Habitat use, growth and movement in relation to bioenergetics of drift-feeding stream fish

Abbas Akbaripasand

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ABSTRACT

The distribution and abundance of fish species is influenced by a range of environmental variables. Information on driving factors in that determines fish habitat use, abundance and distribution is crucial for fisheries and restoration management, especially for species in gradual decline. Habitat use may be structured by interactions between multiple factors including food density, predation risk, competitors, energetic requirements and habitat structure. Habitat selection varies with respect to species, stage of life history and time of day, agonistic interactions between conspecifics may also influence habitat use.

In this study, I selected three streams draining to Otago Harbour in the South Island, New Zealand; Craigs Creek, Deborah Bay Stream and Sawyers Bay Stream. A gradient in riparian vegetation from sparse (Craigs) to dense (Deborah) was the basis of stream selection and they likely differ in food quantity and quality which may affect fish assemblages. I used banded kokopu (Galaxias fasciatus) as an animal model. The fish represent ideal species to study feeding strategies, growth and movement as they appear to form dominance hierarchies that are stable over long periods of time within stream pools. They are also easy to catch, observe and individually tag. High fish density in Craigs Creek and low food density in Deborah Bay Stream and absence of trout in all streams provides an ideal situation to study the role of social hierarchies and intraspecific competition for food and space on patterns of individual growth, residency and movement. Thus the main goals of this dissertation were to elucidate the long-term patterns of banded kokopu habitat selection, growth and movement in relation to their social status, energetic requirements and food supply. Local habitat selection was measured at microhabitat scale to determine if large fish share habitat with or segregate from small conspecifics. Growth of fish across sizes
(hierarchical ranks) was investigated to determine whether agonistic encounters influence habitat use and variation in growth among individuals. Food density and quality (energy availability) and metabolic rates of fish (energy requirements) were measured to assess whether stream pools were capable of providing sufficient energy. Fish movement patterns were monitored to determine whether the fish would change their habitats if energetically unsuitable.

This thesis tests several hypotheses. I assumed that a social dominance hierarchy exists among banded kokopu with larger fish outcompeting smaller fish to gain access to the most profitable patches and this would impact smaller individuals’ growth. I also hypothesised that the banded kokopu population would exhibit evidence of energy limitation based on an assessment of energy consumption in relation to energy supply in the form of drifting invertebrate prey. Fish of low social status would exhibit more movement in an effort to improve their social rank and gain access to more food in new pools.

The results of my first study of banded kokopu habitat use showed that water depth, focal velocity, adjacent fastest velocity and substrate were the factors most strongly associated with banded kokopu position. Patch use by fish was clearly size-related with small fish occupying shallow pools with fast velocities over fine substratum and large fish selecting deeper pools with slower water velocities and coarse substratum. Although the different patterns of habitat use by individuals may be due to ontogenetic shifts in habitat preferences, evidence from multiple published studies suggests that observed pattern of microhabitat partitioning is likely due to agonistic intraspecific interactions and a social hierarchy among individuals of varying size.

Social hierarchy in banded kokopu assemblages appears to influence individual feeding and growth. The growth of high ranked fish in the social hierarchy (large fish) was
correlated with food abundance and biomass (energy available in habitat). This emphasises the ability of large fish to outcompete small ones given their high status in social hierarchy.

The banded kokopu diet study showed that the fish favour food items with high caloric values. Invertebrate drift was insufficient to meet banded kokopu energetic requirements; hence fish must access other sources of energy in the habitat such as terrestrial invertebrate inputs and benthic prey. The fish appeared to be likely energetically constrained in all seasons as they could obtain no more than 70% of their total energy expenditure from drifting invertebrates alone, which based on observations of their feeding behaviour, was their primary food source.

Akaike’s information criterion (AIC) showed that the best candidate model used to predict fish abundance was the one that included food density, pool area, undercut banks and water velocity. Pool size determines the number of small fish, and the energy available determines total fish biomass in pool and also growth of large fish. The growth of subordinate fish is determined by an interaction between food supply and the large dominant fish in the social hierarchy.

Dominant fish exhibited higher growth rates and a reduced tendency to move compared to subordinate fish, suggesting that high-ranked fish monopolise food intake to some extent in pools. In contrast subordinate fish changed pools more often, most likely as consequence of intraspecific competition that resulted in lower growth rates. The growth of fish improved after relocation to a new pool only if a higher social status was gained in the new habitat, suggesting that fish movement was intraspecific competition-oriented rather than food-related.
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CHAPTER 1

General introduction
INTRODUCTION

1.1. HABITAT REQUIREMENTS

Habitat use and home range are crucial elements in the ecology of animals, and can be interpreted as occurrence of a species or individual in space and time (Kernohan et al. 2001). Habitat selection and the distribution of an animal depend on environmental parameters such as habitat structure, habitat suitability, food, breeding opportunities, predation risk and competitors. Knowledge of habitat requirements of biota is of value for conservation management, particularly for threatened animals. Habitat selection is a crucial action carried out by an organism and making this decision is not necessarily easy. A perfect patch for foraging may not provide adequate cover from predators or may offer poor-quality nest sites. Although these problems can be eased for mobile animals, the energetic cost of movement between habitats can be significant (see Orians & Wittenberger 1991 for review).

Research on the role of abiotic and biotic factors on animal distribution and habitat selection started several decades ago (Gleason 1917; Grinnell 1917; Allee et al. 1949; Odum 1953). For example, halictine bees (Halictus rubicundus) prefer softer soils with southern slope, as such habitat types are easier to dig into and absorb the maximum amount of solar radiation (Potts & Willmer 1997). Bechstein's bat (Myotis bechsteinii) has shown marked preference for woodpecker holes in tree trunks as potential roosting sites when selecting a habitat (Dietz & Pir 2009). Juveniles of cutthroat trout (Oncorhynchus clarki) strongly selected pools over riffles to inhabit (Rosenfeld et al. 2000) which resulted in faster growth (Rosenfeld 2003).

Habitat use of a species may result from interactive abiotic and biotic effects in the environment. A study on the frog species Phrynobatrachus guineensis demonstrated that the
relative use of a breeding site was determined by a combination of the full range of environmental factors (Rudolf & Rödel 2005). The frogs were able to estimate the water holding capacity of breeding sites. Moreover, the ovipositing individuals were attracted to presence of conspecific offspring, which was a sign of low predation risk. In an interesting example, (Riedel et al. 2008) indicated that red-backed salamander (*Plethodon cinereus*) habitat use was associated with cover of herbaceous vegetation. Although Riedel et al. (2008) considered vegetation cover as a physical feature, it may be related to higher food abundance on vegetation as surface of leaf litter was considered a foraging spot for the species (Heatwole 1962). Soberón (2010) discussed the theoretical framework that abiotic variables affect the growth rate of populations at large scales and biotic factors influence fitness at smaller scales.

Food supply is a critical determinant of abundance and dynamics of organisms in habitats. For instance, combined density of three wood warbler species (*Dendroica* spp.) in grass willow habitat was 12 times greater than that of species in Lodgepole Pine habitat, and food density in the former habitat was 13 times greater than that in the latter habitat (Hutto 1985). Several empirical studies on a variety of animals, including black bears, *Ursus americanus* (Costello & Sage 1994), moose, *Alces alces* (Dussault et al. 2005), coho salmon, *Oncorhynchus kisutch* (Rosenfeld et al. 2005) and songbird phainopepla, *Phainopepla nitens* (Crampton et al. 2011), have shown that habitat selection can be highly food-oriented. An increase in food density may reduce home range size and an animal’s foraging efforts (Rödel & Stubbe 2006). However, excess food can result in an increase in the number of individuals in the habitat boosting competition when resources become limiting (Hixon 1980; Perrin & Johnson 1999).
It is crucial for animals to know where, when and how to find food of the right type and quality. The “Optimal Foraging Theory” (Emlen 1966; MacArthur & Pianka 1966) proposes that animals preferentially choose abundant food with high energy gain. For example, the downy woodpecker selectively fed on the large goldenrod gall fly (*Eurosta solidaginis*) as small galls are likely to have larvae of parasitic wasp (*Eurytoma gigantea*) which makes the galls a less rewarding meal energetically (see Yahnke 2006 for review). In another study in agreement with optimal foraging theory, Lacher *et al.* (1982) documented that greater proportions of foods of high quality observed in the diet of a herbivorous rodent (*Kerodon rupestris*) in response to overall food abundance increase. Smith & Follmer (1972) also reported that gray squirrels are able to distinguish the quality of food and feed on nuts with greater energy contents. Based on optimal foraging theory, animals maximise the rate of energy intake by feeding on food of high rank in the habitat. However, a patch with abundant low-quality food may be selected over sparse high-quality food (Lewis 1980; Anderson 1984; Abrahamson & Weiss 1997). For example, Van Beest *et al.* (2010) showed that female moose (*A. alces*) feed on high-quality species in summer and switch to low-quality species in winter when high-quality forage resources became scarce or depleted. Lehman (1976) observed that filter feeders capture their food first and then decide to ingest or reject the particles after assessing the quality. However, they may take less favourable food particles if preferred food items are scarce.

1.2. COMPETITION

Competition is one of the main factors influencing habitat selection and segregation among and within species (Grant 1972; Schoener 1974). Rosenfeld *et al.* (2005) demonstrated that elevated fish density shaped segregation in habitat use, with dominant
Chapter 1 General introduction

Territorial fish occupying preferred habitats forcing subordinate fish to non-profitable patches. However, individuals may mitigate the negative effects of intraspecific competition by expanding their niche width, such as by adding alternative prey items to their diet or by changing their patterns of diel activity (Schoener 1974; Abrams et al. 2008; Huss et al. 2008; Svanbäck et al. 2008; Martin & Pfennig 2009). For example, in the presence of adults, juvenile signal crayfish (Pacifastacus leniusculus) move more frequently to avoid competition and possible costly battles (Pavey & Fielder 1996; Harrison et al. 2006). Three-spine stickleback (Gasterosteus aculeatus) increased the variety of prey items in their diet as population density and intraspecific competition elevated (Svanbäck & Bolnick 2007). Similarly, the neotropical rodent (Necromys lasiurus) varies foraging times to avoid intraspecific competition (Vieira et al. 2010).

1.3. FISH AS RESEARCH ANIMALS

Fish are ideal animals for ecological studies. They are widespread in various aquatic systems from shallow creeks to deep marine ecosystems, from freshwater to high salinity oceans, and from very cold water (<0 °C) at the Poles to high temperatures (up to 45 °C) in Death Valley. Their ability to respond to adverse conditions or move to preferred environments (Claireaux et al. 1995; Dahlgren & Eggleston 2000; Vieira et al. 2010) makes them ideal candidates for assessing environmental conditions and testing theories of habitat selection and optimal foraging. They can be captured using uncomplicated methods, tagged, released to their habitats and recaptured for further investigation such as distribution and movement patterns, growth rate, reproduction cycles and so on. Fish can be subjected to environmental stressors to study land-use and habitat change effects. They can be kept and monitored in the laboratory and they are perfect animals for behavioural and manipulative
studies. Their habitat use patterns, intra- and interspecific interactions and dietary regimes can be easily studied and monitored in the ecosystems, especially in small freshwater streams, as is the case in this thesis.

1.4. POPULATION DYNAMICS OF FRESHWATER FISH

There is substantial work that has elucidated the dynamics of stream fish, such as habitat preference (Gosselin et al. 2010), food requirements (Ferreira et al. 2012), bioenergetic demands (Hayes et al. 2000; Guénard et al. 2010), dominance hierarchies (Chen et al. 2011) and distribution and movement patterns (Morrissey & Ferguson 2011). However, lack of knowledge of functional interactions of these ecological concepts leaves a gap in lotic fish ecology. I know of no study that has investigated how freshwater fish food and energetic requirements influence habitat selection, and the relationship of this to social hierarchy and the movements of individuals. Hence, this thesis is aiming to address this yet unanswered concept for the first time.

1.5. SIGNIFICANCE OF THIS STUDY AND STUDY APPROACHES

Despite the wide-spread use of fish to investigate relationships between species habitat use and abiotic and biotic variables, there is a paucity of knowledge on how the two environmental factors jointly influence stream fish habitat selection. Habitat use by bullhead (Cottus gobio) has been associated with a particular physical structure of streams (Gosselin et al. 2010). Salas & Snyder (2010) documented that there is a difference in habitat use by coho salmon (O. kisutch) over 24 hours, with a preference for using undercut banks during the day and for large woody debris during the night. While food supply plays a key role in fish habitat selection, physical stream characteristics selected by brown trout (Salmo trutta) have been linked to minimising energy expenditure (Heggenes 1988b). A trade-off between
foraging and predation risk may result in using different habitats by Atlantic salmon (*Salmo salar*) when feeding or hiding (Hiscock *et al.* 2002). Intra- and/or interspecific competition among fish populations has also been suggested to drive species habitat use (Glova 1986; Whiteman & Côté 2004). These examples merely show the influence of particular variable/s on fish habitat use without providing insight into a model that incorporates a broad range of environmental factors. Thus, this thesis is the first aiming to 1) integrate abiotic and biotic factors including food quality and fish social hierarchy to study which factors drive stream-dwelling fish habitat selection and 2) observe the possible role of social status in movement patterns of fish and 3) measure metabolic rate and energy expenditure by fish to illustrate if food supply in habitat is energetically sufficient to meet fish metabolic requirements. This thesis will shed light onto long-term patterns of stream fish habitat selection, growth, movement, social hierarchy and metabolic rate in relation to drifting invertebrate density.

1.6. **BANDED KOKOPU (GALAXIIDAE) AS EXPERIMENTAL MODEL**

I used banded kokopu (*Galaxias fasciatus* Gray; Family Galaxiidae; Order Salmoniformes) as a freshwater fish to approach the aims of this study. The fish are endemic to New Zealand (McDowall 1990) and occur in small first to third order tributaries and rivers at relatively low elevations (McDowall 1990; Jowett *et al.* 1998; Rowe *et al.* 2002). They prefer shallow backwater pools (McCullough 1998) and typically live for at least 9 years, with males and females becoming mature at 110-130 mm (2 yrs) and 170-180 mm (4 yrs), respectively (Hopkins 1979a, b). As diadromous species, adults of banded kokopu spawn in freshwater from late April to mid-June, and offspring usually migrate to sea. After spending 4 to 6 months at sea, juveniles return to freshwater as ‘whitebait’ and live until they reach the adult stage. The juveniles of banded kokopu are one of the five species that contribute to the
whitebait fishery in New Zealand (McDowall 1984). The abundance of banded kokopu and their contribution to the whitebait fishery has declined over the past decades due to habitat loss through land-use change (Hanchet 1990; Rowe et al. 1999; McDowall 2000). Despite a decline in the fish populations, they are not on the list of threatened species (Allibone et al. 2010). Banded kokopu communities offer an excellent system to address how habitat use by species is shaped by different environmental factors at spatial scales especially when they are present in habitats in which trout are absent. Eliminating the effects of interspecific competition (such as trout) may provide more accurate information on species habitat selection as trout impacts on various galaxiid species has been widely reported (see Townsend & Crowl 1991; Crowl et al. 1992 for review; McIntosh et al. 1992, 1994; McIntosh 2000).

1.7. CHAPTER OUTLINE

This dissertation is organised into six chapters, with four data chapters and a concluding synthesis. The following shows the brief objectives and hypotheses of each core chapter.

Chapter 2. Is microhabitat use in banded kokopu size-related?

It has been documented that habitat segregation occurs among conspecifics of drift-feeding stream fish due to the existence of a stable social hierarchy based on size (Hindar & Jonsson 1982; Hegge et al. 1993; Hansen & Closs 2009). Dominance hierarchy among banded kokopu is expected as 1) they are drift-feeding fish and 2) fish of different sizes coexist within a single pool (pers. obs.). Social hierarchy has been observed among fish assemblages with such characteristics (Bachman 1984; Nakano 1995; David et al. 2007). Size-based variation in habitat selection is of importance as it may impact the fitness of
individual fish (Hansen & Closs 2009). Therefore, I hypothesised that such social hierarchy would exist among banded kokopu and that it would influence the distribution patterns of fish of different sizes. The primary aim of this study was to measure environmental factors related to microhabitat selection of banded kokopu, to determine the microhabitat characteristics of fish and to assess if patch structures of small fish were different from those of large fish. This study was designed to answer the question whether social hierarchy gives large fish benefits by gaining profitable positions and forces small fish to occupy less favourable positions in the available habitat. If such segregation happens among fish assemblages, then one would expect that the growth of subordinate fish would be impacted by larger dominant fish. This would illustrate how the social status of fish together with habitat structure would interact with fish habitat selection and individual fitness.

Chapter 3. *Spatial and seasonal variation in food abundance and diet composition in relation to growth of banded kokopu*

Fish social status may play a key role in intraspecific interactions and it may govern an individual’s feeding and growth (Gustafsson et al. 2010; Van Leeuwen et al. 2011). For instance, it may benefit dominant fish by gaining them access to optimum foraging positions and negatively influence subordinate fish. In Chapter 2, I demonstrated that banded kokopu habitat use was size-based, with dominants (larger fish) occupying profitable microhabitats (i.e. lower current flow and deeper pools) and forcing subordinates (smaller fish) to less favourable positions. Given this, I infer that dominance hierarchies may occur among banded kokopu. In the current chapter, I assumed that such habitat segregation among fish assemblages would influence individual feeding and growth as fish occupy patches with different characteristics. Thus, the aim of this study was to measure food density in the
habitat and to determine if growth of fish was related to food supply. I also aimed to investigate if discrepancy in growth of fish of different sizes was influenced by individual fish status in the social hierarchy.

Chapter 4. *Is food supply energetically sufficient to meet banded kokopu metabolic requirements?*

Food abundance has been regarded as a main factor driving fish habitat selection (Nislow *et al.* 1998; Giannico 2000). However, the role of the energetic value of the food supply entering each pool as a determinant of fish habitat quality and use has received relatively limited study. In Chapter 3, I observed that the biomass of banded kokopu in pools was dependent on the density of drifting invertebrates entering each pool. It was hypothesised that caloric value and size of food may also be a key element influencing growth and fitness of banded kokopu. I also predicted that banded kokopu would be at or close to energy-limitation, corresponding with the predictions of the “input-matching rule” proposed by Parker (1978) in which fish biomass is in balance with energy available. Hence, the primary aim of this study was to measure the caloric value of drifting invertebrates in pools to determine whether fish diet was related to food quality (as determined by energy content). The second aim was to measure basal energy consumption of banded kokopu to compare it with energy available in pools and to determine whether food supply was adequate to meet fish energetic demands.

Chapter 5. *Banded kokopu habitat selection, movement and growth in relation to abiotic and biotic factors*

Given the results of Chapters 3 and 4, it became evident that biotic factors such as food quantity and quality are determinants of banded kokopu habitat use. Abiotic factors
such as pool physical structures have been reported to be as important as biotic variables in fish habitat selection (Ayllón et al. 2009; Gosselin et al. 2010; Salas & Snyder 2010). In this chapter, I integrate a broad range of environmental factors into a model to illustrate what variables most influence habitat use of banded kokopu. My hypothesis was that the factors driving banded kokopu abundance would be likely to result from interactions between both biotic and abiotic factors in the habitat. In chapter 3, I demonstrated that fish social rank influences an individual’s growth. In the current chapter, the possible movement of fish was monitored to determine if fish of low ranks move around more than established dominant fish to find a better location with less agonistic competition with larger conspecifics. Hence, I hypothesised that fish movement and growth would be influenced by the structure of social hierarchy among fish, with high growth and less movement for fish of high ranks and the opposite patterns for fish of low ranks. Taken together, the main aims of this chapter were applying a model selection to determine the best supported set of variables for predicting banded kokopu abundance and growth. Furthermore, I aimed to determine whether fish relocation patterns were strongly associated with social status.

Chapter 6. General discussion

Widespread decline of freshwater fish species spurs a need for assessing habitat requirements for effective management in the restoration of species. To do this, we need to know how habitat use mechanisms interact with the dynamics of fish populations. Hence, the main goals of this dissertation were to elucidate the long-term patterns of habitat selection of freshwater drift-feeding fish such as banded kokopu, together with growth, movement, social hierarchy and metabolic rate in relation to drifting invertebrate density. In the previous chapters, I illustrated these contexts separately. In this chapter I integrate all these
approaches to discuss how social hierarchy drives activity patterns of individual fish in the habitat and demonstrate what sort of environmental factors interact with habitat selection patterns of drift-feeding fish such as banded kokopu. It can be argued that an understanding of freshwater ecological components, fish habitat requirements, fish social interactions and their interactions are crucial for fisheries and restoration management of declining or endangered freshwater fish species.
CHAPTER 2

*Is microhabitat use in banded kokopu size-related?*

Banded kokopu (*Galaxias fasciatus*). Photo by Rod Morris
ABSTRACT

To assess habitat selection by small and large banded kokopu (Galaxias fasciatus), a total of 215 fish were observed using spotlight along 350 m of Sawyers Bay Stream in southern New Zealand. Multiple microhabitat variables were measured at the focal point position of each observed fish. A correlation analysis showed that depth, focal velocity, adjacent fastest velocity and substrate were the factors most strongly associated with fish position. The results exhibited for the first time that patch use by banded kokopu was clearly size-related. Small fish (≤90 mm) occupied shallow pools with fast velocities over fine substratum while large fish (>90 mm) preferred deeper pools with slower water velocities and coarse substrates. I suggest that such microhabitat partitioning could be due to agonistic intraspecific interactions and a social hierarchy among individuals.

The results presented in this chapter were published as follows;

CHAPTER 2 Is microhabitat use in banded kokopu size-related?

2.1. INTRODUCTION

Factors known to influence microhabitat selection in stream fish include biotic variables such as predator avoidance, food supply and intra-or interspecific competition (Gilliam & Fraser 1987; Holbrook & Schmitt 1988; McIvor & Odum 1988; Roussel & Bardonnet 1999; Hansen & Closs 2005) and abiotic variables such as depth, flow and substrate (Rimmer et al. 1984; Jackson et al. 2001). Heterogeneous stream environments provide a range of habitats that enable coexistence of a variety of fish species and size classes, each of which may have varying requirements (Heggenes 1996) but still, habitat segregation within each species population may occur. For instance, length-related microhabitat selection has been reported in stoneroller (Campostoma anomalum) and longnose dace (Rhinichthys cataractae) in Coweeta Creek, where larger individuals of both species occupy areas with faster velocities than smaller fish (Grossman & Ratajczak 1998).

The dynamic physicochemical conditions of streams and their influence on habitat characteristics are central to understanding patterns of fish community diversity (Gorman & Karr 1978). Depth, velocity and substrate have been repeatedly shown to play a primary role in determining individual habitat selection (Kershner & Snider 1992; Johnson & Douglass 2009). However, those primary variables also interact with biotic variables; for example, juvenile and adult salmonids occupy different microhabitats due partly to direct agonistic interactions between individuals, but also differing individual requirements as a consequence of size and feeding preferences (Ayllón et al. 2009; Nagayama et al. 2009). Sometimes prey abundance per se is a better predictor of microhabitat selection by fish than physical factors alone (Petty & Grossman 1996). Habitat selection can also be the result of a trade-off between factors that either restrict or enhance energy intake or incur energetic costs (Hughes & Dill 1990; Hill & Grossman 1993). Thus, the latter authors reported that large rosyside
dace (*Clinostomus funduloides*) and rainbow trout (*Oncorhynchus mykiss*) held positions with higher velocities and consequently captured more prey than smaller individuals in lower velocity patches.

The social status of individuals within a species has been recognised as an important determinant for habitat segregation and coexistence in some stream fish (David *et al.* 2007; Hansen & Closs 2009). A hierarchical social structure within drift-feeding fish particularly benefits dominant individuals, allowing them to gain access to optimum foraging positions, but may also benefit subordinate fish by reducing the intensity of competitive and agonistic interactions (Alanärä *et al.* 2001; Hansen & Closs 2005; David *et al.* 2007).

Banded kokopu (*Galaxias fasciatus*) are most commonly encountered in first- and second-order steep coastal streams (Jowett *et al.* 1996; Rowe *et al.* 2000), but descriptions of microhabitat use have to some extent been contradictory. They have been recorded across a variety of depths from shallow to deep (Halstead 1994; McCullough 1998; Chadderton & Allibone 2000), although a preference for shallow pools has been reported (Rowe *et al.* 2000; Kater 2004; Baker & Smith 2007). Banded kokopu have also been associated with backwater and slow current flow areas in streams (Jowett *et al.* 1998; Chadderton & Allibone 2000). Such variation may be size and/or age related; McCullough (1998) found that juvenile banded kokopu occupied habitats with higher water velocity than adults. This pattern suggests that social status mediated through size-based dominance hierarchies may determine banded kokopu microhabitat use, similar to patterns observed for closely related giant kokopu, *G. argenteus* (Whitehead *et al.* 2002; David & Stoffels 2003; Hansen & Closs 2005, 2009; David *et al.* 2007). Indeed, the relative large sizes of banded kokopu and coexistence of fish of different sizes within a pool is likely to cause aggressive interactions among fish assemblages and force smaller fish to occupy less profitable positions. An
ontogenetic shift in microhabitat use of giant kokopu has been described by (Whitehead et al. 2002) but the possibility of age or size related partitioning of nocturnal microhabitat use by banded kokopu has not been studied in detail. Different size/age classes of fish often have different habitat requirements, hence, understanding habitat requirements across all size/age classes in the life cycle is a key step to improving management and restoration of the species to its former status (Bonnett & Sykes 2002).

The current study comprised two objectives, namely to 1) determine the characteristics of microhabitat used by banded kokopu, and 2) investigate whether or not there is a difference in habitat use between small and large fish. Based on observations on size/age dominance hierarchies in cyprinids, salmonids and other large galaxiids, I hypothesise that small banded kokopu will occupy areas of shallow depth and large fish will reside in deeper pools. I predict that small fish will inhabit faster velocities and large fish will prefer low current pools and also water velocity at the focal point of both small and large fish will be lower than water flow in 20 cm diameter of focal point. This means that the fish will be adjacent to areas with faster water velocity to capture food while resting in low energy cost microhabitat with low flow.

2.2. METHODS

2.2.1. Study site

The study was conducted between March and April 2009 in Sawyers Bay Stream (170°35’E; 45°48’S) in the South Island, New Zealand (Figure 2.1). Sawyers Bay Stream is characterised by an average width and depth of 1.5 m and 0.2 m, respectively. The substratum of the stream was dominated by fine and small-medium gravels. Landuse along the stream comprised low intensity grazing; riparian vegetation was comprised of rank
grasses with occasional sparse patches of native shrubs and small trees (<5 metres tall). Sampling was conducted over nine nights when conditions were suitable (clear water, no wind). This stream was chosen for two reasons. Firstly, it supports high densities of banded kokopu across the full range of sizes that can be expected in this species (Kater 2004). Secondly, apart from an occasional longfinned eel (*A. dieffenbachii*) and common bully (*G. cotidianus*), banded kokopu are the only common large fish in this stream, hence, the confounding effects of interactions with other aggressive species such as giant kokopu or trout affecting habitat use could be excluded (McDowall 1990; David & Closs 2003; Hansen & Closs 2005).

![Map of the study site](image)

**FIGURE 2.1.** The study site on the South Island, New Zealand (top left) and the geographical location of the sampling site, Sawyers Bay Stream. An approximate 350 m length of study reach is represented by two bars.


2.2.2. Sample collection

2.2.2.1. Microhabitat use and availability

To locate banded kokopu, I used non-invasive spotlighting as described by McCullough & Hicks (2002), Whitehead et al. (2002) and Hickey & Closs (2006). A 350 m reach of the stream was divided into sub-reaches that could be surveyed on a single night as sampling the entire study reach in one night was not logistically possible. Each sub-reach was surveyed only once, and fish were assumed to be recorded in the database only once as site fidelity is high in Sawyers Bay Stream. Indeed, studies on movement of banded kokopu (using mark-recapture) in this stream have shown that at least 84% of the fish remained in the same pool for a period of one year (pers. obs.). Each survey was commenced at least one hour after sunset to allow the fish to move into their nocturnal foraging positions. The sampling was conducted along sections of stream where free movement along the stream bank was possible thus allowing me to move quietly upstream along the banks and avoid disturbing the fish (David et al. 2002; Whitehead et al. 2002). Sections of bank with dense vegetation that prevented free movement or uninterrupted viewing of fish were avoided.

When located by spotlight, most banded kokopu remained in position for long enough to accurately mark their focal point position with weighted, numbered floats (Whitehead et al. 2002). Fish that were disturbed and moved away prior to positional marking were not included in this study. The total length of all the undisturbed fish sighted was estimated by eye. The visual estimates were accurate to within 1 cm for all sized fish (based on fish size estimates of more than 100 fish caught and measured prior to this survey; actual length 111 ± 3.6mm, estimated length 110 ± 3.7mm). This also accords with other observations (Whitehead et al. 2002; David et al. 2007). On the following day, microhabitat parameters at each focal point position were measured. Physical habitat variables at fish
focal and random habitat points were measured following the methods of Grossman & Freeman (1987). The depth of water at the vertical position of each observed fish was recorded using a metre stick. Mean water velocity at the focal point and fastest velocity within 20 cm of each fish, was measured using an electronic flow metre (Marsh-McBirney Inc., Frederick, MD, USA; Flo-mate, accuracy ±0.02 m s\(^{-1}\)). Mean velocity in the water column was also measured by recording velocity at 60% of the depth below the water surface (Bonnett et al. 2002). Other variables measured included distance to bank and distance to the nearest cover that could accommodate the total length of the fish, nearest undercut bank width, adjacent bankside floating vegetation width and density, and presence or absence of overhanging vegetation. Dominant substrate was assessed by measuring the longest axis of the nearest stone at the position of each sighted fish. Substrate was categorised into 10 size classes using Wolman (1954): sand & silt 1 mm, coarse sand 1–2 mm, small gravel 2–4 mm, gravel 4–8 mm, large gravel 8–16 mm, pebbles 16–32 mm, large pebbles 32–64 mm, cobbles 64–128 mm, large cobbles 128–256 mm and boulders>256 mm.

To determine whether banded kokopu actively selected microhabitat within the stream, the same microhabitat variables were measured the following day at random points along the stream with the exception of the fastest current velocity within 20 cm of the fish focal point. Random points were selected along the stream using the point-transect method described by Whitehead et al. (2002).

2.3. DATA ANALYSIS

To determine whether sized-based partitioning of habitat occurred in the population of banded kokopu, the fish were categorised into small (≤90 mm) and large (>90 mm) size classes. McCullough (1998) observed that banded kokopu became resident within pools and
appeared to defend territories once individuals were over 90 mm. The fish were divided into
two group sizes because the competitive ability of fishes in social hierarchies is related to
body size (David & Stoffels 2003), and hence size-based shifts in habitat use could be
reasonably expected. The Kolmogorov-Smirnov and the Levene’s tests were employed to
ascertain normality of the distribution and homogeneity of variances in the microhabitat
variables measured, respectively. All data were log10(x+1) transformed to approximate
normality. To detect relationships between each fish size-class and the measured
microhabitat parameters, a two-tailed Pearson’s correlation test was used. After selection of
the factors that significantly correlated (depth, focal velocity, adjacent fastest velocity and
substrate) with fish length, a further analysis of variance (ANOVA) followed by a Tukey
post hoc test was used to determine the degree of difference of microhabitat use between
these variables for each fish size-classes and local microhabitat availability. I also used an
independent samples t-test to address whether microhabitat variables used by small fish are
statistically different from those used by large fish. An adjusted level of significance for
statistical analysis was applied using the method outlined by Benjamini & Hochberg (1995).
A principal component analysis (PCA) was conducted to determine which of the measured
variables explained most of the variance in the data for each of the fish size-classes. To
standardise the data variables in PCA analysis, a correlation matrix was used due to different
units of measurement of the variables. Statistical software SPSS version 15 was used for all
data analysis.
2.4. RESULTS

2.4.1. Fish frequency distribution

In this study, a total of 215 individual fish at different points were observed along the 350 m study reach of Sawyers Bay Stream as surveyed in March and April 2009. The fish size ranged from 30 to 230 mm. Small (≤90 mm) and large (>90 mm) fish comprised 57 and 158 of the total, respectively. The most common size categories were 111–120 mm and 121–130 mm with 9.3% of all fish in both categories, followed by a peak at 81–90 mm comprising 8.4%.

2.4.2. Microhabitat occupied

Small and large banded kokopu selected different microhabitats in terms of depth, velocity, fastest adjacent velocity and substrate (Figures 2.2a-d). Only 30.8% of large fish were observed in water <12 cm deep, yet water of this depth comprised 63.1% of available habitat, and was used by 53.7% of the small fish observed (Figure 2.3a). There was a significant difference in depth used by small and large fish (t\textsubscript{197} = -3.445, \(P<0.001\), \(P_{\text{Adjusted}}=0.025\)). Whilst banded kokopu were found in water velocities ranging from -0.25 to 0.21 m s\textsuperscript{-1}, most small (90.9%) and large (95.5%) fish were recorded in water velocities <0.15 m s\textsuperscript{-1} (Figure 2.3b). Areas with water velocities <0.15 m s\textsuperscript{-1} comprised only 41% of the available habitat. The mean velocity used by small and large banded kokopu was significantly different (t\textsubscript{197}=4.129, \(P<0.001\), \(P_{\text{Adjusted}}=0.012\)). However, whilst small fish actively selected low velocity water, they were usually close to higher velocity water; more than 70% of small fish were recorded within 20 cm of water velocities higher than 0.05m s\textsuperscript{-1} while over half of all large fish resided in areas with flow rates below 0.05 m s\textsuperscript{-1} (Figure 2.3c). Fastest adjacent velocity for both size classes was significantly different (t\textsubscript{197}=2.883, \(P=0.004\),
$P_{\text{Adjusted}}=0.037)$. A majority of small fish (60%) were located over substrate ranging from sand and silt to gravel, whilst 82.1% of large fish were found over substrates ranging from gravel to large pebbles (Figure 2.3d). Available habitat was dominated by gravel (60.2%) followed by 34.8% for pebble. Substrate types used by both fish sizes were not significantly different ($t_{197} = -1.400, P =0.163, P_{\text{Adjusted}} =0.05$).

FIGURE 2.2. Habitat parameters of depth (a), focal velocity (b), fastest adjacent velocity (c) and substrate (d) used by small and large banded kokopu ($Galaxias fasciatus$) and available habitat with 95% confidence intervals in Sawyers Bay Stream. Negative velocity values correspond to the upstream current flow in backwater areas. Substrate longest axis (cm) was measured in the study stream.
CHAPTER 2 Is microhabitat use in banded kokopu size-related?

Principal component analysis for banded kokopu showed that PC1 and PC2 explained 63.4% of the variation which was associated with depth, substrate, focal velocity and fastest adjacent velocity (Table 2.1). The ordinations indicated that 44.2% of small fish (top left of Figure 2.4a) were associated with shallow water, fine substrates, faster water velocity and faster adjacent water velocity. In contrast, 44.9% of large fish (bottom right of Figure 2.4b) were located in deeper areas, coarse substrates, low water velocity and low adjacent water velocity.

FIGURE 2.3. The frequency of microhabitat used by small (□) and large (■) banded kokopu (*Galaxias fasciatus*). Negative velocity values correspond to the upstream current flow in backwater areas.

![Graphs](https://example.com/graphs)
CHAPTER 2 Is microhabitat use in banded kokopu size-related?

FIGURE 2.4. PCA ordinations of the microhabitat environmental factors used by small (a) and large (b) banded kokopu (*Galaxias fasciatus*) in Sawyers Bay Stream. The first two components explained 63.4% of the variation.
CHAPTER 2 Is microhabitat use in banded kokopu size-related?

TABLE 2.1. Eigenvalues from data on microhabitat used in Sawyers Bay Stream.

<table>
<thead>
<tr>
<th>Environmental factors</th>
<th>PC1</th>
<th>PC2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth</td>
<td>0.807</td>
<td>-0.031</td>
</tr>
<tr>
<td>Velocity</td>
<td>0.030</td>
<td>0.783</td>
</tr>
<tr>
<td>Fastest adjacent velocity</td>
<td>0.004</td>
<td>0.792</td>
</tr>
<tr>
<td>Substrate</td>
<td>0.765</td>
<td>0.177</td>
</tr>
<tr>
<td>Total variance accounted for (%)</td>
<td>32.2</td>
<td>31.1</td>
</tr>
</tbody>
</table>

2.4.3. Habitat availability

The same environmental variables were measured for the fish at 749 random points along 350 metres of stream. The depth used by large banded kokopu was significantly different from that available in the habitat ($df_{2,971}=29.503, P<0.001, P_{Adjusted}=0.008$). Furthermore, both small and large fish actively selected velocities that were lower than the current velocities typically available in the stream ($df_{2,971}=59.025, P<0.001, P_{Adjusted}=0.025, P_{Adjusted}=0.016$). I also compared the substrate occupied by fish to that available at random points in the habitat and concluded that substrate used by small and large fish was also significantly different from the average available substrate types ($df_{2,971}=24.177, P<0.001, P_{Adjusted}=0.041, P_{Adjusted}=0.033$).

2.5. DISCUSSION

Smaller banded kokopu tended to use shallow pools over fine substrates, whereas larger fish preferred deeper pools and coarse substrates. Previous studies on banded kokopu reported small fish in shallow areas (Kater 2004) and large fish in deep pools (Halstead
1994; McCullough 1998) but none of these studies investigated whether this habitat use was a random or selective behaviour. Hence, the results of this study showed for the first time that active size-based nocturnal microhabitat selection occurs in banded kokopu. There are two possibilities for explaining such spatial microhabitat partitioning in banded kokopu. First, size-based intraspecific competition for space and preferred feeding territories could cause this segregation. This has been shown to be the case for giant kokopu, a species closely related to banded kokopu (Whitehead et al. 2002; David & Stoffels 2003; Hansen & Closs 2005, 2009). Hansen & Closs (2005) showed that smaller giant kokopu occupied different patches from larger competitively dominant conspecifics thus minimising agonistic interactions. Dominant larger individuals occupied entire pools at night and small subordinate fish were forced to either use suboptimal riffle habitats at night or to feed by day. Banded kokopu also have the potential to grow relatively large (up to 280 mm L Pham, pers. comm.) and size-based habitat partitioning may reduce intraspecific competition and predation. Spina (2000) showed how intraspecific competition is reduced among size and age classes of rainbow trout by using different patches. Given similar patterns of nocturnal microhabitat use by banded kokopu, it is likely that the observed patterns in banded kokopu are the result of intraspecific competition for space and/or food. Secondly, the threat of predation posed by larger conspecifics may also influence microhabitat use as cannibalism has been reported in large galaxiids (Kusabs & Swales 1991; Bonnett & Lambert 2002; West et al. 2005).

Banded kokopu of different sizes inhabited patches that differed in water velocity. Higher mean velocity was recorded for small fish whereas large fish occupied microhabitats with slower flow, a pattern that has also been found in giant kokopu. Velocity at the focal point of feeding fish is seen as a crucial element in microhabitat selection by drift-feeding
stream fish (Hill & Grossman 1993; Muhlfeld et al. 2001). Although a faster current delivers more drifting invertebrates to feeding fish, strike efficiency and hence food capture rate declines as water velocity increases (Hughes & Dill 1990; Grossman et al. 2002). Some studies documented that drift-feeding fish intend to shift their habitat to low flow areas as their sizes increase (Heggenes 1988b; Pert & Erman 1994; Heggenes 2002). This habitat change has been related to higher energetic demand of using faster water (Fausch 1984; Facey & Grossman 1992) and also higher strike efficiency that results from using slower water (Grossman et al. 2002).

The suitability of a particular point is crucial in patch use but the range of habitat types adjacent to this location should also be taken into account (see Maddock 1999). The results of current study indicated that the water velocities adjacent to both small and large banded kokopu were higher than the flow at their resting positions. Many studies have shown that stream-dwelling fish species such as trout or galaxiids hold positions in slow current pools next to faster velocities to capture drifting food items (Hill & Grossman 1993; Vondracek & Longanecker 1993; Hayes 1996; Spina 2000; Whitehead et al. 2002; Banish et al. 2008). As mentioned earlier this tactic may be a balance between net energy gain and energetic costs. This also benefits small banded kokopu which are likely to be displaced by larger conspecifics to less profitable foraging areas of faster velocities but they still prefer holding positions where water velocities are as low as possible.

The ideal test of whether the habitat use of small banded kokopu is determined by larger conspecifics would be a large fish removal experiment, as conducted by David et al. (2007). Nonetheless, the patterns observed in this study in relation to size-structured habitat use are consistent with one mediated by social status, a pattern seen repeatedly in many large-bodied drift feeding fish species (Bachman 1984; Hughes 1992a, b; Nakano 1995;
Brännäs & Alanärä 1997; Alanärä et al. 2001; Maclean & Metcalfe 2001). An alternative assumption that an ontogenetic niche shift may have been responsible for different habitat use by individuals was also considered. Although, aggressiveness of bigger fish towards smaller fish may also cause differentiation in habitat use, it cannot be purely related to size of fish especially when the results in the next chapter (Chapter 3) is considered that growth of fish of different size is different, a further evidence which supports dominance hierarchy structure in banded kokopu.

The habitat within the study stream is also typical of streams in which banded kokopu are generally abundant (Rowe et al. 2000). Hence, there is no reason for the results to be markedly different in other streams where banded kokopu are present. However, a year-round investigation is ultimately recommended as seasonal differences in microhabitat use of the fish may exist.

### 2.6. CONCLUSION

Overall, the study results showed for the first time that small and large banded kokopu exhibited size-based microhabitat selection which is in accordance with the hypothesis of this study. The preference of large banded kokopu for slow velocity water and deep pools is in accordance with that of many larger New Zealand galaxiid fish (Whitehead et al. 2002; Baker et al. 2003; David & Closs 2003; Martínez-Capel et al. 2004). However, small sizes of banded kokopu seem to have been forced to occupy shallower areas with higher velocities in this study. This pattern of microhabitat use is most likely due to interactions between individuals competing for drifting invertebrates and space. This competition may affect the overall growth rate of fish, and in the next chapter it will be
examined whether growth of smaller fish with low social hierarchical ranks is lower than that of larger fish with higher ranks.
CHAPTER 3

Spatial and seasonal variation in food abundance and diet composition in relation to growth of banded kokopu

A drift net to capture drifting invertebrates
ABSTRACT

Invertebrate drift and banded kokopu were sampled once a month from Craigs Creek, Deborah Bay Stream and Sawyers Bay Stream from June 2008 to May 2009. The freshwater snail *P. antipodarum* was the dominant taxon in Craigs Creek and Sawyers Bay Stream and springtails (Collembola) were the most abundant taxa in Deborah Bay Stream. Ostracoda were the dominant prey item found in the fish diet from Craigs Creek whereas *Deleatidium* spp. were highly favoured by the fish in the other streams. Slugs and isopods in Craigs Creek, and slugs and a beetle (*Cylomiscus*) in the other streams had the highest prey selection indices in the fish diet, suggesting that large taxa were a more rewarding meal for banded kokopu. Low prey selectivity on Collembola and water mites indicate that feeding on small taxa is energetically costly for fish. Banded kokopu preyed on more terrestrial taxa than aquatic taxa in Deborah Bay Stream but the opposite pattern was seen in the other streams. Abundance of terrestrial taxa exceeded that of aquatic taxa in Deborah Bay Stream whereas the opposite pattern was observed in Craigs Creek. Summer appeared to be the season with highest invertebrate drift density and highest fish feeding activity. The biomass of fish in pools was related to the invertebrate drift density suggesting that fish biomass is proportional to food supply. Banded kokopu growth did not differ between streams and was related to the invertebrate drift abundance only in Deborah Bay Stream, however, a positive correlation was found between the growth of high ranked fish (based on relative size) and food abundance from the other streams. The growth of banded kokopu was also related to the biomass of prey in Deborah Bay and Sawyers Bay Streams, however, only the growth of fish with the highest social rank was related to prey biomass in Craigs Creek. High correlation between fish growth and biomass of terrestrial taxa in Deborah Bay Stream indicates the significant role of large allochthonous prey in the diet of fish from this stream.
This study suggests for the first time that social hierarchy in banded kokopu assemblages affects individual feeding and growth, and that growth of fish is influenced by abundance of invertebrate drift.
3.1. INTRODUCTION

Suitable physical habitat and prey availability are key determining factors for fish populations in streams. In this regard, the importance of small streams in providing low-flow refuges to maintain fish assemblages over time has been discussed (White 2003; Schrank & Rahel 2004). In addition, prey abundance and net energy intake are important elements in shaping a profitable habitat for salmonids (Fausch 1984; Railsback & Harvey 2002), especially in small streams that are food-limited. Fish distribution patterns can be driven by food abundance (Nislow et al. 1998; Giannico 2000), hence variation in food density may impact on fish populations. Indeed, there are several studies that have shown drift-feeding fish to be affected by variation in invertebrate drift abundance (Sagar & Glova 1988; Dedual & Collier 1995; Shannon et al. 1996; Hayes et al. 2000; Hansen & Closs 2005). Drifting invertebrate abundance is highly correlated with the biomass of trout (Wilzbach et al. 1986), and can govern the maximum biomass of fish that a pool can host (Grant et al. 1998; Imre et al. 2004; Hansen & Closs 2009).

Drifting aquatic and drifting terrestrial invertebrates are important energy sources supporting fish production in freshwater ecosystems (Cloe & Garman 1996). However, the importance of such prey may vary between streams and fish species (see Hicks 1997). Streams running through forest appear to have more terrestrial-derived than aquatic invertebrates (Kawaguchi & Nakano 2001). Cadwallader et al. (1980) reported higher terrestrial prey in the diet of mountain galaxiid (Galaxias olidus) in streams with much much overhanging vegetation than in streams with sparse vegetation. In contrast, some fish such as giant kokopu, Galaxias argenteus (Bonnett & Lambert 2002), upland longjawed galaxias, G. prognathus (Bonnett et al. 1989), alpine galaxias, G. paucispondylus (Bonnett et al. 1989), dwarf galaxias, G. divergens (Hopkins 1971), Canterbury galaxias, G. vulgaris (Glova &
Sagar 1989b), koaro, *G. brevipinnis* (Glova & Sagar 1989a), shortfinned eel, *Anguilla australis* (Sagar et al. 2005) and longfinned eel, *A. dieffenbachii* (Sagar et al. 2005), predominantly prey on aquatic taxa. Shortjawed kokopu (*Galaxias postvectis*) consumed both aquatic and terrestrial prey, depending on availability (McDowall et al. 1996). Many terrestrial invertebrates are larger than aquatic invertebrates (Nakano et al. 1999b) and this makes them more energetically valuable, especially for salmonids (Wipfli 1997; Nakano et al. 1999b, c). Many drift-feeding fish have been shown to selectively prey on large terrestrial invertebrates (Furukawa-Tanaka 1985; Main & Lyon 1988; Sagar & Glova 1988; Nakano 1995; Nakano et al. 1999b). Fish feeding behaviour may be also related to habitat as seen in koaro which consume terrestrials if residing in riffles, and forage on benthic aquatic invertebrates when in still water (Main & Winterbourn 1987). The physical characteristics of streams are also important, as riparian vegetation has been reported to be a source of terrestrial invertebrates which were major prey item in the diet of trout (Cada et al. 1987a).

Diel variation in the consumption of terrestrial or aquatic invertebrate prey may occur. Giant kokopu and trout have been linked to feeding on terrestrial-derived invertebrates by day and on aquatic drift by night (Elliott 1973; Hansen et al. 2004). This may reflect the composition of invertebrates in the drift which typically varies over a diel cycle, with terrestrial invertebrates more abundant in the diurnal drift (Elliott 1973; Furukawa-Tanaka 1985) and aquatic invertebrates more abundant at night (Brittain & Eikeland 1988; Sagar & Glova 1992a). Seasonal variation in the composition of drifting invertebrates may also influence patterns of fish prey selection. Trout were reported to feed mainly on terrestrial invertebrates in late summer (Bridcut 2000) when the density of terrestrial drift is typically highest (Sagar & Glova 1992b; Edwards & Huryn 1995; Cloe &
Garman 1996) and aquatic benthic invertebrates when abundance is low (Hunt 1975; Stoneburner & Smock 1979).

The biomass and size of drifting invertebrates can also influence fish distribution and growth. Hayes et al. (2000) suggested that the limited availability of large invertebrate prey in drift could impact trout growth. Feeding preference on large prey items in drift-feeding fish such as trout (Ringler 1979; Wańkowski 1981; Bannon & Ringler 1986) and various galaxiids including giant kokopu, koaro and banded kokopu (Main & Winterbourn 1987; West 1989; West et al. 2005) may be due to relatively high energy value of these items.

Fish activity is related to prey availability and changes in food abundance can result in intraspecific competition which may affect individual growth rates especially in small streams which are food resource-limited (Hansen & Closs 2009). Amundsen et al. (2007) showed that stock depletion of Arctic charr (Salvelinus alpinus) alleviated intraspecific competition and resulted in enhanced growth and food consumption rates. Another experiment on juvenile steelhead trout (Oncorhynchus mykiss) illustrated that intraspecific antagonism as a result of food competition resulted in size variation among surviving individuals (Keeley 2001). Formation of social hierarchies among fish species living in patches with food scarcity has been extensively discussed in the literature. Social rank is highly correlated with fish size as aggressive contests among individuals are most often won by larger fish (Grand & Grant 1994). In a laboratory study by Whiteman & Côté (2004), dominant large gobies (Elacatinus prochilos) were territorial on patches with high food abundance forcing subordinate fish to less efficient feeding positions. In the absence of territorial dominant fish, the subordinate individuals occupied profitable patches that had been previously monopolised by larger fish. Large brown trout similarly exhibited higher food capture rates than smaller fish in a laboratory when fed with both benthic and surface
food (Gustafsson et al. 2010). Alanäärä et al. (2001) also reported that dominant brown trout foraged early in the night forcing smaller fish to feed at less profitable times. Social status has been studied in galaxiid fish in New Zealand. David et al. (2007) suggested that diel activity and feeding of individuals of giant kokopu is influenced by dominance hierarchies. Moreover, behavioural changes have been observed in large individuals of the same species by restricting resources to subordinate fish (Hansen & Closs 2005). Further details by Hansen & Closs (2009) also showed social ranks in giant kokopu caused segregation in feeding times and consequent negative effects on growth of subordinate kokopu.

Long-term studies of fish growth in relation to food and fish density/biomass and social hierarchies have received less attention to my knowledge (but see Hansen & Closs 2009). Although establishment of social hierarchy has been reported in large fish such as giant kokopu (David et al. 2007; Hansen & Closs 2009), there has been little investigation into if such interactions exist among assemblages of other species of smaller size than the former species. Banded kokopu (Galaxias fasciatus) represent an ideal fish species in which to study feeding strategy, growth and the influence of social status. They can be caught and tagged easily and they do not often move when approached by spotlighting. The fish have been shown to favour large terrestrial invertebrates at foraging times (Main & Lyon 1988; West et al. 2005). It has been reported that intraspecific competition occurs in giant kokopu assemblages due to the existence of social hierarchy (Hansen & Closs 2009). Banded kokopu are closely related to giant kokopu, however, they may have lower energetic constraints at an individual level due to their relatively smaller size compared to the former species. In Chapter 2, I inferred that habitat segregation amongst individuals is most likely due to intraspecific competition. Furthering this finding, the main focus of current chapter is to investigate if this competition affects the fitness of fish of low competitive ability. This
chapter is based on inferences drawn from the study by Hansen & Closs (2009) to investigate how banded kokopu growth interacts with dominance hierarchy. This study consisted of three main objectives. The first objective was monitoring composition, and spatial and temporal variation of drifting invertebrates from streams with different riparian vegetation density (with a gradient from low to high) to investigate if proportion of aquatic and terrestrial prey vary across streams, and if growth of fish is related to food supply. The second aim was to determine banded kokopu diet to determine if fish favour specific prey types (aquatic or terrestrial) and whether growth of fish is influenced by invertebrate variation across different streams. The third objective was to determine if banded kokopu density and biomass are related to drifting invertebrate abundance. The last aim was to address if fish growth is related to drift abundance and if this relationship is mediated by social hierarchy among individuals.

I hypothesise that I will see less total food but more terrestrial invertebrates in the stream with high riparian vegetation density and conversely more food including more aquatic items in the stream with low riparian vegetation density with the medium-vegetated stream site as an intermediate. The reason for this assumption is that streams with dense riparian vegetation are subsidised by terrestrial invertebrates from riparian vegetation (Kawaguchi & Nakano 2001) compared to streams with less riparian vegetation. On the other hand, streams with less riparian vegetation have often been reported as being more productive than streams with native bush (Thompson & Townsend 2005) which may affect total invertebrate abundance. I predict that terrestrial items will be high in abundance and biomass in the diet of fish in all types of streams, as such taxa have been documented to be main prey items in banded kokopu (Main & Lyon 1988; West et al. 2005). I further predict that fish growth rate will be related to food abundance in all types of streams and that growth
will be positively correlated with fish social rank in a pool, with high growth for dominant fish and lower growth for subordinate fish. This assumption was based on the size-based differences in microhabitat use as described in Chapter 2 and previous research on ecologically similar giant kokopu by Hansen & Closs (2009) where dominant fish were shown to exhibit aggressive behaviour towards subordinate fish in pool to enable occupation of the most energetically profitable patches. Thus, dominant fish are expected to get the benefit of higher growth rate in the long term.

3.2. METHODS

3.2.1. Study sites

Three streams flowing into Otago Harbour, in which banded kokopu were relatively abundant, namely, Craigs Creek (170°37'54"E; 45°7'38"S), Deborah Bay Stream (170°37'29"E; 45°47'43"S) and Sawyers Bay Stream (170°35'32"E; 45°48'43"S), were selected. The streams were located approximately 15 km north of Dunedin, South Island, New Zealand (Figure 3.1). Apart from very low numbers of longfinned eel (A. dieffenbachii) and common bully (G. cotidianus), banded kokopu were the only commonly encountered fish in these streams. Craigs Creek is characterised by 75% upstream pastoral land use whereas Deborah Bay Stream consists of 65% indigenous forest/scrub upstream land use. Sawyers Bay Stream is intermediate, with occasional sparse patches of native shrubs and small trees comprising 25% indigenous forest and 50% pastoral land use (Kater 2004). This gradient of riparian vegetation in each catchment was intended to provide some contrasting patterns of terrestrial and aquatic invertebrate prey in the invertebrate drift available to the fish across the three streams.
3.2.2. Sample collection

3.2.2.1. Invertebrates

In order to assess the density of drifting invertebrates in the water column, 7 permanent pools were selected in Craigs Creek and Sawyers Bay Stream and 6 pools in Deborah Bay Stream. Drift sampling was conducted once a month from June 2008 to May 2009. Exception to this sampling regime was during July and August (due to the low probability of sighting and counting fish in mid-winter, see Hansen & Closs 2009) in Craigs Creek and Sawyers Bay Stream, and August in Deborah Bay Stream. Drifting invertebrates were sampled by placing cone-shaped drift nets of 400-μm-mesh size, 250 mm mouth diameter and 80 cm length above each pool where the riffle met the pool. The drift nets were
left for at least 8 hours in the streams at each sampling effort (over night and the following day). The drift nets were set in streams shortly after official sunset and between 9 to 11 am on the following day in each sampling event and they were all in for the same amount of time. The samples were preserved in 90% ethanol in the field and transferred to the lab where they were counted and identified to the lowest possible taxonomic level under a dissecting microscope using Winterbourn et al. (2000) where appropriate.

The water depth and water velocity (see Chapter 2, section 2.2.2.1 for details on velocity measurement) at the mouth of each drift net, and retrieval time were recorded in order to calculate the volume of water passing through the drift nets. This was done by multiplying water velocity by the time span of having the net in the water and by the area of water at the mouth of the drift net. This was calculated as below:

\[
A = [R^2 \times \cos^{-1}((R - h) / R)] - [(R - h) \times (2Rh - h^2)^{0.5}]
\]

Where \( A \) is the area of water at the mouth of drift net (cm\(^2\)), \( R \) is the radius of drift net mouth (cm), \( h \) is the water depth at the mouth of net (cm).

The drifting invertebrate density per m\(^3\) in each pool was calculated as below:

\[
D = N / (V \times (A / 10000) \times T \times 60)
\]

Where \( D \) is the drift density per m\(^3\), \( N \) is the total number of invertebrates in the drift net, \( V \) is the water velocity at the mouth of the net (m/s), \( A \) is the area of water at the mouth of the drift net (cm\(^2\)) and \( T \) is the retrieval time of the net (min.).

3.2.2.2. Fish

Banded kokopu are often abundant in small coastal streams and are considered to be primarily nocturnal invertebrate drift feeders (McDowall 1990; Halstead 1998; McCullough 1998). They can be easily caught by spotlight and hand-net, and tagged, and their pool
fidelity is high (West et al. 2005). They live in shallow pools with low water velocities which makes invertebrate drift sampling to assess prey availability relatively simple. They feed on both aquatic and terrestrial invertebrates (Main & Lyon 1988; West et al. 2005). Thus, they are ideal subjects to study relationships between food supply, social status and long-term growth rates in a natural setting.

Fish sampling was undertaken once a month for a period of one year from June 2008 to May 2009. There was no attempt to sample fish in the winter months of July (except for Deborah Bay) and August due to low probability of sighting fish. Prior to pool selection, trial sampling was conducted to confirm that the selected study pools had relatively permanent fish assemblages. Non-destructive spotlighting and hand-netting was used to capture fish. Fish surveys commenced one hour after official sunset and were done by walking slowly upstream in order to avoid disturbing the fish. Fish were captured and transferred into a bucket and then anaesthetised using 2-phenoxyethanol at 12 ml l⁻¹. The length and weight of each fish was recorded. To enable individual monitoring of growth, each captured fish was given a unique tag using different colours of acrylic paint injected into the epidermis at the base of dorsal and anal fins and caudal peduncle. Tagging has been shown to have no measurable effects on fish (See Hansen & Closs 2009; Phillips & Fries 2009 for more details).

3.2.2.3. Fish stomach contents

In order to investigate banded kokopu feeding habits, prey items were collected by stomach flushing (Kamler & Pope 2001; Castro et al. 2008; Vehanen et al. 2009). Stomach flushing has previously been successfully used to collect the full range of prey items from banded kokopu (McDowall et al. 1996; West et al. 2005) and giant kokopu (Hansen et al. 1996; Vehanen et al. 2009).
2004). The gastric lavage technique was modified by connecting some plastic tubes with 2.5, 2, 1.5 and 1.2 mm (inner diameter) to a 60-cc syringe in order to avoid damage to the oesophagus in fish as small as 60 mm. After flushing, the fish were placed in buckets with stream water to recover, and were returned to the stream at the point of capture. The gut contents were collected and preserved in 90% ethanol. In the laboratory, freshly consumed prey items (recognised as items with little evidence of digestion) were counted and identified under a dissecting microscope using Winterbourn et al. (2000) where appropriate. The number of fish with empty stomachs was recorded, and unidentified partially digested items were also noted. Finally, all invertebrates in the fish’s stomach and drift were oven dried at 60 °C for 48 hours and then weighed to the nearest 0.1 mg using a Mettler Toledo AX205 (Switzerland) for further prey biomass analysis.

3.2.3. Prey selectivity

To determine whether banded kokopu had a preference for eating particular taxa, Pearre’s (1982) index was calculated as follows:

\[ V = \frac{(a_d b_e - a_e b_d)}{(a b d e)}^{0.5} \]

Where \( V \) is prey selectivity index which ranges from -1 to +1 indicating a gradient from no selection to high selection for a prey, respectively, \( a_d \) and \( a_e \) are the numbers of a given species in the fish stomach and drift, respectively, \( b_e \) and \( b_d \) are the numbers of total other species in the drift and fish stomach, respectively, and \( a = a_d + a_e \), \( b = b_d + b_e \), \( d = a_d + b_d \), \( a = a_e + b_e \). Values were not calculated when the species was not present in both the drift and diet.
3.2.4. **Fish growth rate**

The growth rate of fish was calculated in two ways: absolute growth rate and relative growth rate. The absolute growth rate is increase in weight per day \[
\frac{\text{last reading weight} - \text{initial reading weight}}{\text{days between two readings}}
\] and relative growth rate is % increase in body weight \[
\frac{\text{last reading weight} - \text{initial reading weight}}{\text{initial reading weight}} / \text{days between two readings}
\]. The growth rates were calculated between July 2008 and March 2009 in order to avoid bias in weight fluctuations in spawning season (late April to middle of June). The existence of dominance hierarchies in drift-feeding fish has been observed (Alanäärä et al. 2001; Gowan & Fausch 2002) and suggests that social hierarchy causes interactions between fish of different sizes in a pool on patch selection and feeding competition. Hansen & Closs (2005) and David et al. (2007) reported that social hierarchies among giant kokopu can result in variable growth rates. To investigate growth rate among banded kokopu, the fish were ranked from 1 (large fish) to 6 (small fish) in each pool where possible (there was no pool for which fish could possibly be ranked lower than 6 in the streams). For instance, fish with the highest weight was given rank of 1 and the next smaller fish (with a considerable gap in weight) was given rank 2 and etc.

3.3. **DATA ANALYSIS**

Differences in the mean density and biomass of drifting invertebrates between streams were compared using One-way ANOVA. The same procedure was applied to examine diel and seasonal variation in the abundance of terrestrial or aquatic drifting invertebrates. The data were log_{10}(x+1) transformed where necessary to meet assumptions of normality and homogeneity of variances. The diet data for individual fish were pooled for each stream. Comparisons between density and biomass of prey of different origins in
different seasons and streams were determined using ANOVA. To avoid pseudo-replication, all invertebrate samples for individual pools over one year of sampling were averaged and the mean of each was used for the analysis. The prey selectivity indices were not normally distributed so a non-parametric Kruskal-Wallis test was used for comparisons between streams. Linear regression was employed to investigate relationships between fish abundance/biomass and density of drifting aquatic/terrestrial invertebrates. The growth rate of fish was compared across the streams using linear regression. Relationships between the growth of fish across different ranks with abundance and biomass of drifting aquatic and terrestrial invertebrates entering pools within each stream were explored using linear regression. All data were analysed using SPSS version 18.

3.4. RESULTS

3.4.1. Invertebrate drift

3.4.1.1. Invertebrate composition

Drifting invertebrates were sampled, identified and counted once a month in the three streams from June 2008 to May 2009. In each stream, more than 70 invertebrate taxa were identified belonging to 20 orders (Appendix 1). The most frequently-found taxa in Craigs Creek were *Potamopyrgus antipodarum*, Oligochaeta and CollemboIa comprising 26.5%, 12.7% and 8.5% of the drift, respectively. The dominant drifting taxa in Deborah Bay Stream were CollemboIa (23.3%), *Deleatidium* spp. (19.9%) and Diptera adults (11.5%), whereas in Sawyers Bay Stream *P. antipodarum* (44.3%), CollemboIa (10.8%) and *Deleatidium* spp. (7.8%) were the dominant taxa.
3.4.1.2. Seasonal variation in invertebrate drift

Seasonal drift patterns showed that the freshwater snail (*P. antipodarum*) was the most frequent item in almost all seasons in Craigs Creek, with the exception of spring in which Oligochaeta were marginally more abundant (Figure 3.2a). More than one quarter of the drift consisted of springtails (Collembola) in all seasons in Deborah Bay Stream; however, mayflies (*Deleatidium spp.*) comprised 31.6% of the drift in autumn (Figure 3.2b). Snails clearly dominated in the drift from c. 30% to 56% in three seasons in Sawyers Bay Stream, whereas springtails were the dominant taxon in winter (Figure 3.2c).

3.4.1.3. Total drift abundance and diel variation

The mean density of drifting invertebrates varied significantly across the three streams (df$_2$,17=12.21, $P$=0.001), being highest in Craigs Creek and lowest in Deborah Bay Stream. The same pattern was found between the streams when comparing the biomass of drifting invertebrates (df$_2$,17=9.63, $P$=0.002). Diel comparison of drifting invertebrate density showed no significant difference in the abundance of drifting invertebrates at night and day in all streams: Craigs Creek (df$_1$,12=0.52, $P$=0.48), Deborah Bay Stream (df$_1$,10=1.85, $P$=0.20) and Sawyers Bay Stream (df$_1$,12=0.79, $P$=0.39). However, the biomass of drift was higher at night compared to day in all streams: Craigs Creek (df$_1$,12=46.61, $P$<0.001), Deborah Bay Stream (df$_1$,10=15.78, $P$=0.003) and Sawyers Bay Stream (df$_1$,12=4.36, $P$=0.05; Figures 3.3a, b).
FIGURE 3.2. Seasonal variation in relative abundance of the most abundant invertebrate taxa in the drift from Craigs Creek with sparse riparian vegetation (a), Deborah Bay Stream with dense riparian vegetation (b) and Sawyers Bay Stream with medium riparian vegetation (c) from June 2008 to May 2009.
3.4.1.4. Spatial variation in aquatic and terrestrial drift

Analyses showed a significantly higher density and biomass of aquatic species than terrestrial species in Craigs Creek (df\textsubscript{12}=10.42, \(P=0.007\)) and Sawyers Stream (df\textsubscript{12}=6.98, \(P=0.022\)). However, terrestrial invertebrates were numerically dominant in Deborah Bay Stream (df\textsubscript{10}=5.32, \(P=0.044\)) but aquatic taxa dominated gravimetrically (Craigs Creek;
df_{1,12}=59.00, P<0.01, Deborah Bay Stream; df_{1,10}=8.77, P=0.014, Sawyers Bay Stream; (df_{1,12}=24.16, P<0.01, Figures 3.4a, b and Table 3.1).

**FIGURE 3.4.** Mean ± S.E. of log_{10} density (a) and biomass (b) of aquatic (■) and terrestrial (□) drifting invertebrates from three streams from June 2008 to May 2009.
3.4.1.5. *Seasonal variation in aquatic and terrestrial drift*

The density of drifting aquatic taxa was higher than that of terrestrial taxa in summer from Craigs Creek and Sawyers Bay Stream, whereas terrestrial taxa from Deborah Bay Stream were more numerous than that of aquatic taxa in summer (Figure 3.5a and Table 3.1). The biomass of aquatic invertebrates was significantly greater than that of terrestrial invertebrates from all streams year round except during spring and summer from Deborah Bay Stream (Figure 3.5b and Table 3.1).

**FIGURE 3.5.** Seasonal variation (mean ± S.E.) in log_{10} density (a) and biomass (b) of aquatic (■) and terrestrial (●) drifting invertebrates from Deborah Bay Stream (D), Sawyers Bay Stream (S) and Craigs Creek (C) from June 2008 to May 2009.
TABLE 3.1. ANOVA results for log_{10} density (m^{-3}) and biomass (mg m^{-3}) of aquatic and terrestrial invertebrate comparison from three streams in different seasons (June 2008 to May 2009). Significant differences between aquatic and terrestrial invertebrate densities and biomasses are presented with *. The significance levels were tested against sequential Bonferroni adjustments.

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<td>10.60</td>
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<td>1,12</td>
<td>8.60</td>
<td>0.013*</td>
<td>0.05</td>
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<tr>
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<td>3.63</td>
<td>0.081</td>
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<td>1,12</td>
<td>24.08</td>
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</tr>
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</table>
3.4.2. Banded kokopu diet

3.4.2.1. Prey composition

The stomach contents of 651 banded kokopu (different fish) were examined. The stomachs of 22 fish (3.4%) were empty. Sixty-eight prey taxa were identified in the banded kokopu diet. Ostracoda (15%), Paracalliope fluviatilis (12.7%), Chironomidae (12.5%) and Oxyethira albiceps (9.4%) numerically comprised almost half of the items recorded in banded kokopu stomachs from Craigs Creek. In Deborah Bay Stream, 45.2% of the diet consisted of Deleatidium spp., Diptera adults, Collembola and P. fluviatilis. Deleatidium spp. made up 17.4% of the items recorded in fish from Sawyers Bay Stream followed by P. antipodarum, P. fluviatilis and Diptera adults (Appendix 1). More than half of the prey items in the stomachs belonged to 5 orders; Diptera, Ephemeroptera, Ostracoda, Crustacea and Trichoptera.

3.4.2.2. Seasonal changes of prey species in the diet

Temporal analyses of diet showed that Ostracoda and Chironomidae were the most commonly recorded prey in Craigs Creek in winter and summer, respectively, and amphipods (P. fluviatilis) were predominant in the other seasons. In Deborah Bay Stream, fish diet was dominated by Deleatidium spp. year round. Deleatidium spp. was also the main taxa recorded in the diet of fish from Sawyers Bay Stream in all seasons except autumn, when the snail P. antipodarum predominated (Figures 3.6a-c).
FIGURE 3.6. Seasonal variation in number of major prey taxa (mean ± S.E.) represented in banded kokopu (*Galaxias fasciatus*) diet in winter (■), spring (■), summer (■) and autumn (□) from Craigs Creek (a), Deborah Bay Stream (b) and Sawyers Bay Stream (c) from June 2008 to May 2009.
3.4.2.3. Spatial variation in prey of aquatic and terrestrial origin in diet

Prey of aquatic origin was numerically more abundant than terrestrial prey in the diet of fish from Craigs Creek (69.2%) and Sawyers Bay Stream (62.2%), whereas this figure dropped to 48.8% in Deborah Bay. However, invertebrate food items of terrestrial origin comprised a major proportion of the diet by weight ranging from 62.4% to 74.7% in all streams (Appendix 1). Statistical analyses showed that the average number of aquatic invertebrates was significantly higher than that of terrestrial items in the fish diet from Craigs Creek and Sawyers Bay Stream. Furthermore, average biomass of terrestrial prey was substantially higher than that of aquatic prey in all streams (Figures 3.7a, b and Table 3.2).

3.4.2.4. Seasonal variation in prey of aquatic and terrestrial origin

The number of aquatic prey items in the stomach of banded kokopu was significantly greater than that of terrestrial items from Craigs Creek and Sawyers Bay Stream in all seasons except autumn. The same trend was observed in Deborah Bay Stream in winter and autumn (Figure 3.8a and Table 3.3). However, taxa of terrestrial origin were more important than aquatic taxa gravimetrically in almost all seasons in all streams but the difference was not statistically significant in all cases (Figure 3.8b and Table 3.3).
FIGURE 3.7. Mean ± S.E. abundance (a) and biomass (b) of aquatic (■) and terrestrial (●) prey in stomachs of banded kokopu (*Galaxias fasciatus*) from three streams from June 2008 to May 2009.

TABLE 3.2. ANOVA results for abundance and biomass (mg) of aquatic and terrestrial prey from three streams from June 2008 to May 2009. Significant differences between aquatic and terrestrial prey abundances and biomasses are presented with *.

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<th>Stream</th>
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<th>Prey biomass in diet</th>
</tr>
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<td></td>
<td>df</td>
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<tr>
<td>Craigs</td>
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<tr>
<td>Sawyers</td>
<td>1,522</td>
<td>18.6</td>
</tr>
</tbody>
</table>
FIGURE 3.8. Seasonal changes (mean ± S.E.) in abundance (a) and biomass (b) of prey of aquatic (●) and terrestrial (■) origin in stomachs of banded kokopu (*Galaxias fasciatus*) from Deborah Bay Stream (D), Sawyers Bay Stream (S) and Craigs Creek (C) from June 2008 to May 2009.
TABLE 3.3. ANOVA results for aquatic and terrestrial prey [abundance and biomass (mg)] from three streams in different seasons (June 2008 to May 2009). Significant differences between aquatic and terrestrial prey abundances and biomasses are presented with *.

<table>
<thead>
<tr>
<th>Season</th>
<th>Prey abundance in fish stomach</th>
<th>Prey biomass in fish stomach</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>F</td>
</tr>
<tr>
<td><strong>Winter</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Craigs</td>
<td>1.38</td>
<td>5.2</td>
</tr>
<tr>
<td>Deborah</td>
<td>1.58</td>
<td>8.2</td>
</tr>
<tr>
<td>Sawyers</td>
<td>1.60</td>
<td>17.9</td>
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<td><strong>Spring</strong></td>
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</tr>
<tr>
<td>Craigs</td>
<td>1.146</td>
<td>5.8</td>
</tr>
<tr>
<td>Deborah</td>
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<td>Sawyers</td>
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<td>14.9</td>
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<tr>
<td><strong>Summer</strong></td>
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</tr>
<tr>
<td>Craigs</td>
<td>1.110</td>
<td>9.9</td>
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<tr>
<td>Deborah</td>
<td>1.118</td>
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<td>Sawyers</td>
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<td>7.0</td>
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<tr>
<td><strong>Autumn</strong></td>
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<tr>
<td>Craigs</td>
<td>1.82</td>
<td>2.7</td>
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<td>Deborah</td>
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<tr>
<td>Sawyers</td>
<td>1.106</td>
<td>0.03</td>
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</table>


3.4.3. Prey selectivity

Total numbers of 69, 73 and 67 taxonomic groups gave 429, 477 and 525 prey selectivity indices of diet to compare to drifting invertebrate composition from Craigs Creek, Deborah Bay Stream and Sawyers Bay Stream, respectively. There was a strong difference in prey selectivity between the three streams (Kruskal-Wallis, \( P < 0.001 \)). Comparisons of indices between seasons in each stream showed a significant difference in only Deborah Bay Stream (Kruskal-Wallis, \( P = 0.01 \)). Food selection analysis indicated that slugs were strongly preferred by banded kokopu in Craigs Creek (0.55), Deborah Bay Stream (0.68) and Sawyers Bay Stream (0.49). The second most-preferred taxa were isopods (0.52) in Craigs Creek and Cylomiscus (Coleoptera, c. 0.41) in Deborah Bay and Sawyers Bay Streams. \( P. \ antipodarum \) and Oligochaeta (-0.10) in Craigs Creek, Collembola and water mites (-0.07, -0.06, respectively) in Deborah Bay Stream and \( P. \ antipodarum \), Collembola and water mites (-0.13, -0.04 and -0.03, respectively) in Sawyers Bay Stream were selected against by the fish. Investigation on temporal food selection indices showed that while freshwater snails, springtails and water mites were least selected in most seasons, banded kokopu preferred quite a range of invertebrates over the year from the three streams (Figures 3.9, 3.10).
FIGURE 3.9. Prey selectivity indices (V) by banded kokopu (*Galaxias fasciatus*) in winter (■), spring (●), summer (▲) and autumn (□) from Craigs Creek (top), Deborah Bay Stream (bottom) from June 2008 to May 2009. The first two most- and least-preferred prey items are shown on the right and left sides of the vertical axes, respectively.
FIGURE 3.10. Prey selectivity indices (V) by banded kokopu (Galaxias fasciatus) in winter (■), spring (□), summer (■) and autumn (□) from Sawyers Bay Stream from June 2008 to May 2009. The first two most- and least-preferred prey items are shown on the right and left sides of the vertical axes, respectively.

3.4.4. Banded kokopu abundance in relation to prey availability

3.4.4.1. Fish abundance, biomass and drifting invertebrate

Linear regression results indicated that there was no relationship between the number of banded kokopu present and invertebrate drift density in individual pools from three streams (Figures 3.11a-c). In contrast, the biomass of fish was positively related to the density of food in all three streams (Figures 3.11d-f). The abundance of banded kokopu in a pool was not related to aquatic or terrestrial invertebrate density from the three streams but
the biomass of fish did show a positive relationship with number of aquatic items from Craigs Creek ($y=143.5x + 12.0$, $R^2=0.272$, $P=0.002$), Deborah Bay Stream ($y=134.1x + 46.28$, $R^2=0.123$, $P=0.018$) and Sawyers Bay Stream ($y=129.1x + 110.8$, $R^2=0.129$, $P=0.007$).

### 3.4.4.2. Fish growth, body mass and fish ranks

The mean absolute growth rate for banded kokopu was 0.034, 0.046 and 0.040 g/day from Craigs Creek, Deborah Bay Stream and Sawyers Bay Stream, respectively. A significant positive relationship was observed between the absolute growth rate and fish weight (g) from Craigs Creek ($R^2=0.473$, $P<0.001$), Deborah Bay Stream ($R^2=0.426$, $P<0.001$) and Sawyers Bay Stream ($R^2=0.419$, $P<0.001$). The relative growth rate of fish (% increase in body mass) was negatively related to fish weight from Craigs Creek ($R^2=0.203$, $F=13.97$, $P<0.001$) and Sawyers Bay Stream ($R^2=0.099$, $F=9.29$, $P=0.003$). The comparison between the absolute growth rate of fish with different ranks was significant from Craigs Creek ($df=5,55=2.37$, $P=0.05$) and Sawyers Bay Stream ($df=5,81=7.43$, $P<0.001$; Figures 3.12a-c). For example, the average growth rate of fish ranked 1 in a pool was higher than that of fish with a low rank of 3 from Craigs Creek ($df=1,24=5.81$, $P=0.024$). Hence, fish of immediate lower rank (rank 2) had the same growth as dominant fish. The same trend was observed between fish with rank 1 and with lower ranks of 4 ($df=1,31=10.28$, $P=0.003$) and 5 ($df=1,26=9.82$, $P=0.004$) from Sawyers Bay Stream. As noted earlier there was a positive relationship between absolute growth and body mass, but there were several cases in the three streams in which some fish with higher ranks in pools were smaller than fish with smaller ranks in other pools, but with better growth rate (Figures 3.12d-f). For instance, some fish with rank 1 ($n=4$) and mean body weight of 9.6 g had an average growth rate of
0.036 g/day while other fish with rank 2 averaging 19.75 g in body weight (n=4) grew just 0.018 g/day in Craigs Creek.

FIGURE 3.11. The relationships between number (left column) and biomass (g, right column) of banded kokopu (*Galaxias fasciatus*) and log\(_{10}\) density of drifting invertebrates (m\(^{-3}\)) per pool from Craigs Creek (a, d), Deborah Bay Stream (b, e) and Sawyers Bay Stream (c, f) from June 2008 to May 2009.
FIGURE 3.12. The absolute growth rate (g/day, left column) and weight (g, right column) of individual banded kokopu (*G. fasciatus*) by their social ranks from Craigs Creek (a, d), Deborah Bay Stream (b, e) and Sawyers Bay Stream (c, f) from July 2008 to March 2009.
3.4.4.3. *Fish growth and drifting invertebrate density/biomass*

There was no relationship between the absolute growth of individual banded kokopu and density of drifting invertebrates within pools from Craigs Creek and Deborah Bay Stream. However, a pattern was observed when the relationship was investigated among individual ranked groups from the former stream. The growth rate of fish of all ranks was related to the average density of drifting invertebrates from Craigs Creek and Sawyers Bay Stream, with the exception of fish of rank 4 in the latter stream (Table 3.4). The correlations between growth of fish with rank 6 (and rank 5 from Deborah Bay Stream) and drifting invertebrate density was not included in Table 3.4 because of the small number of observations. Considering the relationship between fish growth and invertebrate origin, the absolute growth rates of banded kokopu of all ranks, with the exception of fish of rank 4, were highly correlated with the density of aquatic invertebrate drift from Craigs Creek and Sawyers Bay Stream. No such correlation between fish growth and the number of terrestrial drifting invertebrates was detected in any of the streams (Table 3.4).

The analyses indicated that absolute growth of banded kokopu was positively related to invertebrate drift biomass in Deborah Bay Stream ($R^2=0.113$, $F=5.48$, $P=0.024$) and Sawyers Bay Stream ($R^2=0.141$, $F=14.12$, $P<0.001$). In Craigs Creek, the growth of only dominant fish (rank 1) correlated with invertebrate drift biomass ($R^2=0.595$, $F=11.77$, $P=0.009$). A positive relationship between the growth of dominant fish and biomass of terrestrial invertebrate drift from Deborah Bay Stream ($R^2=0.400$, $F=9.33$, $P=0.009$) highlighted the importance of large terrestrial taxa to fish in this stream.
TABLE 3.4. Regression results for the absolute growth rate (g/day) of banded kokopu (*Galaxias fasciatus*) with different ranks and log$_{10}$ total invertebrate drift density (m$^{-3}$) and log$_{10}$ aquatic invertebrate drift density (m$^{-3}$) from Craigs Creek, Deborah Bay Stream and Sawyers Bay Stream from July 2008 to March 2009. Significant relationships between fish growth and densities of total invertebrate drift and aquatic invertebrate drift are presented with *.

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<td>P</td>
<td>R$^2$</td>
<td>P</td>
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</tr>
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<tr>
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3.5. DISCUSSION

The scope of this study was to investigate the relationships between banded kokopu abundance, food abundance and growth in three streams differing in land use. The presence of a variety of terrestrial and aquatic taxa in the diet of the fish suggested that banded kokopu feed opportunistically on whatever is available in the habitat. Studies of individual pools exhibited a positive correlation between food abundance and total fish biomass indicating that fish biomass is proportional to food supply in a pool. A positive relationship between growth of high ranked (larger) fish and food abundance suggested that the social hierarchy among fish in a pool is a key determinant of access to food amongst individuals.

3.5.1. Invertebrate drift and fish diet

The prediction to see more aquatic drift in stream with low riparian vegetation, more terrestrial drift in the stream with dense riparian vegetation and a high contribution of terrestrial items to the fish diet in all streams was partially supported. Aquatic invertebrate taxa outnumbered terrestrial taxa in the drift from Craigs Creek and Sawyers Bay Stream, whereas terrestrial taxa were marginally higher in abundance in Deborah Bay Stream. A similar pattern was observed in the prey abundance in the diet of banded kokopu from the three streams. While the biomass of aquatic species was significantly greater than that of terrestrial invertebrates in the drift (due to huge numbers of snails), the opposite pattern was observed in the diet. This shows the importance of large terrestrial invertebrates in the diet of banded kokopu. The abundance of large terrestrial items in the diet of banded kokopu has been previously documented by Main & Lyon (1988). West et al. (2005) also reported that terrestrial items comprised 75% of abundance and 89% of biomass in the diet of banded kokopu. Terrestrial species were similarly found to constitute a large proportion of the diet in
giant kokopu (*G. argenteus*), a species closely related to banded kokopu (West 1989; Bonnett & Lambert 2002) and koaro, *G. brevipinnis* (Main & Winterbourn 1987). My hypothesis that biomass of terrestrial invertebrates would be higher than that of aquatic invertebrates in the diet was supported in this study. However, the main limitation in this study was that some crawler invertebrates such as mayflies may have escaped the nets, especially in low current velocities, possibly leading to underestimation of these species. A collar on the drift net is recommended for collecting drifting invertebrates for future studies.

Long-term monitoring of banded kokopu diet indicated different feeding habits in different streams. Banded kokopu preyed upon species that simply were more available in a given habitat, however, this was not the case in Craigs Creek in this study. The latter stream was dominated by freshwater snails, Oligochaeta and Collembola, which seem less rewarding to fish, perhaps due to the availability or structure of snails and the small sizes of the latter two taxa. Thus, banded kokopu searched for alternative prey items. The fish preyed mostly on Ostracoda, amphipods (*P. fluviatilis*) and Chironomidae in Craigs Creek, *Deleatidium* spp. in Deborah Bay Stream, and *Deleatidium* spp., snails (*P. antipodarum*) and amphipods in Sawyers Bay Stream. In Craigs Creek and Sawyers Bay Stream, snails did not make a significant contribution to the diet as reflected in their relative frequency of occurrence in the drift. The frequency of this item in the diet would have been even lower if the couple of fish with 10-30 snails in the stomach in each stream had been removed from the analysis. The hard shell of snails may explain this avoidance behaviour; indeed, most of the snails in the diet of banded kokopu were intact and seemed to have not been digested. Vinson & Baker (2008) reported that more than half of the snails eaten by rainbow trout passed through the gut alive and that the growth and condition of brown and rainbow trout with snails in their stomachs were significantly lower than that of fish which did not feed on
such items. The small contribution of snails to the diet of eel and trout has already been documented (McCarter 1986; Jellyman 1989; Sagar & Glova 1998). Furthermore, Bonnett et al. (1989) discussed that snails were comparatively scarce in the diet of longjawed and alpine galaxias despite being abundant in the benthos.

Banded kokopu showed interest in preying on species such as Deleatidium spp. when they are available in the habitat in all seasons (Deborah Bay and Sawyers Bay Streams). This finding accords with the results by West et al. (2005) that found a high abundance of Ephemeroptera in the diet of banded kokopu especially in spring and summer. It has been documented that invertebrate richness and EPT taxa (Ephemeroptera, Plecoptera and Trichoptera) occur more often in bushy streams than open streams as these taxa are enrichment-sensitive (Harding & Winterbourn 1995; Quinn et al. 1997; Harding et al. 1998). The banded kokopu dietary shift from mayflies in Deborah Bay Stream (with high riparian vegetation density) and Sawyers Bay Stream (with medium riparian vegetation density) to other species such as Ostracoda in Craigs Creek could be due to habitat catchment characteristics which may have caused the lower abundance of mayflies in the latter stream (5% in Craigs Creek vs. 21% in Deborah Bay Stream). A change in the habitat structure (vegetation removal) and consequent dietary change has been studied in other fish such as Perca fluviatilis (Diehl 1993). This study showed that banded kokopu feed on invertebrates in proportion to their abundance in the habitats, a similar pattern to that which was observed in trout (Angradi & Griffith 1990; Hilderbrand & Kershner 2004b). Overall, drifting invertebrate and prey composition relates to the habitat characteristics and varies across the steams – in other words, fish feed opportunistically and adjust their diet to what is available in the stream.
The importance of drifting invertebrates, especially terrestrial species, in drift-feeding freshwater fish, has been reported by several authors (Wipfli 1997; Kawaguchi & Nakano 2001; Allan et al. 2003; West et al. 2005; Romaniszyn et al. 2007). Moreover, availability of prey may play a role in influencing the feeding activities of stream-dwelling fish. In this study, the highest abundance of both aquatic and terrestrial invertebrates (total invertebrates) in the diet occurred in summer in all streams when the invertebrate density was also at its peak in the drift. The lowest number of prey in fish stomachs occurred in the winter season in two streams, whereas the lowest density of drift was recorded in autumn; however, a note of caution is required here to emphasise that there were no data available in June and July for drift abundance analysis for winter from two streams. No attempt was made to investigate the diet of banded kokopu during daytime in this study as this species has been considered to be primarily nocturnal (McDowall 1990; Halstead 1998; McCullough 1998) but diurnal feeding among other galaxiid fish such as Canterbury galaxias (G. vulgaris), giant kokopu and koaro has been documented (McIntosh & Townsend 1995; Hayes 1996; David & Closs 2003; David & Stoffels 2003; Hansen et al. 2004). Apart from occasional events, active large fish were not observed by day in this study.

The prey selection indices indicated that slugs were preferentially consumed by banded kokopu in all streams. However, this is difficult to be interpreted as slugs are of importance in the diet of fish for two reasons. First, the absence of slugs in the drift resulted in high preference on these items. Second, the occurrence of such taxa was very low in the fish stomachs, comprising about 2% of the diet of fish from all three streams. Isopods and a beetle, Cylomiscus, were also highly prevalent items in the fish stomachs. Considering the sizes of these items, it appears that banded kokopu may be interested in large invertebrates as discussed earlier. Moreover, salmonids have shown strong preference for large invertebrates.
which contain higher energetic value (Dunbrack & Dill 1983; Bannon & Ringler 1986; Kreivi et al. 1999). Freshwater snails and small taxa of springtails (Collembola) and water mites were least selected by the fish as feeding on small items to reach satiation may be energetically costly. Bachman (1984) stated that brown trout would ignore small items in the drift if energy expended would be far higher than what they would have achieved by capturing those items. Overall, banded kokopu preyed on a variety of invertebrates in different streams and this may reflect opportunistic feeding habits of this fish.

3.5.2. Fish abundance, growth and drifting invertebrates

The results of this study did not show any significant increase in the number of banded kokopu residing in individual pools as the abundance of drifting invertebrates increased, however, the biomass of fish in a pool was dependent on the drifting invertebrate density. It can therefore be assumed that the biomass of fish per pool was more closely related to the supply of prey than was the number of fish per pool. Hansen & Closs (2009) also reported a similar pattern for giant kokopu. The biomass of salmonids in Horonai Stream was shown to be proportional to the prey availability, especially that of terrestrial invertebrates (Kawaguchi et al. 2003). When the relationship between fish and invertebrate origin was studied, a positive relationship between fish biomass and number of aquatic items from all streams was observed. This result was expected as the number of aquatic invertebrates was greater than the number of terrestrial items in the drift and diet of fish from two streams. West et al. (2005) found a positive relationship between fish abundance (rather than fish biomass in this study) and aquatic drift abundance, but they reported a limitation in statistical power due to small sample size. My results here support the “input-matching” hypothesis discussed by Parker (1978). The theory suggests that the proportion of individuals
in a patch should be equal to the proportion of available resources in that patch. Abrahams (1989) showed that the distribution mechanism of guppies (*Poecilia reticulata*) was in accordance with the predictions of the “input matching” hypothesis. The distribution of small fish was shown to be related to food abundance, however, large fish biomass distributions within a stream were related to other factors (such as predation by birds), rather than food supply (Angermeier & Karr 1983).

The social status of a fish is a key determinant in individual interactions with others in a pool. Some studies on giant kokopu (Hansen & Closs 2005; David *et al.* 2007) showed that dominance hierarchy affects the activity of fish through the claiming of profitable patches by dominant fish at night and the forcing of subordinate fish to forage at day. Although the drift density did not differ significantly from night to the day in this study, the drift biomass was higher by night relative to the day. Further investigation is needed to determine if such similar ontogenetic shifts in diel feeding activity occur in banded kokopu assemblages, as prey biomass has been shown to be smaller by day and this may affect growth of subordinate fish. In this study, growth was positively related to fish weight in all streams, implying that larger fish had a greater increase in weight per day (absolute growth) relative to small fish. This result compliments the findings by others on salmonids (Chapman 1962; Metcalfe *et al.* 1989; Nakano *et al.* 1991; Nakano 1995). However, when relative growth was calculated, small fish displayed a greater gain. This pattern is expected as small fish direct all their energy into somatic growth, unlike mature fish for which a large proportion of energy is directed into gonadal development. The absolute growth rate of dominant fish was higher than that of subordinate fish from two streams. This was expected as the basis for the rankings was fish weight but some fish with higher ranks and better
growth rate in a pool were smaller in weight than other low ranked fish in other pools. The present findings seem consistent with research on giant kokopu by Hansen & Closs (2009).

It is interesting to note that individual-based (fish ranks) growth analyses in relation to food reveal a pattern that was concealed at the population level. The growth of fish of the first three ranks (1, 2 and 3) was positively related to drifting invertebrate abundance (and also aquatic drift) in Craigs Creek and Sawyers Bay Stream, indicating an ability of large fish to seize drifting invertebrate and deprive subordinates of food supply. Gustafsson et al. (2010) stated that brown trout (S. trutta) of larger size showed higher food capture rates than smaller trout. They demonstrated size-specific differences in foraging among brown trout such that large fish were able to keep positions close to the water surface to capture food and force small conspecifics to find refuge between foraging efforts. A significant positive relationship was also found between absolute growth of fish and biomass of drifting invertebrates from Deborah Bay Stream and Sawyers Bay Stream. In Craigs Creek, growth of only fish rank 1 was dependent on food biomass. Another important finding was that the high correlation between fish growth and biomass of terrestrial items from Deborah Bay Stream could magnify the role of large allochthonous invertebrates in the diet and consequently, the growth of fish from streams with dense riparian vegetation. Montori et al. (2006) and Teixeira et al. (2006) reported that guts of large trout contained more terrestrial invertebrates than that of small trout. The size of terrestrial invertebrates has been reported to be four times larger than that of aquatic invertebrates (Nakano et al. 1999b) and a great proportion (up to 90%) of terrestrial prey in salmonid diets (Nakano et al. 1999b; Kawaguchi et al. 2003) may give fish the benefit of improved growth. It has been shown that terrestrial invertebrate depletion resulted in growth reduction among large trout (Erős et al. 2010). These examples and results from the current study highlight the significance of streams
running through bushes in providing large terrestrial subsidy and influencing growth of drift-feeding fish. My prediction that fish growth would be correlated with food abundance and fish ranks were supported in this study but not without a cautionary footnote that growth was not dependent on food abundance from one stream.

3.6. CONCLUSION

In general, the growth of banded kokopu was related to fish rank, indicating that high-ranked fish grew faster than low-ranked ones. There were some cases in which small fish that held high ranks in a pool had better growth than other, large, fish with lower ranks in other pools. It may be that the smaller fish benefited from being dominant in their own pools. There is extensive literature indicating that fish of high social status access better energetic positions than individuals of low ranks. For instance, dominant Atlantic salmon (*Salmo salar*) had larger otoliths than subordinate conspecifics, indicating faster growth rates (Metcalfe *et al.* 1992). Dominant coho salmon (*Oncorhynchus kisutch*) exhibited higher growth than subordinates when food supply was adequate, however, the opposite pattern occurred at low food ration because subordinates had lower energy requirements (Van Leeuwen *et al.* 2011). This corroborates with the results of current study as a positive relationship between dominant fish growth and drifting food supply was observed. Larger drifting invertebrates appeared to enhance fish growth rate and terrestrial items seemed to be more important than aquatic items. Diet analysis of banded kokopu suggests that the fish are opportunistic feeders that may prey on whatever is available in the habitat. Numerous aquatic prey species in the diet of the fish may be related to high numbers of the same items in the drift, but a heavy terrestrial invertebrate representation in the diet suggested that fish selected the larger prey items in the drift.
This chapter has discussed that prey availability may drive banded kokopu to feed on certain invertebrates but whether individual prey nutritional quality plays a role in food selectivity is a matter that needs to be addressed. On the other hand, subordinate fish seemed to face fierce competition as dominants intercepted great proportions of the food supply. This prompts the question whether fish of low rank compensate for low growth rates by relocation, which will be discussed in Chapter 5. In the next chapter the caloric values of the main invertebrates drift items that contributed to banded kokopu diet will be investigated in order to gain a better understanding of the fish dietary habits. The energetic demands of the fish will also be discussed and compared with the energy available in the habitat to infer if the food energetically meets the fish metabolic requirements.
CHAPTER 4

Is energy content in food supply sufficient to meet banded kokopu metabolic requirements?
ABSTRACT

The relationships between total energetic value of drifting invertebrates, biomass and growth of banded kokopu, and fish oxygen consumption and metabolic demand, were studied in two New Zealand South Island streams. The fish metabolic rate was determined by measuring oxygen consumption rates using a respirometer at 5.5, 10.5 and 15.5 °C, reflecting the typical seasonal variation in water temperatures (5.7 to 16.8 °C) in the study streams over an annual cycle. The metabolic rates were converted to energy expenditure estimates for fish at different temperatures. To calculate energy available in each pool, the energy contents of 20 key invertebrate prey taxa were measured. The study shows that invertebrate drift was likely insufficient to meet banded kokopu energetic requirements and fish may access other sources of energy in the habitat such as terrestrial invertebrate inputs. The fish seemed to be living on an energetic “knife edge” in all seasons as they could obtain only c. 70% and 60% of their total energy expenditure from drifting invertebrates in Craigs Creek and Deborah Bay Stream, respectively. Fish biomass and growth of dominant fish were dependent on pool quality, suggesting that variation in the energy source may affect fish size structure and fitness in pools. Furthermore, the nutritional quality of individual invertebrate drift taxa was identified as a key determinant in fish prey selection. The low caloric values for taxa such as water mites, Oligochaeta and Potamopyrgus antipodarum may relate to their relatively small sizes or hard shells and this may explain why banded kokopu were deterred from feeding on these items.
4.1. INTRODUCTION

The interaction between energy pathways in freshwater ecosystems and the bioenergetic demands of fish is a key determinant of fish production (see Wipfli & Baxter 2010). Fish obtain food from their habitat and use the energy from its catabolism for maintenance, activity, growth and reproductive products (Brett & Groves 1979). In a normal situation, dietary energy (exogenous source) must equal energy for maintenance, activity and to maintain body mass; and energy stored in tissues (endogenous source) is used to meet metabolic requirements during periods of insufficient energy supply. If starvation continues, then fish growth, and ultimately reproduction, may be impacted in the long term (Brett & Groves 1979). Hence, it is essential to know whether energy resources in the ecosystem meet the energy requirements of inhabiting fish to inform fisheries management strategies.

It has been demonstrated that trout populations are energy-limited in many streams despite the consistent production of prey items (Warren et al. 1964; Allan 1983; Cada et al. 1987b; Waters 1988; Ensign et al. 1990; Filbert & Hawkins 1995; Huryn 1996). In contrast, an availability of sufficient energy to support rainbow trout (Oncorhynchus mykiss) populations has been reported by Nakano et al. (1999b) in the Honorai Stream. Energy shortfalls in streams were first discussed by Allen (1951) who found that there was scarcely enough energy to support trout production in a New Zealand stream. His finding is known as “Allen’s paradox” (Hynes 1970). Allen’s paradox suggests that the deficit in energy available for trout may relate to an underestimation of food sources other than benthic aquatic invertebrates, such as allochthonous (terrestrial) prey in streams (Waters 1988, 1993). The importance of terrestrial energy inputs into streams has been assumed to be equal to that of energy available from the benthic community (Cloe & Garman 1996). These terrestrial subsidies are considered to be important sources of energy for consumers at high
trophic levels (Fisher & Likens 1973; Triska et al. 1982; Allan et al. 2003; Romaniszyn et al. 2007), as their large size makes them potential prey with high energetic values (Wipfli 1997; Baxter et al. 2005). Although it is not clear if quality of allochthonous invertebrates is different from that of autochthonous invertebrates, predatory fish have been shown to select high-quality food resources regardless of their origins (Marcarelli et al. 2011).

Bioenergetic information enables us to understand the conceptual framework of fish growth interactions with their environments (Warren & Davis 1967). Bachman (1982) proposed a bioenergetic model for drift-feeding salmonids in which fish growth is determined by energy availability based on density of drifting invertebrates. A considerable amount of literature has been published on the impact of food limitation on growth of salmonids in streams and rivers (Cada et al. 1987b; Ensign et al. 1990; Filbert & Hawkins 1995; Weiland & Hayward 1997; McKinney & Speas 2001). Moreover, Hayes et al. (2000) showed that growth of trout is limited in the absence of large prey items, as longer foraging times on small drifting invertebrates (with low energy value) to reach satiation may impact fish growth. They also stated that the maximum trout size (biomass) would be constrained by the energy available in the drift unless the fish move to profitable patches or forage on alternative prey items. Imre et al. (2004) demonstrated that the total salmonid biomass in pools increased following increases in energy resources in the habitat. These suggest that pool quality, in terms of how energy influences fish biomass, affects the fitness of its individuals.

To better understand patterns of energy flow in an ecosystem, it is vital to know the energetic value of its prey items (Rodgers & Qadri 1977). Although the energy value of a large number of invertebrates has been measured, few studies (mostly on trout) have attempted to elucidate the relationships between food quantity and quality and the metabolic
requirements of secondary consumers such as fish. Banded kokopu, *Galaxias fasciatus*, are a native galaxiid fish in New Zealand (McDowall 1990) and represent an ideal species to investigate relationships between fish growth, energy supply and expenditure. The fish are often resident in their home pools throughout the year, and hence, the biomass and abundance of fish within a pool should reflect the long-term patterns of energetic quantity and quality of the food supply (drifting invertebrates) entering the pool (see Hansen & Closs 2009). Despite some studies on banded kokopu feeding patterns (Main & Lyon 1988; West *et al.* 2005), their energetic demand in relation to their prey availability is uncertain.

This research had three main aims. The first objective was to measure the energetic content of drifting invertebrates entering individual pools in two streams to assess the availability of total energy from drifting invertebrates at the pool level. The second objective was to investigate if growth of banded kokopu is influenced by the pool quality in terms of energy. The last aim was to estimate banded kokopu oxygen consumption and consequently their energy expenditure to elucidate whether food is in short supply, in equilibrium, or in excess when considering the total energy from drifting invertebrates in individual pools. As metabolic rate is temperature dependent, metabolic rates of banded kokopu were measured at different temperatures using a respirometry instrument. The metabolic rates were converted to energetic consumption using the method described by Elliott & Davison (1975). Two streams were selected for this study, Craigs Creek and Deborah Bay Stream. The first stream is characterised by high numbers of banded kokopu (0.72 vs. 0.43 fish/m² in Deborah Bay Stream) and the second stream is defined by low invertebrate (food) density (see Chapter 3). I hypothesise that banded kokopu growth will be determined by the total energy available in the form of drifting invertebrates in each pool in both streams. I also predict that banded kokopu will be food-limited in both streams, given that Craigs Creek is more densely
populated with banded kokopu and Deborah Bay Deborah Bay has a low density of drifting invertebrates.

4.2. METHODS

4.2.1. Study site

Two streams flowing into Otago Harbour, in which banded kokopu were relatively abundant, i.e., Craigs Creek (170°37′54″E; 45°47′38″S) and Deborah Bay Stream (170°37′29″E; 45°47′43″S), were selected. Seven and six pools were selected for the sampling in Craigs Creek and Deborah Bay Stream, respectively. Craigs Creek is characterised by 75% upstream pastoral land use whereas Deborah Bay Stream consists of 65% indigenous forest/scrub upstream land use. The two streams were selected because they were like to vary in the quantity and quality of drifting invertebrate prey due to contrasting patterns of catchment land use. More than 64% of drifting invertebrates consisted of aquatic taxa from Craigs Creek whereas dominant taxa (60%) from Deborah Bay Stream were terrestrial species (Appendix 1).
4.2.2. **Sample collection**

4.2.2.1. **Fish collection and oxygen consumption measurements**

The basal metabolic rate of banded kokopu was determined using a closed system respirometry instrument (Strathkelvin Instruments, Scotland). Although measurement of resting oxygen consumption rate using a closed system is often used (Graham 1949; Wells 1987; Robinson 2008) and has several advantages, it also has limitations such as poor resolution of short-term metabolic rates (Chappell & Bachman 2002). A total of 30 fish was captured during several sampling outings in September and October 2009 from Craigs Creek and Deborah Bay Stream. The fish were kept in a bucket with stream water and aeration.
prior to transport, and were transferred to a temperature-controlled room at the University of Otago. The fish were left for 4 hours to acclimatise at the pre-set room temperature before being transferred to aerated aquaria with dimensions of $90 \times 60 \times 70$ cm. Fish were starved for 48 hours in the aquaria prior to the experiment to avoid overestimating metabolic rate measurements due to digestion of the remaining food in the fish’s stomach (Alsop & Wood 1997). The fish were kept at a photoperiod of 12L:12D.

The fish were placed in specifically designed circular respirometer containers (0.75 or 1.55 litres capacity, depending on fish size) and then left for 12 hours with slow, fresh water inflow, to acclimatise to the new environment and allow the fish to stabilise their metabolic rate. The respirometer containers were covered with black plastic to minimise stress and disturbance. Prior to taking oxygen measurements in the closed system, the inflow water was disconnected and the container completely sealed. Approximately 1 ml of water was sampled from the container and injected into an oxygen metre (Oxygen Metre 781, Strathkelvin Instruments, Scotland) to read the oxygen partial pressure values. Three readings were taken at 10 minute intervals and all readings occurred 2 minutes after the injection to allow the instrument to stabilise. The average of the 3 readings was taken for data analysis. All experiments were conducted under conditions of absolute darkness and extra care was taken to minimise stress to the fish throughout the trial. All measurements were made at the same time of night (around 11 pm) to avoid possible variation in metabolic rates over a diel cycle. The respirometry experiment was conducted at three temperature levels, i.e., 5.5, 10.5 and 15.5 °C, reflecting the typical seasonal variation in water temperatures (5.7 to 16.8 °C) in the study streams over an annual cycle. Each fish was used only once for the experiment at a particular temperature. After recording the data, each fish
was sedated using 2-phenoxyethanol at 12 ml l⁻¹ and the length and weight were recorded. All fish were returned to their original streams at the completion of the measurements.

The oxygen consumption rate of banded kokopu was estimated using the following equation (Robinson 2008);

\[ \Delta P O_2 \times C \times V \times 31.99 / (M \times t) \]

Where \( \Delta P O_2 \) is change in oxygen partial pressure over the measurement period (mm Hg), \( C \) is \( O_2 \) capacitance of water at the experimental temperature (1.7 \( \mu \text{mol L}^{-1} \text{ mm Hg}^{-1} \)), \( V \) is volume of the respirometer (L), 31.99 is molecular weight of oxygen, \( M \) is mass of fish (g) and \( t \) is duration of experiment (h).

### 4.2.2.2. Energetic content of invertebrate taxa

To measure the caloric content of individual invertebrate taxa, drifting invertebrates were sampled from March to July 2010 using the methods described in Chapter 3 (section 3.2.2.1) from Craigs Creek and Deborah Bay Stream. The main prey taxa found in the diet of banded kokopu (Appendix 1, Table 4.2) were collected, identified and picked whilst still alive to determine the fresh caloric values of the individual taxa. A few species that were not important in the diet (but abundant in the drift) were also included to evaluate if the lack of selection of these potential prey items by fish, reflected low caloric values. The fresh invertebrates were snap frozen using dry ice then stored in −20 °C until processing. To determine caloric values, all invertebrates were oven dried at 60 °C for 48 hrs and weighed to the nearest 0.01 mg using a Mettler Toledo AX205 (Switzerland). The samples were then ground into a homogenous powder using a mortar and pestle and their caloric values measured using a Carlo Erba Elemental Analyser EA 1108 (CEEA 1108) at Campbell
Microanalytical Laboratory, Department of Chemistry, University of Otago. The values obtained from combustion in the instrument were presented as net heating values (Cal g⁻¹).

### 4.2.2.3. Energy available to feeding fish by pool

To determine the energy available to fish in each pool, the drifting invertebrates entering each pool were collected from June 2008 to May 2009 (see Chapter 3, section 3.2.2.1). The drift nets were set in the streams after official sunset and were left for 10 hrs. The biomasses of collected drifting invertebrates were measured and oven dried at 60 °C for 48 hrs and weighed to the nearest 0.01 mg using a Mettler Toledo AX205 (Switzerland). The energetic contents of dried biomass of drifting invertebrates were calculated using the values presented in Table 4.2. For taxa for which caloric values were not available (these terrestrial or rare aquatic taxa comprised c. 13 and 14% of the drift and fish diet from Craigs Creek and c. 21 and 23% of the drift and fish diet from Deborah Bay Stream, respectively), the grand-average energy content of species listed in Table 4.2 was used. In the biomass calculations, the biomass of *P. antipodarum* was adjusted to compensate for 90% of the snail’s weight being shell (Forsyth & McCallum 1981). The average volume of each pool (m³) in each month was used to calculate the mean energy available (cal per 24-h) using the density of drifting invertebrates (m⁻³ h⁻¹) in each pool. There was no significant difference between invertebrate drift densities at night and day, hence, the invertebrate drift density at night was used for the calculations.

As energy expenditure of fish was measured at three temperature levels of 5.5, 10.5 and 15.5 °C, the temperature profile of the streams was also recorded and integrated into these three categories in order to compare fish energy expenditure with the energy available in the form of invertebrate drift in pools (see section 4.2.2.6 for more details on this
The water temperature was recorded using HOBO temperature loggers (HOBO Water Temp Pro, Model H20-001, Onset Computer Corporation, Pocasset, MA, USA) once a month from June 2008 to May 2009. June to October and April to May were assigned a mean water temperature of 10.5 °C and November to March a temperature of 15.5 °C in Craigs Creek. In contrast, June to October and November to May were given a mean of 5.5 °C and 10.5 °C, respectively, in Deborah Bay Stream (see section 4.4.1 for more details on water temperature from the streams). The comparison of fish energy expenditure and energy available as drifting invertebrates was also made at season level for each stream to study if trends varied across seasons.

4.2.2.4. Fish biomass and growth in relation to energy available in pool

The biomass (kg) and absolute growth rate of fish (g/day) were measured (see Chapter 3, section 3.2.4. for more details on fish growth measurements) to determine the relationships between these parameters and the energy available as drifting invertebrates in pools in Craigs Creek and Deborah Bay Stream. The absolute growth rates were calculated between July 2008 and March 2009 in order to avoid bias in weight fluctuations in the spawning season (late April to middle of June).

4.2.2.5. Converting oxygen consumption rate to energy expenditure

As fish oxygen consumption is temperature dependent, three regression lines were plotted between oxygen consumption rate (mg O₂ kg⁻¹ h⁻¹) and fish weight (kg) at 5.5, 10.5 and 15.5 °C (Figure 4.3a). I used these equations to calculate the oxygen consumption rate of each fish in each pool at the relative temperature. For instance, the oxygen consumption rate of a fish weighing 0.06 kg in a pool with an average water temperature of 5.5 °C was estimated at 21.95 mg O₂ kg⁻¹ h⁻¹ [-1011 × 0.06 + 82.61 (equation 1)]. The oxygen
consumption rate measured for each fish was converted to an energy expenditure rate assuming that 1 mg O\textsubscript{2} is used to generate 3.24 calories of energy (Elliott & Davison 1975). This conversion factor has been used by several authors for a variety of fish species (Grisdale-Helland et al. 2008; Guénard et al. 2008, 2010; Jennings et al. 2008; Clark et al. 2010). For the above mentioned example, a fish weighing 0.06 kg and consuming oxygen at a rate of 21.95 mg O\textsubscript{2} kg\textsuperscript{-1} h\textsuperscript{-1} used an estimated 4.27 cal h\textsuperscript{-1} (21.95 × 3.24 × 0.06). The total energy expended by fish biomass in each pool was obtained by summing up the energy expenditure of individual fish and calculating the total energy consumption for 24 hrs (cal per 24-h).

4.2.2.6. Comparison of fish energy expenditure and energy available in pool

To compare banded kokopu energy consumption to the energy available as drifting invertebrates entering a pool, average foraging time (hrs) was estimated in each night (due to their nocturnal behaviour). Estimating foraging time in the field is difficult as length of night and temperature vary throughout the year. Foraging length also varies among fish of different sizes (pers. obs.). It was assumed that banded kokopu feed on average for 8 hours during the night throughout the year. Based on my personal observations, the fish may feed for up to 12 hrs (early evening to early morning) during summer because of their higher metabolic rates and feed for up to 4 hrs during winter as their metabolic demands decrease. Variability in feeding activity among assemblages of giant kokopu, a species closely related to banded kokopu, has also been reported (Hansen et al. 2004). Hence, I used the total energy equivalent of biomass of drifting invertebrates (cal per h) to calculate the energy available as drifting invertebrates entering a pool for banded kokopu for 8 hrs. The contribution of drifting invertebrates to the daily energy budget of banded kokopu (%) was
calculated using the values of daily energy consumption and energy available in the form of invertebrate drift in the streams.

4.3. DATA ANALYSIS

The relationship between fish oxygen consumption rate and fish weight at three different temperatures was studied using a linear regression. To study if the mean oxygen consumption of fish at three temperature levels were significantly different, an ANCOVA was applied with fish weight as covariate. Furthermore, a Bonferroni adjustment was used due to multiple comparisons. A one-way ANOVA was used to determine whether the energetic content of the invertebrate drift in the two streams differed. The mean caloric value of uncommon invertebrates was compared with that of abundant invertebrates in the diet of fish using an independent-samples t-test. A linear regression was applied to investigate the relationship between total fish biomass and absolute growth of dominant fish, and energy available in the form of drifting invertebrates in each pool. A one-way ANOVA was used to compare available energy and fish energy expenditure in pools from both streams at three temperature levels and in different seasons. The data were log_{10}(x+1) transformed when necessary to meet assumptions of normality and homogeneity of variances. All data were analysed using SPSS version 18.

4.4. RESULTS

4.4.1. Temperature variations in the study streams

The mean monthly water temperature of Craigs Creek was higher than that of Deborah Bay Stream throughout the study (Figure 4.2). The lowest mean monthly water
temperatures were recorded in August as 7.5 and 5.7 °C and the highest were recorded as 16.8 and 12.2 °C in January in Craigs Creek and Deborah Bay Stream, respectively.

FIGURE 4.2. Monthly variation in the mean water temperature (°C) of Craigs Creek (■) and Deborah Bay Stream (□) from June 2008 to May 2009.

4.4.2. Fish oxygen consumption in relation to energy expenditure

The average oxygen consumption rate of banded kokopu at rest was measured at 5.5, 10.5 and 15.5 °C (Table 4.1). ANCOVA results showed that the covariate, fish weight, was significantly related to the oxygen consumption rate (mg O₂ kg⁻¹ h⁻¹) of banded kokopu (df₁,26=16.07, P<0.01) as small fish consumed more than large fish per unit of body, whereas the opposite pattern was observed when oxygen consumption per animal was calculated (Figure 4.3). The mean oxygen consumption rate of fish at 5.5 °C was significantly different from that of fish at 15.5 °C (df₁,15=18.39, P=0.001). The mean energy consumption of fish in
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The energy content in the food supply for banded kokopu was 2.5 ± 0.33 (n=48), 3.45 ± 0.21 (n=286) and 5.25 ± 0.51 (n=124) Cal h⁻¹ at 5.5, 10.5 and 15.5 °C, respectively.

FIGURE 4.3. The relationships between oxygen consumption rate per unit weight of banded kokopu (*Galaxias fasciatus*, mg O₂ kg⁻¹ h⁻¹, a) and per individual (mg O₂ h⁻¹, b) at 5.5 °C (1, ♦), 10.5 °C (2, □) and 15.5 °C (3, ▲).
4.4.3. Caloric value of invertebrates

The invertebrate taxa with the highest energy content in Craigs Creek were *Zelandobius* (Plecoptera), *Microvelia mcgregory* (Hemiptera), *Deleatidium* (Ephemeroptera) and Diptera adults, whilst lowest values were observed for Ostracoda and millipedes. In Deborah Bay Stream, Diptera adults, spiders (Arachnida), Lepidoptera larvae, Diptera pupa and *Zelandobius* were the most energetically nutritious taxa whereas amphipods (*Paracalliope fluviiatilis*) had the lowest energy value (Table 4.2). There was no significant difference between caloric values of the same species from Craigs Creek and Deborah Bay Stream except for Diptera adults (df\textsubscript{1,4}=11.01, \(P=0.029\)).
The mean caloric value of three taxa, *M. mcgregory*, Oligochaeta and water mites (Arachnida), which were not abundant in the diet but fairly abundant in the drift from Craigs Creek, were compared with the mean caloric content of other taxa (Ostracoda and millipedes values excluded) and no significant difference was observed. The same analysis was performed to compare mean caloric value of *Zelandobius*, *P. antipodarum* and water mites with other taxa (all values included) from Deborah Bay Stream but no significant difference was observed.

### 4.4.4. Fish biomass and growth in relation to energy available in pool

A positive relationship was observed between total fish biomass (kg) and the energy available as drifting invertebrates (cal/24-h) in each pool when the data from Craigs Creek and Deborah Bay Stream were pooled (Figure 4.4). A positive relationship was also observed between absolute growth (g/day) of dominant fish (rank 1) and the energy available as drifting invertebrates (cal/24-h) in each pool when the data from both streams were pooled (Figure 4.5).
### TABLE 4.2. C, H and N compositions (%), mean ± S.E. caloric values of dry weight of invertebrates in banded kokopu (*Galaxias fasciatus*) diet.

Species with low frequency in the diet of fish but relatively abundant in the drift from Craigs Creek and Deborah Bay Stream are shown with * and †, respectively. Three replicates were used for each species/taxa from each stream.

| Species/Taxa        | C (%) | H (%) | N (%) | Energetic value (Cal g⁻¹) | Species/Taxa        | C (%) | H (%) | N (%) | Energetic value (Cal g⁻¹) |
|---------------------|-------|-------|-------|---------------------------|---------------------|-------|-------|-------|---------------------------|---------------------|-------|-------|-------|---------------------------|
| Ostracoda           | 24.8  | 2.6   | 3.8   | 2598 ± 0.88               | Ostracoda           | –     | –     | –     | –                         |
| Lepidoptera larvae  | –     | –     | –     | –                         | Lepidoptera larvae  | 50.7  | 7.5   | 10.6  | 6297 ± 242.91              |
| Chironomidae        | 48.7  | 7.2   | 10.6  | 5835 ± 170.06             | Chironomidae        | –     | –     | –     | –                         |
| Spider              | –     | –     | –     | –                         | Spider              | 50.7  | 7.5   | 10.6  | 6297 ± 242.91              |
| Oxyethira           | 51.9  | 7.5   | 10.1  | 6043                      | Oxyethira           | –     | –     | –     | –                         |
| Trichoptera adult   | –     | –     | –     | –                         | Trichoptera adult   | 49.5  | 7.3   | 12.2  | 6079 ± 375.0               |
| Millipede           | 30.3  | 4.6   | 5.3   | 3636 ± 177.68             | Millipede           | –     | –     | –     | –                         |
| Cylomiscus          | –     | –     | –     | –                         | Cylomiscus          | 50.4  | 7.4   | 10.7  | 5726 ± 236.77              |
| M. mcgregory*       | 50.8  | 7.0   | 10.4  | 5976 ± 124.39             | M. mcgregory*       | –     | –     | –     | –                         |
| Paradixia           | –     | –     | –     | –                         | Paradixia           | 49.8  | 7.8   | 11.3  | 5979 ± 179.02              |
| P. fluviatilis      | 40.3  | 6.1   | 8.3   | 5255 ± 334.98             | P. fluviatilis      | 39.2  | 6.0   | 8.3   | 4545 ± 45.17               |
| Diptera adult       | 51.1  | 7.5   | 9.8   | 5835 ± 137.81             | Diptera adult       | 50.3  | 7.3   | 11.7  | 6324 ± 51.6                |
| Collembola          | 48.7  | 7.1   | 12.8  | 5442 ± 136.68             | Collembola          | 49.6  | 7.4   | 12.5  | 5925 ± 275.04              |
| Hemiptera adult     | 50.1  | 6.9   | 11.8  | 5685 ± 116.92             | Hemiptera adult     | 49.9  | 7.1   | 11.8  | 5794 ± 210.99              |
| Diptera pupa        | 48.7  | 7.2   | 10.9  | 5684 ± 142.51             | Diptera pupa        | 50.4  | 7.6   | 10.9  | 6293                      |
| Zelandobius†        | 49.6  | 7.4   | 9.9   | 5965 ± 199.30             | Zelandobius†        | 50.6  | 7.7   | 9.7   | 6233 ± 238.13              |
| P. antipodarum†     | 43.4  | 6.7   | 8.7   | 5028 ± 148.84             | P. antipodarum†     | 45.7  | 6.9   | 9.3   | 5580 ± 250.72              |
| Deleatidium         | 50.3  | 7.7   | 9.1   | 5934 ± 59.22              | Deleatidium         | 46.7  | 7.4   | 10.2  | 5913 ± 68.89               |
| Oligochaeta*        | 47.1  | 7.6   | 12.0  | 5618 ± 207.56             | Oligochaeta*        | 45.8  | 7.4   | 10.0  | 5579 ± 246.41              |
| Water mite*†        | 46.8  | 6.7   | 10.9  | 5875                      | Water mite*†        | 46.9  | 6.7   | 9.5   | 5640 ± 401.6               |
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FIGURE 4.4. The relationship between log_{10} energy available as drifting invertebrates (cal/24-h) and total banded kokopu (*Galaxias fasciatus*) biomass (kg) in each pool. The data from Craigs Creek and Deborah Bay Stream were pooled.

\[ y = 0.063x - 0.039 \]
\[ R^2 = 0.242 \]
\[ P < 0.001 \]

FIGURE 4.5. The relationship between log_{10} energy available as drifting invertebrates (cal/24-h) and absolute growth (g/day) of dominant (rank 1) banded kokopu (*Galaxias fasciatus*) in each pool. The data from Craigs Creek and Deborah Bay Stream were pooled.

\[ y = 0.177x - 0.228 \]
\[ R^2 = 0.72 \]
\[ P < 0.001 \]
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4.4.5. Fish energy expenditure relationship with energy available in pool

The total energetic requirement of all fish (cal/24-h) in each pool was calculated by summing up individual energy expenditures and comparing this to the energy available (cal/24-h) as drifting invertebrates entering the same pool. This comparison was made for water temperatures of 5.5, 10.5 and 15.5 °C. The mean energy expended by banded kokopu was significantly higher than the mean energy available as drifting invertebrates in pools at both 10.5 °C (df1,48=56.35, P<0.001) and 15.5 °C (df1,40=38.59, P<0.001) in Craigs Creek (Figure 4.6a). The same trend was seen at 5.5 °C (df1,28=17.38, P<0.001) and at 10.5 °C (df1,48=73.00, P<0.001) in Deborah Bay Stream (Figure 4.6b).

4.4.6. Seasonal comparisons of fish energy expenditure and energy available in each pool

The mean energy expended by banded kokopu was significantly higher than the mean energy available as drifting invertebrates in pools in winter (df1,4=10.84, P=0.03), spring (df1,32=75.30, P<0.001), summer (df1,22=25.99, P<0.001) and autumn (df1,26=9.25, P=0.005) in Craigs Creek (Figure 4.7a). The same trend was seen in winter (df1,20=10.33, P=0.004), spring (df1,12=22.75, P<0.001), summer (df1,26=28.50, P<0.001) and autumn (df1,14=38.08, P<0.001) in Deborah Bay Stream (Figure 4.7b). When the data for all seasons were pooled, banded kokopu could potentially obtain c. 70% and 60% of their total energy expenditure from invertebrates in Craigs Creek and Deborah Bay Stream, respectively.
FIGURE 4.6. Available energy ($\log_{10}$ mean ± S.E.) as drifting invertebrates (cal/24-h, ■) in pools (June to October 2008 and April to May 2009 were considered with the mean water temperature of 10.5 °C, November 2008 to March 2009 with the mean of 15.5 °C in Craigs Creek and June to October 2008 and November 2008 to May 2009 were considered with the mean of 5.5 and 10.5 °C, respectively, in Deborah Bay Stream) and mean energy expenditure by banded kokopu ($Galaxias fasciatus$) biomass (cal/24-h, □) in pools at different temperature levels from Craigs Creek (a) and Deborah Bay Stream (b).
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4.5. DISCUSSION

The results of this study shed light on the energetic demands of banded kokopu and their interaction with the energy available in the form of drifting invertebrates in streams. Fish biomass and growth of dominant fish were positively correlated with food energy available in pools, suggesting that energy supplied in the invertebrate drift determines the

FIGURE 4.7. Seasonal variation in energy available (log₁₀ mean ± S.E. ) as drifting invertebrates (cal/24-h, ■) in pools and mean energy expenditure (cal/24-h, ■) by banded kokopu (Galaxias fasciatus) biomass in pools, at different seasons from Craigs Creek (a) and Deborah Bay Stream (b).
biomass of fish supported in each pool and that growth of fish would be affected if energy intake by fish failed to surpass or meet maintenance energy requirements. The chief aim of this study was to determine if food supply is energetically limiting or in surplus for banded kokopu in the two study streams. My results indicated that banded kokopu energy expenditure was likely higher than energy available as drifting invertebrates in different habitats across the range of temperatures assessed. Given the fact that fish did grow in the study streams, it seems that the fish gained some of the energy needed from other sources that were not measured here. Regardless, banded kokopu seem to regulate the population size based on available food in the habitat, as not much food was left in the system, supporting the hypothesis tested by Chapman (1966).

4.5.1. Oxygen consumption rate

As the oxygen consumption rate of banded kokopu was measured for the first time in this study, there is no intraspecific data available with which results can be compared. However, the average oxygen consumption rate of 80.24 mg O$_2$ kg$^{-1}$ h$^{-1}$ recorded in this study is comparable to the metabolic rates of other stream fish, including salmonids. A value of 50 mg O$_2$ kg$^{-1}$ h$^{-1}$ was reported for rainbow trout, Oncorhynchus mykiss (Steffensen 2002), 61.6 and 83-92 mg O$_2$ kg$^{-1}$ h$^{-1}$ for Atlantic salmon, Salmo salar (Grøttum & Sigholt 1998; Grisdale-Helland et al. 2002) and 104 and 117.1 mg O$_2$ kg$^{-1}$ h$^{-1}$ for Arctic char, Salvelinus alpinus (Beamish 1980; Lyytikäinen & Jobling 1998). Large fish exhibited a higher overall metabolic rate than small fish, whereas small fish had higher oxygen consumption/metabolic rate per unit of body mass, patterns consistent with other studies (Saint-Paul et al. 1988; Jobling 1993). The higher basal metabolic rate of large fish may also be associated with their dominance in social structures (Metcalfe et al. 1995).
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Temperature is an important variable that controls fish metabolic rate and oxygen consumption (Winberg 1956; Clarke & Johnston 1999; Clarke & Fraser 2004), and variation in metabolism due to temperature variation has been reported to occur at a constant rate (Schmidt-Nielsen 1975). At 15.5 °C banded kokopu had a resting oxygen consumption rate that was c. 2 times higher than that of fish at 5.5 °C which is in agreement with Jensen et al. (1993) who suggested a 2-3 fold increase in metabolic rate for a 10 °C rise in temperature. This pattern indicates that the fish need to increase their foraging rate and double their food intake to meet their metabolic requirements, which could lead to energy limitation in the warmer months, especially in small food-limited streams. Longer days in summer also limit the time that nocturnal fish such as banded kokopu can feed, potentially forcing fish to extend their foraging effort into the day, a pattern that has been documented in giant kokopu (David & Closs 2001, 2003; Hansen et al. 2004). The possibility of 24-h food feedings by fish at higher temperatures in stream to achieve maximum growth potential cannot be ruled out as this hypothesis has already been accepted on trout by Hayes et al. (2000) and on giant kokopu by Hansen & Closs (2005). McCullough & Hicks (2002) also reported that small banded kokopu (age-0) were active during the daylight hours in some streams, a similar pattern reported by Hansen & Closs (2005). Observation of occasional fish activity by day in this study (pers. obs.) may further support this idea.

4.5.2. Caloric value of invertebrates

The findings of the current study are consistent with those from a limited number of other studies that have examined the energy content of New Zealand stream invertebrates. A caloric value of 17561 J g⁻¹ (4197 Cal g⁻¹) was reported for Paracalliope fluviatilis by Ryan (1982), and 22066 J g⁻¹ (5273 Cal g⁻¹) for Chironomidae by McCarter (1986), both of which
are close to the values recorded in this study. However, a range of 3567-6615 J g⁻¹ (825-1581 Cal g⁻¹) and an average of 6000 J g⁻¹ (1434 Cal g⁻¹) for *Potamopyrgus antipodarum* was reported (Ryan 1982; McCarter 1986), both of which are considerably lower than results of this study (5028-5580 Cal g⁻¹). It is possible that this may relate to the specifics of the sampling sites. Both authors collected their samples from lakes whereas the samples of this study were collected from shallow streams. A possible difference in the quantity and quality of algae between the two ecosystems might have caused this discrepancy (Hill *et al.* 1995).

This study found that the three rarely selected drift taxa had the same energy content as the most frequently selected prey taxa, suggesting that other factors influenced prey selection by banded kokopu. McCarter (1986) proposed that fish predation rate may be determined by the habitat and behaviour of the prey, prey size, palatability or other factors. Prey size has been shown an important factor in salmonids when choosing their prey (Allan 1981; Sagar & Glova 1988; Nakano 1995; Nakano *et al.* 1999b). The results of this study may be explained by the fact that the small size of taxa such as water mites may deter banded kokopu from feeding on these items. Although Oligochaeta were common in the drift, the (mostly) small individual size and their generally cryptic nature may limit their availability to fish. Englund *et al.* (1999) showed that drift-feeding fish ignored small-size prey such as chironomid midges; the number of prey even increased in the presence of fish, however, there is lack of information on the mechanisms influencing prey selection in galaxiid fish. As discussed in the previous chapter, the minor contribution of species such as *P. antipodarum* to the fish diet may be explained by low selectivity of these species as they were often found undigested with intact shells in the gut samples. However, banded kokopu prey selection towards snails seems to be different from that of trout, which have
compensated for the low energy content of snails by eating them in large quantities (Wells & Clayton 2001).

4.5.3. Fish biomass and growth in relation to energy available

This study proposes that the biomass of banded kokopu is correlated with energy available in the form of drifting invertebrates in the pool. A pool may be occupied by one large fish, lots of small fish, or a proportionate full range of fish sizes depending on the pool quality in terms of energy. However, pool characteristics such as depth, velocity, etc., determine how fish biomass in pool is divided up (see Chapter 2). The results here corroborate the reports by Wilzbach (1985) and Imre et al. (2004) who found a positive correlation between trout biomass and pool quality, and more emigration was observed in pools in energetically poor conditions with the same pattern having been observed for giant kokopu (Hansen & Closs 2009). Energy available can interact with social hierarchy to determine fish biomass in a pool. For instance, Hughes (1992a, b) showed that Arctic grayling (Thymallus arcticus) rank the quality of patches and then sort themselves into those patches based on their social status. This hypothesis had been successfully tested on coho salmon (Oncorhynchus kisutch) by Fausch (1984). Faster absolute growth of dominant banded kokopu in high-quality pools also highlights how fish fitness can be influenced by availability of energy in a habitat. Fausch (1984) and Nakano (1995) showed that dominant fish will grow fastest by occupying the most profitable positions. A higher relative growth rate for trout in high-quality streams compared with that in low-quality streams has been observed by Edwards et al. (1979) and Wilzbach (1985). The growth of trout is also substantially affected if high-quality drifting invertebrates (large prey) are limited in the habitat (Bannon & Ringler 1986; Hayes et al. 2000; McKinney & Speas 2001). The current study’s results also accords with the earlier observations by Preall & Ringler (1989) who
found that limitation in energy availability is likely responsible for the growth setback of trout in Furnace Brook, New York.

4.5.4. In-stream energy yield and fish energy expenditure

The results showed that banded kokopu are likely energy-limited, being able to potentially obtain c. 70% and 60% of their energy needed from the invertebrate drift (based on assumption of 8-h feeding per day) in Craigs Creek and Deborah Bay Stream, respectively. The food supply appeared unlikely to meet metabolic requirements of the fish at all temperatures in all seasons. The results here accord with previous research (Allen 1951; Mundie 1974; Mason 1976; Allan 1983; Cada et al. 1987b; Waters 1988; Preall & Ringler 1989; Ensign et al. 1990; Elliott 1994; Huryn 1996; Ashley & Slaney 1997; Railsback & Rose 1999) that showed that many stream fish populations were food-limited.

Given the fact that banded kokopu survived and were able to grow consistently over the time in the study streams (Chapter 3), there must have been other sources of energy that banded kokopu access. Hence, the possibility of underestimating of the food biomass and consequently the energy available in the habitat cannot be ruled out for two reasons. First, infall terrestrial invertebrates into the streams may be detected and eaten by banded kokopu before reaching the sampling drift nets, resulting in imprecise measurement of the drift. Second, banded kokopu may switch to consume benthic prey which was not measured in this study. The ability of banded kokopu to detect and capture terrestrial invertebrates from water the surface has been reported (West et al. 2005). The high biomass of terrestrial items found in many fish stomachs (see Chapter 3, section 3.4.2.3; Dahl 1998; Nakano et al. 1999b; Kawaguchi & Nakano 2001; Nakano & Murakami 2001) further supports this hypothesis in that terrestrial arthropods can be a substantial energy source for drift-feeding fish. Fausch et al. (1997) and Nakano et al. (1999a) observed that Dolly Varden char (Salvelinus malma)
shifted their foraging mode from drifting prey to benthos when the former prey was scarce. Rainbow trout have also been shown to feed almost exclusively on terrestrial invertebrates in streams during evening when such prey are most available (Nakano et al. 1999b) but then switch to foraging on aquatic invertebrates or benthos when terrestrial prey are not available (see Fausch et al. 2002 for review). These examples suggest that drift-feeding fish such as banded kokopu may forage on different types of prey, or switch from one to another to meet their energetic demands. Further research might explore if the strategy of feeding on alternative prey (such as benthos) is coupled with reducing oxygen consumption rate (lowering energy consumption) when drifting food is limited, a pattern which has been seen in Atlantic salmon (Cook et al. 2000). Taken together, invertebrates appeared to be likely insufficient to meet the energetic requirements of banded kokopu especially in warmer months and must be supplemented by terrestrial invertebrates or other sources of prey. However, this study presents a limitation when the results on the energy expenditure by fish in the laboratory extrapolated to the field condition where the energy availability was estimated. In this study, the basic energy expenditure by fish was estimated which might have been slightly different with the figures if were measured in the field condition.

4.6. CONCLUSION

This study set out to determine the influence of variation in food quality on banded kokopu abundance, biomass and growth, and also to investigate whether food in the habitat is energetically adequate to maintain fish bioenergetic demands. The first major finding was that the biomass of fish was determined by the amount of food energy available in the form of drifting invertebrates in the habitat, suggesting that food quality determines the biomass of fish, whereas fish number and size is determined by habitat characteristics. This study found
that the growth of dominant banded kokopu was also dependent on the energy source, suggesting that prey abundance together with high-quality prey items may be a key element benefitting drift-feeding fish. The second main finding was that the oxygen consumption and energy expenditure by fish increased as temperature rose and that the supply of aquatic invertebrate drift appears to be energetically deficient at all temperature levels. Fish may compensate for this energy deficit by foraging on terrestrial subsidy input. However, the interactions between fish and other biotic and abiotic factors (i.e. fish abundance, social status, habitat structure) must be taken into account to better understand the driving factors in banded kokopu habitat selection which is the subject of the next chapter.
CHAPTER 5

Banded kokopu habitat selection, movement and growth in relation to abiotic and biotic factors

Measuring physical features of pools in Sawyers Bay Stream
ABSTRACT

Banded kokopu abundance, habitat selection, growth and movement were investigated in relation to their individual social status in multiple pools from three streams. Multiple linear regression rankings (Akaike’s information criterion) were used to evaluate the interactions and influence of abiotic and biotic factors on fish habitat use. The most parsimonious candidate model used to predict fish abundance was the one that included pool area, undercut banks, water velocity and invertebrate drift density suggesting that the factors driving fish abundance are likely to result from interactions between physical and biological factors in the habitat. Dominant fish had a higher growth rate and less of a tendency to relocate compared to subordinate fish, suggesting that high-ranked fish monopolise food intake to some extent in pools. Subordinate fish changed pools more often, most likely as a consequence of intraspecific competition that resulted in lower growth rates. The growth of fish improved after relocation to a new pool only if a higher social status was gained in the new habitat, suggesting that fish relocation was intraspecific competition-oriented rather than food-related. Overall, social hierarchy of fish plays a key role in mediating individual growth, residency and relocation.
5.1. INTRODUCTION

Knowledge of freshwater fish abundance and distribution is of importance to conservation, restoration and fisheries management, especially for fish of high conservation value (Bonnett et al. 2002; Bonnett & Sykes 2002). Fish distribution has been associated with a variety of environmental factors, including predation, competition, physical and chemical habitat variables, availability of food and potential energy intake and the fish status within the social hierarchy (Freeman & Stouder 1989; Harvey 1991; Hill & Grossman 1993; Fausch et al. 1994; Hughes & Reynolds 1994; Grand & Dill 1997; Grossman et al. 1998; Hughes 1998, 2000; Metcalfe et al. 1999; Nakano et al. 1999a; Alanärä et al. 2001; Jackson et al. 2001; Grossman et al. 2002; Railsback & Harvey 2002; Milner et al. 2003; Hansen & Closs 2005, 2009). Moreover, habitat use of a particular species may vary from one stream to another depending on the combination of environmental factors specific to each stream (Rosenfeld 2003).

The importance of physical habitat features such as water velocity, undercut banks and overhanging vegetation in fish habitat selection have been investigated extensively in freshwater systems (Main 1988; Inoue et al. 1997; Bonnett et al. 2002; Rowe & Smith 2003; Baker & Smith 2007; Parasiewicz & Walker 2007; Ayllon et al. 2009; Johnson & Douglass 2009; Gosselin et al. 2010; Salas & Snyder 2010). However, assuming that only abiotic factors control fish habitat selection may be less convincing compared to that when biotic components are integrated. Menge & Olson (1990) stated that both physical and biological factors interact to regulate community structure. Hence, fish habitat use patterns need to be understood in the context of multiple interacting ecological factors. Fish abundance and its relationship with environmental characteristics may be influenced by social status within a community of interacting conspecifics. Hansen & Closs (2009) found that the number of fish
in a pool was strongly influenced by pool area, but the biomass of fish within a pool was controlled by food supply, and that food supply was independent of pool area. Hansen & Closs (2005) found that giant kokopu (*Galaxias argenteus*) assemblages consisted of just one or two big fish in a pool, or lots of small fish. However, their proportions would change depending on the physical structure of a pool.

In a competitive social group, fish of high ranks have the ability to monopolise food supply in foraging territories (Holbrook & Schmitt 1992; Hasegawa & Yamamoto 2010), and as a consequence, fish of low competitive ability may increase their foraging rates (Dill & Fraser 1984) or change their feeding position (David & Closs 2003; David & Stoffels 2003; Hansen *et al.* 2004) to compensate for a low level of food intake. Increased foraging activity has been observed among stream gobies (*Rhinogobius* sp.) in response to competition in an attempt to exploit habitat efficiently (Inoue *et al.* 2005). Poor competitors may also shift to less-favoured dietary items (Milinski 1982; Schluter 1993). Fish may come to the decision that they should leave their current home range and find another if competition affects individuals and reduces foraging rate below a critical level (see Ward *et al.* 2006). It has been shown that dominant fish primarily tend to remain within habitats where their foraging rates are at a maximum level, and subordinate fish exhibit more relocation (Nakano 1995; Hansen & Closs 2009). Bachman (1984) showed that larger dominant brown trout force smaller fish to move and that movement is energetically costly (Gowan & Fausch 1996; Hilderbrand & Kershner 2004a). However, this relocation may be a beneficial action especially if they gain habitat with less agonistic competition. Webster & Hixon (2000) found that feeding rates of subordinate fish increased by up to 60% when dominant fish were excluded from habitat. Agonistic interactions may occur more amongst fish of high social ranks due to their higher metabolic demands. Hansen & Closs (2009)
showed that fish of intermediate ranks were more severely affected than any other fish in the social hierarchy by fish of highest dominance rank. In a dominant-subordinate relationship, the growth setback of subordinate fish has been shown to be dominance-related (Brown 1946; Abbott & Dill 1989; Metcalfe et al. 1989; Metcalfe et al. 1992; Hansen & Closs 2009), however, the opposite pattern has also been observed (Huntigford & de Leaniz 1997). Hence one would expect that if subordinate fish relocate themselves to another pool with less agonistic interactions (then obtaining higher ranks) then they may grow faster. This hypothesis was accepted by Hansen & Closs (2009) who found that high growth rate was a reward for permanently relocated giant kokopu when they gained higher ranks in the new habitats, however, relocation is a risky action and may not always result in finding a profitable habitat.

There is little information available on the relationship between fish abundance and physical habitat structure in relation to other variables, such as invertebrate drift density and fish social status. In Chapter 2, I indicated that banded kokopu habitat selection is associated with some physical environmental factors (such as depth, velocity and substrate) at the microhabitat level in Sawyers Bay Stream. In the present chapter, I built on my previous work by integrating biotic factors, such as food supply, to study how fish habitat selection interacts with both abiotic and biotic factors at mesohabitat level in three streams. Furthermore, there is a paucity of knowledge on residency and mobility patterns of fish in relation to dominance hierarchy (Höjesjö et al. 2007). Given the results in Chapter 4 that fish are energetically constrained, social hierarchy structure is expected to have a strong influence on movement patterns of fish. This study therefore comprised two objectives, namely to 1) generate the most parsimonious model predicting fish abundance regarding physical environmental variables and invertebrate drift density in the habitat and 2)
determine if fish pool residency and relocation is a consequence of intraspecific competition and if movement influences fish growth. This long-term study will enhance the understanding of fish habitat use patterns and how fish movement is determined by dominance hierarchy in the fish assemblages. To do this, I monitored banded kokopu (*G. fasciatus*; see Chapter 3, Introduction section, for more details on rationale for the use of this species) in three Otago Harbour streams. The streams selected in this study had no record of brown trout and this made the habitat assessments more accurate due to lack of predation risk by the latter species (Chadderton & Allibone 2000). I predict that I will see relationships between banded kokopu abundance and interactions of physical and biotic factors in pools. I also predict that movement will occur more among fish of intermediate social status and that movement as a consequence of intraspecific competition with dominant fish will impact on the growth of these fish.

5.2. METHODS

5.2.1. Study site

Three streams flowing into Otago Harbour were selected in which banded kokopu were relatively abundant: Craigs Creek (170°37′54″E; 45°47′38″S), Deborah Bay Stream (170°37′29″E; 45°47′43″S) and Sawyers Bay Stream (170°35′32″E; 45°48′43″S; Figure 5.1). Seven pools in Craigs Creek and Sawyers Bay stream and six pools in Deborah Bay Stream were selected for sampling (see Chapter 3, section 3.2.1 for more details on the streams).
5.2.2. Sample collection

5.2.2.1. Habitat characteristics

The habitat survey, including measurement of abiotic and biotic parameters of pools, was carried out once a month for each stream at night from June 2008 to May 2009. To investigate the relationships between fish abundance and individual pool physical factors, pool area, velocity and substrate were measured using the methods described in Chapter 2, Section 2.2.2.1. Undercut banks, overhanging vegetation, in-stream vegetation and log and woody debris were recorded if they were present.
5.2.2.2. *Invertebrates and fish collections*

To assess the mean density of drifting invertebrate supply in each pool, invertebrate drift was sampled once a month for a period of one year (from June 2008 to May 2009) from 7 pools in Craigs Creek and Sawyers Bay Stream and from 6 pools in Deborah Bay Stream (see Chapter 3, sections 3.2.2.1 for more details on invertebrates sampling). Invertebrates were identified to the lowest possible taxonomic levels and their densities (m$^{-3}$) were calculated for each pool (see also Chapter 3, section 3.2.2.1). Abundances of banded kokopu were determined by counting fish once a month from June 2008 to May 2009 in the same 7 pools in Craigs Creek, 7 pools in Sawyers Bay Stream and 6 pools in Deborah Bay Stream from which habitat and invertebrate drift data were obtained. There was no attempt to sample fish (and also drifting invertebrates) in the winter months of July (except for Deborah Bay) and August due to the low probability of sighting fish (see Chapter 3, section 3.2.2.2 for more details on fish sampling). The growth rate of banded kokopu was calculated between July 2008 and March 2009 in order to avoid bias due to weight fluctuations related to spawning (late April to middle of June). To do this, fish were captured and given unique tags. The relative growth rate was calculated as the % increase in body weight [(last reading weight – initial reading weight) / initial reading weight / days between two readings]. Each fish in a pool was given a hierarchical rank based on its weight relative to that of other fish in the pool, with highest rank of 1 for the largest fish, down to the lowest rank of 6 for the smallest fish (see Chapter 3, sections 3.2.4 for more details on fish growth and rank).

Fish were considered residents if they never left their original home pool for the entire period of this study. If they left their pool at least once or more, then they were identified as movers. If they left their pool and resided in another pool for at least 3 months, it was considered a permanent relocation (see Hansen & Closs 2009 for more details).
5.3. DATA ANALYSIS

The Kolmogorov-Smirnov and the Levene’s tests were employed to ascertain normality of the distribution and homogeneity of variances in the variables measured, respectively. Data were log_{10}(x+1) transformed if necessary to homogenise variances as required. A two-tailed Pearson’s correlation test was used to identify the critical physical habitat variables that related to fish abundance in pools (the data were scanned to check for possible unimodal relationships but none were found). After selection of these factors (pool area, pool velocity, undercut banks and overhanging vegetation), a linear regression was used to examine the relationships between these variables and fish abundance in detail. To achieve this, the data from the three streams were pooled. Due to multiple tests, significance levels for regressions were adjusted using a sequential Bonferroni adjustment (Holm 1979). Multiple linear regression rankings were generated using Akaike’s information criterion (AIC, Akaike 1973) to create the set of candidate models used to predict fish abundance in the pools. When AIC models were calculated, the relative likelihood of each model was evaluated using Akaike weights (Burnham & Anderson 1998). Akaike weights range from 0 to 1 and candidate models with the lowest AIC and highest Akaike weight represent the most parsimonious model. The natural average method (Burnham & Anderson 2002) was performed for model averaging of candidate models using 95% confidence model set (see also Grueber et al. 2011 for more details on model averaging). Due to multiple sampling of each pool and to avoid pseudo-replication, the model in the multiple linear regression rankings was considered with the inclusion of random effects. A chi-square test was applied to detect if differences between the proportions of fish movement across different ranks were significant. A two-way ANOVA was used to compare relative growth rates of resident and mover fish (across different ranks), and a paired t-test was used to compare relative growth
of fish before and after permanent relocation. Statistical software SPSS version 18 and R
version 2.11.1 were used for data analysis.

5.4. RESULTS

5.4.1. Do environmental factors affect fish abundance?

Among the physical factors measured in pools from Craigs Creek, Deborah Bay Stream and Sawyers Bay Stream (Tables 5.1 and 5.2), banded kokopu abundance correlated with pool area ($R^2=0.12$, $P<0.001$, $P_{\text{Adjusted}}=0.025$), overhanging vegetation ($R^2=0.09$, $P<0.001$, $P_{\text{Adjusted}}=0.0125$), undercut banks ($R^2=0.08$, $P<0.001$, $P_{\text{Adjusted}}=0.016$), and water velocity ($R^2=0.04$, $P=0.004$, $P_{\text{Adjusted}}=0.01$). The model that best explained the variation in fish abundance in pools included invertebrate drift density and aforementioned abiotic factors (Table 5.3, Model 1). Model averaging showed that pool area and invertebrate drift density were the most important components in the candidate models predicting fish abundance (Table 5.4).

TABLE 5.1. Mean ± S.E. physical characteristics of pools. The data were pooled from Craigs Creek, Deborah Bay Stream and Sawyers Bay Stream from June 2008 to May 2009.

<table>
<thead>
<tr>
<th>Pool characteristics</th>
<th>Craigs</th>
<th>Deborah</th>
<th>Sawyers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pool area (m$^2$)</td>
<td>3.20 ± 0.21</td>
<td>6.18 ± 0.27</td>
<td>5.49 ± 0.39</td>
</tr>
<tr>
<td>Velocity (m s$^{-1}$)</td>
<td>0.03 ± 0.005</td>
<td>0.04 ± 0.005</td>
<td>0.05 ± 0.006</td>
</tr>
<tr>
<td>Substrate (cm)</td>
<td>16.41 ± 0.62</td>
<td>21.78 ± 0.78</td>
<td>19.86 ± 0.36</td>
</tr>
<tr>
<td>Undercut banks (m$^2$)</td>
<td>0.30 ± 0.06</td>
<td>0.38 ± 0.05</td>
<td>0.43 ± 0.08</td>
</tr>
<tr>
<td>Overhanging vegetation (m$^2$)</td>
<td>0.17 ± 0.05</td>
<td>0.91 ± 0.14</td>
<td>1.90 ± 0.45</td>
</tr>
<tr>
<td>In-stream vegetation (m$^2$)</td>
<td>0.32 ± 0.06</td>
<td>0.005 ± 0.003</td>
<td>0.44 ± 0.08</td>
</tr>
<tr>
<td>In-stream log (m$^2$)</td>
<td>–</td>
<td>0.09 ± 0.02</td>
<td>0.12 ± 0.03</td>
</tr>
<tr>
<td>Woody debris (m$^2$)</td>
<td>–</td>
<td>0.01 ± 0.006</td>
<td>0.08 ± 0.04</td>
</tr>
</tbody>
</table>
TABLE 5.2. Pearson’s correlation coefficient matrix of fish abundance (n=1184) and habitat abiotic factors. The data were pooled from Craigs Creek, Deborah Bay Stream and Sawyers Bay Stream from June 2008 to May 2009. Significant correlations are shown in bold.

<table>
<thead>
<tr>
<th></th>
<th>Fish abundance</th>
<th>Pool area</th>
<th>Pool velocity</th>
<th>Substrate</th>
<th>Undercut banks</th>
<th>Overhanging vegetation</th>
<th>Woody debris</th>
<th>In-stream vegetation</th>
<th>In-stream log</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fish abundance</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pool area</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pool velocity</td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Substrate</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Undercut banks</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Overhanging vegetation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Woody debris</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>In-stream vegetation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>In-stream log</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
</tr>
</tbody>
</table>

Significant correlations are shown in bold.
TABLE 5.3. Candidate set of models for predicting banded kokopu (*Galaxias fasciatus*) abundance determined by Akaike’s information criterion (AIC). AICc is corrected AIC and ΔAIC is the difference between the highest ranked model and the candidate model; $w_i$ is Akaike weight which is the probability that a particular model is the most parsimonious model among the candidate models (Burnham & Anderson 1998).

<table>
<thead>
<tr>
<th>Rank</th>
<th>Candidate models</th>
<th>AIC</th>
<th>AICc</th>
<th>Δi</th>
<th>$w_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Pool area + undercut banks + water velocity + invertebrate drift density</td>
<td>696.7</td>
<td>697.8</td>
<td>0.00</td>
<td>0.584</td>
</tr>
<tr>
<td>2</td>
<td>Pool area + water velocity + invertebrate drift density</td>
<td>698.8</td>
<td>699.7</td>
<td>1.83</td>
<td>0.233</td>
</tr>
<tr>
<td>3</td>
<td>Pool area + undercut banks + water velocity + overhanging vegetation + invertebrate drift density</td>
<td>700.6</td>
<td>702.1</td>
<td>4.25</td>
<td>0.070</td>
</tr>
<tr>
<td>4</td>
<td>Pool area + undercut banks + water velocity + overhanging vegetation</td>
<td>1131</td>
<td>1132</td>
<td>434.0</td>
<td>0.000</td>
</tr>
</tbody>
</table>

TABLE 5.4. Summary results of effects of abiotic and biotic variables on banded kokopu (*Galaxias fasciatus*) abundance after model averaging.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Estimate</th>
<th>S.E.</th>
<th>Confidence interval</th>
<th>Relative importance</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>5.93</td>
<td>0.655</td>
<td>(4.640, 7.210)</td>
<td></td>
</tr>
<tr>
<td>Pool area</td>
<td>2.49</td>
<td>0.699</td>
<td>(1.120, 3.860)</td>
<td>1.00</td>
</tr>
<tr>
<td>Invertebrate drift density</td>
<td>1.94</td>
<td>0.596</td>
<td>(0.777, 3.110)</td>
<td>1.00</td>
</tr>
<tr>
<td>Undercut banks</td>
<td>1.13</td>
<td>0.587</td>
<td>(-0.016, 2.280)</td>
<td>0.76</td>
</tr>
<tr>
<td>Overhanging vegetation</td>
<td>0.29</td>
<td>0.681</td>
<td>(-1.050, 1.620)</td>
<td>0.37</td>
</tr>
<tr>
<td>Velocity</td>
<td>-1.29</td>
<td>0.556</td>
<td>(-2.380, -0.203)</td>
<td>0.87</td>
</tr>
</tbody>
</table>
5.4.2. *Fish growth in relation to fish ranks and drifting invertebrates*

Banded kokopu absolute growth interacted with individual fish rank and drifting invertebrate density (m$^{-3}$) in pools. The data pooled from the three streams showed that banded kokopu of highest rank grew faster in pools with high drifting invertebrate density (Figure 5.2 and Table 5.5).

FIGURE 5.2. Three-dimensional graph showing the relationships between banded kokopu (*Galaxias fasciatus*) absolute growth rate (g/day) and log$_{10}$ invertebrate drift density (m$^{-3}$) across fish of different social status from highest rank of 1 to lowest rank of 6. The graph shows that fish growth rate increased as the rank of fish and the density of invertebrates in pools increased. The data obtained from three streams, Craig Creek, Deborah Bay Stream and Sawyers Bay Stream, were pooled.
TABLE 5.5. Parameter estimates of the relationships between banded kokopu (*Galaxias fasciatus*) absolute growth rate (g/day) and $\log_{10}$ invertebrate drift density (m$^{-3}$) across fish of different social status. The data obtained from three streams, Craigs Creek, Deborah Bay Stream and Sawyers Bay Stream, were pooled.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>S.E.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>0.0895</td>
<td>0.0359</td>
</tr>
<tr>
<td>Fish rank</td>
<td>-0.0259</td>
<td>0.0124</td>
</tr>
<tr>
<td>Invertebrate drift density</td>
<td>-0.0027</td>
<td>0.0476</td>
</tr>
<tr>
<td>Fish rank * Invertebrate drift density</td>
<td>0.0106</td>
<td>0.0150</td>
</tr>
</tbody>
</table>

5.4.3. *Fish movement in relation to growth and social hierarchy*

Pool fidelity among banded kokopu from the three streams was high with only c. 12% of fish relocating permanently (Table 5.6). There was no significant difference between the proportion of movers of rank 1 and 2 whereas fish of rank 3 moved twice as much as did fish of rank 1 ($\chi^2 =4.29$, df=1, $P=0.038$) and rank 2 ($\chi^2 =4.03$, df=1, $P=0.045$). The average relative growth rate of fish that remained in their pools for the whole period of this study was $0.46 \pm 0.03\%$ (n=144) while the figure for fish that moved to other pools (before moving) was $0.34 \pm 0.04\%$ (n=43). The average relative growth rate of fish ranked 2 and 3 that remained in their home pools and those that changed their pools (before leaving) was significantly higher [rank 2 (df$_{1,74}$=4.588, $P=0.035$) and fish of rank 3 (df$_{1,22}$=6.538,
$P=0.018$). Differences in the relative growth rates of movers and stayers of other ranks were not significant (Figure 5.3).

The relative growth rate of fish that changed their home pools permanently, increased significantly after relocation ($t_{21}=2.164$, $P=0.042$; Figure 5.4). The invertebrate drift density of original home pools and new pools after relocation was compared and the result showed no significant difference between two pools ($d_{f,42}=0.549$, $P=0.463$). Of the 22 fish that changed their pools permanently, 14 fish either held their rank or gained a higher rank in their new pool. Fish of low social status (ranks 5 and 6) remained in their home pools for the duration of this study, however, the number of these fish were low in the study.

**TABLE 5.6.** The average length and weight of banded kokopu (*Galaxias fasciatus*) of different ranks with the number of residents in their home pools and number of movers obtained from Craigs Creek, Deborah Bay Stream and Sawyers Bay Stream.

<table>
<thead>
<tr>
<th>Fish Rank</th>
<th>Average length (mm)</th>
<th>Average weight (g)</th>
<th>Number of fish remained</th>
<th>Number of fish moved</th>
<th>Number of fish relocated permanently</th>
<th>Proportion of fish moved (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>145.4</td>
<td>39.2</td>
<td>52</td>
<td>13</td>
<td>5</td>
<td>20</td>
</tr>
<tr>
<td>2</td>
<td>107.6</td>
<td>15.4</td>
<td>60</td>
<td>16</td>
<td>8</td>
<td>21</td>
</tr>
<tr>
<td>3</td>
<td>101.2</td>
<td>11.5</td>
<td>14</td>
<td>10</td>
<td>5</td>
<td>41.7</td>
</tr>
<tr>
<td>4</td>
<td>93.9</td>
<td>8.8</td>
<td>13</td>
<td>4</td>
<td>4</td>
<td>23.5</td>
</tr>
<tr>
<td>5</td>
<td>87.2</td>
<td>6.9</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
<td>84.2</td>
<td>5.9</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
FIGURE 5.3. Banded kokopu (*Galaxias fasciatus*) relative growth rate (mean ± S.E.) of residents (○) and movers (♦) across different ranks from Craigs Creek, Deborah Bay Stream and Sawyers Bay Stream. The growth rates were measured before the fish moved permanently. The number of samples (n) is shown for each data point. The data from the three streams were pooled.

FIGURE 5.4. Mean ± S.E. relative growth of banded kokopu (*Galaxias fasciatus*, n=22) before and after permanent relocation from pools in Craigs Creek, Deborah Bay Stream and Sawyers Bay Stream. The data from the three streams were pooled.
5.5. DISCUSSION

In this chapter, I aimed to quantify the key environmental factors influencing fish habitat selection, with the role of food abundance being of particular interest. The abundance of banded kokopu within pools correlated with water velocity, undercut banks, overhanging vegetation and invertebrate drift abundance, suggesting that habitat selection of fish should be defined by considering interactions between abiotic and biotic factors. Social hierarchy appeared to influence patterns of residency and relocation of fish to new habitats along a stream. High-ranked fish exhibited a low tendency for relocation and high growth rate. In contrast, intermediate-ranked fish showed more frequent relocation and their growth was impacted by dominant conspecifics. Monitoring growth of fish before and after relocation showed that growth of fish improved if a higher rank was achieved in the new habitat. This re-emphasises that intraspecific competition is triggered by food deficit (Chapter 4) in the study streams and that has a significant influence on individual banded kokopu.

5.5.1. Is pool structure of importance to fish habitat selection?

Banded kokopu abundance was related to the size of pool, water velocity and the presence of undercut banks and of overhanging vegetation. Pools with a large surface area supported higher numbers of fish. Roni & Quinn (2001) reported a positive relationship between pool area and coho salmon (*Oncorhynchus kisutch*) abundance in winter, however, no such relationship existed in summer and this may be attributed to use of a variety of habitat types such as glides by fish in summer. Positive correlations between estimates of fish abundance and pool size (and also between fish biomass and food supply, see Chapter 3, section 3.4.4.1) suggest that small fish coexist with large ones by occupying shallower margins of pools with larger surface areas. This finding corresponds with previous research
on giant kokopu (Hansen & Closs 2009) that larger pools tended to support more fish of small sizes. Moreover, pools of different surface areas did not differ in invertebrate drift density in the current study; hence, higher numbers of fish in larger pools were not food-related, suggesting that the increased area reduces agonistic interactions, allowing smaller fish to coexist with larger fish. This is of importance for small fish as small pools in the study streams limited the habitats for fish of low ranks to coexist with large conspecifics. Undercut banks are suggested to act as refuges for the fish at daytime hours. In-stream cover seems a critical physical habitat factor to explain the presence of many galaxiid fish in New Zealand streams (David & Closs 2003; Rowe & Smith 2003; West et al. 2005; Baker & Smith 2007). The positive correlation between banded kokopu abundance and overhanging vegetation in this study emphasises the role of riparian vegetation in providing terrestrial invertebrates (Edwards & Huryn 1996; Nakano & Murakami 2001; see Gowan & Fausch 2002). While fish from Craigs Creek and Sawyers Bay Stream took twice as many aquatic invertebrates as terrestrial invertebrates, the terrestrial species were numerically as important as aquatic species in the fish diet from Deborah Bay Stream with dense riparian vegetation (see Chapter 3, section 3.4.2.3).

The role of biotic factors such as food abundance in fish habitat selection has been investigated by many authors (Giannico 2000; Hayes et al. 2000; Hansen & Closs 2005, 2009). Petty & Grossman (1996) reported that mottled sculpin (Cottus bairdi) habitat use was based on macroinvertebrate abundance rather than the physical characteristics of the patch. However, this finding may not be applicable to banded kokopu. It was showed that variation in invertebrate drift density per se did not affect fish numbers in pools (see Chapter 3, section 3.4.4.1), hence, its interaction with pool physical structures was the subject of interest in current study. The analysis showed that the most parsimonious model to predict
banded kokopu abundance was the one that included both abiotic habitat components (such as pool area, undercut banks, water velocity) and a biological factor (invertebrate drift density). However, the role of each factor in a complex model may vary over a yearly cycle. For instance, Gasith & Resh (1999) demonstrated that environmental (abiotic) controls had more influence than biological (biotic) controls on stream communities during flood events or dry season. These examples suggest that fish habitat use patterns need to be evaluated across several environmental descriptors, and long-term monitoring is essential in elucidating such patterns.

5.5.2. *Is fish movement determined by interactions of social hierarchy and fish growth?*

Banded kokopu exhibited a high fidelity for their home pools with 88% of the fish either remaining in a single pool or only leaving temporarily over the course of this study. Their restricted home range and relatively stationary habits seem to be similar to that of salmonids (Bohlin 1977; Bachman 1984; Hesthagen 1988; Heggenes 1988a; Bohlin *et al.* 2002; Höjesjö *et al.* 2002; Økland *et al.* 2004) and giant kokopu (David & Closs 2001, 2003). The less-tendency-to-move behaviour among banded kokopu may cause agonistic competition when there is inadequate energy in the habitat to meet their metabolic requirements. I showed in Chapter 4 (section 4.4.5) that banded kokopu were energetically constrained, thus, individuals of low competitive ability in the social hierarchy may stay and suffer or decide to move to find another potentially more profitable place, especially over the periods of low food supply. The current study showed that socially dominant fish exhibited less relocation. Dominant coho salmon showed a great tendency to remain in stream channels whereas subordinate conspecifics had to leave the habitat in the presence of dominant fish (Chapman 1962; Mason & Chapman 1965). Nakano *et al.* (1991) also documented that smaller red-
spotted masu salmon (*Oncorhynchus masou rhodurus*) exhibited more movement between pools than did larger fish during the non-breeding season. Hansen & Closs (2005) reported that subordinate fish had larger home ranges (movement) than dominant fish and they were consistently diurnally active compared to the latter. The result in this study is contrary to what has been reported by others (Sundström *et al.* 2004; Höjesjö *et al.* 2007) on dominant brown trout that moved more than subordinate conspecifics. This discrepancy can be attributed to the unpredictable distribution of food in some habitats that increases aggression and forces dominant fish to show more exploratory behaviour (Grant 1997; MacLean *et al.* 2005).

This study showed that low-ranked fish had a lower growth rate than fish of higher ranks and that the latter grew faster than fish of any other ranks when a high density of invertebrate drift was available. The ability of dominant fish to monopolise food supply can be coupled with food limitation in the study streams (Chapter 4) to impact growth of subordinate fish and force them to leave the pool as they become food constrained. Boss & Richardson (2002) demonstrated that cutthroat trout (*Oncorhynchus clarki*) were food-limited and their growth was influenced by variation in the food resources. Moreover, Chapman (1962) suggested that if growth of individuals is impacted then fish may leave original home pools. The results here indicated that the relative growth rate of fish prior to changing location was significantly lower than that of fish that were sedentary for the entire study period. The lower growth rate for fish of low ranks compared to that of fish of high ranks coexisting in the same pool has been reported by Hansen & Closs (2009). These interesting findings explain that relative growth of intermediate hierarchy groups can be impacted if the fish cannot establish themselves in the habitats and struggle to coexist with other fish of higher status, or
they simply grow and their higher energetic demands intensified competition with the dominant fish.

The relative growth of the limited number of fish that permanently changed their home pools increased significantly after movement. This habitat relocation was not related to drifting invertebrates as no significant change in invertebrate drift density from the two habitats was observed. This is the first study to show that banded kokopu relocate to find a habitat with less intraspecific competition. This can be supported by the fact that fish benefited by gaining higher social rank in the new habitats and consequently they grew faster after relocation. My results support previous work by MacLean *et al.* (2005) who found that Atlantic salmon (*Salmo salar*) movement was in response to agonistic interactions rather than to changing food supply. In contrast to fish of other ranks, fish rank 4 did not experience significant variation in relative growth after relocation. This may strengthen the idea that fish of low ranks can fit anywhere in the habitats as their energetic requirements are relatively low. Moreover, Rosenfeld & Boss (2001) stated that despite greater metabolic demands per unit weight for small fish, their lower absolute energetic requirements allow them to disperse everywhere and coexist with larger fish in small streams or shallow habitats in rivers. Fish of low ranks seemed to be tolerated and less impacted by large fish as they tend to use shallower marginal habitats, findings that concur with those reported for giant kokopu (David & Stoffels 2003; Hansen & Closs 2005, 2009) and trout (Jonsson & Jonsson 2011). It is noted that the number of fish with lowest ranks 5 and 6 were few in this study and no relocation was recorded for these fish. Overall, although invertebrate density is important in fish habitat use, the social hierarchy within fish assemblages has a prominent role in food intake, growth and movement of individuals.
5.6. CONCLUSION

The current study shows that banded kokopu population dynamics are linked to their habitat. To define these linkages, a wide range of environmental variables should be taken into consideration. For instance, food resources have been shown to be essential factors considered by fish when selecting a habitat (Power 1984; Kawaguchi et al. 2003). The role of food supply in banded kokopu habitat selection was obscured in this study until other variables such as pool physical characteristics were integrated. Thus, focusing solely on one single variable would result in misleading information on the relationship between fish and the environment (Hayes et al. 1996). Many banded kokopu remained in their home pool for the duration of this study. In a dominance hierarchy triggered by deficit of food resources (Chapter 4, section 4.4.5), fish of high ranks were able to maintain their dominance in the pools and rigorously impact fish of immediate lower ranks. The movement pattern shown in the present study is in agreement with previous studies (Gerking 1959; Hansen & Closs 2005, 2009) in which the degree of movement is determined by dominance hierarchy and the scale of territorial behaviour by fish assemblages. The negative influence of intraspecific competition on fish of low competitive ability is clearly reflected in the growth and movement patterns of such fish. Most subordinate fish experienced low growth rates before movement and they gained higher hierarchical ranks and achieved better growth once they successfully moved to new permanent habitats. This pattern makes a compelling argument for the idea that decisions on relocation of banded kokopu to find a habitat are made to reduce competition; however, it is not clear if fish have a pre-existing knowledge of habitats beyond their home range or instead, whether they simply cruise around to find such profitable habitats (see Gowan & Fausch 2002 for more details). It has been suggested that the searching and acquisition of information are two components in habitat selection of
freshwater fish (Milinski 1984; Gowan & Fausch 2002). All in all, this study showed that interactions of environmental factors influence banded kokopu abundance and social dominance and fish growth drive fish movement.
CHAPTER 6

General discussion
6.1. INTRODUCTION

The central goals of this thesis were to elucidate the long-term patterns of banded kokopu distribution, habitat selection, growth, movement, social hierarchy, and metabolic demand in relation to drifting invertebrate density. To do this, fish and drifting invertebrates were sampled from 3 streams (Craigs Creek, Deborah Bay Stream and Sawyers Bay Stream) draining into Otago Harbour in the South Island, New Zealand. In this chapter, the results of all previous chapters were integrated and banded kokopu interactions with conspecifics and the environment and the influences of social hierarchy on the activity patterns of individual fish in the habitat will be discussed.

6.2. DOES SOCIAL HIERARCHY AND/OR ONTOGENIC SHIFT CONTROL HABITAT SEGREGATION AND FITNESS AMONGST DRIFT-FEEDING FISH?

Individuals within populations may use different resources in a habitat, a concept known as the “niche variation theory” (Van Valen 1965). Based on this theory, individuals of a given species may use the full range of available resources, but some may use different patches to avoid competition with conspecifics (see Bolnick et al. 2007 for review). A size-based linear dominance hierarchy has been demonstrated amongst giant kokopu (Galaxias argenteus) assemblages, with larger and smaller fish being dominant and subordinate in a given pool, respectively (David & Stoffels 2003). Dominant fish tend to occupy profitable patches and force subordinate fish to use less valuable areas (see Finstad et al. 2011). Chapter 2 showed that the size-related microhabitat use of banded kokopu was varied. Smaller subordinate fish were forced to occupy shallower pools with faster current. These results accord with niche variation theory as size of fish has been documented as a
component in structuring social hierarchy among conspecifics (David & Stoffels 2003; Hansen & Closs 2009; Paull et al. 2010).

Habitat segregation can be assumed to be one of the behavioural strategies to lessen agonistic interactions between competing individuals (Alanäärä et al. 2001; Whitehead et al. 2002; Hansen & Closs 2005; David et al. 2007; Ayllón et al. 2009; Nagayama et al. 2009). If habitat segregation amongst small and large fish (Chapter 2) is driven by dominance hierarchy, one would expect that the fitness of subordinate fish is influenced by dominant fish through competition. The results in Chapter 4 showed that the growth rate of dominant fish (rank 1) depended on the energy available in a pool, suggesting that fish of high rank limit food access to subordinate fish. Furthermore, the growth rate of high-ranked fish (large fish) was on average higher than that of low-ranked fish (Chapter 3). Although the growth rate of fish is size-dependent to some extent, it seems that this discrepancy in growth rate is associated with a reduced competitive ability of subordinate fish. This can be supported by the results in Chapter 3 in which the growth rate comparisons of dominant fish (rank 1) across different pools showed that some fish grew faster despite being smaller (yet being dominant in their pools) compared to others.

Whilst different patterns of size-based habitat use could be due to ontogenetic shifts in habitat preferences, the evidence collected, particularly size-based variation in growth of fish as presented in Chapter 3 provides strong support for the assumption that a dominance hierarchy structure exist among assemblages of banded kokopu. Evidence of overall food limitation in Chapter 4, and the dependency of the growth of dominant fish on food density also suggest that competition for resources is intense, and mediated by the social hierarchy of fish both within and between pools. Whilst the assumption of a social hierarchy was not tested directly, indirectly the evidence presented in this thesis strongly suggests that a
dominance hierarchy structure exists in banded kokopu population. This conclusion suggests that individual fitness of banded kokopu is determined by their relative position within pool dominance hierarchy, a pattern consistent with the results of multiple studies on drift-feeding stream fish (Metcalfe *et al.* 1990; Sloman *et al.* 2000a, b, 2002; Hansen & Closs 2005).

6.3. **DOES HABITAT MAINTAIN FISH ENERGETIC REQUIREMENTS?**

Evaluation of quality of habitat is a fundamentally important component in freshwater ecosystem management. It is also vital to understand resource acquisition by individual fish and to relate this to habitat capacity to provide essential information to stream management planning. There is a body of evidence (Warren *et al.* 1964; Allan 1983; Cada *et al.* 1987b; Waters 1988; Ensign *et al.* 1990; Filbert & Hawkins 1995; Huryn 1996) in which trout were shown to be food-limited in many freshwater streams.

The quantitative results in Chapter 4 showed that the supply of drifting invertebrates was insufficient to meet the energy requirements of banded kokopu, and fish were likely food-limited (with the assumption of 8 hours foraging period) in the study streams. Given that banded kokopu grew in the habitats, there must be energy surplus left for growth after the energy devoted to metabolism. It can be inferred that the energy sources available in the food web may have been underestimated and/or fish foraged longer than 8 hours in this study. The lack of data on the accurate estimation of terrestrial inputs and the possibility of benthic feeding by the fish, may explain this uncertainty. Furthermore, it has been documented that large giant kokopu force small conspecifics to change their foraging behaviour from preferred night time to day time as a consequence of intraspecific competition (Hansen & Closs 2005; David *et al.* 2007). Hence, such daytime feeding may also have occurred in banded kokopu assemblages in this study. Regardless, it seems that
there was not a huge amount of surplus energy available to the fish due to the unequal growth rate of individuals in the assemblages. The growth of fish was shown to be at least partly dependent on the energy available as drifting invertebrates in pools (Chapter 4) and based on the ability of dominant fish to most likely control access to that food source (Holbrook & Schmitt 1992; Hasegawa & Yamamoto 2010; also Chapter 5). Further, variation in the growth rate of individuals within the social hierarchy can be expected (Chapter 3). It seems that the energetic requirements of banded kokopu approximately matched the energy available in the habitats in the three study streams, which is in agreement with the “input matching rule” (Parker 1978) where the proportion of individuals in a patch should be equal to the proportion of available resources in that patch.

6.4. IS FISH MOVEMENT DRIVEN BY INTERACTIONS BETWEEN FOOD LIMITATION AND INTRASPECIFIC COMPETITION?

It has been argued that the ability of species to find and maintain profitable patches is determined by their social ranks in the dominance hierarchy (MacLean et al. 2005). Banded kokopu are mostly sedentary with respect to pool residency. Although social hierarchy can moderate the possible encounters between individuals, the food-limited nature of pools in the present study streams may increase aggression among individuals within a pool. Grossman (1980) found that aggressive behaviour built up among bay gobies (*Lepidogobius lepidus*) when food presence was limited. Intraspecific aggression is known as an adaptive phenomenon that determines to what extent limited food sources should be allocated to individuals (Grossman 1980). Hence, one would expect that increased segregation and/or relocation are observed among individuals when resource limitation occurs, especially amongst subordinates when their growth rates are reduced. All these expectations were met
in this study. Chapter 2 showed that the subordinates use different habitats than dominants, and more movement between pools among smaller, most likely subordinate, fish was shown in Chapter 5. These patterns used by subordinate fish are likely to avoid further costs involved in the interactions with dominant fish (Hughes 1992a; Nakano 1994, 1995; David & Stoffels 2003).

The variation in the growth rates of individual fish further supports the hypothesis that fish relocation is also driven by intraspecific competition. It has been suggested that fish move in search of a place with greater food access and higher growth rate (Fausch 1984; Hughes & Dill 1990; Hughes 1998; Railsback et al. 1999). Subordinate fish achieved a better growth rate once they relocated (Chapter 5). Their improved fitness in the new pools can be attributed to their improved rank in the social hierarchy structure, and consequently, better access to food after relocation. This supports the hypothesis of “habitat matching” (Pulliam & Caraco 1984) that fitness of individuals in energy-limited habitats is dependent on the share of resources used by them. Fierce competition appeared to occur among fish of high and intermediate ranks due to their similarly high energetic requirements, and that competition may be much less severe for fish at the bottom of the social hierarchy given the rare relocation among smaller fish (see also David & Stoffels 2003; Hansen & Closs 2005, 2009). Fish of low ranks (smaller fish) are not considered as potential competitors by the large dominants due to their relatively low net metabolic demands and usage of less profitable habitats, hence, their presence is tolerated by larger fish (Rosenfeld & Boss 2001).

There is a body of literature (Northcote 1997; Lucas & Baras 2001) that suggested a link between fish movement and food supply. The movement pattern in this study was more dominance- than food-related as the invertebrate drift density did not vary significantly between the pre- and post-movement pools. The findings in the present study may further
support the idea of the “optimality rule” (Railsback et al. 1999; Gowan & Fausch 2002) that fish depart their home pools to locate to a new patch with a higher expected fitness compared to that achieved in their initial pools.

6.5. DOES HABITAT STRUCTURE OR FOOD SUPPLY DETERMINE FISH ABUNDANCE?

It has been argued that community organisation is governed by multiple processes (Dunson & Travis 1991). There is substantial evidence that demonstrates the effects of abiotic factors (Vannote et al. 1980; Poff 1997; Ayllón et al. 2009; Gosselin et al. 2010; Salas & Snyder 2010) and biotic variables (Holbrook & Schmitt 1988; Roussel & Bardonnet 1999; Hansen & Closs 2005) on species distribution and abundance in freshwater ecosystems. However, as few researchers have focused on the integrative role of abiotic and biotic factors in determining fish abundance and habitat selection, this study aimed to fill this gap. Multiple linear regression rankings postulated that a combination of both abiotic and biotic factors determine banded kokopu abundance in streams (Chapter 5). Fish presence was best predicted by factors including pool area, undercut banks, water velocity and food abundance. Food supply together with physical and hydrological features in streams has been shown to have a great influence on the distribution of juvenile coho salmon (Oncorhynchus kisutch) in summer (Giannico 2000). It has been argued that pool foraging quality determines both coho salmon abundance and the fish’s response towards in-stream physical structure such as woody debris (Giannico 2000). Hansen & Closs (2005) showed that the habitat use of both dominant and subordinate fish can be affected by drifting invertebrates under both normal and manipulative food supply conditions. These examples together with the results of the current study concord with the theory discussed by Evans et al. (1987) and
Jackson et al. (1992) that fish communities are highly structured, and individuals non-randomly select their patches. Overall, both habitat structure and drifting invertebrates as food drive the fish abundance and habitat selection as fish preferred a subset of environmental surrounding variables and not the entire habitat was suitable (also Chapter 2).

6.6. IMPLICATIONS FOR FRESHWATER MANAGEMENT

Juveniles of banded kokopu contribute to the “whitebait fishery” which is a recreational and commercial industry in New Zealand (McDowall 1990). Although banded kokopu have not been classified as a threatened species (Hitchmough et al. 2007), their population is declining mainly due to the anthropogenic habitat degradation from forest to pasture (Hanchet 1990; McDowall 1990; Rowe et al. 1999). Thus, identifying the environmental factors that fish interact with in the habitat can be crucial for conservation management of freshwater fish including banded kokopu (Orth & White 1993; Peterson & Rabeni 2001).

This thesis provides evidence that banded kokopu habitat selection is determined by a number of physical environmental factors and invertebrate drift density (Chapter 5). Cover and low flow pools appeared essential elements in the fish habitat. Riparian vegetation provides in-stream refuge for fish through fallen trees (McDowall 1990), causes pool-riffle formation and slows water current in pools (Baillie & Davies 2002), and also provides terrestrial invertebrate input (Edwards & Huryn 1996; Nakano & Murakami 2001; see Gowan & Fausch 2002). This may explain why banded kokopu favoured overhanging vegetation in streams sampled in this study (see also Eikaas et al. 2005). The morphological and biological characteristics of habitats also have strong implications for freshwater fish larvae. The streams in this study did not appear to be recruitment-limited. Based on my
personal observations using a spotlighting method, a substantial number of juveniles enter the streams from Otago Harbour every year. However, the rate of successful establishment for these juveniles most likely depends on the amount of energy and the physical suitability of habitat (Post & Evans 1989; Eikaas et al. 2005).

This thesis highlights the necessity for understanding the nutritional capacity of the habitat, which is important for effective fisheries management in the ecosystems. It has been shown in this study that the pool foraging quality determines the biomass of banded kokopu in stream. Moreover, several researchers have demonstrated that food sources also influence the growth rate of freshwater fish (Cada et al. 1987b; Chappaz et al. 1996; Johnson et al. 2006) and limitation in food supply can affect fish fitness. Food scarcity coupled with low water level and high temperature, especially in summer, can negatively influence banded kokopu abundance and recruitment. Overall, in a successful predictive model to determine stream fish abundance, all biological and physical factors in the ecosystem should be incorporated to ensure sustainable stream management (McDowall 1993).

6.7. FUTURE RESEARCH

The results of this study gave insight into the mechanisms of habitat selection by banded kokopu in three streams in Otago, New Zealand. There is still plenty of scope for further study that can be integrated with the results presented here to be used as a tool for ecosystem management. For example, one of the biotic factors influencing habitat selection by fish is predation risk (Gilliam & Fraser 1987; Clark & Levy 1988; Brown & Moyle 1991; Harvey 1991; Grand & Dill 1997; Metcalfe et al. 1999) which was not included in this study. Although banded kokopu were the major species in the study streams and no other aquatic predators were detected, the presence of terrestrial predators (such as shags, rats and stoats;
see Rowe & Smith 2003) and their possible effects on habitat selection (Power 1983) should be scrutinised. Monitoring daytime activity of banded kokopu is also recommended for future studies. Given the strong formation of social hierarchy and the existence of agonistic competition among conspecifics of banded kokopu shown in the current study, an ontogenetic shift in diel activity may occur which warrants further study.
APPENDIX 1

The relative occurrence of invertebrates in the drift and banded kokopu stomach from Craigs Creek, Deborah Bay and Sawyers Bay Streams from June 2008 to May 2009.

<table>
<thead>
<tr>
<th>Invertebrates</th>
<th>Craigs Drift %</th>
<th>Craigs Diet %</th>
<th>Deborah Bay Drift %</th>
<th>Deborah Bay Diet %</th>
<th>Sawyers Bay Drift %</th>
<th>Sawyers Bay Diet %</th>
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<td>Sawyers Bay Diet %</td>
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REFERENCES


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