the refuge in this time it was recorded as 300+ seconds.

**Boldness 2**

The second boldness assay measured the latency time for an individual fish to come within 5 cm of a novel object (a black cylinder). After the acclimatisation period, recording began and the novel object was placed approximately 20 cm away from the head of the fish. The fish was given five minutes to approach the object.

When analysing the videos, a timer was started when the novel object was placed in the container, and stopped when the individual swam to within 5 cm of the object. If the
individual did not approach the object to within this distance, then latency was recorded as 300+ seconds.

**Exploratory behaviour**

The exploratory behaviour trials assayed the latency for an individual fish to enter a novel space. At the beginning of acclimatisation, a divider with a covered hole at the bottom was placed halfway across the container. The cover was removed to provide access to the other side of the divider, and the fish left for 5 minutes.

During the video analyses, a timer was started when the cover on the divider was lifted, and stopped once the fish’s head entered the novel space. If the individual failed to enter the space within 5 minutes the latency was recorded as 300+ seconds.

**Aggression**

The aggression assay measured the amount of aggressive movement displayed by an individual fish in a five-minute period of exposure to a mirror in the container, which mimics the presence of a conspecific. This aggressive movement was defined as “lunging” and “active movement against the mirror”, as opposed to passive swimming. The covered mirror was placed in the container at the beginning of acclimatisation. Once acclimatisation was finished, the cover was removed and the fish was left for five minutes.

The amount of time a fish acted aggressively in a five-minute period was analysed in each video by starting and stopping a timer when the fish was displaying aggressive movements against the mirror.

2.2.4 Field sampling II

On the 15th of February 2016 the second session of fish collection took place. This was needed due to the unforeseen extent of fish death that occurred during the first trial period, but was also taken as an opportunity to account for any diet preferences that fish that had been housed in the lab for three months may have picked up. Including a set of fish that had not spent two months in the lab before the mesocosm portion of the study also allowed the effect of potential acclimatisation to captivity to be accounted for within the study and allowed assessment of the effects of prior captivity during the mesocosm part of the project (Chapter 3). For this round of sampling, 30 traps were set on the afternoon of the 15th of February. They were set from shore and collected the following morning. The first 40
common bullies that were more than 4 cm in length were collected, individually tagged, and transferred to the mesocosms in 2 L containers containing cool source water, with no more than four fish per container. All other fish were released.

2.2.5 Fish size and parasite load
At the beginning of the mesocosm study, the total length of each fish was measured. After the mesocosm study, all fish from session one were euthanized using AQUI-S (AQUI-S New Zealand Ltd., Lower Hutt, NZ) and immediately frozen. These session one fish were then dissected and all tissues were examined to determine the parasite load of each fish. Parasite load was defined as the total number of parasites per fish and the parasites that were examined were all trematode or nematode species.

2.2.6 Behavioural trials II
After the two-month mesocosm study (10 February 2016 – 13 April 2016), six 40 L glass fish aquaria were set up in an aquarium room at the zoology department, using 1/3 salt water to 2/3 fresh water in each tank to reduce risk of parasite or fungal outbreaks. The climate-controlled room used to analyse the first session of behavioural trials was not available during the second session, therefore an aquarium room with ambient temperature was used. Fish were treated in a salt-water bath in the same way as the fish in the first round of trials. Six or seven fish were placed in each aquarium, as this seemed to be the optimum density to stop cannibalism without having a large number of aquaria. Fish were maintained in the same way as previously explained, however they were fed only bloodworms (six grams) from the beginning.

Behavioural trials began on the 27th of April 2016 and were undertaken using the same methods and equipment as all previous behavioural analyses. All 37 fish (three died in the mesocosm experiment) were tested three times for each behavioural assay, and euthanized with AQUI-S after their last trial was finished. In total, 97 fish (from sessions one and two combined) had at least one measure of all four behavioural parameters.

2.2.7 Statistical analyses
All statistical analyses were carried out using RStudio (version 0.99.467). Data exploration was undertaken to determine whether the behavioural data fit the assumptions of linear mixed modelling, and transformations were performed where necessary. Linear mixed effects models were run on the behavioural variables aggression, boldness 2 (latency to
approach novel object) and exploration with fish ID and aquarium as the random effects and sex and behavioural analysis session (before or after mesocosm trial) as the fixed effects to account for these potentially confounding factors. A generalised linear mixed effects model was run on the boldness 1 measure. This is because after analysing the videos, it became clear that whether or not a fish actually entered the refuge was a better determinant of boldness, rather than entering and then emerging, as a lot of fish never entered the refuge at all and therefore their boldness could not be quantified. This measure was therefore treated as binomial and analysed separately. Session was found to have a large effect on the behavioural response variables, therefore each session was analysed separately as it became clear that the sessions were not representative or comparable to each other. The intra-class correlation coefficient (ICC) was then calculated using the variance of ID and the variance of the residuals (Nakagawa and Schielzeth 2010) (i.e. the between individual variation in behaviour and the within individual variation) for the continuous data (aggression, boldness 2 and exploration) using the formula:

$$R = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_e^2}$$

Where R is the repeatability, $\sigma_a^2$ is the between-group variance and $\sigma_e^2$ is the within-group variance ($\sigma_a^2 + \sigma_e^2$ is the total phenotypic variance). The repeatability of the binary boldness 1 measure was also calculated using the variance of ID and the residual variance. The residual variance was calculated using the binomial dispersion parameter ($\omega$), which is a measure of the lack of fit to a binomial error structure, and the latent-scale distribution-specific variance for the logistic model ($\pi^2/3$). Hence the latent-scale residual variance is:

$$\sigma_e^2 = \omega(\pi^2/3)$$

And the latent-scale repeatability for proportion data with multiplicative overdispersion is therefore:

$$R_{logitM} = \frac{\sigma_a^2}{\sigma_a^2 + \omega(\pi^2/3)}$$

These measure the repeatability of certain behaviours over time for each individual and range from 0.0 (no repeatability in behaviour) to 1.0 (consistent repeatability in behaviour) (Nakagawa and Schielzeth 2010). Behavioural types were also compared through
Pearson’s product-moment correlation tests to analyse whether the behaviours an individual displayed were correlated with each other.

A Principal Components Analysis was run on the Best Linear Unbiased Predictor values (BLUPs) for each of the aggression, boldness and exploratory variables of fish from session one. BLUPs are the differences between the population-level average predicted responses for a given set of fixed-effect values, and the responses predicted for a particular individual (Robinson 1991, McGilchrist and Yau 1995). To construct these BLUP matrices, linear mixed effects models were run on three of the behavioural parameters (aggression, boldness 2 and exploration). Tank and ID were set as the random effects and sex and sampling round were the fixed effects. PC1 accounted for nearly 70% of the variation in the behavioural data, and was the only PC axis that explained a significant amount of behavioural variation relative to a null broken-stick model. Linear models were then run on PC1 against the total length of fish from both sessions and the parasite load of individuals from session one to infer the effect of size and parasites on the individual behaviour of common bullies.

2.3 Results

2.3.1 Individual Behaviour

The data in all behavioural parameters showed a lot of non-normal distributions, with most having high numbers of zeroes. Transformations did not seem to improve any of the behavioural data. Tank, sex and round did not have any significant influence on the behaviours of individuals; however, fish in session two tended to be less active and aggressive, and be to be slower in all of their latency responses (Fig 2.1).

Session one behavioural trials were undertaken before the mesocosm study and session two were undertaken afterwards. After exploratory data analysis it was decided that each session would be statistically analysed separately due to differences in conditions where the trials took place and session having a very large effect in the generalised linear mixed effects models. Examination of the residual variances of each behavioural parameter showed reasonably normal distributions.
Fish from session one displayed repeatability over time in all of their behaviours (Fig 2.2). This was reflected in ICC values showing between 0.26-0.46 repeatability in the four behaviours. Whether or not a fish entered a refuge had the highest repeatability (ICC = 0.46) and aggression also had moderate repeatability (ICC = 0.39). The latency to approach a novel object (ICC = 0.29) and exploration (ICC = 0.27) had lower but still
relevant repeatability. The repeatability of behaviours of fish during session two was much more variable than session one (Fig. 2.2), with behavioural types ranging from practically no repeatability (aggression ICC = 0.05) to repeatability of nearly 60% for the boldness 1 measure (entering a refuge ICC = 0.59). The repeatability for the latency to enter a novel space was also reasonably high (ICC = 0.42). Approaching a novel object still showed some repeatability, but was fairly low (ICC = 0.19). The boldness 1 measure had the highest repeatability in both sessions one and two. For session one, significant correlations amongst behavioural types were found between aggression and boldness 2 (p = 0.008, df = 58), aggression and exploration (p = 0.0028, df = 53), boldness 1 and boldness 2 (p = 0.044, df = 57), boldness 2 and exploration (p = <0.001, df = 53), and exploration and boldness 1 (p = 0.0018, df = 53). The only behavioural types that did not display a significant correlation were aggression and boldness 1 (p = 0.23, df = 57). Aggressive fish tended to be bolder (in boldness 2 measures) as well as more exploratory, whilst bullies that were shyer were also less aggressive and had lower exploratory tendencies. Pearson’s product-moment correlation coefficients indicated that these relationships were moderate to strong, with significant correlations ranging from 0.25 to 0.60. These correlations imply the presence of an exploratory-bold-aggressive behavioural syndrome in these common bullies.

For session two there were three significant correlations among behavioural types. These

![Figure 2.3](image-url) The Pearson’s product-moment correlation coefficients with 95% confidence intervals of the four behavioural parameters assayed in common bullies (*Gobiomorphus cotidianus*) for sessions 1 and 2. Agg is aggression, Bold1 is boldness 1, bold2 is boldness 2 and Exp is exploration. Because latency was used in boldness 2 and exploration, a lower boldness 2 or exploration score corresponds to shorter latency, which means the fish was bolder or more exploratory.
were between aggression and boldness 1 (p = <0.001, df = 35), aggression and exploration (p = <0.001, df = 45) and exploration and boldness 1 (p = 0.0025, df = 35). The remaining measures ranged from near-significant correlations (boldness 2 and exploration, p = 0.067, df = 35), to clearly non-significant correlations (aggression and boldness 2, p = 0.44, df = 35; boldness 2 and boldness 1, p = 0.55, df = 35). Significant correlations, however, proved to be relatively strong, with all of these correlation coefficients sitting at around 0.50. This, again, suggests the emergence of an exploratory-bold-aggressive behavioural syndrome within the session two common bullies, however only in the boldness 1 measure (Table 2.1, Fig. 2.3, Fig. 2.4). Overall, fish that were bolder tended to be more aggressive and more exploratory and vice versa.

<table>
<thead>
<tr>
<th>Session</th>
<th>Behaviour</th>
<th>Correlation coefficient</th>
<th>p-value</th>
<th>df</th>
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<tr>
<td>1</td>
<td>Agg-Bold2</td>
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<td>**0.0082</td>
<td>58</td>
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<td></td>
<td>Agg-Bold1</td>
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<td>0.23</td>
<td>57</td>
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<td>**0.0028</td>
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</tr>
<tr>
<td></td>
<td>Bold2-Bold1</td>
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<tr>
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<td>53</td>
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<tr>
<td></td>
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<td>**0.0018</td>
<td>53</td>
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<td>Bold1-Exp</td>
<td>-0.482</td>
<td>**0.0025</td>
<td>35</td>
</tr>
</tbody>
</table>

Table 2.1 The Pearson’s product-moment correlation coefficients, p-values and degrees of freedom of the four behavioural parameters assayed in common bullies (Gobiomorphus cotidianus). Agg is aggression, Bold1 is boldness 1, bold2 is boldness 2 and Exp is exploration. Significance: * <0.05, ** <0.01, *** <0.001.

2.3.2 Fish Size and Parasitism

There was a significant effect of fish total length on the PC1 behavioural axis of common bullies in fish from session one (p = 0.041, df = 35). The total length of fish decreased as boldness, aggression and exploration increased, however the effect size of this response was very weak ($R^2 = 0.08$). There was no effect of total length on the behaviour of fish overall (p = 0.3, df = 73) or from session 2 (p = 0.3, df = 35) (Fig. 2.5).
The parasites found in the fish were mostly trematode cysts, often up to hundreds per fish, and a small number of nematodes. Parasites were also found in multiple tissues. There was

Figure 2.4 The correlations of the mean behaviours of individual fish of the four behavioural parameters assayed in common bullies (Gobiomorphus cotidianus) for sessions one and two. Significance: * <0.05, ** <0.01, *** <0.001.
a significant effect of total parasite load on the behaviour of common bullies ($p = 0.04$, df = 35). As parasite load increased, PC1 decreased, demonstrating that more aggressive, exploratory and bold individuals had fewer parasites than their more reactive (shyer, less exploratory and less aggressive) conspecifics. This relationship, however, was very weak, with an extremely small $R^2$ of 0.09 (Fig. 2.6).

### 2.4 Discussion

#### 2.4.1 A behavioural syndrome in bullies

It was found that common bullies displayed consistent individual proactive/reactive personalities across time, showing that this bold-exploratory-aggressive behavioural syndrome does indeed exist in this species, which supports hypothesis one. A previous study on individual behaviour of common bullies also discovered a very similar behavioural syndrome using comparable behavioural assays (Hammond-Tooke et al.)
There seems to be some repeatability in nearly all behavioural types for both sessions in the population, and they were generally of moderate strength. This indicates that repeatability in these behavioural types is present across the population, however there is likely plasticity in these behavioural types, which is shown in these moderate ICC scores. This plasticity is advantageous as it gives the fish more opportunity to respond accordingly to different environmental changes and challenges (Delarue et al. 2015), which may aid in survival and reproduction. Lower repeatability may also be from measurement error or subtle differences in environmental conditions such as temperature or time of day between rounds.

The difference in responsiveness to performing behaviours between sessions suggests that behaviour could have changed or been affected during the mesocosm experiment which carried through to the second session of behavioural trials. The fish may have become less active over the course of the mesocosm study, perhaps due to the high abundance of food present in the mesocosms (Chapter 3). This could have resulted in decreased need for foraging and therefore reduced activity through this acclimatisation (Laskowski and Bell 2013, Sebastien et al. 2016). It may also have been caused by differences in experimental conditions between sessions one and two. Session two was not in a temperature-controlled room and on average fish took longer to perform behaviours or did not perform them at all. Because session two was undertaken in winter and the room was at ambient temperature (generally between 4-13°C, compared to 16-18°C during session one), it likely slowed the fish’s metabolism, thereby decreasing energy output and acting to slow activity levels. Metabolism and behaviour have been closely linked in previous studies (Cutts et al. 2001, Biro and Stamps 2010, Careau and Garland 2012) and energetics are related to temperature. Therefore, the decreased temperatures during session two may have caused the decrease in overall performance of behaviours (Fig. 2.1).

Three of the four behaviours of fish during session one were significantly correlated with each other. These correlations ranged from 0.15-0.59, which indicates that there were some strong correlations between behaviours, and that all were biologically relevant. It was found that as aggression increased, so did boldness 2 (latency to approach a novel object) and exploratory tendencies, suggesting the emergence of a proactive-reactive behavioural syndrome. Aggression and boldness 1 (whether or not a fish entered a refuge after a predator strike), and boldness 1 and boldness 2 were not significantly correlated. In session two similar patterns were found, where aggression, boldness 1 and exploration were all
significantly correlated. It can be concluded that individual *G. cotidianus* that were on average bolder also tended to be more aggressive and more exploratory, and bullies that were shyer were less aggressive and less exploratory. These results are comparable to other fish studies where boldness, exploration and aggressive behaviours have been found to recurrently correlate with each other (Huntingford 1976, Sneddon 2003, Brown et al. 2005, Harris et al. 2010, Conrad et al. 2011, Hammond-Tooke et al. 2012, Kareklas et al. 2016). This indicates that common bullies do in fact display consistent differences in individual behaviour, with behaviours that correlate with each other in suites of syndromes; however, these behaviours are not always repeatable through time and show some plasticity.

### 2.4.2 The influence of parasites and fish size on individual behaviour

Parasite load was found to have a significant effect on the personality of fish that had their behaviour analysed after the mesocosm study (Chapter 3). Parasite exposure was thought to have occurred mostly prior to collection. Fish that scored higher on the PC1 axis generally had less parasites than those with lower scores, which indicates that parasite load and animal personality were linked, with shyer, less exploratory and less aggressive fish being more highly infected. This partly supports hypothesis two, where there was an effect of parasite load on behaviour, however it was in the opposite direction to the predicted relationship. Whilst this relationship proved to be statistically weak ($R^2 = 0.09$), the correlation may have been caused through either parasitic manipulation, parasites causing sickness and altering behaviour, or the behaviour of the fish meant they were more likely to be infected. Parasitic manipulation causes infected individuals to behave in a way that benefits the parasite’s chances of completing its life cycle and infecting its definitive host. This often results in behaviours that may increase predation, such as increased activity (Thünken et al. 2010) and increased phototaxis (Kaldonski et al. 2008, Jacquin et al. 2014). Hammond-Tooke *et al.* (2012) specifically examined the correlation between parasite type and load with the personality of *G. cotidianus*, however found the opposite trend to my results in one behavioural measure: higher trematode infection was correlated with increased aggression. This suggests that host manipulation by parasites may not have played a role in the behaviour of fish in my study, and infection may be more prevalent in shyer, less aggressive individuals as the spaces these fish utilise may overlap more, therefore increasing the chances of contact transmission between individual fish. Parasitic infection may have also caused fish to become less proactive as they may have caused sickness in the fish therefore making them less able to perform these behaviours. In order
to fully deduce the mechanism behind this correlation, the species of parasite infecting the fish and their modes of transmission would need to be more closely examined.

The total length of fish from session one had a significant correlation with the behaviour of these fish, where increased length was correlated with decreased boldness, aggression and exploration. This partially supports hypothesis two, where an effect was present, however, again, this was in the opposite direction to the correlation that was expected. This correlation, however, was extremely weak, with just 8% of the variation in behaviour being accounted for by fish size. There have been varied results in other studies, where morphological characteristics have influenced personality in some (Toscano and Griffen 2014, Thomas et al. 2016) and there has been no association in others (Harris et al. 2010). The significant but weak trend shown here in *G. cotidianus* is the opposite of what the pace-of-life hypothesis, and therefore hypothesis two, predicts. This could be due to smaller fish needing to gain more energy in order to grow faster, therefore their exploratory and boldness traits may be heightened to increase foraging success. However, ultimately the weak correlation here and the non-significance of session two and the combined sessions does suggest that size does not play a large role in predicting the behaviour of common bullies. A limitation of this analysis was that total length was only measured during the mesocosm portion of the study, and not whilst the fish were undergoing behavioural trials. Therefore, although interesting, length is possibly not directly comparable with individual behaviour in this study.

2.4.3 The role of individual behavioural variation in ecology

Similar correlated behaviours were found in common bullies in a previous study (Hammond-Tooke et al. 2012), where aggression, boldness and activity were correlated, which suggests that *G. cotidianus* do display a consistent proactive-reactive behavioural syndrome and corroborates that common bullies that are more aggressive are also more likely to be both bold and exploratory. These consistent, correlated behaviours likely arise through some advantage in having suites of related behaviours (van Oers et al. 2005, Sih et al. 2012). For example, an exploratory individual may also need to be aggressive in order to find and utilise new resources that are occupied by other fish, and bold in order to venture away from known or potentially safer areas. Likewise, a fish that is more shy would likely need to be less aggressive in order to stay in more confined areas, such as under refugia where the population density might be higher. This behavioural syndrome is common and is consistent with personalities found across many other freshwater fish
species (Conrad et al. 2011, Mittelbach et al. 2014). This proactive-reactive personality axis may prove to aid in the survival and reproduction of individuals. A proactive (bold-aggressive-exploratory) common bully may be able to gain access to more nutritionally dense or a higher abundance of food through their ability to forage more effectively and in areas less frequented by the reactive members of the population. This behavioural syndrome is likely to persist as it could also decrease intra-specific competition. This behavioural syndrome may be advantageous as individuals may be able to find and gain access to more or superior mates, therefore enhancing reproduction chances. On the other hand, an individual on the reactive (shyer, less exploratory, less aggressive) side of the spectrum would be more conspicuous, and therefore the chances of predation would likely be decreased, as they would not be prone to endeavouring far from cover or into novel areas that may be more exposed. Reduced aggression would also be advantageous in conjunction with these behaviours, as it would allow individuals to live in closer proximity, such as under refugia, without suffering the consequences of aggressive attacks.

The occurrence of these behavioural syndromes in common bullies could have implications for the population, on the other species with which G. cotidianus interact, and on the ecosystem as a whole. Conspecifics may be forced to employ certain behaviours different to those with which they share habitats with so as to decrease competition and conflict. When other members of the population behave in a consistent way, competition or social conflict may be heightened, which may force more plastic members of the population to alter their own behaviours (Bergmuller and Taborsky 2010). If this behavioural differentiation occurs, which has been seen in my study in common bullies, then the avoidance of competition may result in increased productivity for members of the population (Biro and Stamps 2008, Duckworth 2008). Should behavioural plasticity not occur, this competition due to behavioural syndromes might concurrently result in individual relocation to new habitats. Behavioural types such as boldness have also been shown to influence migratory tendencies in fish species (Chapman et al. 2011), therefore the reactive/proactive personalities found in common bullies could result in changes to population abundance and structure if these syndromes are a driver for certain individuals emigrating from the population.

How an individual fish reacts to changing environmental parameters may be influenced by its personality. For example under predation pressure, rainbow trout (Oncorhynchus mykiss) that exhibited less risky behavioural syndromes had 68 % higher survival rate than
their more bold, exploratory counterparts (Biro et al. 2003b). This demonstrates that more proactive personalities may be disadvantageous should there be higher predator presence, and this could therefore alter individual survival and population demography. Variation in behaviour, however, can additionally enhance population stability and resilience (Sih et al. 2011). Whilst certain behavioural types may be more susceptible to risks, these alternative behaviours might benefit the whole common bully population, as they provide varied responses to environmental change, with some behavioural responses likely being more beneficial than others (Dwyer et al. 2014). Moreover, the variation in repeatability that was revealed in my study highlights the possibility for common bullies to modify their behavioural types. Whilst a proactive/reactive personality axis is certainly present in the common bully population studied here, the plasticity seen in behavioural types over time could be beneficial when facing changes to the environment. This has been documented in rainbow trout where the ability to vary activity and boldness levels enabled the fish to cope in hypoxic conditions (Thomson et al. 2012). The variation in behaviour observed in my study could therefore be imperative to population survival. Individual behavioural variation may be an element on which natural selection acts upon (Réale et al. 2010a, Sih et al. 2011, Yuen et al. 2016), providing a basis for behavioural evolution, should behavioural syndromes prove to be heritable (van Oers and Mueller 2010, Wolf and Weissing 2012).

The behavioural syndrome uncovered here in common bullies will likely have further-reaching effects on the lake community. Individual behavioural variation can ultimately alter the interactions bullies have with their predators and prey, such as risk avoidance for shyer fish, or increased foraging for bolder, more exploratory individuals. This can ultimately affect predator and prey abundances (Post et al. 2008), or it may result in changes to aspects such as predator growth or fecundity should their prey’s behaviour cause them to become more elusive (Conrad et al. 2011, Delarue et al. 2015).

For the management of fish populations, an individual-level approach may be important as it might reveal information about diversities that could be missed if individual variation is not taken into account. Whilst common bully populations are not actively managed in New Zealand as the species is not threatened, the consistent behavioural syndromes exposed here and in other studies of freshwater fish do emphasise the possibility that our more highly endangered native species, such as galaxiids, may also need to be studied at the individual level if we are to be able to manage their populations more effectively.
2.4.5 Conclusions

*Gobiomorphus cotidianus* displayed moderately consistent behavioural syndromes on a proactive/reactive personality axis, where bolder individuals were more exploratory and aggressive. This was demonstrated in two separate population samples of fish, tested approximately three months apart, confirming that behavioural syndromes are consistently present in this species. These personalities present within the population were significantly but not strongly correlated with fish size or parasite load. This suggests that other mechanisms, such as trade-offs between foraging ability and predation risk aversion, may also be drivers in syndrome emergence. Understanding how *G. cotidianus* vary in their individual behaviours gives us important insights into how the population, and how other fish species, may cope under changing environmental pressures, and how individual fish might play an important role in shaping population dynamics and community structure. It is becoming evident that studying animals at the individual level may be imperative if we are to fully understand the role a species plays in its ecosystem.
Chapter Three

Implications of individual behavioural variation on individual niche and fitness in *Gobiomorphus cotidianus*
3.1 Introduction

3.1.1 Individual niche variation

In a population, no two individuals will interact with the ecosystem in exactly the same way (Bolnick. et al. 2003). Many studies have found populations to consist of individuals that are specialists and utilise a subset of the resources used by the whole population (Bolnick et al. 2011, Dall et al. 2012, Stamps et al. 2012). Therefore, categorising individuals as interchangeable members of a population may conceal important differences in resource use that could have substantial consequences for a population’s influence on a food web (Bolnick. et al. 2003). The total niche width of the population (TNW) is made up of the variation in resource use between individuals (between individual component, BIC) and the average variation of resource use within an individual (within individual component, WIC) (Bolnick et al. 2002). Thus, niche variation, which can be defined as within-population niche differentiation, is common and likely important in a species’ ecology.

Causes of individual specialisation are likely linked to trade-offs where an individual is more adept at utilising a certain resource type, and is worse at using others (Dall et al. 2012). These trade-offs have been associated with aspects of an individual’s morphology (Brandl and Bellwood 2013); however, the relationships between variation in ecological, morphological and behavioural parameters of individuals remain understudied. The degree of niche variation within a population can depend on a number of ecological factors, such as competition and predation (Svanbäck and Bolnick 2007, Ingram et al. 2012). Interspecific competition may drive niche variation in either direction, where individuals could become further generalised so as to gain access to enough resources of a wide variety, or more specialised so as to drive out other potential competitors. Intraspecific competition may facilitate niche variation through the need for individuals to specialise on certain resource types so as to successfully gain the resources needed in order to maintain their fitness, and in doing so minimise the competition for these resources (Huss et al. 2008, Bolnick et al. 2010, Laskowski and Bell 2013). This is also more likely to occur if there are a wide variety of resource types that individuals are able to utilise (Huss et al. 2008). Predation can also influence aspects of resource use such as foraging ability or habitat preference, where individuals might avoid certain areas with predators, therefore driving them out of particular habitats (Toscano and Griffen 2014).
Niche variation in a species can have effects on a number of ecological processes. A population that displays more diversity in its resource use will have more interactions with different facets of the food web, and the degree of specialisation within this variation may affect the strength of these interactions (Araújo et al. 2008, Rossman et al. 2015). Niche variation can therefore alter predator-prey interactions and may result in certain prey items being utilised or depleted to a greater extent than others. Within a population, niche variation can lead to niche shifts whereby individuals specialise so intensely on certain resource types that it leads to a permanent alteration in the population’s total niche width (Clutton-Brock and Sheldon 2010, Knudsen et al. 2010, Cachera et al. 2017), and may be accelerated under environmental changes or ecological stress (Smallegange and Coulson 2013). This could lead to changes in the trophic position of both the species undergoing the niche shift and the animals with which it interacts within the food web (Ingram et al. 2012). Niche shifts may also lead to evolutionary changes within the species, should the variation among individuals be heritable (Dall et al. 2012, Smallegange and Coulson 2013). How individuals behave and interact with their environment may well give us insight into their ability to cope with future environmental change and the extent to which an individual can influence their ecosystem. Ultimately, the key to understanding an entire ecosystem may lie within the individual animals that make that ecosystem their home.

### 3.1.2 How forms of individuality can influence each other

Populations are composed of individuals that vary in their morphology, behaviour, physiology and ecology (Wolf and Weissing 2012). They may utilise a subset of the resources that the population uses (Robertson et al. 2015) or individuals may be consistently different in the way they react to new situations (Sih et al. 2012). Ultimately it is likely that many of these forms of individuality will influence each other. The morphology of an individual may determine what type of prey it is able to consume, or correlate with the utilisation of certain habitats (Kern et al. 2016), and metabolism has been linked to individual differences in behaviour in multiple studies (Cutts et al. 2001, Biro and Stamps 2010, Dwyer et al. 2014, Toscano and Monaco 2015). Understanding these connections between forms of individuality is important to fully deduce how individual variation can influence the population, community and ecosystem within which an individual resides and interacts. An animal’s life history can be altered, which can go on to affect fitness aspects such as their growth or susceptibility to pathogens and parasites (Pruitt et al. 2012, Wolf and Weissing 2012) and ultimately influence both population dynamics and evolutionary adaptation (Smith and Blumstein 2008). It is intuitive that how
individuals within a population vary in their behaviour may correlate with differences in
other aspects of their niche such as diet or habitat use; understanding these individualities,
both on their own and in combination, is imperative in fully deducing a species’ ecology
and in understanding how an individual might affect an ecosystem.

3.1.3 The connection between individual variation in behaviour and resource use
How an individual behaves can impact other aspects of its ecology. Whether an animal is
active or bold may influence how far it forages for food (Bergvall et al. 2011). Further, an
aggressive behavioural type could impact interactions with mates (Briffa et al. 2015) or a
non-exploratory fish may be limited in its access to certain habitats (Yuen et al. 2016).
These examples highlight the potentially crucial interplay between an individual’s
behaviour and its resource use (Han et al. 2016). If this link exists it could go on to
influence aspects of an individual’s fitness, and shows how individual variation in
behaviour may play a role in determining food web interactions.

Metabolism has been linked to behavioural syndromes in previous studies (Cutts et al.
2001, Biro and Stamps 2010, Careau and Garland 2012, Dwyer et al. 2014, Mathot and
Dingemanse 2015, Toscano and Monaco 2015). Energy needs may cause an individual to
behave in certain ways to gain access to certain energy sources (Han et al. 2016), or
alternatively, an animal with a faster metabolism may therefore be able to have a more
proactive personality (Toscano and Griffen 2014). Behavioural types and animal
personalities appear to be linked in some way to energy, both in the acquisition and
expenditure of it (Bolnick. et al. 2003, Biro and Stamps 2010). It could then be expected
that these behavioural types may influence both the amount and type of food an animal
eats. And this could be both in the sense of what an individual is able to gain access to
because of its behaviour, or what it needs to consume in order to consistently display their
personality.

Behavioural differences are often connected to life history strategies. Certain behaviours
can be linked directly to mortality/fecundity; they may result in an individual using certain
habitats, and with that comes exposure to different resources, predators, competitors or
parasites; or, lastly, behavioural variation has been correlated with alternative pace-of-life
syndromes (Tuomainen and Candolin 2011, Zhao et al. 2016). If an animal behaving in a
certain way can improve its fitness and survival this may consequently feed back to
promote this individual behavioural variation (Smith and Blumstein 2008). As an example,
a bold or exploratory animal may be less averse to predators and more willing to venture farther from shelter, and could therefore gain better access to resources, whereas a shyer individual, whilst potentially limiting itself in food availability, could avoid predation to a greater extent and save energy. Ultimately these behavioural types can correlate to complement each other and form a behavioural syndrome or animal personality, as was found in *Gobiomorphus cotidianus* (Chapter 2). The more risky, dangerous behaviours of aggression, boldness and exploration may complement each other (Sih and Del Giudice 2012) as they would lead to an animal that should be able to grow fast and reproduce more efficiently through more access to resources, better territory or mate choice (Wolf and Weissing 2012). However, negatives of the potential increased risk of predation or injury present the trade off that individuals may face if they are less plastic in their behaviours. Therefore the benefits that certain behavioural types bring – less competition, more resource access or lower predation risk may be a driver of the consistent animal personalities we see across the animal kingdom.

We currently lack understanding of how resource use and individual behaviour are linked, as very few studies have directly looked at the relationship between an individual animal’s diet or resource use and its individual behaviour or personality. In one such study, the personality and foraging decisions of 15 fallow deer (*Dama dama*) were examined; specifically looking at boldness and dominance and how this affected the amount and type of food a deer ate (Bergvall et al. 2011). It was found that boldness, but not dominance, was strongly and positively related to the amount of food a deer ate in both familiar and novel settings. This study, however, was limited in examining the deer’s food preference by not giving individuals a large, natural range of resources to select from. In another study, Han *et al.* (2016) examined the nutritional preference for macronutrients (protein or carbohydrates) and explorative and aggressive behaviours of field crickets (*Gryllus bimaculatus*). They found that personality did not predict nutritional preference at the individual level in these crickets; however there was a positive correlation with body weight where larger crickets consistently consumed a higher carbohydrate to protein ratio. Yet again, this study was conducted in a highly controlled environment and only gave the crickets a small range of food (protein or carbohydrate) to choose from; therefore, it may be less applicable to individuals’ diets in wild populations. The last study that has directly looked at food intake and personality was of mud crabs (*Panopeus herbstii*), where it was found that small crabs that displayed a more active behavioural type also ate more (Toscano and Griffen 2014). None of these studies gave the animals the chance to forage
in natural or semi-natural environments, where the full range of their natural diet was present. Although these studies yield some very promising results, highlighting the potential link (or lack of it) between personality and diet in these three species, it also accentuates the deficiency of research where the animals being studied are not in ecosystems that resemble individuals’ normal environment. The study presented here addresses this shortcoming by comparing the individual behaviour of common bullies *Gobiomorphus cotidianus* to their use of food and habitat resources in an environment that mimicked their natural ecosystem. This is the first study of its kind and gives us the crucial comparison of repeated individual resource use, individual behavioural variation and how this may be related to other individual fitness parameters in a semi-natural environment.

3.1.4 The effects of an individual’s characteristics on fitness

How an animal behaves exposes it to different aspects of the ecosystem, such as different habitats or co-occurring species (Rossman et al. 2015). These altered interactions within the ecosystem can then result in an animal being exposed to different risks or benefits, such as predation (Toscano and Griffen 2014), competition (Laskowski and Bell 2013), or parasites (Thomas et al. 2010, Poulin 2013). Alternatively it may make food sources or mates more readily available to the individual, which will ultimately play a role in an individual’s growth, reproduction and survival (Smith and Blumstein 2008, Sih et al. 2012, Feldhaar 2014). Individual behaviour has also been found to correlate with parasite infection in many species (Dianne et al. 2014, Horký et al. 2014), including common bullies (Hammond-Tooke et al. 2012). This parasite load can affect fitness levels through parasites causing sickness or depleting energy stores. It may also be a link with behavioural manipulation, where parasitic infection alters an individual’s behaviour to increase its chance of transmission to its definitive host, which often results in an increased risk of predation (Sánchez et al. 2007, Stone and Moore 2014, Gopko et al. 2015). Individual niche and behavioural variation also can influence the nutritional quality and amount of energy an individual may gain, which could impact fitness aspects such as growth.

3.1.5 Aims and hypotheses

The primary aim of this study was to investigate individual niche variation of common bullies (*Gobiomorphus cotidianus*) by examining their repeated diet and habitat use, and to explore how individual resource use is related to individual behavioural variation in these fish. The second aim was to examine how the personality and individual niche
variation of common bullies affects their fitness. The individual behaviour of 120 common bullies was repeatedly assayed to deduce possible behavioural syndromes present within the fish (Chapter 2). The diet, habitat use and growth of these same fish were also examined in pond mesocosms over two months. It was hypothesised that there would be individual specialisation in the diet and habitat use of common bullies and that the personality of individual fish would affect the resource use of these same individuals. Proactive personalities can result in more risk-taking behaviour (David et al. 2011), which may cause these individuals to specialise on resources that are in more exposed areas, less frequented by others and thus potentially more abundant or nutrient-rich. Therefore it was predicted that:

1) Individuals that had more aggressive, bold and exploratory behavioural syndromes would spend more time out of refugia and off the bottom of the mesocosms.
2) That the diets of these individuals would be more specialised towards pelagic food sources.
3) That these individuals would consume prey of larger mass due to the ability to access a wider range of habitats throughout the mesocosm
4) That fish with proactive personalities would have higher growth rates, again because they would have access to a larger range of resources.

3.2 Materials and Methods

3.2.1 Mesocosm set-up
Twenty 1200L polyethylene cattle troughs (Wilson’s PolyProducts, Palmerston North, New Zealand) were set up as mesocosms to mimic pond ecosystems and the Lake Waihola environment. Mesocosms were set up outdoors in Sawyers Bay, near the Otago Harbour in Dunedin, New Zealand. Each tank was first rinsed and scrubbed clean, then filled with approximately 1200L of water from the city water supply. Water was sprayed through a fire hose then left for two weeks to volatise any chlorine present. Wood structures were built to provide shelter and a depth gradient for the fish to utilise. They were constructed using 9mm thick plywood ramps with “steps” added to hold sediment (see below) and stones. These structures were 1.2 metres in length and covered a depth range between 0-55cm. At Sawyers Bay, the structures were placed in the water, all facing the same way. In order to provide enough benthic habitats, along with the sediment, for both bullies and
invertebrates, 10L of washed beach sand (Nichols Garden Group Ltd., Dunedin, New Zealand) was evenly spread into each of the mesocosm tanks.

Four days after the tanks were filled, 80L of sediment/water slurry was collected from Lake Waihola in the areas where bullies were originally caught. Zooplankton sweeps were also carried out at Lake Waihola in order to seed a pelagic plankton community in the mesocosms. A long-handled fine net was swept through water three times, for 20 seconds each. Sediment and zooplankton were transported to Sawyers Bay, where 4L of sediment was evenly spread into each of the mesocosms. Water containing zooplankton from the zooplankton sweep was also divided equally among the mesocosms. This set up was left for two weeks prior to the addition of fish to allow the mesocosms to develop a community of invertebrates for the bullies to feed on.

On the 16th of February 2016, 40 fish that had been collected in the first session of field sampling (November 2015) were randomly selected from the remaining 46 fish, and 40 that were collected in the second session were transported to Sawyers Bay in the same way as all other transportation trips (Chapter 2). At the site, the 40 fish that were collected in the second field sampling trip were uniquely tagged using elastomer tags in the same way as the first session. Each fish from both sampling periods was weighed (after first patting with a damp paper towel to remove excess water), and its total length was measured. Fish were then sorted into groups of four, based on which fish they had been previously housed with in tanks (for fish from the first sampling session), as these fish did not display adverse behaviour toward each other, or on size (for fish from session two) so as not to promote aggression or cannibalism. Each group of four was then randomly assigned to a mesocosm, with separate spatial blocks for fish from the first and second sampling sessions. Each group of four fish was transported to Sawyers Bay and carefully placed into their assigned
mesocosms. Prior pilot studies have shown that four fish per mesocosm was likely to correspond to moderate density in the wild and good food availability (Ingram, personal communication). All methods involving animals were approved by the University of Otago Animal Ethics Committee (protocol 85-15).

3.2.2 Habitat sampling

On the 19th of February 2016 the first habitat analysis took place. Each mesocosm was first viewed from a distance of approximately a metre to observe any fish without creating any disturbance/shadows. Once all fish that could be seen from a distance had been recorded, closer observations were made: as fish were generally similar in colour to the substrate, some searching was often required to both find a fish and identify it by its ID tags.

If a fish was observed and identified its habitat was immediately recorded. This included:

- The depth at which the fish was first observed (to the nearest 5cm)
- The distance of any part of the fish to the closest refuge which were defined as either a PVC tube, the depth structure or riverstones (to the nearest 5cm, if any part of a fish was under a refuge it was recorded as 0cm)

Each observation period lasted approximately 5 minutes per tank, or until all fish had been accounted for. Habitat analyses were repeated three times per week (Mondays, Wednesdays and Fridays); however, on some days sampling did not occur due to heavy rain on the surface of the mesocosm making it impossible to find fish. Half of the analyses were carried out before 12pm, the other half after 12pm to account for potential differences in activity levels at different times of the day, and no sampling took place prior to 8am or after 5pm.

An algal bloom began on approximately the 22nd of February in tank 6, and by the following week thirteen tanks had algal blooms where the bottom of the mesocosm was not visible. This meant habitat observations were seriously hindered throughout these tanks for a number of observation days. 30mL of Algae killer (Wunder algae killer, Hollywood Fish Farm, Auckland, New Zealand) was added to all tanks on the 14th of March, and all but four mesocosms had cleared up completely within ten days.

3.2.3 Gastric lavage

Gastric lavage took place on the 7th March, 28th March, 8th April, and 18th April. Two minnow traps were placed in each mesocosm on either side of the depth structure. They
were left for at least 1 hour before being checked for fish and any fish in the traps were collected and placed in 2L plastic containers containing cool water from that mesocosm. If all fish were trapped, traps were removed and fish underwent gastric lavage; if not all fish were trapped the traps were replaced in the mesocosms. They were checked again at 2 hours since first being placed in the mesocosms and again, if fish were present they were collected. If there were still fish that had not been trapped, the traps were again replaced and left until 3-3.5 hours after they were first set. At this point the traps, and any fish in them were collected and the traps were not reset. The maximum time any trap was left for was 3.5 hours, which generally provided sufficient time for the fish to be caught and lavage to take place throughout the day. This also reduced the chance that the stomach contents will reflect the food a fish may have consumed inside the trap rather than before trapping. Hand-netting was attempted for fish close to the surface or resting on raised structures, but was abandoned as it generally proved ineffective and had the adverse effect of stirring up sediment.

Gastric lavage was performed to obtain a diet sample from each fish at each sampling date. The fish was securely held with its head angled downward and over a receptacle. A thin polyethylene tube attached to a syringe filled with tap water was inserted into the mouth of the fish and carefully moved to the back of the stomach, then 1-3mL of water (the amount of water depended on the size of the fish, with larger fish requiring more water) was pushed from the syringe and into its stomach. This water then washed back out through the mouth, flushing the stomach contents with it, and was collected in the receptacle. Subsequently, the fish was placed in a bucket containing cool water for recovery for at least five minutes. Each fish was carefully monitored after flushing, and no fish showed adverse reactions to gastric lavage. Once all of the fish that were collected from a mesocosm had undergone gastric lavage, and had at least five minutes to recover, they were placed back into their mesocosms. Fish were checked the following day to observe if the gastric lavage was in any way harmful to the fish, however, again, there was no observed mortality or other adverse effects following lavage. The last round of gastric lavage marked the end of the mesocosm study, so the fish that were caught in the first session of field trapping were euthanized using an overdose of AQUI-S (AQUI-S New Zealand Ltd., Lower Hutt, NZ), and the fish from the second session were transported back to the zoology department to undergo behavioural assays.
3.2.4 Diet identification

Diet samples taken during the mesocosm study were identified under a dissecting microscope to the lowest taxonomic level possible, usually family level. Abundance of each prey type was recorded and the length of the first ten individuals of each prey type was measured using an ocular micrometer. Fish that were euthanized directly after the mesocosm study were dissected to inspect the remaining stomach contents that were not recovered with gastric lavage. Fish sex was also confirmed during dissections.

3.2.5 Growth

The total length and weight of each fish were taken before they went into the mesocosms. Every fish that was caught for gastric lavage over the next two months had these measurements taken again. Because every fish (except for five that died) were caught on the last lavage date then each fish had at least two measurements for total length. This information was converted to a growth rate of mm per day.

3.2.6 Statistical analyses

All statistical analyses were carried out using RStudio (version 0.99.467).

3.2.6.1 Resource Use

Exploratory data analysis of the habitat variables “depth” and “distance from a refuge” showed highly skewed distributions where fish were either mostly on or close to the bottom of the mesocosms or under or close to a refuge (i.e. close to 0cm for both). Transformations did not improve any of these distributions, so the data was converted to binomial measures. Therefore depth was recorded as fish either on or off (either swimming or on the structure) the bottom of the mesocosm, and refuge use was recorded as either exposed or under a refuge. The habitat use of each individual was analysed through generalised linear mixed models, which was run on each of the depth and distance from refuge variables. Repeatability of the habitat use was then calculated using the same method as repeatability of the boldness 1 measure (Chapter 2).

The diversity of an individual’s diet (hereafter termed prey type) and the prey mass of prey type an individual consumed were the two diet measures that were analysed. Both diet measures were statistically analysed to measure the degree of individual specialisation within the population by calculating the between-individual and within-individual components of the total niche width of the population (Bolnick et al. 2002).
Degree of individual specialisation = WIC/TNW

= WIC/(BIC+WIC)

= residual variance / (ID variance + residual variance)

This is the ratio of the average individual niche width to the population niche width, and it ranges from 1, where all individuals consume the same prey in the same proportions (no individual specialisation), to 0, where each individual utilises a unique type of prey (maximal individual specialisation).

For prey type, the data for the number of times a prey type was consumed by an individual was aggregated and a matrix of this was created. Because prey type is a categorical variable, the components of niche variation for prey type were extracted using Shannon diversity indices as proxies for variances (Bolnick et al. 2002). The index “E” was also calculated, which is an alternative measure of individual specialisation calculated as the mean pairwise diet dissimilarity of individuals (Araújo et al. 2008).

Prey mass of each prey item was estimated using the length-weight regressions of invertebrates identified (Dumont et al. 1975, Grant et al. 1983, Culver et al. 1985, Yan and Mackie 1987, Benke et al. 1999, Baumgärtner and Rothhaupt 2003a). This is so mass can be analysed as a measure of prey size for each item. Prey item was nested within individual ID and session of sampling. For unmeasured prey items, the average prey type sizes for that individual were substituted. The data were log transformed as this fitted the assumption of normality as the non-transformed data were heavily skewed due to the large number of very small items that were eaten. A linear mixed effects model was run with the mass of individual prey items as the response variable, round and session as fixed variables and ID and mesocosm as the mixed (random) effects.

To analyse the relationship between resource use parameters Pearson’s product moment correlation tests were run on the Best Linear Unibased Predictors (BLUPs; how these were obtained is detailed in Chapter 2) of the four individual niche parameters of prey mass, prey type, whether or not a fish was on the bottom of a mesocosm (depth) and whether or not a fish was in a refuge (distance).
3.2.6.2 Relationship between individual behaviour and resource use

In order to compare the relationship between individual behaviour and individual niche parameters, the parameters had to be converted into variables that had all differences accounted for. To do this, values called Best Linear Unbiased Predictors (BLUPs) were generated for each of the eight behavioural and niche parameters for all of the fish, and separately for fish from session one and session two. These are the differences between the population-level average predicted responses for a given set of fixed-effect values, and the responses predicted for a particular individual (Robinson 1991, McGilchrist and Yau 1995). To construct these BLUP matrices, linear mixed effects models were run on three of the behavioural parameters (aggression, boldness 2 and exploration) and prey biomass. Tank, for the behavioural parameters, or mesocosm, for the biomass parameter, and ID were set as the random effects and sex and sampling round were the fixed effects. Generalised linear mixed effects models were run on the boldness 1 behavioural parameter, the habitat variables (depth and refuge use) and whether or not prey consumed was pelagic as these were all binomial parameters. ID and tank (boldness 1) or mesocosm (habitat and pelagic food source) were the random effects, the fixed effects were sex and sampling round, and the link function used was the logit function. From these models, the random effects due to fish ID were found, which gives the conditional modes or the individual-level effects or the BLUPs.

To analyse the relationship between individual behaviour and individual niche variation, a canonical correlation analysis was used under the package CCR in R, which took the two matrices constructed from the behaviour and niche BLUPs and compared them. The canonical correlation analysis rotated the matrices to form the most highly correlated dimensions present in each of the data sets. It allowed us to examine how each variable is related to each canonical correlation and tested each canonical correlation for significance. Canonical correlations were run for all fish together and for fish from separate sessions due to the differences found in behaviour between sessions (Chapter 2).

3.2.6.3 Individual parameters and growth

Principal Components Analyses (PCA) were run separately on the four behavioural parameters and on the four niche parameters in order to determine how these individual characteristics were related to the growth rate of each fish. These were run on all of the fish (overall) and fish from session one and two separately to account for the differences that occurred in behaviour before and after the mesocosm trials (Chapter 2). Using a
broken stick analysis, it was determined that PC1 was the only PC axis that explained more variation than a null model would for all parameters in all sessions. Therefore, the PC1 scores were extracted from each of these and linear models were run against the growth rate and the start length of each fish for behaviour and niche PC1 scores for each session.

3.3 Results

Five fish in total died during the course of the mesocosm study (two from session one and three from session two). All of these were from separate tanks. There were no evident reasons why the fish had died (i.e. no obvious injuries, starvation or external parasites/fungus).

3.3.1 Habitat

There was some repeatability in habitat use for individuals, which was low to moderate. Repeatability, which can range between 0 (no repeatability) and 1 (consistent repeatability), was at about 0.20-0.25 where individual fish utilised the same depth and were in a refuge over time (depth ICC = 0.25, distance ICC = 0.203). For both habitat use parameters, round (sampling date) did have some significant effects, and mesocosm accounted for a large portion of the variance for the distance variable (variance = 0.69), when compared to the between individual variation (variance = 0.81). The Pearson’s product-moment correlation coefficient between between depth and whether or not a fish was in a refuge was weakly positive (0.18) but not significant (p = 0.12, df = 76) (Fig. 3.1).

**Figure 3.1** The relationship between whether or not individual *Gobiomorphus cotidianus* were on the bottom of the mesocosm (Proportion on benthos) and whether or not a fish was in a refuge (Proportion shelter use), where 0 = on bottom/in refuge and 1 = off bottom/not in refuge. Each data point is the average depth and refuge use of an individual fish observed over 22 sampling rounds (N = 77).
3.3.2 Prey type
Stomach flushing showed sufficient efficacy, where on average 72% of the stomach contents of each fish were flushed through gastric lavage. There did not seem to be any apparent bias with the prey sizes that lavage was able to extract from the fish, although lavage can miss very large items. The degree of individual specialisation in prey type using the variance from the between- and within-individual components of the total niche width was about 50% (WIC/TNW = 0.498, where BIC = 0.904, WIC = 0.91 and TNW = 1.814), showing that 50% of the total niche width can be accounted for by individual specialisation. E, an alternative index that calculates diet specialisation using pairwise diet dissimilarity between individuals was 0.697, which also indicated high diet specialisation in the common bullies sampled.

3.3.3 Prey mass
The degree of individual specialisation of the biomass of each prey type consumed by common bullies was similar to that of prey type consumed, about 50% (WIC/TNW = 0.53), which means that half of the total niche width of the population can be accounted for by the within-individual variation in diet biomass of the fish. Mesocosm, sample round and whether or not the fish had been in the lab previously did not have an effect on the degree of individual prey biomass specialisation. The individual components of the niche were BIC = 0.73, WIC = 0.81 and TNW = 1.54.

3.3.4 Overall resource use
Individual fish’s mean prey type consumed was significantly correlated with individual mean prey mass, where prey mass decreased when a higher proportion of pelagic prey was consumed (Fig. 3.2) in both sessions combined (p < 0.001, df = 62), session one (p = 0.0012, df = 32) and session two (p < 0.001, df = 32). There were no significant correlations between any of the other resource use variables, and all Pearson’s product correlations were weak or negligible. There were, however, two near-significant correlations, where the prey mass consumed was larger when individuals from session one did not use refugia (p = 0.052), and the prey mass was also larger when individuals from both sessions combined were off the bottom of the mesocosms (p = 0.081) (Fig. 3.2).
3.3.5 Relationship between individual behaviour and resource use

Canonical correlation analysis found an overall (session one and two combined) correlation of 0.36 for canonical correlation coefficient 1, between the individual behaviour and resource use of common bullies, however, this canonical correlation was not significant ($p = 0.71$, $df = 62$). The only individual behavioural correlation score (in canonical 1) that was potentially biologically relevant was boldness 1 (correlation score = 0.51). The niche parameters were much more strongly correlated with canonical
correlation coefficient 1, with scores ranging from 0.66 to -0.97 and showed that fish that ate larger prey and consumed a higher amount of pelagic prey tended to spend more time off the bottom of the mesocosm and exposed (not using a refuge) (Tab. 3.1; Fig. 3.3).

Session one, however, did show a significant canonical correlation between behavior and resource use ($p = 0.0018$, df = 32) where more exploratory, less bold fish utilised shallower habitats and ate larger prey. The canonical correlation was 0.76 between individual behaviour and resource use for canonical correlation coefficient 1. (Tab. 3.1; Fig. 3.4).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Canonical Coefficient 1</th>
<th>Canonical Coefficient 1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overall</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>Aggression</td>
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</tr>
<tr>
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<td></td>
<td>Exploration</td>
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<tr>
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<td>Depth</td>
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<tr>
<td></td>
<td>Distance</td>
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<tr>
<td></td>
<td>Prey mass</td>
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<tr>
<td></td>
<td>Pelagic</td>
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<tr>
<td>Session One</td>
<td>0.76 (p = 0.0018)</td>
<td></td>
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<tr>
<td></td>
<td>Aggression</td>
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</tr>
<tr>
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<tr>
<td></td>
<td>Pelagic</td>
<td>-0.64</td>
</tr>
</tbody>
</table>

Table 3.1 The canonical correlation coefficients for the behavioural and niche parameters of *Gobiomorphus cotidiana*. This is split into canonical coefficient 1 in all fish (overall, both sessions 1 and 2 combined, $N = 63$) and fish from sessions one ($N = 33$) and two ($N = 30$) separately. The canonical coefficient 1 scores show how each parameter is correlated with its respective canonical correlation coefficient.

In session two there was no significant canonical correlation ($p = 0.51$, df = 29) and the overall canonical correlation coefficient 1 was 0.54 between the behaviour and resource use data. (Tab. 3.1; Fig. 3.5).
Figure 3.3 The relationship between the behaviour and niche of individual *Gobiomorphus cotidianus* for all fish (N = 63). Each data point corresponds to an individual fish. A higher behaviour canonical score corresponds to fish that were more bold, and a higher niche canonical score corresponds to fish that spent more time on the bottom of the mesocosms, more time in refugia and consumed larger, more pelagic prey.

Figure 3.4 The relationship between the behaviour and niche of individual *Gobiomorphus cotidianus* for fish from session one (N = 33). Each data point corresponds to an individual fish. A higher behaviour canonical score corresponds to fish that were more exploratory and more bold, and a higher niche canonical score corresponds to fish that spent less time on the bottom of mesocosms and ate larger prey.
3.3.6 Individual parameters and growth

Total length of fish at the beginning of the mesocosm study was significantly and strongly negatively correlated with growth in fish from all sessions across both behaviour and niche (p < 0.001) (Fig. 3.6).

Behaviour PC1 of fish overall and of fish from session one were not significantly related to growth rate (p = 0.322 and 0.9, respectively). The behaviour of fish from session two was very close to significant (p = 0.053, partial eta² = 0.11, df = 35) suggesting that the behaviour of fish from session two may have had some effect on the growth of fish. The partial eta-squared showed that 11% of the variation in individual growth could be explained by PC1 behaviour, demonstrating a weak relationship. Fish that had a larger PC1 (a more exploratory, bold and aggressive fish) had a slower growth rate over the mesocosm testing (Fig. 3.7).

Niche PC1 from fish overall, and from fish from each separate session was not significantly correlated with fish growth (p value = 0.54, 0.52 and 0.63 respectively).

Figure 3.5 The relationship between the behaviour and niche of individual Gobiomorphus cotidianus for fish from session two (N = 30). Each data point corresponds to an individual fish. A higher behaviour canonical score corresponds to fish that were less bold, and a higher niche canonical score corresponds to fish that spent more time in refugia and ate less pelagic prey.
3.4 Discussion

3.4.1 Individual habitat use

There was some repeatability in individual habitat use throughout the mesocosm study, which supports hypothesis one, however this was reasonably low across both sessions. This low consistency indicates a large amount of within-individual variation in the use of refugia and different depths, and also suggests that individuals were rather flexible over
time in their habitat choices. Whilst common bullies have previously been thought to be a reasonably sedentary fish (Wilhelm et al. 2007), this diverse habitat use highlights that they perhaps relocate themselves more often than previously thought. Although activity levels could still be low, the mesocosms used in my experiment were reasonably small and provided the opportunity for fish to move about freely. Lack of predators and therefore any predator cues such as kairomones may also influence the habitat use of individuals (Thünken et al. 2010, Zhao et al. 2016). Whilst the behavioural portion of this study indicates that some fish do take more risks than others, the lack of perceived risk in the mesocosms may result in fish consistently changing where they position themselves, which may cause the low repeatability (Huntingford 1982, Bell and Sih 2007, Harris et al. 2010, Thünken et al. 2010, Hammond-Tooke et al. 2012, Toscano and Griffen 2014).

There were also a number of difficulties that occurred during the habitat analyses in the mesocosm study. The most apparent was the fact that individuals could often not be found due to fish either being completely hidden under refugia or camouflaging with the substrate. Therefore only a subset of the individuals could be sampled at each habitat analysis occasion. Whilst 22 sampling dates did provide many opportunities for fish to have their habitat preference observed, these problems often resulted in less than a third of the sample population being identified and having their habitat use recorded on any given sampling date. This could have biased the habitat results toward individuals that did not use refugia as often. It was also difficult to get good fine-scale measures of the habitat variables, as using any measurement tools in the water would disturb the fish too much, therefore the habitat measures were fairly imprecise. An algal bloom caused poor visibility in many of the tanks over multiple sampling dates; at one point all but 4 tanks had such poor visibility that the substratum on the bottom of the mesocosms was not detectable. This meant there was a period during the mesocosm study (about 7 sampling occasions) where it was difficult to analyse many of the mesocosms reliably as it was impossible to see any fish that were utilising the deeper areas of the mesocosm. Based on these results, overall there seemed to be little consistent individual preference for different depths or distances from a refuge; however, this likely cannot be confidently concluded due to the issues that arose during sampling.

3.4.2 Individual diet

Individual specialisation was higher for diet than habitat, with about 50% individual specialisation in both prey type and prey size. This supports hypothesis two and indicates
that half of the total niche width for prey type and mass was accounted for by individual specialisation in these parameters. Individual diet specialisation has been documented previously in other freshwater fish species (Bolnick et al. 2010, Ingram et al. 2012, Laskowski and Bell 2013); however this is the first time it has been studied in bullies. It presents an interesting result as bullies have often been classified as a generalist species (Rowe 1999, Vanderpham 2012), where any member of the population can consume any prey item, and is essentially interchangeable. The diet specialisation in 50% of the population shown here, nonetheless, indicates that certain individuals are more specialised on particular prey types and prey sizes, and that individuals in the population are therefore more unique in their ecology.

This individual diet specialisation may be the result of competition avoidance, where certain individuals specialise on prey different to that from others in the population, so as to avoid the depletion of resources and gain more energy individually (Svanbäck and Bolnick 2007, Laskowski and Bell 2013, Rossman et al. 2015). Intraspecific competition was found to cause divergence in the resource use of threespine sticklebacks (Gasterosteus aculeatus) where individuals were more specialised on certain prey types when more conspecifics were present (Svanbäck and Bolnick 2007, Laskowski and Bell 2013). The lack of interspecific competition was also shown to increase individual specialisation in sticklebacks (Bolnick et al. 2010). Although the mesocosms mimic the Lake Waihola ecosystem, they do lack other fish species that bullies may compete with, such as European perch (Perca fluviatilis) (Rowe 1999). The absence of interspecific competitors may drive niche expansion in individual fish, therefore allowing them to specialise on certain prey types and sizes within the mesocosms without the competitive pressure imposed by other species.

Diet specialisation can have distinct effects on different facets of the ecosystem. For common bullies, this specialisation suggests individuals may exert a marked effect on population dynamics and interactions with other community members and it highlights the potential for individuals to have varied interactions with prey. This could then lead to changes in the abundance of certain prey types (Tinker et al. 2012, Eloranta et al. 2013) should individuals be highly specialised on particular resources. These shifts within the community may then flow on to exert changes on other trophic levels (Araújo et al. 2011, Ingram et al. 2011, Eloranta et al. 2013). Individual specialisation in both prey type and mass may lead to changes in the fitness of individuals (Roughgarden 1972), as the growth,
fecundity and survival of a fish may depend on the availability of its prey. Therefore, specialising on one or few prey types may be detrimental if that prey were to become depleted and the fish were not very plastic in their diet (Araújo et al. 2011). This decreased food intake may result in the reduced fitness of individuals through the inability to obtain sufficient energy and may even result in mortality (Bolnick. et al. 2003, Clutton-Brock and Sheldon 2010). On the other hand, the resilience of a population may be improved by individual specialisation and diet variation (Feldhaar 2014). A varied diet within the population could be beneficial when there are changes in prey abundances, as it provides a number of different resources for members of the population to utilise (Wolf and Weissing 2012). This individual variation therefore can also aid in the survival of a population.

Most resource use variables were not correlated with each other in my study. The only significant correlation was between prey size and the proportion of benthic prey; this is simply because benthic prey such as chironomids tend to be much larger than pelagic taxa such as *Daphnia* and copepods (Baumgärtner and Rothhaupt 2003b). There was a nearly significant result, where fish that spent more time out of refugia consumed prey with larger mass. Because refugia could have higher densities of individuals (smaller area of the mesocosms than the exposed areas and many individuals utilising it), the bigger prey may be less abundant. Therefore individuals that ventured away from refugia could have had access to larger prey. The other near-significant correlation was that fish on the bottom of the mesocosms consumed smaller prey. This seems counterintuitive, as benthic prey should be larger (with the exception of mosquito pupae (*Culicidae* spp.)), as shown by the only truly statistically significant result here. However, few fish were ever swimming when observed. This result could be that the high number of fish that were on the bottom did utilise the water column when not being surveyed. It is curious that there were no strong correlations in most of the parameters. This result suggests that fish, even though they were specialised in diet, do not have affinities for certain areas even though those areas may contain more of the individual’s preferred prey type. Nevertheless, we again cannot be completely certain on the reliability of the habitat results, due to their borderline significance and the issues raised earlier, but this does still pose interesting findings on the individual resource use of common bullies.

3.4.3 The relationship between behaviour and resource use

The first canonical correlation coefficient was significant in fish that underwent behavioural trials before having their individual niche analysed. This reveals that there
were meaningful correlations between the individual behavioural variation and resource use of common bullies, where exploration and shyness were predictive of fish that were found in shallower habitats and consumed larger prey items. This result partially concurs with hypothesis three. It was thought that animals with more proactive personalities would venture to shallower, more exposed depths where prey were likely pelagic and therefore smaller. More exploratory individuals did utilise shallower areas, however these individuals were also shyer and ate larger prey. This suggests that behavioural types, but not behavioural syndromes (correlated behavioural types), influenced individual niche. Risk-taking individuals may be able to gain access to more or better resources due to their ability to inhabit areas that others cannot (Roughgarden 1972, Svanbäck and Bolnick 2007, Robertson et al. 2015). The trade-off between predator aversion and foraging success likely causes some individuals to exhibit these more risky behaviours (Araújo et al. 2011) and these findings support this, where individuals that were more exploratory ate larger prey items in areas that were likely more exposed (shallower). This novel result demonstrates a relationship between the individual behavioural types of an animal and the resources that that same individual utilises within an environment that is close to its natural ecosystem.

Fish that had their behaviour analysed after the mesocosm study did not show significant correlations between their individual personalities and niche parameters. Being in a mesocosm for two months prior to the laboratory, where prey was abundant and there was no predation risk, may have altered individual behaviours. The lack of predator avoidance needed could have caused individuals to become less variable in their behaviours (Harris et al. 2010, Urszan et al. 2015). Animals are able to learn and modify their behaviour to fit the experiences they undergo (Schneirla 1941). Therefore, the fish learning that there was no predation threat in the mesocosms may have resulted in these fish altering their individual behaviour in the laboratory, regardless of their individual resource use. It also highlights that both individual behaviours and resource use are not necessarily fixed and can be plastic over time (Dall et al. 2012, Mittelbach et al. 2014). Consequently, even though fish did show individualities in separate parameters, their behaviour did not influence the foraging or habitat use capabilities of fish from session two. Although there is likely some sort of relationship between resource use and individual behaviour (Bergvall et al. 2011, Toscano and Monaco 2015), the results shown here suggest that it is probably more complicated than straight correlations between animal personality and individual niche. How behaviour influences resource use might be mediated by other biotic factors
such as competition and predation (Toscano and Griffen 2014), both of which were lacking at least partly in the behavioural trials and in the mesocosms. Predation and competition have both been shown to facilitate prey consumption (Svanbäck and Bolnick 2007, Toscano and Griffen 2014) and change behavioural reactions (Yuen et al. 2016) and their presence may be important in causing more obvious specialisation in habitat utilisation. Finding this one correlation between resource use and animal personality in common bullies is evidence that resource use is impacted by behaviour; however how this occurs is likely more complicated than a simple correlation and bullies may be more plastic than previously thought.

3.4.4 Growth and individual behaviour and resource use

The growth of individuals was not significantly impacted by their personality in my study, which does not support hypothesis four. The role of behavioural types in shaping an individual’s fitness is likely complicated, and involves many aspects of the animal’s individual ecology (Stephens 1982, König and Schmid-Hempel 1995, Adriaenssens and Johnsson 2010, Wolf and Weissing 2012). Whilst fitness aspects such as mortality from predation (Biro et al. 2003a, DiRienzo and Montiglio 2016) or injury through aggression (Biro et al. 2003b) may be more directly comparable to that individual’s risk taking and therefore its behavioural syndrome, the growth of an animal likely has many more aspects that have varying degrees of importance in shaping an individual’s growth. Some of the bullies reproduced, or became reproductive during the study which may account for the correlation between starting size and growth. The only close-to-significant result in my experiment was that individuals from session two that had more reactive personalities grew faster. Fish that were smaller at the beginning of the mesocosm trials did grow the fastest. However there was no link between individual behaviour and starting length, therefore it cannot be concluded that shyer fish were smaller to begin with. In brown trout (Salmo trutta) it was also found that less exploratory trout grew faster, which challenges the hypothesis four (where bolder/aggressive/exploratory individuals forage more and grow faster) (Adriaenssens and Johnsson 2010). Behaviour that saves energy, such as shyness and reduced exploration, may contribute more to growth than more risky behaviours that promote higher foraging (Careau et al. 2008), therefore resulting in individuals with reactive personalities growing faster. Adriaessens and Johnsson (2010) also found no correlations between any behavioural parameters other than exploration with growth, which concurs with these results. Moreover, the high abundance of prey within the
mesocosms could have resulted in all fish, regardless of their foraging ability or risk taking tendencies, being able to gain access to nutrient dense food sources.

3.4.5 Conclusions

Never before has the individual resource use of an animal population been compared to the animal’s personality in a setting where individuals had access to their natural range of diet resources. Consequently, the finding that individual common bullies that were more exploratory and less bold in their behavioural types also utilised shallower habitats and consumed larger prey is an important, novel result. It highlights the potential for individual behavioural variation to have critical effects on an individual’s ecology and it can also impact their fitness. These results confirm that there is indeed a link between animal personality and individual resource use; however they also demonstrates the complexity of these interactions and how they may depend on a number of other factors such as prior learning. Ultimately, finding this correlation gives us the first insight into how the individual parameters of an animal’s niche and behaviour are inherently connected.
Chapter Four

General Discussion
4.1 The relationships between forms of individuality

This thesis found that *G. cotidianus* exhibit individual variation in both behaviour and resource use, however these were only correlated in half of the fish and were generally not related with individual growth. Common bullies were found to have a proactive/reactive personality axis, where individuals that were bolder in their behaviours were also consistently more aggressive and exploratory, and vice versa (Chapter 2). This confirms that these fish do display consistently correlated behaviours, corroborating previous research (Hammond-Tooke et al. 2012). This proactive/reactive behavioural syndrome has also been found throughout the animal kingdom (Bell 2007, Dingemanse et al. 2010, Réale et al. 2010a, Conrad et al. 2011, Sih et al. 2012, Cleasby et al. 2015, Mathot and Dingemanse 2015), and these correlated behavioural types do tend to complement each other in an ecological sense. Thus a bolder individual would explore more, as it takes more risks, and may encounter more unknown conspecifics and thus require heightened aggression. It has been proposed that these behavioural syndromes can alter the variety and strength of ecological interactions with individuals (Wolf and Weissing 2012), through different personalities accessing varying resources (Chapman et al. 2010, Han et al. 2016).

It was also found that individual common bullies specialised in diet, and to a lesser extent in habitat use (Chapter 3). About 50% of the total niche width of individuals was accounted for by individual specialisation in both prey type and prey mass, where fish would eat larger, benthic prey or smaller, pelagic prey. The absence of interspecific competitors, and perhaps predators, can facilitate specialisation as a result of intraspecific competition. (Svanbäck and Bolnick 2007, Bolnick et al. 2010, Laskowski and Bell 2013). The low repeatability in habitat use demonstrates little individual affinity with particular depths or refuge use in common bullies. However, less refuge use was correlated with individuals consuming more benthic, large prey, which suggests that utilising habitats that are exposed may prove advantageous in foraging for larger prey.

Perhaps the most important insight resulting from this study was that there was a relationship between the individual behaviour of fish and their resource use (Chapter 3). Shyness and more exploratory behaviours were predictive of fish spending more time in shallower areas and consuming larger prey. This result confirms the hypothesis that animal personalities can affect the resource utilisation of individuals. However, this was only found in fish that had their behaviour analysed prior to their resource use, which suggests
fish may be quite plastic in their behaviours and resource preferences depending on what they have experienced prior.

There was no significant correlation between fish growth and individual behaviour or resource use (Chapter 3). However, the growth rate of fish that were not in the lab before resource use analysis did have a near-significant correlation with their behavioural syndrome where shyer, less aggressive, less exploratory fish tended to grow faster than their proactive conspecifics. Whilst non-significant, this relationship does suggest that shyer fish have a fitness advantage when it comes to growth. Energy conservation is one potential cause of this (Adriaenssens and Johnsson 2010). Therefore, despite these fish eating smaller prey, the energy saved by exhibiting these behaviours may be more beneficial to the individual than the extra energy that may be gained from more risky behaviours such as exposed foraging. Because it was only fish from session two that had this significant result, this suggests that aspects such as laboratory feeding may have broken the link between an individual’s growth and behaviour.

4.2 Study weaknesses

During the course of the study, there were a few weaknesses that might have affected some of the parameters analysed. However, these were largely addressed either during the execution of the study, or accounted for in statistical models so as to avoid obtaining potentially false results. The difference in behavioural trial conditions was one such imperfection. The behavioural trials were carried out in different rooms before and after the mesocosm study. These rooms therefore had different temperatures (one being cooler), which was the likely cause of some of the major differences in the behaviour of individuals between the sessions. While this seemed to alter the mean behaviours, it didn’t seem to have any effect on the magnitude of the correlations between behavioural types or behavioural repeatability. Whilst the differences between sessions meant it was hard to compare behavioural parameters using all fish, having separate sessions revealed important insight into the effects that being in a laboratory had on the fish and of their plasticity in behaviour. This shows the importance of considering the effect captivity may have when studying an animal’s behaviour and ecology.

Habitat analyses, whilst repeated regularly, could have been biased towards repeatedly identifying the same individuals if they had an affinity for certain habitat, or individuals that only utilised exposed areas. However, a range of individuals were sampled throughout the mesocosm study, with all individuals having at least one measure of habitat. The algal
bloom that occurred during the mesocosm experiment could have its affected results because a large number of mesocosms could not be analysed. The fact that habitat analyses were repeated many times may have mitigated this, as it provided many opportunities for individuals to have their habitat repeatedly sampled. However, the algal bloom could have also biased results to only sample individuals that were in shallower areas, as these were the only visible spaces during the algal bloom. This algal bloom may have also altered behaviours as the low visibility could be taken as increased cover for fish, therefore decreasing the threat of predation and altered risk-taking behaviours. This low visibility may have also hindered individual’s ability to forage. If bullies rely on vision when searching for prey, then the low visibility caused by the algal bloom may be detrimental to foraging, which could impact how much an individual can specialise on certain resources. This may have led to more opportunistic feeding, rather than individuals specifically choosing prey types or sizes.

Repeatedly sampling fish stomach contents gives a more accurate insight into an individual’s diet than simply a “snapshot” which would be obtained from only one sample. However on the first three diet sampling rounds during the mesocosm experiment, only about half of the fish were caught in the traps each time. Some fish were caught repeatedly whereas others were caught only on the final sample, which, whilst giving some idea of diet, may not capture the entire prey range of individual common bullies. Also, if the stomach was empty it resulted in some individuals not having any data recorded for their diet at all. Despite these difficulties that occurred during analysis, there did seem to be sufficient samples to quantify the individual resource use of individual common bullies reasonably reliably, and specialisation in diet was found.

The use of Best Linear Unbiased Predictors (BLUPs) in statistical analyses has received some criticism (Hadfield et al. 2010). It has been noted that BLUPs can give anticonservative and biased estimates if not used correctly. The random effects due to fish ID calculated in the linear mixed-effects models (or generalised linear missed-effects models for binomial factors) provided the individual effects of that predictor, which are the BLUPS. These BLUPS are the differences between the population-level average predicted responses for a given set of fixed-effect values, and the responses predicted for a particular individual (Robinson 1991, McGilchrist and Yau 1995). Bias in BLUPs occurs because they are often used to estimate effects that are not explicitly accounted for in the model used to make the predictions (Hadfield et al. 2010). However, careful selection of model
parameters used to calculate the BLUPs in this study should account for any variation caused by anything other than fish ID, therefore bias should not be a weakness here. Another problem is that BLUPs are point estimates of quantities that are sometimes known with little certainty and failure to account for uncertainty can lead to anticonservatism (Hadfield et al. 2010). In my study, however, the quantities used in this study were reasonably well known, and multiple sampling (at least three repeats for each behavioural variable in each fish, and likely many habitat and at least one but likely more diet ones) should make quantities reasonably accurate. Also, quantities were analysed without using BLUPs for some analyses, and similar results were yielded. There will always be uncertainty in ecology, especially when measuring parameters that can be very plastic, such as behaviour. Nevertheless the concerns that can come with BLUPs should not influence the results of this study because all models accounted for potential confounding factors and therefore should give the true variation caused by individual ID.

4.3 Study implications

My study is the first to directly compare animal personality with multiple measures of resource use in a semi-natural setting. First, the findings obtained in this research are important as they challenge the conception that common bullies are a generalist species (Stephens 1982, Rowe 1999). Instead, these results corroborate the idea that each individual is more unique than previously thought, in both the way they behave and in how they interact with their ecosystem. Second, the correlation found between behaviour and resource use (and also the lack of such a correlation) provides important new information on the consistencies found between different facets of an individual, and gives further evidence that individual behaviour can play a role in determining the diet and habitat use of individuals within a population (Bergvall et al. 2011, Zhao et al. 2016). The latter has far-reaching implications. When certain personalities are correlated with utilisation of certain resources, it means that personalities can directly affect the strength and the range of interactions an individual has within its ecosystem (Réale et al. 2010a, Bergvall et al. 2011, Bolnick et al. 2011, Sih et al. 2012, Wolf and Weissing 2012, Mittelbach et al. 2014, Kern et al. 2016). The individual interactions with prey that have been shown in my study highlight that personality can alter the effect a predator population might have on the prey populations with which it interacts. Predator personality could alter prey abundances (Johnson et al. 2009, Pruitt et al. 2012, Toscano and Monaco 2015) – if a number of individuals specialise on one particular prey type, then that prey type can become depleted, which may even lead on to affect trophic levels that the prey interacts with too, causing a
trophic cascade (Post et al. 2008). Whilst there is a correlation between behaviour and resource use in some fish, in others this correlation was not statistically significant. This suggests that other mechanisms can also come into play in how an individual can exert its effects on resources, such as cognitive learning from past experiences (Urszun et al. 2015, Stamps and Biro 2016), competition (Svanbäck and Bolnick 2007, Araújo et al. 2011, Laskowski and Bell 2013, Robertson et al. 2015), or predation threat (Pruiitt et al. 2012).

Finally, the relationship between fitness and behaviour also highlights the crucial effects that personality can have on the growth of individuals. Whilst there were no statistically significant relationships, the almost-significant correlation present between individual behavioural variation and individual growth rate does suggest that behaviour may be an important determinant of fitness. However, like resource use, there are likely other factors that also interplay to affect how fast an individual grows (Nakano 1995, Biro et al. 2003b, Adriaenssens and Johnsson 2010, Sebastien et al. 2016). Nevertheless, it is important to understand how behaviour and resource use play their respective roles in growth as this can then go on to affect factors such as mortality (Biro et al. 2003a, b) and reproductive potential (Zhao et al. 2016), which can have effects on the structure of a population.

### 4.4 Conclusions and future research directions

Overall, the results of my study show us that it is likely that individual behaviour does affect resource use. However, this correlation can also be affected by other individual parameters, or by the environment with which an individual interacts. Whilst my findings highlight the importance in treating a population of common bullies as a unique set of individuals, they also capture the fact that individual bullies are ultimately very plastic and can be influenced by any number of different factors. *Gobiomorphus cotidianus* are a central species in food webs in many of New Zealand’s freshwater ecosystems, providing ample prey for many predators, and predating on a wide range of animals. Therefore, understanding these food-web interactions, and what may affect them to a greater extent contributes more accurately to what we know about this key species’ ecology. My findings also suggest that perhaps when managing New Zealand’s more at-risk freshwater fish species, it may be beneficial to understand the individual-level of these animals’ ecology.

In future related research, it would be beneficial to analyse the behaviour of individuals at the same time as their resource use, and it would again be important for this research to be performed in the wild or at least in semi-natural environments, such as the mesocosms used in my study. This future research would give greater insights into how individuals behave in the wild and may provide stronger evidence for the apparent link between
behavioural syndromes and individual niche. Finally, my study provides some of the first evidence that the personality of an animal can influence that individual’s natural resource use, and highlights the importance of studying animals at the individual level, if we are to fully understand a species’ role within the ecosystem.


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