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Diet overlap between coexisting populations of
native blue ducks (*Hymenolaimus*
malacorhynchos) and introduced trout (Family:
Salmonidae): Assessing the potential for
competition.

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Abstract

I investigated diet overlap between blue ducks and trout, to assess the possibility that introduced trout (Family: Salmonidae) may be acting as an agent-of-decline on New Zealand's endemic blue ducks (*Hymenolaimus malacorhynchos*). Blue ducks inhabit fast-flowing rivers and streams. Both rainbow (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) were liberated into New Zealand's rivers and streams in the 1870s. Stream macroinvertebrates are consumed by both blue ducks and trout raising the possibility that the two animals may compete for food resources.

The importance of different prey in the diets of trout and blue ducks was assessed both in terms of numbers of prey consumed and prey dry weight. To analyse each predator's diet in terms of prey dry weight, I developed regression equations for commonly eaten macroinvertebrates. These allowed for the estimation of dry weight from prey head width and body length measurements. A power equation, $y = ax^b$ is used to express the relationship. The precision of dry weight estimation varied between taxa ranging between $\pm 10\%$ and $\pm 40\%$. For the majority of taxa, dry weight could be estimated with greatest precision from body length.

The relative abundance of macroinvertebrate prey was measured in trout stomachs and faeces of adult blue ducks collected from Tongariro, Manganuiateao, Ikawetea and Makaroro Rivers in 1991/92. Trichoptera and Ephemeroptera larvae were the most abundant macroinvertebrate prey in the diet of blue ducks inhabiting all rivers. Diptera were also consumed in large numbers by blue ducks on Tongariro and Manganuiateao Rivers but were less important than Trichoptera and Ephemeroptera in terms of dry weight. Prey consumed by blue ducks were also of high importance in the diets of trout in all four rivers. A maximum diet overlap value of 0.69 (Schoener's index) was found using numeric data while a maximum value of 0.89 was found when dry weight data were examined. The highest overlap occurred between blue ducks and trout on

Manganuiateao River. Blue ducks on all four rivers were found to take macroinvertebrates having a smaller mean body length than that occurring on average in the benthos. Trout were found to consume prey having a larger mean body length than that occurring in the benthos. The body length of prey consumed by trout was positively correlated with trout fork-lengths ($r_s = 0.49$ $p < 0.05$). However, the mean body length of prey consumed by small trout (FL < 250mm) was significantly larger than that taken by blue ducks ($T_{199} = -2.74$ $p = 0.007$).

To test the hypothesis that foraging by rainbow trout alters the composition of the aquatic macroinvertebrate community, data were compared from reaches of river above and below waterfalls on Ikawetea and Makaroro Rivers. Discriminant analysis indicated that the macroinvertebrate communities occurring in sections of river free of trout were not consistently dissimilar from those in sections inhabited by trout. However, an enclosure / exclosure experiment conducted in Tongariro River in April, 1993 found that in the absence of rainbow trout the density of Trichoptera, Ephemeroptera and Plecoptera in the benthos significantly ($F_{2, 33} = 3.615$ $p = 0.038$) increased. In addition, in those enclosures containing trout the density of large macroinvertebrates (body length > 7.1 mm) was less than in enclosures free of trout after 6 days.

To examine the response of blue ducks to trout-induced changes in the benthos I conducted an experiment to assess the foraging behaviour of blue ducks in artificial stream channels varying in prey availability. Blue ducks showed a graded response in respect to relative food availability, with a significant correlation between prey density and number of foraging visits to channels ($r_s = 0.738$, $p < 0.05$). In addition a significant correlation was found between the proportion of total foraging time spent in a channel and the proportion of total insect numbers in that channel ($r_s = 0.833$, $p < 0.05$).

For those endeavouring to develop a strategy to ensure the long term survival of this unique waterfowl my research indicates that where trout and blue ducks coexist resource partitioning may result in little interspecific competition occurring and hence competition appears unlikely to be a principal agent-of-decline of blue ducks.

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Table of Contents

Abstract.....ii

Acknowledgments.....iv

Table of Contents.....vi

List of Tables.....x

List of Figures.....xii

List of Plates.....xiv

Chapter One.....1

**Diet overlap between native blue ducks and introduced trout:
Assessing the potential for competition.**

1.1 Ecological interactions between trout species and blue ducks 1

1.2 Competition and coexistence of species: The role of introduced organisms..... 8

1.3 Thesis Format 14

1.3.1 Chapter Two 14

1.3.2 Chapter Three 15

1.3.3 Chapter Four 16

1.3.4 Chapter Five 16

1.3.5 Chapter Six..... 17

Chapter Two..... 18

**Conversion of prey availability and utilization data to dry
weight estimates from body size measurements.**

2.1 Introduction 18

2.2 Methods..... 19

2.2.1 Macroinvertebrate collection sites 19

2.2.2 Macroinvertebrate collection and measurement protocol 19

2.2.3	Data analysis.....	20
2.2.3a	Dry weight regression analysis	20
2.2.3b	Body length - head width regression analysis.....	21
2.3	Results.....	21
2.3.1	Body length - dry weight relationship.....	21
2.3.2	Head width - body length relationships	29
2.4	Discussion.....	32

Chapter Thre.....3 4

Macroinvertebrate fauna in the benthos and diets of trout and blue ducks on four North Island rivers.

3.1	Introduction	34
3.2	Methods.....	35
3.2.1	River and study site descriptions.....	35
3.2.2	Sampling of benthic macroinvertebrate fauna.....	44
3.2.3	Blue Duck diets from droppings.....	44
3.2.4	Trout diet from stomach samples.....	46
3.2.5	Sampling timetable.....	48
3.2.6	Data analyses	48
3.3	Results.....	50
3.3.1	Benthic macroinvertebrate fauna in Tongariro and Manganuiateao Rivers.....	50
3.3.2	Benthic macroinvertebrate fauna in Makaroro and Ikawetea Rivers	54
3.3.3	Trout characteristics in Tongariro and Manganuiateao Rivers.....	60
3.3.4	Trout diet in Tongariro and Manganuiateao Rivers.....	60
3.3.5	Trout characteristics in Ikawetea and Makaroro Rivers.....	63
3.3.6	Trout diets in Ikawetea and Makaroro Rivers	63
3.3.7	Blue duck diets on Tongariro and Manganuiateao Rivers	64
3.3.8	Blue duck diets on Ikawetea and Makaroro Rivers.....	66
3.3.9	Comparison of trout and blue duck diets.....	69
3.3.10	Relative importance of prey	71
3.3.11	Comparison of prey size selection by blue ducks and trout.....	76
3.3.12	Blue duck and trout diet overlap	78
3.4	Discussion	82
3.4.1	Composition of the benthic macroinvertebrate communities	82
3.4.2	Composition of trout die.....	82
3.4.3	Effect of trout foraging on macroinvertebrate communities in Ikawetea and Makaroro Rivers	83
3.4.4	Composition of blue duck diet.....	85
3.4.5	Implications of the similarity in the diets of blue ducks and trout.....	87

Chapter Four.....9 1

Field experiment to investigate responses of benthic macroinvertebrates to presence and absence of trout

4.1	Introduction	91
4.2	Methods	92
4.2.1	Study site	92
4.2.2	Experimental design	92
4.2.3	Sampling	96
4.2.4	Data Analysis	96
4.3	Results	97
4.3.1	Macroinvertebrate assemblages	97
4.3.2	Trout diet	98
4.3.3	Trout effect	98
4.4	Discussion	105

Chapter Five.....1 08

Foraging by blue duck in artificial streams stocked with trout

5.1	Introduction	108
5.2	Methods	109
5.2.1	Experimental system	109
5.2.2	Macroinvertebrate prey	110
5.2.3	Trout	110
5.2.4	Blue ducks	111
5.2.5	Experimental design	111
5.3	Results	115
5.3.1	Prey mortality	115
5.3.2	Effects of trout on benthic macroinvertebrates	119
5.3.3	Blue duck foraging behaviour	120
5.3.4	Patch use in a depleting environment	124
5.4	Discussion	126
5. 4. 1	Macroinvertebrate mortality	126
5. 4. 2	Trout foraging	126
5. 4. 3	Foraging by blue duck and optimal foraging theory	127
5. 4. 4	Optimal foraging theory and its ecological relevance for blue ducks	128

Chapter Six.....130

General Discussion

6.1 Review of field and experimental work..... 130

6.2 Diet overlap and its relationship with competition..... 132

6.3 Conservation biology and competition theory: The role of introduced species . 134

6.4 Implications for blue duck conservation strategies 139

6.5 Summary 141

Appendices 143

Appendix A Reprint of: *Predicting dry weight of New Zealand aquatic
macroinvertebrates from linear dimensions*..... 143

Appendix B Relative composition (%) of the major aquatic food
categories in the diets of trout and blue ducks..... 144

References 153

List of Tables

Table 2.1	Number of individuals, ranges of body lengths (BL), head widths (HW), dry weights (DW) and collection source (T=Tiritea, K=Kahuterawa) of insects utilised in the derivation of dry weight predictive equations.....	22
Table 2.2	Values for the constants ln _a and b obtained from the regression of lnDry Weight (DW, mg), lnBody Length (BL, mm) and lnHead Width (HW, mm) for selected aquatic insect taxa	23
Table 2.3	Regression parameter estimates using weighted data for the relationship between body length (BL, mm), or head width (HW, mm) and dry weight (DW, mg) for four aquatic insect orders.....	26
Table 2.4	Values for the constants a and b obtained for the linear relationship between head width (HW, mm) and body length (BL, mm) for selected aquatic insects.	30
Table 2.5	Regression parameter estimates using weighted data for the relationship between head width (HW, mm) and body length (BL, mm) for four aquatic insect orders.....	31
Table 3.1	The taxa identified in blue duck droppings and the formulae used for converting numbers of fragments to numbers of individuals	47
Table 3.2	List of benthic macroinvertebrate taxa collected from the Manganuiateao (Mang.), Tongariro (Tong.), Ikawetea (Ik.) and Makaroro (Mak.) Rivers.....	51
Table 3.3	Comparison of the mean body length (mm) of benthic macroinvertebrates collected from Ikawetea and Makaroro Rivers above and below their respective waterfalls.....	56
Table 3.4	Number of trout stomachs collected per season from Manganuiateao and Tongariro Rivers.....	60
Table 3.5	Number of trout stomachs collected per season from Makaroro and Ikawetea Rivers.	63
Table 3.6	Prey-selection indices calculated from dry weight of macroinvertebrates in each of the major categories in the diets of trout and blue ducks from Tongariro and Manganuiateao Rivers in relation to that found in the benthos.....	72
Table 3.7	Prey-selection indices calculated from dry weight of macroinvertebrates in each of the major categories in the diets of trout and blue ducks from Ikawetea and Makaroro Rivers in relation to that found in the benthos.....	72

Table 3.8	Indices of the relative importance (IRI) of common prey consumed by blue ducks and trout from Tongariro River	74
Table 3.9	Indices of the relative importance (IRI) of common prey consumed by blue ducks and trout from Manganuiateao River	74
Table 3.10	Indices of the relative importance (IRI) of common prey consumed by blue ducks and trout from Ikawetea River	75
Table 3.11	Indices of the relative importance (IRI) of common prey consumed by blue ducks and trout from Makaroro River	75
Table 3.12	Mean body length of Manganuiateao and Tongariro River macroinvertebrates in the diet of trout and blue ducks, and in the benthos	77
Table 3.13	Mean size of Ikawetea and Makaroro River macroinvertebrates in the diet of trout and blue ducks, and in the benthos.....	77
Table 3.14	Diet overlap values for blue ducks and trout inhabiting Tongariro and Manganuiateao Rivers calculated by the Schoener (1970) proportional differences method. Overlap values are presented for the six sampling occasions and the combined numerical and dry weight data	79
Table 3.15	Diet overlap values calculated by the Schoener (1970) proportional differences method between blue ducks and trout of Ikawetea and Makaroro Rivers. Overlap values are presented for the six sampling occasions for both abundance and dry weight data	81
Table 3.16	Diet overlap values calculated by the Schoener (1970) proportional differences method between blue ducks above and below the Ikawetea River waterfall. Overlap values are presented for the six sampling occasions for both abundance and dry weight data	81
Table 5.1	Treatment allocation for the eight trials involving blue duck	112
Table 5.2	Percentage composition at zero and 24 hrs, and relative mortality rates for taxa in experimental channels	118
Table 5.3	Diet composition of trout stomachs.....	119
Table 5.4	Mean macroinvertebrate densities and numbers of taxa (\pm 1 SE) in channels after 96 hrs	120
Table 5.5	Number of foraging visits made by blue duck to "Trout" and "No trout" channels during each trial	121
Table 5.6	Proportion of food resource (based on insect density) in channel A and B for the eight trials.....	124

List of Figures

Fig. 2.1A	Log/log plot of the regressions for dry weight (mg) versus body length (mm) for the five macroinvertebrate orders plus Gastropoda	26
Fig. 2.1B	Log/log plot of the regression for dry weight (mg) versus head width (mm) for macroinvertebrate orders.....	27
Fig. 2.2	Log/log plots and regression lines of dry weight versus head width for the groups of Diptera, Aphrophila neozelandica, Chironomidae and Austrosimulium sp. The weighted regression for the order is also presented	27
Fig. 2.3	Regression lines and associated 95% intervals for <i>Olinga feredayi</i> , <i>Zelandobius</i> sp. and Hydrobiosidae.....	28
Fig. 2.4	Plot of the regressions for body length (mm) versus head width (mm) according to macroinvertebrate order	31
Fig. 3.1	Location of Tonariro River and sampling sites.....	38
Fig. 3.2	Location of Manganuiateao River and sampling sites.....	39
Fig. 3.3	Location of Ikawetea River and sampling sites.....	41
Fig. 3.4	Location of Makaroro River and sampling sites.....	43
Fig. 3.5	Mean (± 1 SE) relative numerical abundance of macroinvertebrate Orders in samples collected from Tongariro River	52
Fig. 3.6	Mean (± 1 SE) relative abundances of macroinvertebrate Orders in samples collected from Manganuiateao	53
Fig. 3.7	Body length distributions of macroinvertebrates collected from Manganuiateao (A) and Tongariro Rivers (B).	55
Fig. 3.8	Mean (± 1 SE) relative abundances of macroinvertebrate Orders recorded in benthic samples collected from Ikawetea River.....	57
Fig. 3.9	Mean (± 1 SE) relative numeric abundance of macroinvertebrate Orders recorded in benthic samples collected from Makaroro River	58
Fig. 3.10	Body length distribution plots for macroinvertebrates collected from Ikawetea (A) and Makaroro (B) Rivers. Shaded bars represent macroinvertebrate data for above the waterfalls while clear bars give below-waterfall data.....	59
Fig. 3.11	Frequency distribution of prey body length consumed by Tongariro (A) and Manganuiateao River (B) trout.....	62

Fig. 3.12	Frequency distributions of prey body lengths consumed by Ikawetea (A) and Makaroro River (B) trout.....	65
Fig. 3.13	Frequency distributions of prey body lengths consumed by blue ducks inhabiting Tongariro (A) and Manganuiateao (A) Rivers	67
Fig. 3.14	Body length distribution of prey consumed by blue duck above and below Ikawetea River waterfall.....	68
Fig. 3.15	Distribution of prey body length consumed by blue duck above and below the Makaroro River waterfall	70
Fig. 4.1	Location of study site on Tongariro River.....	94
Fig. 4.2	Experimental set-up showing position and relative dimensions of plots	95
Fig. 4.3	Relative numerical (A) and biomass (B) composition of the macroinvertebrate community in the benthos and the diet of trout inhabiting and taken from Treatment One enclosures at the end of 144 hours.....	99
Fig. 4.4	Relative percentage (± 1 SE) of the different prey items in the diet of trout removed from enclosures (Treatment One)	100
Fig. 4.5	Relative numerical (A) and biomass (B) composition of the epibenthic macroinvertebrate communities present in each of the three treatments at 0 and 144 hours.....	102
Fig. 4.6	Percentage composition of drift based on numerical data for each treatment at 0 and 144 hours.	103
Fig. 4.7	Size composition of the benthic macroinvertebrate community at 0 (A) and 144 (B) hours in trout enclosures and trout exclosures respectively	104
Fig. 5.1	Diagram of experimental system.	113
Fig. 5.2	Plots of mean insect density (m^2) in channels over time.	116
Fig. 5.3	Plot of $\log_{10}(\text{hour}+1)$ versus mean number of per m^2 for combined data from trials 1 and 2.....	117
Fig. 5.4	Proportion of foraging visits to the richest channel (channel with most food) versus the proportion of food in that channel, for all 8 trials (A). Plot (B) regresses the total time spent foraging in the richest channel against the proportion of food resource, for all 8 trials	123
Fig. 5.5	Proportion of visits (A) and foraging time (B) in relation to food availability during the first and last 24 hour periods	125

List of Plates

Plate 3.1	Collecting a kick sample of benthic macroinvertebrates from Ikawetea River.....	45
Plate 3.2	Examples of "Key fragments" extracted from blue duck droppings	45
Plate 4.1	View of experimental plots in Tongariro River.....	95
Plate 5.1	Experimental channel	114
Plate 5.2	Chart recorder and print out registering foraging activity (spikes) on the two channels	114
Plate 5.3	Blue duck foraging upon aquatic macroinvertebrates in an experimental channel.....	122

Chapter One

Diet overlap between native blue ducks and introduced trout: Assessing the potential for competition.

1. 1 Ecological interactions between trout species and blue ducks

New Zealand's endemic blue duck (*Hymenolaimus malacorhynchos*) was once a common sight throughout the country, inhabiting most rivers and streams with early records even noting their presence on beaches and swimming in the sea (Buller, cited in Fordyce 1976). Pre-1930 records indicate that blue ducks were once so abundant that in some areas they were commonly part of the diet of early settlers (Fordyce 1976).

However, today only fragmented populations occur in the upper reaches of relatively unmodified river catchments, and while the exact number remaining is unknown, it appears that the national population has dramatically declined both in number (Williams 1988) and range (King 1984) in the last one hundred years. This period of decline corresponded with an era of great general modification of the New Zealand environment by people. The country's rivers did not escape the effects of man, being subjected to large-scale alteration through the creation of dams and lakes, abstraction of water, the clearance of forest from river catchments and the direct mining of river beds in the search for precious metals. However, man's effect on the aquatic environment and the communities it supports also came about in less conspicuous ways. The introduction of exotic fish to enhance the recreational freshwater fishery is one such example. The most successful of such introductions was the acclimatisation of brown (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*), which today form the basis of New Zealand's world-renowned trout fishery.

Trout, both rainbow and brown, were first introduced into the country in the late 1800s. Brown trout was one of the first game fish species

introduced into New Zealand lakes and streams with the first consignment arriving in 1867 (McDowall 1990). Although there is some uncertainty about exactly when rainbow trout arrived in New Zealand it is likely many of the country's rainbow trout populations descend from an 1883 importation (see McDowall 1990). Following importation both species of trout were widely liberated. Such liberation programmes and also natural dispersal via sea routes quickly saw trout spread to almost all accessible freshwater habitats. The relative ease and speed of establishment was seen by some as reflecting the fact that trout were simply filling a "vacant niche" and as such the resources they required were readily available (McDowall 1990). Allen (1952) suggested that the successful establishment and subsequent proliferation of trout in New Zealand's rivers and streams was in part due to the abundance of the insect prey upon which trout feed (Allen 1952, Mills 1971, Elliott 1973, Cadwallader 1975).

The feeding and foraging behaviour of brown and rainbow trout have been extensively studied (Mills 1971, Elliott 1973, Sagar & Eldon 1983; McLennan & MacMillan 1984, Bechara 1993, Dedual & Collier 1995). Mills (1971) found that both rainbow and brown trout take their invertebrate prey directly from the substrate, from the drift and from the water surface. Dedual & Collier (1995) in their study of juvenile trout in Tongariro River found a positive correlation ($r_s = 0.89$) between the relative abundance of macroinvertebrate in the stomach of juvenile trout and that in the drift which they suggested provided evidence that such fish feed mainly on drifting organisms. McLennan & MacMillan's (1984) work on the diet and feeding habits of brown and rainbow trout in Mohaka River found that both species obtained the majority of their food by holding a fixed position in the current, either immediately in front or behind a boulder, and intercepted drifting prey. They also recorded trout browsing on insects on the surface of the substrate and on the lee side of rocks in shallow rapids.

Several studies have examined how the feeding sites of trout change as they grow (Everst & Chapman 1972, Sheppard & Johnson 1985, Dedual & Collier 1995). Trout, especially brown trout, are highly territorial and become increasingly so as they grow older (McDowall 1990). Large adult fish hold the best feeding positions at the heads of pools while the small

juvenile fish are restricted to the shallow littoral zones. Studies have found that as trout mature they move into swifter and deeper water to feed, aggressively competing with other trout of similar size for the best positions (Everst & Chapman 1972, Sheppard & Johnson 1985).

Studies of brown and rainbow trout feeding patterns have found that they often feed throughout the day, being particularly active at dusk and dawn (Mills 1971). Glova & Sagar (1991) reported that juvenile rainbow and brown trout in Ryton River, South Island fed mostly during the day, a finding that was consistent with earlier work by Angradi & Griffith (1989). Dedual & Collier (1995) also reported that the foraging activity of juvenile rainbow trout inhabiting the lower Tongariro River appeared to be continuous throughout the day. A similar diurnal feeding pattern among adult rainbow and brown trout has also been documented by Mills (1971). However, Mills (1971) also noted that adult fish do at times feed actively during the night.

Considerable work examining the prey composition of brown and rainbow trout has been conducted in New Zealand. Stomach content analysis undertaken by McLennan & MacMillan (1984) found that mature brown and rainbow trout in Mohaka and Tutaekuri Rivers consumed large numbers of Trichoptera and Ephemeroptera nymphs and that the prey composition of the diets of the two trout were very similar. Mills (1971) also found that the diets of rainbow and brown trout were similar in terms of the type of macroinvertebrate prey consumed. In addition, he also reported that the prey consumed by the two trout were of similar size. Recent studies conducted in other North Island rivers and streams have also shown that aquatic insects, especially larval Trichoptera and Ephemeroptera, compose the greatest proportion of the diet of adult and juvenile trout (Kusabs & Swales 1991, Dedual & Collier 1995). Dedual & Collier (1995) reported that juvenile rainbow trout have a high preference for Trichoptera, particularly caddisflies in general and Hydrobiosidae specifically. These prey made up a greater proportion of the diet relative to their proportion in the drift and benthos. Dedual & Collier (1995) suggested that the high fat content of such prey may account for the trout's selectivity for these prey.

Studies by Bisson (1978), Bechara *et al.* (1993), Dedual & Collier (1995) have documented a correlation between the length of trout and the size of

prey consumed. In general the average length of macroinvertebrate prey consumed by trout increased with increasing fish size. Bechara *et al.* (1993) reported that such size selective predation can result in a significant reduction in the occurrence of larger macroinvertebrates through the direct removal of such organisms.

The ecological consequences of predation by trout on aquatic insect communities have been the focus of a number of investigations (Allan 1982, Reice 1983, Flecker & Allen 1984, Culp 1986, Schofield *et al.* 1988, Feltmate & Williams 1989, Reice 1991, Bronmark *et al.* 1992, Diehl 1992, Power 1992, Bechara *et al.* 1993, Flecker & Townsend, 1995). Bechara *et al.* (1993) found that brook trout (*Salvelinus fontinalis*) inhabiting a stream in Québec, Canada, significantly affected the body size distribution, community structure and densities of aquatic macroinvertebrates in the drift but did not change macroinvertebrate densities. Feltmate & Williams (1989) recorded a 35% reduction in the abundance of stonefly *Paragnetina media* in Pine River system, Ontario. They attributed this reduction to trout predation and active migration of the nymphs from sections of streams where predators occurred. Recent work in New Zealand by Flecker & Townsend (1995) showed that the presence of brown trout in experimental channels had multitrophic effects, reducing aquatic insect densities and biomass. The standing crops of algae in those channels containing high densities of trout were also significantly greater than that in channels containing no trout due to trout depredation of macroinvertebrate grazers.

The effects of introducing exotic trout into the New Zealand lotic environment have therefore not gone unstudied, however to date most research has focused on the impacts of such introductions on the country's native fishery (Fletcher 1919, Cadwallader 1975, McDowall 1990, Kusabs & Swales 1991). Although recent work has cast some doubt on the exact role of trout in the decline of native fish populations it is still widely believed that competition between the native species and trout has in part been responsible for the contraction of the country's native fishery (Flecker & Townsend 1995).

Research examining the wider community effects of exotic insectivorous fish introductions has also investigated the impacts on waterfowl that eat aquatic macroinvertebrates. Eriksson (1979) found that goldeneye

(*Bucephala clangula*) densities on lakes without insectivorous fish in Scandinavia were higher than on neighbouring waters containing high densities of insectivorous fish. Hill *et al.* (1986) showed that broods of mallards (*Anas platyrhynchos*) occurred at twice the density on the river Ouse, which had a low density of coarse fish (*Rutilus rutilus* and *Abramis brama*), than on a reserve where fish densities were much higher. Similar relationships between fish and waterfowl have also been recorded by other studies (Eadie & Keast 1982, Pehrsson 1984). Studies of duckling foraging, growth and survival in relation to the presence and absence of insectivorous fish have also generated interesting results. DesGranges & Rodrigue (1986) recorded the survival of American black ducks (*Anas rubripes*) and goldeneye on three Canadian lakes inhabited by brook trout. After the initial collection of duckling survival data, trout were removed from one lake and used to increase the density in a second. Duckling survival was found to be inversely related to trout density. Similar findings have also been reported by Giles *et al.* (1990) and Phillips (1992) for British waterfowl populations. Phillips (1992) recorded a large increase in numbers of dabbling ducks using a 17 ha lake after the removal of a high density coarse fish population (6.5 tonnes of fish removed). He suggested that the presence of fish needed to be considered in waterfowl management plans with the removal of such fish being a useful technique in the maintenance and enhancement of waterfowl populations.

As with many of the above-mentioned waterfowl species studied overseas, blue ducks rely almost entirely on aquatic macroinvertebrate prey to fulfil their nutritional demands. Blue ducks glean such prey from submerged substrate surfaces by plunging the head and neck beneath the water in shallow areas or diving in deeper water. Studies conducted by Eldridge (1986) and Veltman & Williams (1990), which involved observing blue ducks during the day, found that most foraging occurred close to the edges of riffles in the early morning and late afternoon in late summer and autumn, and throughout the day during winter, spring and early summer. Blue ducks have also been observed foraging during the night on several North Island rivers (pers comm. M Williams). Veltman *et al.* (1995) found blue ducks on Manganuiateao River spent the majority (81 - 99 %) of their foraging time in shallow rapids. Occasionally blue ducks will dive in deeper water to scour the bottom and or the sides of

large boulders. Veltman *et al.* (1995) noted that such diving behaviour was most common amongst the blue ducks being observed on Manganuiateao River in March and July when water levels were high.

Eldridge (1986) also observed paired birds on Manganuiateao River feeding most intensely in the morning and evening with little foraging occurring during the middle of the day. Eldridge (1986) suggested that the dawn and dusk foraging pattern was a result of prey being more available during these periods when their macroinvertebrates prey have a greater propensity to drift. Sub-adults and non-paired birds however, were found to have a less structured feeding pattern and were often observed feeding in the middle of the day (Eldridge 1986). Kear (1972) found that during such feeding activity pairs of blue ducks often cover considerable lengths of territory with mates tending to feeding close together, often in the same rapid throughout their foraging forays.

Kear & Burton (1971) examined the faecal material gathered from several North Island rivers and found Trichoptera nymphs dominated blue duck diet, although Ephemeroptera and Plecoptera larvae were also common in the faeces. Collier (1991) examined the diet of blue ducks resident on the North Island's Manganuiateao River and another seven rivers and streams at East Cape. Blue ducks consumed predominantly cased caddisfly larvae, mainly species of *Helicopsyche*, *Pycnocentroides* and *Beraeoptera roria*, with Plecoptera larvae also being relatively abundant in the blue duck faeces (Collier 1991). Wakelin (1993) examined a sample of blue duck faeces collected from Tongariro River in December 1990. Chironomidae constituted 45% of the diet and Trichoptera larvae, especially cased larvae, 28%. Veltman *et al.* (1995) found the diet of blue ducks on Manganuiateao River to be much the same as that described by Collier (1991). In addition Veltman *et al.* (1995) found that blue ducks selected for the Trichoptera, *Aoteapsyche* sp. while avoiding cased caddisfly larvae. This finding is contrary to that of Collier (1991) who found cased caddisflies to be strongly preferred by blue duck on East Coast rivers. However despite the apparent conflict in findings, neither Veltman *et al.* (1995) nor Collier (1991) found any evidence to suggest that blue ducks are obligate specialists consistently reflecting a preference for certain prey. Interestingly, Collier (1991) reported that the prey consumed by pairs of blue ducks and between

birds of different ages within the same family groups differed although no consistent pattern between sex or age could be identified.

The size of prey consumed by blue duck has not been previously assessed.

Early researchers (Kear 1972, Eldridge 1986) recognised the similarity in the diets of blue ducks and trout, suggesting that there was potential for competition. Kear (1972) offered some anecdotal evidence that trout had directly effected the distribution of blue ducks making the observation that "the birds live more commonly today on streams where the trout are scarce".

A more recent examination (Veltman *et al.* 1991) of the diet and territorial behaviour of blue ducks inhabiting Manganuiateao River indicated that macroinvertebrate density in the benthos far exceeded that required to meet the nutritional requirements of the birds. In fact Veltman *et al.* (1991) suggested that the equivalent of macroinvertebrates occurring in approximately 2 m² of substrate was required to meet the nutritional requirements of an adult blue duck on the river for one day, under normal conditions. As the territory of a typical pair of blue ducks on Manganuiateao River includes approximately 5000 m² of substrate it would appear that competition for food between trout and blue ducks is unlikely. However, as reviewed by Keddy (1989) competition can arise from subtle changes in a resource. Bechara *et al.* (1993) found that foraging by trout in pebble-bottom outdoor channels reduced the density of certain size classes of benthic macroinvertebrates while not reducing the overall density. Feltmate & Williams (1989) documented the decline in certain large benthic prey (*Paragnetina media*) while other taxa actually increased in the presence of rainbow trout.

To assess the effects of foraging by trout on benthic macroinvertebrate communities and consequently the exploitation of such food resources by blue ducks, I collected data from four North Island rivers having coexisting populations of trout and blue duck. In addition I conducted two experiments to assess trout effects on benthic macroinvertebrates in enclosed patches and to investigate blue duck responses to such effects.

1. 2 Competition and coexistence of species: The role of introduced organisms

Competition theory predicts that in evolving communities the occurrence of severe competition will be rare as evolutionary pressures induced by competitive interactions will result in little niche overlap between coexisting species (Connell 1980). However, when a community is invaded by an introduced organism, competition between the invader and pre-existing organisms for certain resources may be acute if resource availability is limited.

The activities of man have facilitated the introduction of numerous species into communities where they did not previously exist. For most countries, the number of documented introductions is within a range of 10^2 - 10^3 species (Lodge 1993). The effect of such introductions and the role of the resultant interspecific competition in the re-structuring of the receiving communities is a topic that has engendered much heated and at times openly hostile debate among ecologists (Connell 1983, Schoener 1983, Strong *et al.* 1984, Diamond & Case 1986). Supporters of the competitionist's paradigm believe that species overlapping in the resources they utilise cannot coexist for any length of time, one ultimately competitively excluding the other from the system (Schoener 1982). This concept is often referred to as Gause's principle although MacArthur and Levins' (1967) theory of "limiting similarity" also relies on the same premise. However others (Strong *et al.* 1984, Diamond & Case 1986) suggest that while at times competition may occur, other interactions, such as predation, play a much more significant role in the dynamics of invaded communities.

Interspecific competition between species for limited resources may manifest itself in two distinct forms. These are commonly referred to as interference competition, where competitors aggressively interact with one another to secure access to a resource; and exploitation competition, where competition is expressed through the depletion of a commonly utilised commodity such as food. Exploitation competition has also been referred to as scramble competition in the literature (Minot 1981). Theory presently predicts that exploitation competition should occur where a resource is widely distributed and the densities of potential competitors are not high thus making it unprofitable to defend the resource directly.

Likewise, interference competition should occur when a limited resource exists in very discrete locations making its successful defence profitable.

Given that the potential invertebrate prey of trout and blue ducks are spread widely over river beds and the ratio of competitor density to resource availability is probably low, it appears that there would be little advantage to either competitor in actively defending the food resource against the other. In addition, the fact that blue ducks have territories of a significantly larger size than trout may also work to reduce the occurrence of interference competition. If a resource becomes limited at one location the energetic cost to blue duck of moving to another within the territory is likely to be less than required to actively defend the resource. Thus any competition that may occur between these two organisms for aquatic macroinvertebrate prey is likely to take the form of exploitation competition.

As a result of the nature of exploitation and interference competition, exclusion of a species is most likely to occur as a result of intense interference competition where one organism totally excludes access to a resource by another. Models of exploitation competition suggest that this form of competitive interaction usually results in a lowering of the density of both competitors over time rather than the exclusion of either organism (Brain 1960). Interestingly, there appears to be little in the literature to support the notion that either type of competition regularly results in species exclusion. Herbold & Moyle (1986), as a result of their research review, suggest that the total exclusion of a species as a result of competition, even following an invasion, is in fact rare.

Simberloff (1981) advanced the concept of vacant niches in communities to explain this apparent lack of extinction as a result of invasion, suggesting that successful invaders simply occupied niches and exploited resources not previously utilised. However this idea was vigorously attacked by Herbold & Moyle (1986) who believed that vacant niches did not exist in pristine communities. This does suggest that the incidence of successful invasions of such pristine communities should be low. Herbold & Moyle (1986) presented data from the literature to support this conjecture.

In an attempt to assess the potential for, and the effects of competitive interactions many researchers have manipulated the density of natural or enclosed populations and then monitored changes in either species density or some fitness parameter, such as fecundity, growth or mortality (Connell 1983). Studies (Schoener 1974, Herbold & Moyle 1986) with a similar objective have also looked for a niche shift where the type of resource being used or microhabitat occupied by potential competitors alters over time. However in those situations where species cannot be translocated or enclosed without ill effect, the similarity in diets has frequently been examined in detail and overlap assessed instead.

In general, interference competition is more easily detected than exploitation because of the direct nature of the interaction (Petren & Case 1996). In the process of demonstrating the potential for the existence of interspecific exploitation competition Petren & Case (1996) suggested that the organisms must be shown to utilise the same resources, and that the presence of one organism has the ability to negatively affect the acquisition of the shared resource of the other. In keeping with this, many studies (Cadwaller 1975, Brown 1982, Glova & Sagar 1991, Sagar & Glova 1994) have examined the degree of diet overlap existing between aquatic organisms. Zaret & Rand (1971), based on their studies of competition amongst communities of tropical fish, suggested that when overlap in the prey items consumed by the two potentially competing organisms passes 0.6 (Schoener index) it is likely that competition will occur when food resources become limited.

However while this approach may be helpful in assessing the potential for competition, the use of such a figure without an assessment of the fluctuations in food availability and more importantly the response of one organism to the competitive presence of the other provides little information on the ultimate role of competition in population dynamics. Hence there is a need to support examinations of diet and diet overlap with experiments designed to measure responses directly. In many studies this has taken the form of enclosure experiments (Power 1992, Petren & Case 1996) or the examination of population parameters in the presence and absence of the potential competitor (Eriksson 1979, DesGranges & Rodrigue 1986, Hunter *et al.* 1986). In keeping with this I

also conducted enclosure experiments and examined the diets of blue ducks in the presence and absence of trout.

To measure the occurrence and effect of interspecific competition in the structuring of communities numerous field and manipulative experiments have been conducted (see reviews by Schoener 1983, Connell 1983). In the majority of studies (77% and 55% respectively), some degree of competition was detected. However, others (Ferson *et al.* 1986) have questioned the ability of these literature reviews to provide a true reflection of the importance and occurrence of competitive interactions within communities suggesting that there is a greater propensity to publish positive results.

In an effort to assess findings of different competition studies, Gurevitch *et al.* (1992) conducted a meta-analysis on field-competition experiments published in six journals between 1980 and 1989. Their analysis showed competition "had a large effect overall" ($d_t = 0.80$) although significant variance was noted between different trophic levels. Of the trophic groups examined competition was found to be least pronounced among competing carnivores ($d_t = 0.25$). Gurevitch *et al.* (1992) suggested this finding was contrary to the original theory advanced by Hairston *et al.* (1960) which predicts greatest competition intensity at higher trophic levels. The fact that carnivores have the ability to move from one resource patch to another thereby reducing the competitive pressures while sessile primary producers do not, may help explain this apparent dichotomy between Hairston's *et al.* (1960) theory and the results obtained by Gurevitch *et al.*

An interesting result from Gurevitch *et al.* (1992) analysis, given the use of enclosure experiments in my study, was their finding that experiments conducted on caged organisms resulted in greater competitive effects than those with free-roaming and unenclosed organisms. They attributed this to the physical scale of the study environment with enclosed animals being "forced to compete". To illustrate this point Gurevitch *et al.* (1992) presented the example of competition between species of mollusc studied under two different regimes, firstly in enclosures and secondly in the natural environment. The effects of interspecific competition measured between caged and uncaged molluscs differed significantly suggesting that either physical or other biological factors (predation) were exerting

greater forces on the mollusc community in the natural setting than competition. In the artificial cage experiments where such additional pressures were absent, competition reached acute levels and was detected. Another example is provided by McLachlan's (1993) investigation of competition in coexisting species of midges (Diptera) amongst puddles of rain water. Where the two species occurred in large natural puddles they coexisted. However, in smaller experimental puddles *Chironomus pulcher* showed total competitive exclusion of *C. imicola* as a result of the homogeneity of the experimental environment and the fact that under the restrictions imposed by the experiment, competition for shared resources was intense. Hence McLachlan's (1993) experiment not only showed the importance of scale but in addition, the influence of habitat structure on competition.

Abrams (1990) also discussed the effects of scale and its influence on competitive interactions. However he considered competitive interactions in terms of time suggesting that competition could exert itself on both a relative short ecological (within one or few generations) and a much longer evolutionary (over many generations) scale. Abrams (1990) suggested that where competition occurs at what he termed the "ecological scale" it was more likely to result in the exclusion of species. However others (Brown & Wilson 1956, Grant 1972) have argued that there is no difference between ecological and evolutionary competition instead suggesting that both are part of the same continuum and it is as a result of this continuum that species eventually coexist successfully. Brown & Wilson (1956), who had previously considered competition in terms of temporal effects, suggested that the effects of competitive pressure on fitness ultimately resulted in the divergence of the resource utilisation traits of competing species. They termed this process "character displacement". Connell (1980) also suggested that such "character displacement" resulted in the development of stable coexisting populations and called this "the ghost of competition past".

In the case of invading species it has also been suggested that coexistence arises as a result of subtle differences in the resources used (Schoener 1974). Schoener (1974) argued that these differences reduce the intensity of competition thus providing the opportunity for further niche divergence without the total displacement of either species. Herbold &

Moyle's (1986) findings indicated that introduced species seldom make the exact same demands on the environment as those occurring in the pre-existing community, with resource use often being subtly different. Resource partitioning, as it was termed by Hutchinson (1959), hypothesises that the intensity of competition is reduced or eliminated as a result of a commonly used resource being exploited in a different manner by what appear to be competing species. However, Schoener (1974) maintained that while successful partitioning is a possibility, if the similarity in either the resources being exploited or the resource itself becomes particularly limited, competition will occur.

A recent study by Kusabs & Swales (1991) of the effects of introduced brown and rainbow trout on populations of the native fish koaro (*Galaxias brevipinnis*) found that, despite a high level of overlap in the diets of the fish, populations of these animals coexist in some Taupo tributaries. On examining the manner in which the two species of fish forage they concluded that coexistence was possible as a result of temporal and spatial partitioning of food resources. Others (Abrams *et al.* 1986, Hayward & Carton 1988, James 1991, Sagar & Glova 1994) have also reported the successful coexistence of species which appear to utilise the same food resources, as a result of the consumption of different-sized prey items, feeding at different times and/or feeding in different microhabitats.

In New Zealand the introduction of exotic species has had significant effects on the fauna resulting in the decline and extinction of several native and endemic species (King 1984). The introduction of exotic fish species, particularly those belonging to the family Salmonidae have been implicated in the reduction of the abundance and distribution of several native fish species (McDowall 1990). Several studies conducted abroad have found competition between waterfowl and introduced fish for limited food resources, often aquatic macroinvertebrates (Eriksson 1979, Eadie & Keast 1982, Pehrsson 1984, Hill *et al.* 1986, Phillips & Traill-Stevenson 1988, Phillips 1992).

As discussed above, while high levels of diet overlap between sympatric populations may suggest the occurrence of competition, it does not in itself confirm its existence or quantify its effect. Hence many studies have endeavoured to quantify the role of exploitation competition within

communities by measuring fitness parameters. However, an inherent problem in adopting this approach is the potential to underestimate the importance of such interactions as a result of the stabilising effects of past competition (Connell 1980). Therefore Petren & Case (1996) in their study of competition among coexisting populations of insectivorous geckos in Hawaii, suggested that a "more sophisticated" approach involving the experimental manipulation of food resources and the measurement of any response (i.e., movement in prey utilisation, use of different feeding patches).

In keeping with the suggestion of Petren & Case (1996) I experimentally tested the response of blue ducks to trout induced changes in the availability of their aquatic prey. Further to this I gathered data on the consequences of trout presence on blue duck diet by examining the prey consumed by blue ducks above and below natural trout barriers. Based on this work I assessed the potential for competition between blue ducks and introduced trout to operate as an agent-of-decline in the reduction of blue duck populations.

1. 3 Thesis Format

1. 3. 1 Chapter Two

Several studies designed to characterise the diet of an organism for the purpose of assessing the magnitude of overlap and competition with another have examined the diets in terms of prey numbers only (Cadwallader 1975, Giles *et al.* 1990, James 1991). However, utilising such a numerical approach may result in a distorted picture of the importance of individual prey types. An example of how this distortion may arise is illustrated by the aquatic insects Chironomidae and *Stenoperla prasina* which are consumed by both trout and blue ducks. *Stenoperla prasina* is substantially larger than chironomids and in terms of dry weight, approximately 50 chironomids are required to equal the dry weight of one *Stenoperla prasina* (Towers *et al.* 1994). This difference, which is likely to be reflected in nutritional returns to the predator and which may to some degree drive prey selection, would not be detected by simple numerical analysis of the diets.

Glova & Sagar (1993) in their examination of the diets and dietary interactions of exotic and native fish species in New Zealand argued that the consideration of diet composition in terms of the dry weight of each individual prey type is important if an accurate picture of the significance and importance of different prey is to be obtained.

Prey dry weight can either be directly measured, a time-consuming task which ultimately leaves the prey useless for further examination, or estimated using relations between body dimensions and dry weight values. Equations for making such estimates were not available for New Zealand's common freshwater macroinvertebrates so I conducted research to define the relations. This involved collecting aquatic macroinvertebrates from rivers and streams and measuring body dimensions followed by dry weights. Based on this work, regression equations for body length-dry weight and body length-length relationships are presented in Chapter 2. Information presented in this chapter is extensively used in Chapter 3 in the examination of the diets of blue ducks and trout.

1. 3. 2 Chapter Three

Chapter 3 presents diet data from samples collected at four North Island rivers. The data are used to explore how blue ducks and trout utilised aquatic macroinvertebrates by measuring the diet composition of each predator and overlap in the diets of the two. This involved detailed examination of the benthic macroinvertebrate assemblages existing at the four study sites. I analysed numbers and biomass of prey consumed by both predator species, as well as the patterns of prey selectivity and the relative importance of the major prey taxa to each predator. The degree of overlap existing between the diets of trout and blue duck was examined by calculating overlap indices for both numeric and dry weight data.

In addition, I compared benthic macroinvertebrate communities above and below the Ikawatea and Makaroro River waterfalls to see if trout presence had altered the macroinvertebrate community composition and size structure in the lower sections. I also examined the diet of blue ducks living above and below the waterfalls to establish if differences

existing in the macroinvertebrate communities above and below the falls were also manifested in the ducks' diet.

1. 3. 3 Chapter Four

Trout can have substantial effects on aquatic insect communities (Angradi & Griffith 1990, Feltmate & Williams 1989, Bechara *et al.* 1993, Flecker & Townsend 1995). Such studies have found that trout reduce total macroinvertebrate densities (Flecker & Townsend 1995), densities of specific prey (Feltmate & Williams 1989) and also alter the size distribution of the community (Bechara *et al.* 1993). These studies have also shown that the effects of trout on the structure of benthic macroinvertebrate communities can be complex and dependent on an array of variables.

To quantify the type and magnitude of the effects associated with trout foraging on the benthic community within a Tongariro River study area, an enclosure/exclosure experiment was conducted. The specific objective of this experiment was to test the hypothesis that trout foraging reduces aquatic macroinvertebrate biomass in patches of substrate. In addition, I also tested the hypothesis that trout presence alters benthic macroinvertebrate community composition and macroinvertebrate drifting behaviour between patches with and without trout.

The experiment involved the erection of 9 enclosures in a small braid of Tongariro River known to be inhabited by trout and used for foraging by the resident blue ducks. Within 6 enclosures the density of trout was manipulated with the remaining 3 being controls. At time intervals following the initiation of the experiment the macroinvertebrate community in each plot was examined.

1. 3. 4 Chapter Five

Overseas studies have shown that waterfowl can detect changes in the availability of their aquatic macroinvertebrate prey and react by reducing their use of those waters (Eriksson 1979, Eadie & Keast 1982, Pehrsson 1984, Hill *et al.* 1986, Phillips & Traill-Stevenson 1988, Phillips 1992). Research conducted by Eriksson (1979) noted that goldeneyes preferred lakes without fish to those containing fish. He also reported that goldeneyes increased their use of an experimental lake following the

removal of fish and the corresponding increase in aquatic insect densities. Phillips (1992) reported a very similar finding from a study he conducted in England. Other research has found that the occurrence of high densities of insectivorous fish can have more direct effects. Pehrsson (1984) found that ducklings raised on waters containing high densities of fish had to forage for longer periods and over greater areas to collect the same amount of aquatic insect food as those ducklings raised on lakes relatively free of fish. Such extended foraging activity exposed the ducklings to greater predation pressure.

Therefore, at the completion of the trout manipulation experiment described in Chapter 4, I conducted another experiment to examine trout-duck trophic interactions by testing the hypothesis that blue ducks perceive and respond to trout-induced alterations of stream macroinvertebrate communities.

This involved constructing an aviary with two identical channels flowing through it. At the beginning of each experimental run, similar numbers of aquatic macroinvertebrates were liberated into each channel and trout were introduced into one channel only. Following an initial period, a captive-reared blue duck was introduced into the aviary and its foraging activity and response to the trout-induced changes in the macroinvertebrate food resources recorded. The experiment was replicated 8 times.

1. 3. 5 Chapter Six

Chapter 6 reviews the results of the field and experimental work and compares the findings with that of recent studies. This chapter also deals with the relationship between diet overlap and competition and I discuss possible ways that organisms which make similar demands on resources may coexist. In addition an attempt is made to rationalise competition theory with conservation biology to apply my research to future conservation strategies for blue ducks.

Chapter Two

Conversion of prey availability and utilization data to dry weight estimates from body size measurements.

2. 1 Introduction

A problem that is often likely to occur when describing the composition of a stream community or the diet of a stream predator in numeric terms is the overestimation of the importance of small animals and underestimation of large ones. The dry weight of aquatic macroinvertebrates within the same community and consumed by predators ranges widely (Towers *et al.* 1994). Many small animals may not be as important to a predator in terms of dry weight and hence kilojoules, as one large prey. Such differences in the dry weight and calorific value of prey may play a role in prey selectivity among predators and thus a taxon of high dry weight and corresponding nutritional value may be a key taxon in any competition between coexisting organisms.

The most common method of determining dry weight has been to directly weigh each individual specimen after drying for at least 30 hours. This approach is very time consuming, and prone to error if the specimens have been previously stored in preservative (Stanford 1972, Donald & Paterson 1977). Direct weighing has the added disadvantage of rendering the specimen useless for further examination as a result of the drying process. An alternative approach is to utilise predictive equations to estimate dry weight from body measurements. Davey (1954), Engelmann (1961), Breymeyer (1967) and Tillbrook (1972) used regression equations for estimating dry weight from body dimensions for species of terrestrial arthropods. Equations for lotic macroinvertebrates have been derived for taxa in North America (Smock 1980) and Europe (Meyer 1989).

I measured head widths and body lengths of some common New Zealand

stream-dwelling macroinvertebrates, and used regression procedures to find their interrelationship with one another and with dry weight. Predictive equations for macroinvertebrate orders were also developed to allow estimation of dry weight when specimen identification was imprecise (as often the case in diet analysis).

2.2 Methods

2.2.1 Macroinvertebrate collection sites

Aquatic macroinvertebrates were collected between November 1991 and March 1992 from the Kahuterawa and Tiritea streams. Both streams originate in the Tararua Ranges and flow westwards into Manawatu River in the vicinity of Palmerston North (40°21'S, 157°37'E). Tiritea and Kahuterawa Streams drain forested headwaters and have well-defined pool-riffle formations. Tiritea Stream is impounded in its mid-reaches to supply water to Palmerston North city. Samples were collected from a site downstream of the dam in a shaded reserve amongst residential development. At that point the stream order was 4. The sample site on Kahuterawa Stream was near a road end at the point where vegetation in the catchment changed from forestry to pastoral farmland. The stream order was 5.

2.2.2 Macroinvertebrate collection and measurement protocol

Aquatic macroinvertebrates were collected on five occasions. All macroinvertebrate specimens of a particular order were collected together to negate seasonal effects. Specimens were obtained by kick sampling with a dip net (0.5mm mesh) and identified using Winterbourn & Gregson (1989).

Living, undamaged macroinvertebrates were measured using a Zeiss dissecting microscope fitted with an ocular micrometer (magnification 6.7-40x). Specimens larger than 10 mm were measured with Vernier callipers. Each macroinvertebrate was placed on moist filter paper and measured when activity stopped. For most taxa, body measurements were head capsule width (HW) and total body length (BL). Head capsule width was always measured across the widest section of the head. Body

length was taken as the distance from the anterior of the head to the end of the last abdominal segment, (excluding cerci or other appendages). Body length measurements were recorded to the nearest 0.1 mm while head width was recorded to 0.01mm. If the body of a macroinvertebrate was not straight it was straightened out with care being taken not to stretch the specimen.

The procedure was modified for some taxa. Hydrobiosidae were measured with the head extended flat along the filter paper. Body lengths of Trichoptera with portable cases were taken to be the maximum length of the case, except for *Helicopsyche* sp. for which the greatest width across the case was substituted. The body lengths of Tipulidae larvae were measured with the head retracted. For the gastropod mollusc *Potamopyrgus antipodarum* shell height was measured. No attempt was made to quantify separately the gut contents of the macroinvertebrates used.

Live macroinvertebrates were placed individually in pre-weighed aluminium foil boats, dried at 104°C for 36 hours (Meyer 1989), and weighed after cooling in a desiccator. Dry weights were recorded to the nearest 0.1mg, with the exception of Chironomidae, Elmidae, and *Helicopsyche* which were weighed to the nearest 0.01mg. Cased Trichoptera were extracted from their cases before drying, case weight therefore was not included. Due to the damage associated with extracting *Potamopyrgus antipodarum* from their shells; shell weight was included.

2.2.3 Data analysis

2.2.3a Dry weight regression analysis

Power functions of the form $Dw=a.L^b$ were fitted by log transforming weights and lengths so that linear equations of the form $\ln Dw=\ln a + b.\ln L$ could be used to estimate dry weight where a, b = regression constants, Dw=dry weight (mg) and L=length parameters (BL or HW) (mm). Analysis of co-variance was undertaken to test whether the regression equations differed significantly among taxa.

I also generated functions suitable for estimating dry weight for macroinvertebrate orders. Because different numbers of individuals had been measured for the species in any order, I weighted all data points by the inverse of sample size for that species. This meant that each species in the order contributed equally to the regression.

2. 2. 3b Body length - head width regression analysis

As the bodies of aquatic macroinvertebrates are damaged when consumed by a predator, a reliable method of estimating body length from measurements of some body part less prone to damage by initial consumption was required. The smaller relatively robust heads of aquatic macroinvertebrates often suffer little damage when ingested and thus regression equations for predicting body length based on head width were obtained. The estimation of body length was particularly important to this study as it allowed for the examination of size selectivity by the two potential competitors.

The relationship between measurements of head width and body length was examined by fitting the linear model $BL=a + b.HW$ to raw length data, and the power function $BL=a.HW^b$ to logged data. Initially both models were applied to determine the best relationship between the two variables. Functions suitable for estimating BL from HW are presented for individual taxa as well as for aquatic macroinvertebrate orders. Weighted regressions were used when calculating order coefficients.

2. 3 Results

2. 3. 1 Body length - dry weight relationship

A total of 618 macroinvertebrate larvae were measured and weighed (Table 2.1). Because of difficulties with species identification all Chironomidae were pooled, and Hydrobiosidae were pooled because of low numbers. Parameters for the regression equations relating body length and head width to dry weight for each taxon are presented in Table 2. 2.

Table 2. 1 Number of individuals, ranges of body lengths (BL), head widths (HW), dry weights (DW) and collection source (T=Tiritea, K=Kahuterawa) of macroinvertebrates utilised in this study.

Taxon	R a n g e			n	Site
	BL (mm)	HW (mm)	DW (mg)		
Ephemeroptera					
<i>Coloburiscus humeralis</i>	8.7-15.5	1.93-2.68	4.0-22.7	53	K
<i>Deleatidium</i> sp.	3.9-10.4	0.88-2.03	0.3-5.7	53	K
<i>Nesameletus</i> sp.	2.0-5.5	1.10-2.00	2.2-20.9	39	K
<i>Ameletopsis perscitus</i>	6.1-19.5	1.10-4.10	0.2-25.1	27	K
<i>Zephlebia</i> sp.	4.3-16.3	1.00-3.25	0.3-10.3	23	K
Plecoptera					
<i>Zelandobius</i> sp.	2.5-10.2	0.63-1.43	0.2-2.7	28	K
<i>Zelandoperla</i> sp.	6.7-15.0	1.23-1.98	2.6-9.7	20	K
<i>Stenoperla prasina</i>	11.5-29.5	2.13-3.95	2.1-51.4	12	K
<i>Austroperla cyrene</i>	6.1-15.8	1.20-2.00	1.0-9.6	33	K
Trichoptera					
<i>Olinga feredayi</i>	3.9-12.2	0.43-1.30	0.1-5.9	41	K
<i>Helicopsyche</i> sp.	1.3-3.1	0.28-0.68	0.1-0.5	17	K
<i>Aoteapsyche</i> sp.	5.2-19.2	1.00-2.50	0.3-20.0	26	K
<i>Pycnocentrodes</i> sp.	3.2-7.0	0.50-1.18	0.2-1.6	25	T
Hydrobiosidae*	4.5-25.0	0.45-1.73	0.1-15.2	43	T/K
Megaloptera					
<i>Archichauliodes diversus</i>	6.5-35.0	0.98-4.00	0.5-75.7	27	K
Diptera					
<i>Aphrophila neozelandica</i>	6.7-16.8	0.33-0.93	0.50-2.50	18	T
Chironomidae	2.1-4.1	0.16-0.32	0.08-0.85	23	T/K
<i>Austrosimulium</i> sp.	2.1-4.7	0.30-0.60	0.06-0.35	21	T
Coleoptera					
<i>Elmidae</i> (larvae)	2.9-6.9	0.25-0.50	0.05-1.19	32	T/K
Adult Coleoptera	2.2-4.2	0.35-0.80	1.4-10.4	22	T/K
Gastropoda					
<i>Potamopyrgus antipodarum</i>	1.7-5.2	no data	0.4-7.9	35	T/K

* Grouped because of low numbers.

Table 2. 2 Values for the constants $\ln a$ and b obtained from the regression of \ln Dry Weight (DW, mg), \ln Body Length (BL, mm) and \ln Head Width (HW, mm) for selected aquatic macroinvertebrate taxa. r^2 is the coefficient of determination. SE = standard error of the estimate. All correlation coefficients of determination were significant at the 0.05% level except those marked *.

Taxon	Conversion	Regression constants		r ²
		ln <i>a</i> ± SE	<i>b</i> ± SE	
Ephemeroptera				
<i>Coloburiscus</i>	BL-DW	-3.6445 ± 0.4672	2.4700 ± 0.1914	0.76
<i>humeralis</i>	HW-DW	-1.5500 ± 0.3983	4.6007 ± 0.4653	0.65
<i>Deleatidium</i> sp.	BL-DW	-5.3800 ± 0.2758	3.0555 ± 0.1394	0.91
	HW-DW	-1.3428 ± 0.1266	4.0807 ± 0.2475	0.84
<i>Nesameletus</i> sp.	BL-DW	-6.8917 ± 0.4041	3.5268 ± 0.1627	0.85
	HW-DW	0.6180 ± 0.1803	3.1721 ± 0.3201	0.75
<i>Ameletopsis</i>	BL-DW	-4.1700 ± 0.9931	2.4294 ± 0.4063	0.58
<i>perscitus</i>	HW-DW	-0.0840 ± 0.3437	2.2115 ± 0.3866	0.55
<i>Zephlebia</i> sp.	BL-DW	-4.3066 ± 0.3656	2.5252 ± 0.1768	0.90
	HW-DW	-0.7747 ± 0.1483	2.9722 ± 0.2383	0.88
Plecoptera				
<i>Zelandobius</i> sp.	BL-DW	-1.5528 ± 0.2603	2.5956 ± 0.4277	0.57
	HW-DW	-3.2054 ± 0.4254	1.7354 ± 0.2314	0.67
<i>Zelandoperla</i> sp.	BL-DW	-2.3001 ± 0.6587	1.7333 ± 0.2314	0.67
	HW-DW	0.2172 ± 0.2595	2.9431 ± 0.4757	0.62
<i>Stenoperla prasina</i>	BL-DW	-6.8350 ± 1.3430	3.2787 ± 0.4397	0.83
	HW-DW	-2.4635 ± 0.7627	4.6465 ± 0.6259	0.83
<i>Austroperla cyrene</i>	BL-DW	-4.7875 ± 0.2294	2.5909 ± 0.0997	0.95
	HW-DW	-0.7739 ± 0.1826	4.3239 ± 0.3933	0.79
Trichoptera				
<i>Olinga feredayi</i>	BL-DW	-6.5681 ± 0.2363	3.3417 ± 0.1079	0.96
	HW-DW	1.1276 ± 0.0575	3.6462 ± 0.1728	0.92
<i>Helicopsyche</i> sp.	BL-DW	-1.4503 ± 0.3191	0.2446 ± 0.3463	0.00*
	HW-DW	-0.3150 ± 0.4624	0.9477 ± 0.4762	0.18*
<i>Aoteapsyche</i> sp.	BL-DW	-6.0016 ± 0.5814	3.0349 ± 0.2309	0.88
	HW-DW	-0.2015 ± 0.3307	3.2061 ± 0.5564	0.56
<i>Pycnocentroides</i> sp.	BL-DW	-4.8730 ± 0.7253	2.5024 ± 0.4434	0.58
	HW-DW	-0.0908 ± 0.0971	2.5264 ± 0.2584	0.80
Hydrobiosidae	BL-DW	-5.2103 ± 0.5732	2.2222 ± 0.2335	0.69
	HW-DW	0.3567 ± 0.1473	1.8327 ± 0.4011	0.34
Megaloptera				
<i>Archichauliodes</i>	BL-DW	-5.5204 ± 0.4329	2.6784 ± 0.1348	0.94
<i>diversus</i>	HW-DW	-0.1064 ± 0.2676	2.9036 ± 0.2380	0.85
Diptera				
<i>Aphrophila</i>	BL-DW	-4.2771 ± 0.3070	1.8086 ± 0.1258	0.92
<i>neozelandica</i>	HW-DW	0.7519 ± 0.1969	1.3047 ± 0.0354	0.43
Chironomidae	BL-DW	-3.8757 ± 0.1697	2.7206 ± 0.1560	0.93
	HW-DW	2.8411 ± 0.4046	2.6356 ± 0.2765	0.80
<i>Austrosimulium</i> sp.	BL-DW	-49029 ± 0.2222	2.4205 ± 0.1689	0.90
	HW-DW	0.2272 ± 0.1941	2.7671 ± 0.2620	0.83
Coleoptera				
<i>Elmidae</i> (larvae)	BL-DW	-6.0784 ± 0.3849	3.0920 ± 0.2471	0.83
	HW-DW	2.2581 ± 0.2702	3.5741 ± 0.2632	0.86
Adult Coleoptera	BL-DW	-2.0076 ± 0.1420	3.2271 ± 0.1226	0.97
	HW-DW	3.1102 ± 0.1081	2.5412 ± 0.1750	0.91
Gastropoda				
<i>Potamopyrgus antipodarum</i>	BL-DW	-2.0961 ± 0.1408	2.4506 ± 0.1126	0.93

For both body length and head width, with the exception of *Helicopsyche* sp., all regression slopes were significant at the $p < 0.05$ level. For 16 of the 20 taxa displaying significant regressions, more of the variance in dry weight was explained (as expressed by the coefficient of determination (r^2)) by body length than by head width (Table 2. 2).

Regression equation parameters relating body length and head width to dry weight for four macroinvertebrate orders are presented in Table 2. 3 (Coleoptera, Megaloptera and Gastropoda not included in Table 2. 3 as coefficients presented in Table 2. 2). Inspection of the natural log/log plots of dry weight in relation to body length (Fig 2. 1A) and in relation to head width (Fig 2. 1B) for each macroinvertebrate order demonstrated that dry weight increased in different ways amongst the organisms and justified separate functions for each taxon. Analysis of covariance confirmed that significant differences existed between equations associated with the different orders (body length-dry weight intercept $F_{6,566}=20.65$, $P<0.005$, slope $F_{6,566}=23.899$, $P<0.005$; Head width-dry weight intercept $F_{5,530}=23.601$, $P<0.005$; slope $F_{5,530}=8.605$, $P<0.005$). Some orders exhibited slopes or intercepts that were not significantly different. Analysis of covariance showed that Ephemeroptera and Megaloptera body-length-to-dry-weight regressions were not significantly different from each other (intercept $F_{1,215}=0.827$, $P=0.364$, slope $F_{1,215}=0.358$, $P=0.550$). Similarly, the equations obtained for Plecoptera, Trichoptera, and Coleoptera larvae did not differ significantly (intercept $F_{2,255}=2.821$, $P=0.061$, slope $F_{2,255}=1.838$, $P=0.161$), but did differ from Ephemeroptera and Megaloptera (intercept $F_{1,476}=21.133$, $P<0.005$, slope $F_{1,476}=50.825$, $P<0.005$).

The possibility that sorting Trichoptera into cased and uncased larvae may increase the precision of predictions was examined. I removed *Helicopsyche* sp. (a cased species) from the analysis due to its low r^2 statistic and found no significant difference between the regressions for relating dry weight to body length of cased and uncased Trichoptera (intercept $F_{1,127}=0.20$, $P<0.888$, slope $F_{1,127}=1.975$, $P<0.162$). Analysis of covariance did show a significant difference between the head-width-dry-weight regressions for cased and uncased caddisfly larvae (intercept $F_{1,129}=8.873$, $P<0.005$, slope $F_{1,129}=19.49$, $P<0.005$) and therefore parameters for dry weight determination for Trichoptera based on case

presence or absence are provided in Table 2. 3.

In the majority of cases greater precision was obtained using equations at the generic and specific levels than that obtained at order level. For example, in all three taxa of Diptera that were investigated, there were significant relationships between linear dimensions and dry weight. This was also true when all Diptera taxa were considered together, but a lower proportion of the variation in the data was explained by the resulting equation (Tables 2. 2 and 2. 3, Fig 2. 3).

To explore the precision of the predictions, the 95% confidence intervals were inspected for the macroinvertebrates with the highest and lowest r^2 values respectively. These were *Olinga feredayi* and Hydrobiosidae for head width, and *Olinga feredayi* and *Zelandobius* sp. for body length (Table 2. 2, Fig 2. 3A and 2. 3B). This exercise showed that the precision of predicting the dry weight of a taxon varied between taxa and with the size of individuals within taxa. On the basis of this examination of precision it can be expected that dry weight estimations will range between $\pm 10\%$ to $\pm 40\%$. Dry weight estimation for small samples or for individual estimations necessarily will be less precise due to the increased variance associated with them.

Table 2. 3 Regression parameter estimates using weighted data for the relationship between body length (BL, mm), or head width (HW, mm) and dry weight (DW, mg) for four aquatic macroinvertebrate orders. SE = standard error of the estimate, r^2 = coefficient of determination, n = number of individuals. All coefficients of determination are significant ($p < 0.001$) except that marked *. †*Helicopsyche* sp. removed from analysis.

Order	Conversion	$\ln a \pm SE$	$b \pm SE$	r^2	n
Ephemeroptera	BL-DW	-4.6453 ± 0.2148	2.7011 ± 0.0936	0.81	195
	HW-DW	-0.2887 ± 0.1293	2.8402 ± 0.1819	0.57	195
Plecoptera	BL-DW	-4.4451 ± 0.1912	2.5044 ± 0.0787	0.92	93
	HW-DW	-0.0985 ± 0.0734	2.8538 ± 0.1028	0.89	93
Trichoptera †	BL-DW	-4.8940 ± 0.2679	2.4364 ± 0.1207	0.75	133
	HW-DW	0.3609 ± 0.0644	2.5200 ± 0.1500	0.68	133
Cased caddis	HW-DW	0.8080 ± 0.0850	3.7390 ± 0.2420	0.79	64
Uncased caddis	HW-DW	0.3890 ± 0.1060	2.1310 ± 0.2260	0.57	69
Diptera	BL-DW	-2.8777 ± 0.1803	1.2445 ± 0.1045	0.69	62
	HW-DW	-0.0806 ± 0.2322	0.9202 ± 0.2349	0.20*	62

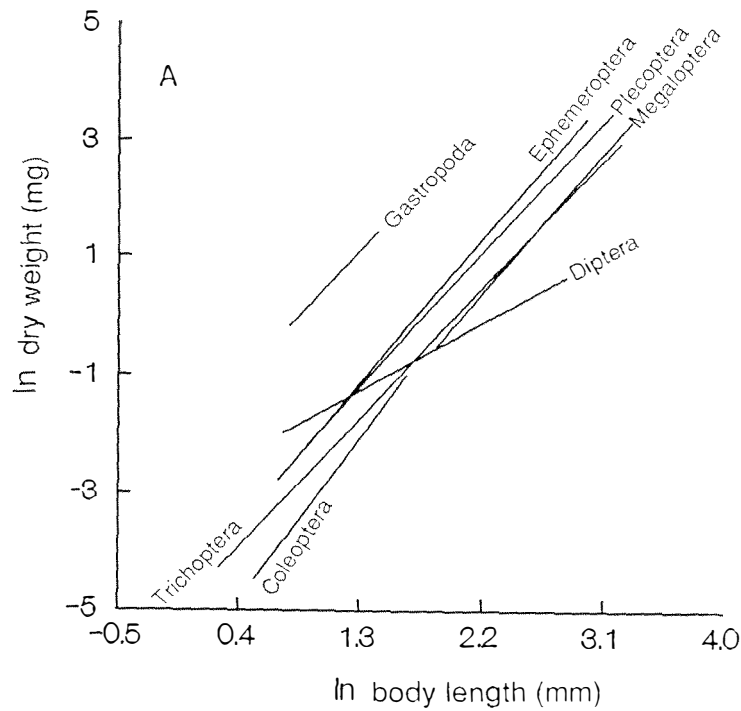


Fig. 2. 1A Log/log plot of the regressions for dry weight (mg) versus body length (mm) for the five macroinvertebrate orders plus Gastropoda.

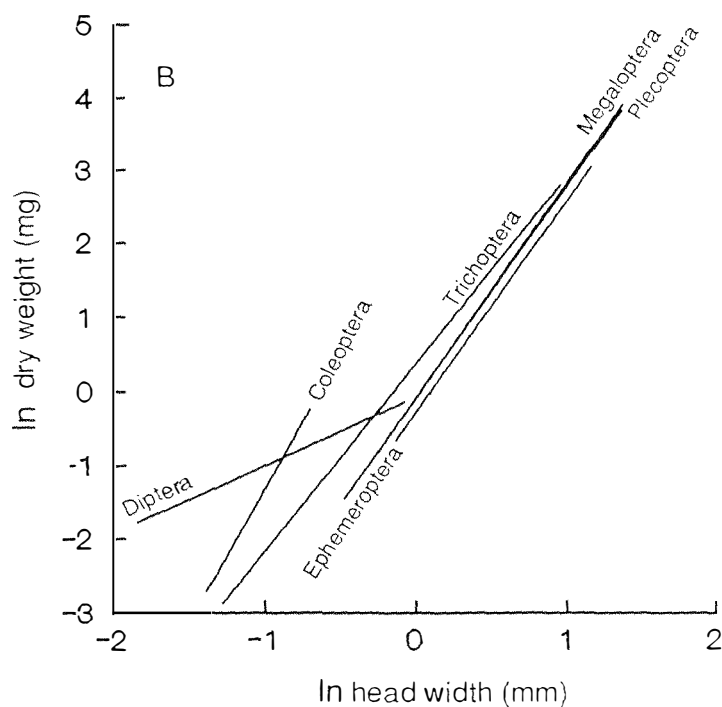


Fig. 2. 1B Log/log plot of the regression for dry weight (mg) versus head width (mm) for macroinvertebrate orders.

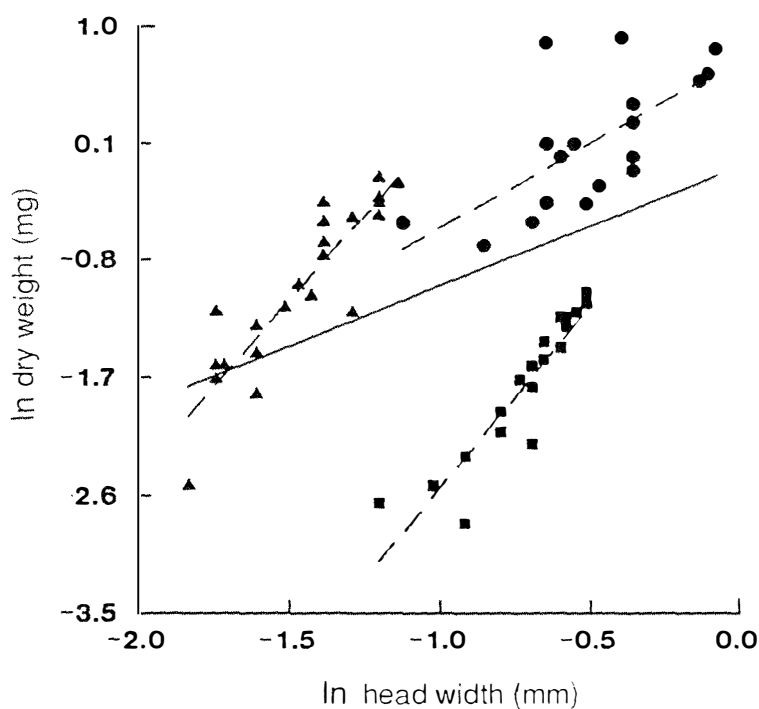


Fig. 2. 2. Log/log plots and regression lines (---) of dry weight versus head width for the groups of Diptera. (• *Aphrophila neozelandica*, Δ Chironomidae and ■ *Austrosimulium* sp.). The weighted regression for the order is also presented (—).

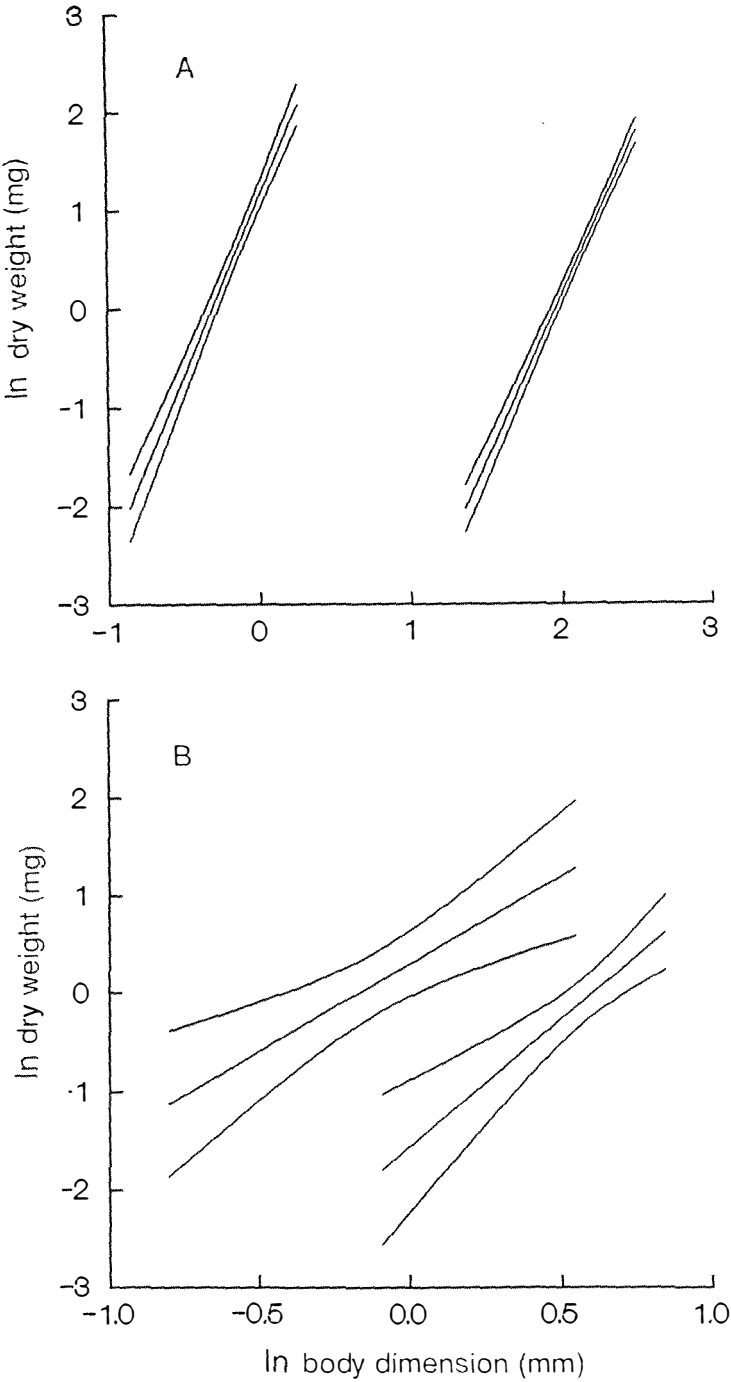


Fig. 2. 3 **A**, Regression lines and associated 95% confidence intervals for *Olinga feredayi*, the macroinvertebrate with the highest r^2 values for body length and head width to dry weight relationships. The body length-dry weight relationship is shown on the right and head width-dry weight on the left. **B**, Regression lines and associated 95% intervals for *Zelandobius* sp. which had the lowest r^2 value for the body length-dry weight relationship (shown on the right) and Hydrobiosidae which had the lowest r^2 value for the head width-dry weight relationship (shown on the left).

2. 3. 2 Head width - body length relationships

Examination of the parameters generated by the two models indicated no significant gain (as indicated by r^2) in precision could be made by applying the power function and therefore coefficients for the linear model relating body length to head width for each taxon are presented in Table 2. 4.

With the exception of *Helicopsyche* sp., all regression slopes were significant at the 0.05 level. The amount of variance in body length explained by head width (as expressed by the coefficient of determination (r^2)) ranged from 0.48 to 0.98, excluding *Helicopsyche* sp. which had an r^2 of only 0.09.

Regression parameters for six aquatic macroinvertebrate orders are given in Table 2. 5. Inspection of the plot relating body length to head width (Fig 2. 4) for each macroinvertebrate order demonstrates that body length for each taxonomic group increases at a different rate justifying separate functions. Analysis of covariance confirmed that significant differences ($P < 0.005$) existed between the equations associated with the different orders.

Due to the obvious morphological differences between cased and uncased Trichoptera the possibility that increased precision could be gained by separating the two groups was examined. *Helicopsyche* sp. was excluded from this examination due to its low r^2 statistic. Significant differences between the regressions relating body length to head width for cased and uncased Trichoptera were found (intercept $F_{1,134} = 48.02$, $P < 0.005$, slope $F_{1,134} = 8.15$, $P < 0.05$). Parameters for body length estimation from head width for Trichoptera based on case presence or absence are presented in Table 2. 5.

Table 2. 4 Values for the constants a and b obtained for the linear relationship between head width (HW, mm) and body length (BL, mm) for selected New Zealand aquatic macroinvertebrates. r^2 is the coefficient of determination. SE = standard error of the estimate. All correlation coefficients of determination were significant at the 0.05% level except that marked *.

Taxon	$a \pm SE$	$b \pm SE$	r^2
Ephemeroptera			
<i>Coloburiscus humeralis</i>	-5.3410 ± 2.4500	7.1810 ± 1.0390	0.48
<i>Deleatidium</i> sp.	-1.8365 ± 0.5365	5.5884 ± 0.3249	0.85
<i>Nesameletus</i> sp.	1.3866 ± 0.7510	5.4274 ± 0.5795	0.70
<i>Ameletopsis perscitus</i>	0.9474 ± 0.5617	4.5705 ± 0.2211	0.95
<i>Zephlebia</i> sp.	-1.4285 ± 0.3693	5.3419 ± 0.1944	0.97
Plecoptera			
<i>Zelandobius</i> sp.	-2.3755 ± 0.9231	8.1242 ± 0.8362	0.78
<i>Zelandoperla</i> sp.	-4.4760 ± 2.6830	8.8830 ± 1.5550	0.65
<i>Stenoperla prasina</i>	-4.8700 ± 5.1270	7.7880 ± 1.5010	0.73
<i>Austroperla cyrene</i>	-6.1920 ± 1.5490	10.4172 ± 0.9759	0.77
Trichoptera			
<i>Olinga feredayi</i>	-0.4821 ± 0.3524	10.4992 ± 0.3729	0.95
<i>Helicopsyche</i> sp.	3.3270 ± 0.7533	-2.1150 ± 1.8520	0.09*
<i>Aoteapsyche</i> sp.	-0.4130 ± 2.0480	7.3060 ± 1.1160	0.66
<i>Pycnocentroides</i> sp.	1.3197 ± 0.4345	4.9473 ± 0.5464	0.78
Hydrobiosidae	2.7130 ± 1.4910	9.4440 ± 1.4560	0.48
Megaloptera			
<i>Archichauliodes diversus</i>	-0.8140 ± 1.9710	8.6170 ± 0.6262	0.88
Diptera			
<i>Aphrophila neozelandica</i>	0.6780 ± 2.1330	27.6600 ± 4.2720	0.72
Chironomidae	0.1089 ± 0.2888	11.9270 ± 1.1780	0.83
<i>Austrosimulium</i> sp.	-0.5918 ± 0.1670	8.7546 ± 0.3329	0.97
Coleoptera			
<i>Elmidae</i> (larvae)	-0.2051 ± 0.3786	13.3109 ± 0.9850	0.86
Adult Coleoptera	0.6314 ± 0.1142	4.3735 ± 0.18899	0.96

Table 2. 5 Regression parameter estimates using weighted data for the relationship between head width (HW, mm) and body length (BL, mm) for four aquatic macroinvertebrate orders. SE = standard error of the estimate, r^2 = coefficient of determination, n = number of individuals. All coefficients of determination are significant ($p<0.001$). [†]*Helicopsyche* sp. removed from analysis.

Order	$a \pm SE$	$b \pm SE$	r^2	n
Ephemeroptera	0.9730 ± 0.2874	4.4834 ± 0.1437	0.84	195
Plecoptera	-0.6823 ± 0.3858	6.6520 ± 0.1801	0.94	93
Trichoptera [†]	2.5466 ± 0.6304	6.4249 ± 0.5230	0.53	137
Cased caddis	-1.5780 ± 0.7580	10.2923 ± 0.8695	0.69	65
Uncased caddis	6.4880 ± 1.1090	4.2063 ± 0.7513	0.31	72
Diptera	-1.9170 ± 1.7490	21.8040 ± 4.035	0.32	65

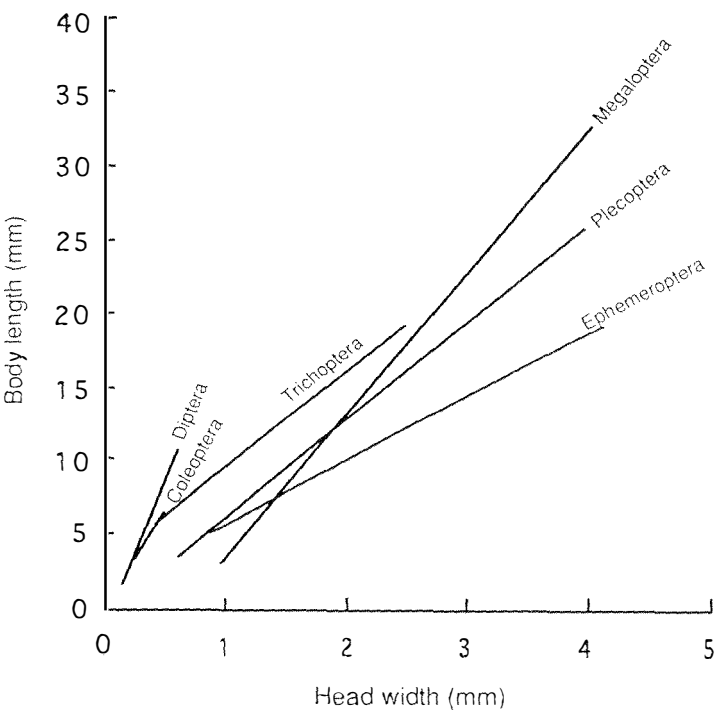


Fig. 2. 4 Plot of the regressions for body length (mm) versus head width (mm) according to macroinvertebrate order.

2.4 Discussion

With the exception of *Helicopsyche*, the r^2 values obtained for estimating dry weight from body dimensions were similar to those found for North American (Smock 1980) and European stream macroinvertebrates (Meyer 1989) for similar taxa and at the order level. The variation in the size of sand grains utilised by *Helicopsyche* larvae in the construction of their cases may in part explain the low r^2 . As size was taken to be the maximum width of the case, a predominance of large or small grains in cases of similar sized larvae may have resulted in low correlation between body length and dry weight. Alternatively, as *Helicopsyche* larvae grow, measurable increases in body length (greatest case width) will be small as a result of the spiralled nature of the case, so even modest inaccuracies in width measurement will result in poor r^2 .

The values of the power function exponents ranged between approximately 2 and 4 for both body length and head-width-to-dry weight relationships. Smock (1980) obtained a mean b value of 2.74 for the relationship between body length and dry weight, and a mean b value of 2.85 when he related head width to dry weight for eight aquatic macroinvertebrate orders and suggested that “the value of b ranged around 3.0”. For those with low b values around 2, dry weight would appear to be more dependent on surface area than volume. Engelmann (1961) suggested that the mass of aquatic macroinvertebrate animals is made up largely by the exoskeleton and attached musculature, and their body weights are more dependent on surface area than on volume. For those with b values ranging around 3 dry weight would appear to be more volume dependent.

The inclusion of gut contents in dry weight measurements contributed some imprecision to the subsequent dry weight predictions. Marchant (1986) suggested that the inclusion of gut contents produced overestimations of dry weight, but that such errors were “probably small compared with the error in using regression estimates rather than actual measurements of dry weight”.

The heavy calcareous shell of *Potamopyrgus antipodarum* explains why its body length-dry weight plot (Fig 2. 1A) had a larger intercept than that of other the macroinvertebrate orders examined. A similar plot may

have been derived for the cased caddis if the cases had not been removed before drying.

Winterbourn *et al.* (1981) noted that throughout New Zealand, unmodified streams tend to have remarkably similar benthic macroinvertebrate faunas with a “nucleus of common genera (*Deleatidium*, *Coloburiscus*, *Nesameletus* (Ephemeroptera); *Stenoperla*, *Zelandoperla*, *Zelandobius* (Plecoptera); *Hydrobiosis*, *Psilochorema*, *Pycnocentria*, *Olinga*, *Aoteapsyche* (Trichoptera); *Archichauliodes* (Megaloptera); *Potamopyrgus* (Gastropoda)) and species”. The equations presented here cover all of these taxa except *Pycnocentria* and are applicable to the majority of aquatic macroinvertebrates consumed by trout and blue ducks in the rivers studied in this thesis. As other macroinvertebrate taxa, for which specific predictive equations are not presented here, may also occur in the diets of the two predators the order level equations will be used for dry weight estimations.

These predictive equations will be used in Chapters 3 and 4 to estimate the dry weight and length of macroinvertebrates captured by predators and also to quantify the dry weight composition of the benthic communities upon which trout and blue ducks forage.

Chapter Three

Macroinvertebrate fauna in the benthos and diets of trout and blue ducks on four North Island rivers.

3. 1 Introduction

New Zealand's aquatic environment has been the recipient of numerous fish introductions (see McDowall 1990). Of such introductions the acclimatisation of trout, both brown (*Salmo trutta*) and rainbow (*Oncorhynchus mykiss*) has been the most successful (McDowall 1985) and today few suitable rivers and streams remain free of these species. The first trout introductions took place during the 1870s. At this time many people considered that the introduced insectivorous trout would simply colonise a vacant niche within New Zealand's aquatic environment. However, several studies of trout and native fish diets have shown this early belief to be incorrect because there is significant similarity in the prey consumed by these fish (Cadwallader 1975, Glova & Sagar 1991, Glova & Sagar 1993).

Cadwallader (1975) examined diet overlap between several New Zealand native freshwater fish species and brown trout. As a result of the similarity in the microhabitats exploited and the prey consumed by brown trout and galaxiids he concluded that direct competition was, in part, accountable for the reduction in galaxiid abundance in those areas where trout also occurred.

New Zealand's blue ducks, like the majority of the country's native fish species, feed almost entirely on aquatic macroinvertebrates (Kear & Burton 1971, Collier 1991, Wakelin 1993). Kear & Burton (1971) noted the similarity in the diets of blue ducks and trout and speculated on the possibility of potential competition for food resources. Several international studies have recorded significant overlap in the diets of waterfowl and fish which in turn has resulted in adverse effects on the sympatric waterfowl populations (Eadie & Keast 1982, Phillips 1992,

Pehrsson 1984, Des Granges & Rodrigue 1986, Hill *et al.* 1986, Hunter *et al.* 1986). Phillips & Wright (1993) found that coarse fish (*Abramis brama* and *Perca fluviatilis*) greatly reduced the densities of chironomids in an English lake, leading to lower waterfowl densities on the lake. Hill *et al.* (1986) found that the survival of mallard ducklings (*Anas platyrhynchos*) raised on ponds containing high densities of insectivorous coarse fish was significantly lower than that of ducklings raised on neighbouring ponds which contained low numbers of such fish. Both studies concluded that modification of the benthic macroinvertebrate communities by the fish had resulted in the observed adverse effects on the waterfowl.

In light of these studies and the comments by Kear & Burton (1971), I collected field data on benthic macroinvertebrate communities and their exploitation by coexisting populations of blue ducks and trout on four North Island rivers to test the hypothesis that such coexisting populations of blue ducks and trout overlap in the use of aquatic macroinvertebrate prey resources. On two of the rivers, I was able to compare macroinvertebrate populations and the diet of blue ducks above and below waterfalls that excluded trout from the upper reaches. Using the data collected from these rivers I tested the hypothesis that trout foraging alters the composition of macroinvertebrate communities and in turn the diets of blue ducks below the falls relative to that above.

3. 2 Methods

3. 2. 1 River and study site descriptions

Data were collected from sites located on Tongariro, Manganuiateao, Ikawetea and Makaroro Rivers. Each river had a resident population of blue ducks and all contained trout. Ikawetea and Makaroro Rivers each had large waterfalls which obstructed upstream migration of trout. On both of these rivers blue ducks were present above and below the waterfalls.

The study sites on Tongariro and Manganuiateao Rivers were located in the middle sections of the two systems where both rivers were characterised by large width, deep water, high flow and stable boulder /

cobble substrate. Conversely, the sampling sites on the two Ruahine rivers were located in the headwaters which were characterised by unstable cobble / gravel substrate, relatively low flows, shallow water and narrow channel width. Due to the similarity in the nature of Tongariro and Manganuiateao Rivers, and Ikawetea and Makaroro Rivers, the discussion of the data from the similar rivers is often combined in the following sections.

A description of each of the four rivers follows.

Tongariro River

Tongariro River originates in the Kaimanawa Ranges. In addition to collecting water from the Kaimanawas, Tongariro River also drains the eastern flanks of the central North Island volcanos, before flowing into Lake Taupo. The river's flow dynamics have been substantially altered since the early 1970s when it became part of a large hydropower scheme. In the area where I collected my samples, the river was approximately 20-30 m wide and fast-flowing with a predominantly boulder / cobble substrate. The riparian forest bordering the river in this region is dominated by silver beech (*Nothofagus menziesii*).

There is a population of blue ducks in the middle and upper reaches of the river while the lower section contains a world-renowned trout fishery. In the middle section of river, where I conducted my study, the trout population is mainly composed of rainbow trout.

From this river I collected trout, blue duck faecal droppings and benthic macroinvertebrate samples at two sites. The first sample site was located immediately upstream of the Pillars of Hercules (S 39° 09' 05", E 175° 49' 02", elevation 620m) while the second was located approximately 0.5 km downstream of Tree Trunk Gorge (S 39° 10' 04", E 175° 48' 05") (Fig. 3.1).

Monitoring of the Tongariro River blue duck population indicates that the adult ducks occur at a density of approximately 1.3 birds per km although numbers have declined by approximately 40% since 1983 (Don 1992 unpublished). Little information exists on the density of juvenile trout in the study area. However, work by Stephens (1989) reported

juvenile trout densities in the lower river increased rapidly in spring to a maximum in December before declining slowly throughout the summer and autumn. As with Stephens (1989), I found by electrofishing that juvenile densities were highest in summer with fish occurring in the littoral substrate at approximately 1 per m².

Manganuiateao River

Manganuiateao River originates in the southwest snow fields of Mt Ruapehu, in the central North Island (Fig 3.2). It flows southwest for approximately 80 km to its confluence with Wanganui River and has a catchment area of 620 km² (Cudby & Strickland 1986). In the middle section of the river from which I collected my samples, the river is characterised by a well defined pool / riffle system. The river substrate is composed of large rounded andesitic boulders and is relatively stable in nature. Mean annual water flow recorded at Ruatiti downstream of my sampling sites is approximately 18.2 m³s⁻¹ and water quality has been reported as uniformly high (Williams 1991). The river in the vicinity of my study area is flanked by pasture and, in places, regenerating native bush.

There is a population of blue ducks in the middle and upper reaches of the river while both rainbow and brown trout occur throughout the river.

Samples for my study were collected from three sites in the middle reaches of the river. These were named Top site (S 39° 19' 06" E 175° 14' 00"), Camp site (S 39° 19' 05" E 175° 14' 03"), and Flying fox (S 39° 19' 05" E 175° 15' 01") which was the most downstream site. Resident pairs of blue ducks occupied territories encompassing each of the sampling sites.

Adult blue ducks within the study area occur at a density of approximately 1 pair per kilometre of river (Williams 1991). Adult trout (FL¹ > 0.2 m) densities have been reported by Cudby & Strickland (1986) to be in the order of 5 fish per pool in the reach from which samples were collected. No published information is available on juvenile trout density in the study area. From my electro-fishing, densities of juvenile trout appeared to be low, being in the order of 0.2 fish per m².

¹ FL = Fork Length - length of fish from tip of snout to central edge of caudal fin.

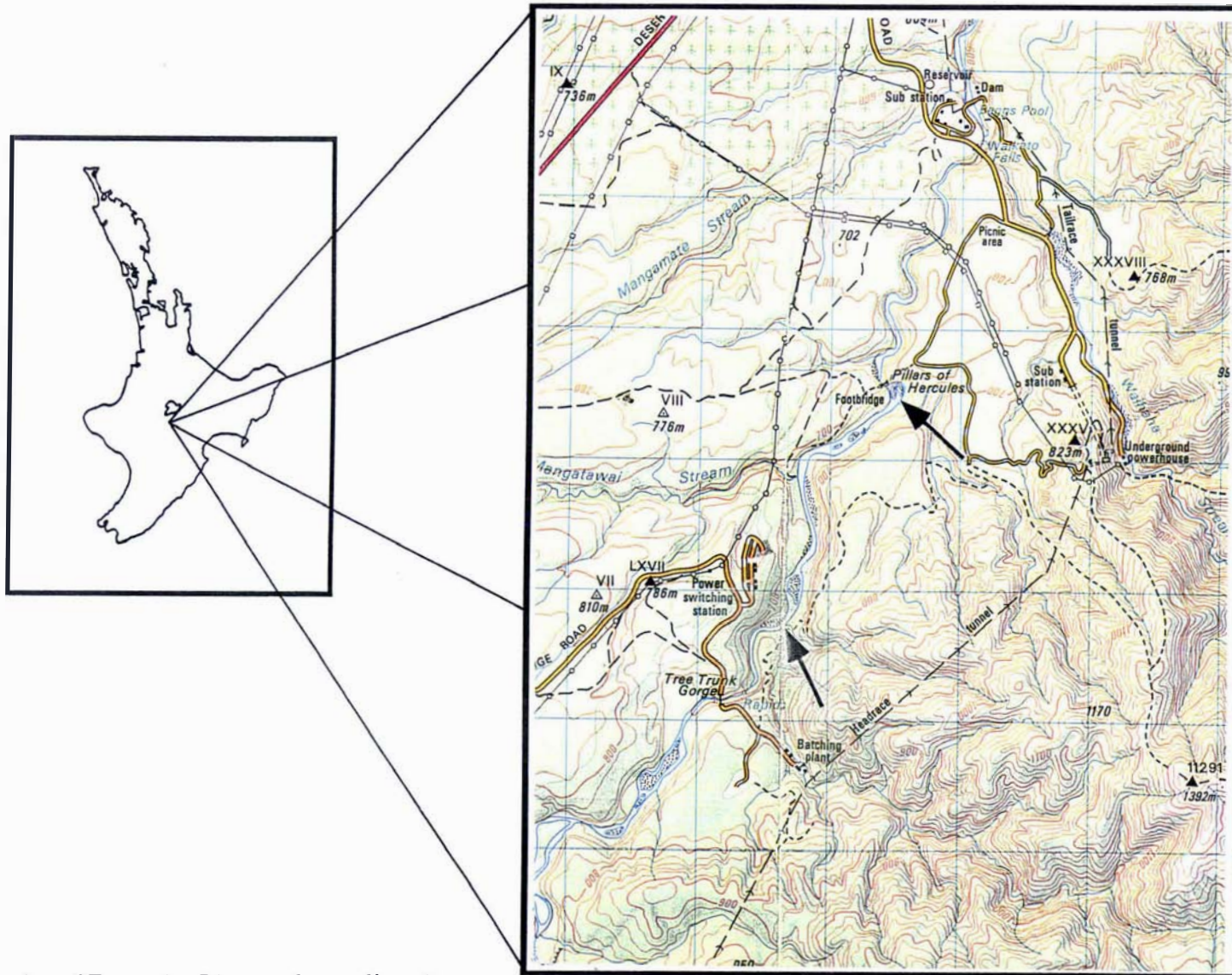


Fig. 3. 1 Location of Tongariro River and sampling sites.

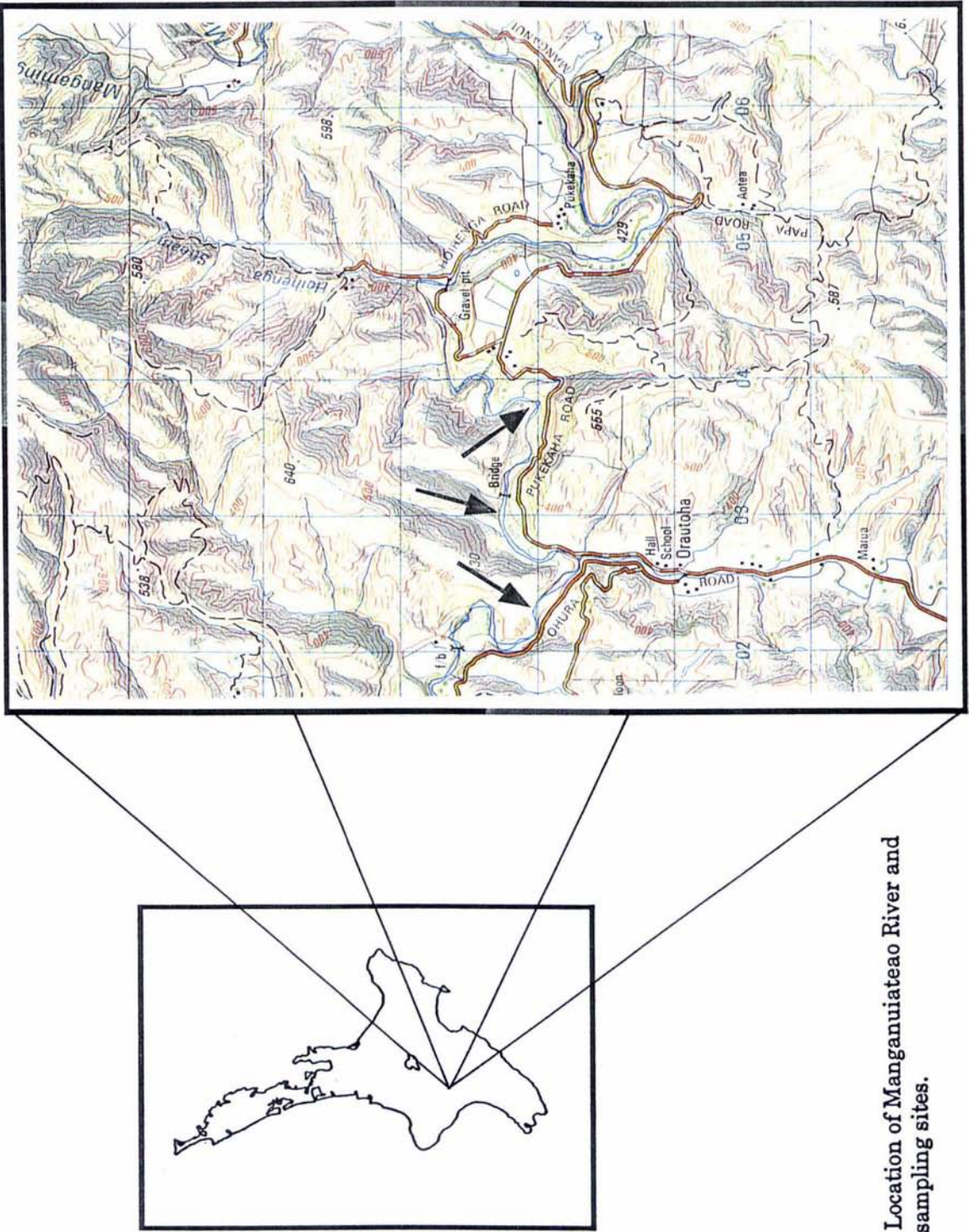


Fig. 3. 2 Location of Manganuiateao River and sampling sites.

Ikawetea River

Ikawetea River originates in the Northern Ruahine Ranges and flows north to join Taruarau River and ultimately Ngaruroro River (Fig. 3.3). The river drains two large valleys, the Ikawetea and the Apis which combined have a catchment area of approximately 80 km². The lower valley slopes are dominated by red beech (*Nothofagus fusca*), the upper slopes by mountain beech (*N. cliffortioides*) and the open tops by leather wood scrub (*Olearia colensoi*) and tussock (*Chionochloa* sp.). The headwaters are relatively devoid of riparian vegetation other than tussock.

The stream bed is composed of a mixture of cobble and gravel-sized material with outcrops of bed rock prominent in upper gorge sections. Mean annual flow was estimated (based on stream width x depth x velocity estimates) to be 0.5 m³s⁻¹ with the stream's flow pattern being punctuated throughout the year by high flow events. A waterfall of approximately 20 m height is situated in the middle section of the river (S 39° 35' 08" E 176° 12' 05").

Benthic, faecal and trout samples were collected from a total of six sites, three sites below the falls and three sites above. The below-fall sites were spaced approximately 1.5 km apart with the first being 300 m downstream of the falls. The first of the three upstream sites was located approximately 100 m above the falls. The second upstream site was approximately 2 kms upstream while the third was 3.5 kms above the falls and 100 m downstream of Rockslide Bivouac (S 39° 37' 03" E 176° 13' 07").

Thirteen blue ducks were recorded between the lower and upper benthic macroinvertebrate sampling sites on the Lower Ikawetea and Apis Rivers during the 1991/92 data collection period. This equates to a density of 1.9 birds per km of river. From visual counts of adult trout in Ikawetea River below the waterfall I estimated trout density to be in the order of 1-2 fish per pool.

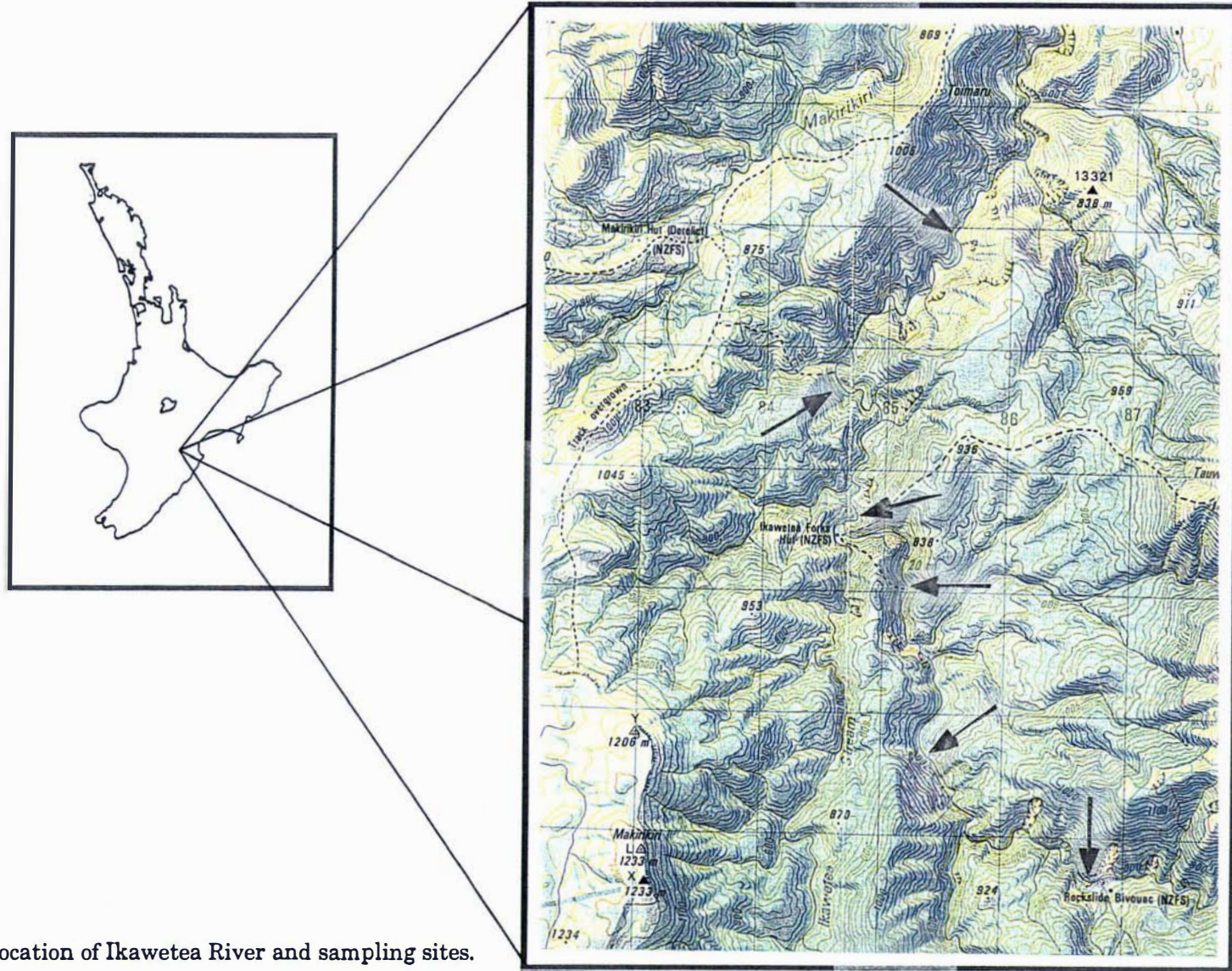


Fig. 3. 3. Location of Ikawetea River and sampling sites.

Makaroro River

Makaroro River, like Ikawetea, originates in the Northern Ruahine Ranges and drains a catchment of approximately 67 km² (Fig. 3.4). The vegetation of the catchment is much the same as that of Ikawetea. The upper reaches of the river flow in a southerly direction before flowing west to join Waipawa River. The stream has a substrate composed predominantly of cobble and gravel-sized material. I estimated the mean annual flow to be in the order of 0.5 m³s⁻¹. A waterfall of approximately 10 metres height is located in the middle section of the river (S 39° 40' 06" E 176° 14' 01").

I collected benthic, faecal and trout samples from three sites below the waterfall and benthic and faecal samples from three sites above the waterfall. Benthic sample collection sites were spaced at approximately 1 km intervals both above and below the falls.

Eight blue ducks were counted between the upper and lower macroinvertebrate sampling sites in 1991/92 equating to a density of 1.6 birds per km of river. The smaller size of trout occurring in Makaroro River made visual trout counts less accurate and the highest density of trout recorded was 0.75 fish per pool.

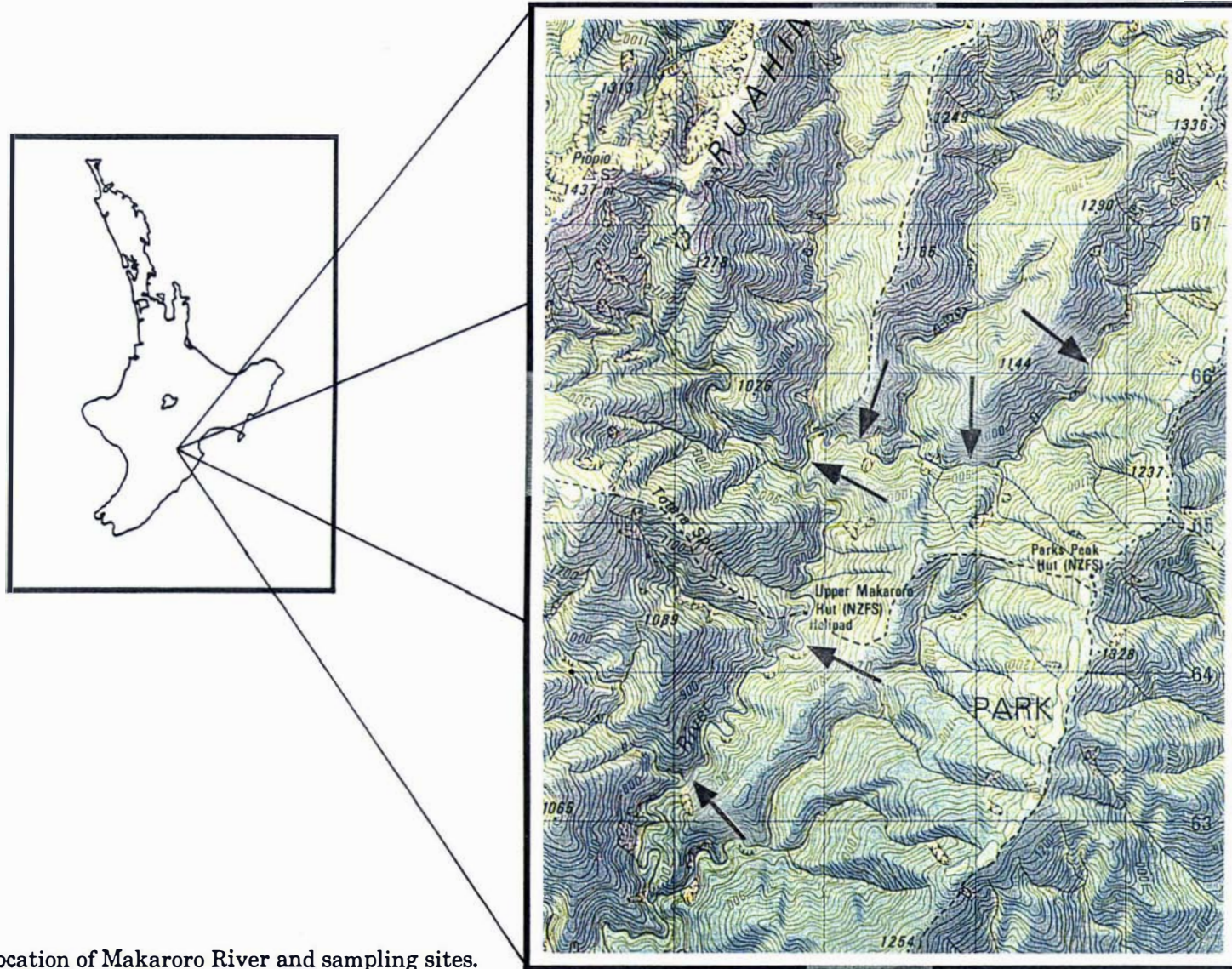


Fig. 3. 4. Location of Makaroro River and sampling sites.

3. 2. 2 Sampling of benthic macroinvertebrate fauna

The macroinvertebrate fauna samples were collected from riffles as blue duck preferentially hunt in such habitat (Veltman & Williams 1990). At each sampling site, 3 x 20 second kick samples were collected (Plate 3. 1). Kick sampling involved placing a hand-held net fitted with 500µm nylon mesh downstream of the site to be sampled. An area of substrate of approximately 0.3 m² was then vigorously agitated using the feet resulting in macroinvertebrates being washed downstream into the net. Macroinvertebrates were placed in 70% ethanol for later sorting, identification and enumeration. Invertebrates were examined using a Zeiss stereoscopic microscope (mag. 10-40x) and identified using the key of Winterbourn & Gregson (1989). Terrestrial invertebrate prey were grouped together in a single category.

3. 2. 3 Blue Duck diets from droppings

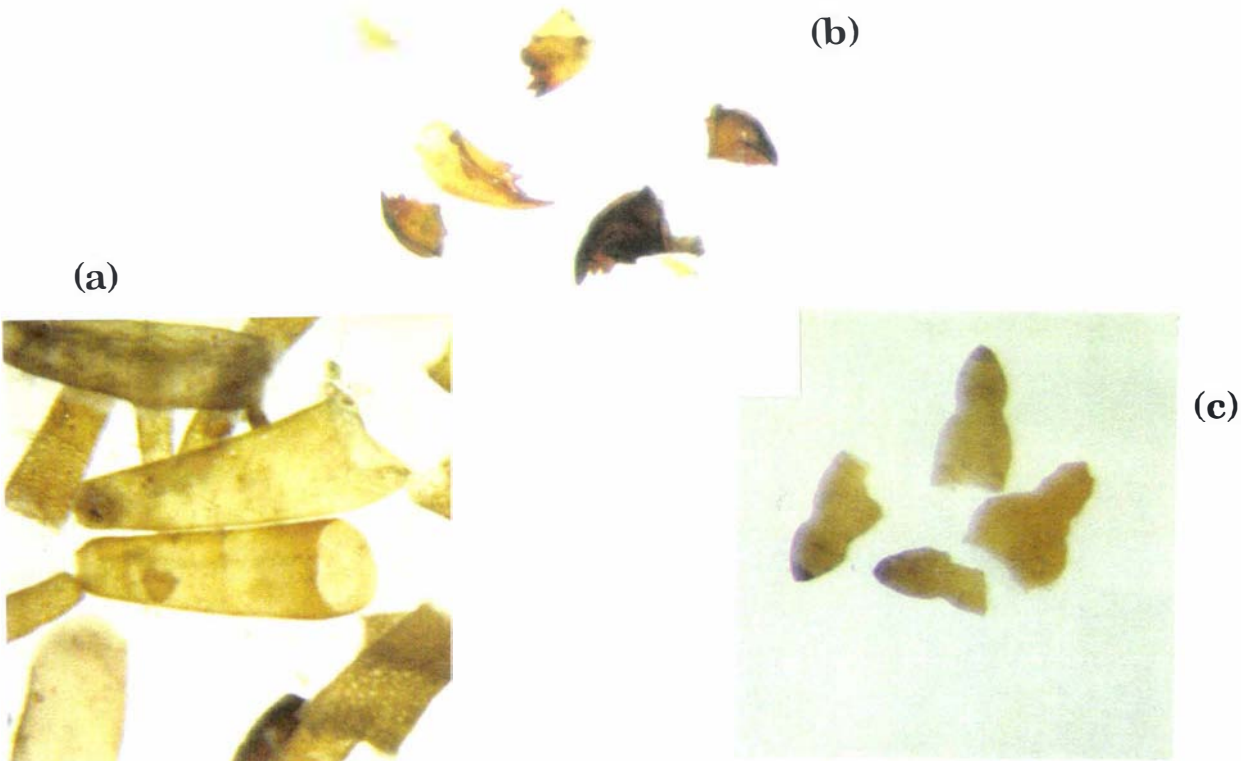
Whenever possible, 5 blue duck droppings were collected from the river margin in the immediate vicinity of the macroinvertebrate sampling sites on the Tongariro River and Manganuiateao River. Due to the irregular distribution of birds and their faeces, droppings from the Ikawetea and Makaroro Rivers were collected between the bottom and top macroinvertebrate sampling sites, both above and below each river's waterfall. Samples collected above and below the waterfalls were kept separate for later analysis of diet composition.

In the laboratory each faecal sample was suspended in distilled water and agitated using a magnetic stirrer to loosen the macroinvertebrate remains. Due to the sclerotised nature of the aquatic insect body parts, fragments of insects eaten could be identified even after passage through the digestive tracts of ducks (Plate. 3. 2). To obtain an unbiased fraction of approximately 1000 insect fragments from each dropping for microscopic analysis the resulting suspension was sub-sampled using a Folsom plankton-splitter (Longhurst & Seibert 1967). Not all fragments could be identified so "key fragments" which consistently travelled through the digestive tract undamaged and were easily distinguishable were counted. Key fragments consisted of mandibles and clypeus although often complete or part heads of consumed macroinvertebrates

Plate 3. 1 Collecting a kick sample of benthic macroinvertebrates from Ikawetea River.



Plate 3. 2 Examples of "Key fragments" extracted from blue duck droppings (a) caddisfly case (b) mandibles (c) clypeus.



remained intact, easing identification. This was particularly so for several Diptera taxa (ie, Chironomidae, *Aphrophila* sp.). Caddisfly cases also passed through the birds relatively undamaged and this assisted in the positive identification of consumed caddisfly prey. Terminal segments of Elmidae larvae were also used in identification.

As samples contained multiple fragments of the same individual macroinvertebrate, formulae were employed to calculate the number of individuals in each prey category in a sample (Table 3.1). Prey identified in the droppings of blue ducks were divided into twenty categories. These prey categories reflected taxonomically workable resolution and thus categories often contained several taxa.

The diet was examined in terms of the number of prey consumed and in terms of the dry weight each prey type represented. Dry weight for different prey was calculated by measuring either the body length (ie, case length) or head widths of a proportion of consumed prey equal to that occurring numerically in the diet and applying the predictive equations presented in Chapter 2.

3. 2. 4 Trout diet from stomach samples

A pulsed DC backpack electro-shocker was used to collect trout from the Tongariro and Manganuiateao Rivers. Electro-fishing was conducted in close proximity to macroinvertebrate collection sites and took place after the collection of macroinvertebrate samples because electro-fishing has been shown to affect aquatic macroinvertebrates (Fowles 1975). Angling and netting were used to collect trout from Ikawetea and Makaroro Rivers due to the remoteness of the location and the associated problems of transporting the necessary gear.

Trout diet was quantified by examining stomach contents. Unlike the prey consumed by blue ducks, the macroinvertebrates in the stomachs of trout were usually intact. This meant that all prey could be measured although where large numbers of macroinvertebrates had been consumed a proportion based on the numeric occurrence of each prey class was measured. Aquatic prey were classified using the same categories as those used for blue ducks (Table 3. 1). Stomach contents were assessed using three methods, the numerical abundance of each prey, dry weight

Table 3. 1 The taxa identified in blue duck droppings and the formulae used for converting numbers of fragments to numbers of individuals. Head (H) refers to a whole head having both mandibles (M) and with its clypeus (C) present. T indicates terminal segment and WC the whole case of Trichoptera.

TAXON	FORMULA FOR ONE INDIVIDUAL
Ephemeroptera	
<i>Deleatidium / Austroclima</i>	$(M/2)+H$
<i>Coloburiscus</i>	$(M/2)+H$
<i>Nesameletus</i>	$(M/2)+H$
Trichoptera	
<i>Aoteapsyche</i>	$((M/2+C)/2)+H$
Hydrobiosidae	$((M/2+C)/2)+H$
<i>Beraeoptera</i>	$((M/2+C)/2)+H$
<i>Pycnocentria</i>	$((M/2+C)/2)+H$
<i>Confluens</i>	$((M/2+C)/2)+H$
<i>Pycnocentrodes</i>	$((M/2+C)/2)+H$
<i>Olinga</i>	$((M/2+C)/2)+H$
<i>Paroxyethira</i>	WC
<i>Oxyethira</i>	WC
<i>Helicopsyche</i>	$((M/2+C)/2)+H$
general cased	WC
Plecoptera	
<i>Austroperla</i>	$((M/2)+T)/2$
<i>Megaleptoperla</i>	$((M/2)+T)/2$
<i>Zelandoperla</i> and others	$((M/2)+T)/2$
Diptera	
Chironomidae	$((M/2+C)/2)+H$
Muscidae	$(M +T)/2$
<i>Aphrophila</i>	$((M/2+C)/2)+H$
Megaloptera	
<i>Archichauliodes</i>	$((M/2+C)/2)+H$
Coleoptera	
Elmidae	$(H+T)/2$
Gastropoda	
Mollusca	Radula
Other Aquatic	H
Terrestrial	H

of each prey and occurrence (ie, presence or absence) of each prey. Dry weight for the different prey consumed was estimated using the equations presented in Chapter 2.

3. 2. 5 Sampling timetable

Samples were collected from each river approximately every 2 months during 1991 and 1992. Due to poor weather and flooding in 1991, sampling in some months had to be postponed either to the following month or to the same month in 1992.

3. 2. 6 Data analyses

To assess the similarity in the composition of the benthic communities in the four rivers and to determine if trout presence in Ikawetea and Makaroro Rivers resulted in differences in the composition of the macroinvertebrate communities occurring above and below the falls canonical discriminant analyses were preformed. These analyses were performed on log transformed (x+1) abundance data with uncommon taxa (< 5 individuals) being excluded from the analyses.

The diets of both blue ducks and trout were examined in terms of numbers of each prey type consumed, the estimated dry weight of each prey type and the occurrence (ie, presence / absence) of a prey type. Hyslop (1980) reviewed diet analysis and concluded that the best method of establishing the importance of a particular prey in the diet was to measure all three parameters. I therefore used Pinkas *et al.*'s (1971) IRI (Index of Relative Importance) as it combines all three data types.

The importance of the more common prey in the diet of each species was assessed by using the relative importance index (IRI) (Pinkas *et al.* 1971). The equation:

$$IRI = (N + W)F \quad \text{(Pinkas *et al.* 1971)}$$

incorporates percentage data on the number of individuals (N), dry weight (W), and frequency of occurrence (F) of prey consumed. Values for this index ranged from 0, when a taxon did not occur in the diet, to 20,000 when one taxon comprised the entire stomach content of a trout.

The relationship between the relative importance (IRI) of prey in the diet of trout and blue duck was assessed by Spearman rank correlation (r_s) analysis. In addition, the IRIs of blue ducks living above and below the two waterfalls were also compared using the same statistical procedure.

To assess how blue ducks and trout used the available aquatic macroinvertebrate resources, prey selectivity by the two predators was examined by comparing the dry weights of certain taxa in the benthos with their dry weights in the diets using analysis of variance (ANOVA). Positive and negative coefficients were used to indicate prey selection and avoidance. This ANOVA approach was also used to test the hypotheses that prey selection by the two insectivores differed amongst seasons. For Makaroro and Ikawetea Rivers trout and blue duck selectivity patterns were analysed separately due to the data not being orthogonal in nature (no trout above the falls).

Diet overlap between fish and ducks was calculated using Schoener's (1970) equation:

$$\alpha = 1 - 0.5 \left(\sum_{i=1}^n |P_{xi} - P_{yi}| \right) \quad (\text{Schoener 1970})$$

in which P_{xi} is the proportion of prey type i in the diet of species x , P_{yi} is the proportion of prey type i in the diet of species y , and n is the number of prey types. Overlap is generally considered to be biologically important when a value in excess of 0.60 is obtained (Zaret & Rand 1971). As Schoener's equation has been widely used in similar studies of diet overlap, it was used in the present work to allow comparison and discussion.

To test the hypothesis that blue ducks and trout consume prey of similar mean body length and to compare the body lengths of consumed prey with that occurring in the benthos, mean body length data were statistically compared by analysis of variance (ANOVA) using an orthogonal procedure. All analyses were conducted on log-transformed data ($x+1$) and statistical significance was set at $p \leq 0.05$.

3.3 Results

3.3.1 Benthic macroinvertebrate fauna in Tongariro and Manganuiateao Rivers

A total of 14,457 benthic macroinvertebrates was collected from Manganuiateao River and 12,923 from Tongariro River. Both rivers had high taxonomic diversity with a total of 46 and 41 taxa being collected from the Tongariro and Manganuiateao Rivers respectively (Table 3.2).

The macroinvertebrate fauna in Tongariro River was dominated by Diptera (45-98%) throughout the year (Fig. 3.5). Chironomidae comprised over 80% of all Diptera collected on each sampling occasion while *Aphrophila neozelandica* dominated the remaining 20%. Trichoptera, in particular the purse caddis *Paroxyethira* sp. and *Oxyethira albiceps* were also abundant, with large numbers of these algae piercers occurring during November, when filamentous algal growth was prolific. Ephemeroptera and Plecoptera species were present on all sampling occasions. Ephemeroptera were most prevalent in April, comprising 18% of the benthic macroinvertebrate community. Plecoptera were also most abundant in April making almost 10% of the sample.

Trichoptera larvae were the most common animals (41-70%) collected from the Manganuiateao River benthos (Fig. 3.6). The cased Trichoptera *Beraeoptera roria* and *Pycnocentroides* sp. along with Hydrobiosidae and the net-spinner *Aoteapsyche* sp. were the most abundant caddisflies. Ephemeroptera were also relatively numerous (15 - 38%), particularly species of the Leptophlebiidae mayfly, *Deleatidium* sp. Plecoptera were collected in samples on all six sampling occasions but only in July did they comprise more than 10% of the community. No other macroinvertebrate taxon comprised more than 10% of the total macroinvertebrate fauna collected in any month.

Table 3. 2 List of benthic macroinvertebrate taxa collected from the Manganuiateao (Mang.), Tongariro (Tong.), Ikawetea (Ik.) and Makaroro (Mak.) Rivers. X denotes presence.

Phylum: Arthropoda									
Class: Insecta	River				River				
	Mang.	Tong.	Ik.	Mak.	Mang.	Tong.	Ik.	Mak.	
Order: Ephemeroptera									
<i>Coloburiscus humeralis</i>	X	X	X	X	<i>Costachorema</i> sp.	X	X	X	X
<i>Deleatidium</i> sp.	X	X	X	X	<i>Psilochorema</i> sp.	X	X	X	X
<i>Nesameletus</i> sp.	X	X	X	X	<i>Plectrocnemia</i> sp.	X	X	X	X
<i>Oniscigaster wakefieldi</i>		X		X	<i>Polyplectropus</i> sp.	X		X	
<i>Ameletopsis perscitus</i>	X	X	X	X	<i>Helicopsyche</i> sp.	X	X	X	X
<i>Zephlebia</i> sp.	X	X	X	X	<i>Oeconesus</i> sp.		X		
<i>Neozephlebia</i> sp.	X		X		<i>Diplectrona</i> sp.			X	X
<i>Mauiulus luma</i>	X		X	X	<i>Philorheithrus</i> sp.				X
<i>Austroclima</i> sp.	X	X	X	X	Order: Diptera				
<i>Acanthophlebia cruentata</i>	X		X	X	Chironomidae	X	X	X	X
Order: Plecoptera					Blephariceridae	X		X	X
<i>Zelandobius</i> sp.	X	X	X	X	Tanyderidae	X		X	
<i>Zelandoperla</i> sp.	X	X	X	X	Muscidae	X	X	X	X
<i>Stenoperla prasina</i>	X	X	X	X	Eriopterini	X	X	X	X
<i>Austroperla cyrene</i>	X	X	X	X	Culicidae	X		X	
<i>Megaleptoperla</i> sp.	X	X	X	X	<i>Aphrophila neozelandica</i>	X	X	X	X
<i>Acroperla</i> sp.	X	X	X	X	Tipulidae	X	X	X	X
Order: Trichoptera					<i>Austrosimulium</i> sp.	X	X	X	X
<i>Olinga feredayi</i>	X	X	X	X	Nothodixa			X	
<i>Beraeoptera roria</i>	X	X	X	X	Ceratopogonidae			X	X
<i>Confluens hamiltoni</i>	X				Order: Megaloptera				
<i>Pycnocentria</i> sp.	X	X	X	X	<i>Archichauliodes diversus</i>	X	X	X	X
<i>Triplectides</i> sp.	X	X			Order: Coleoptera				
<i>Zelolessica cheira</i>	X	X	X	X	Elmidae	X	X	X	X
<i>Oxyethira albiceps</i>	X	X			Hydraenidae	X	X	X	X
<i>Paroxyethira</i> sp.		X			Adult Coleoptera	X	X	X	
<i>Orthopsyche</i> sp.	X	X	X	X					
<i>Aoteapsyche</i> sp.	X	X	X	X	Phylum: Mollusca				
<i>Pycnocentrella eruensis</i>		X	X	X	Class: Gastropoda				
<i>Neurochorema</i> sp.	X	X	X		<i>Potamopyrgus antipodarum</i>	X	X	X	X
<i>Hydrobiosis</i> sp.	X	X	X	X	<i>Latia neritoides</i>	X			

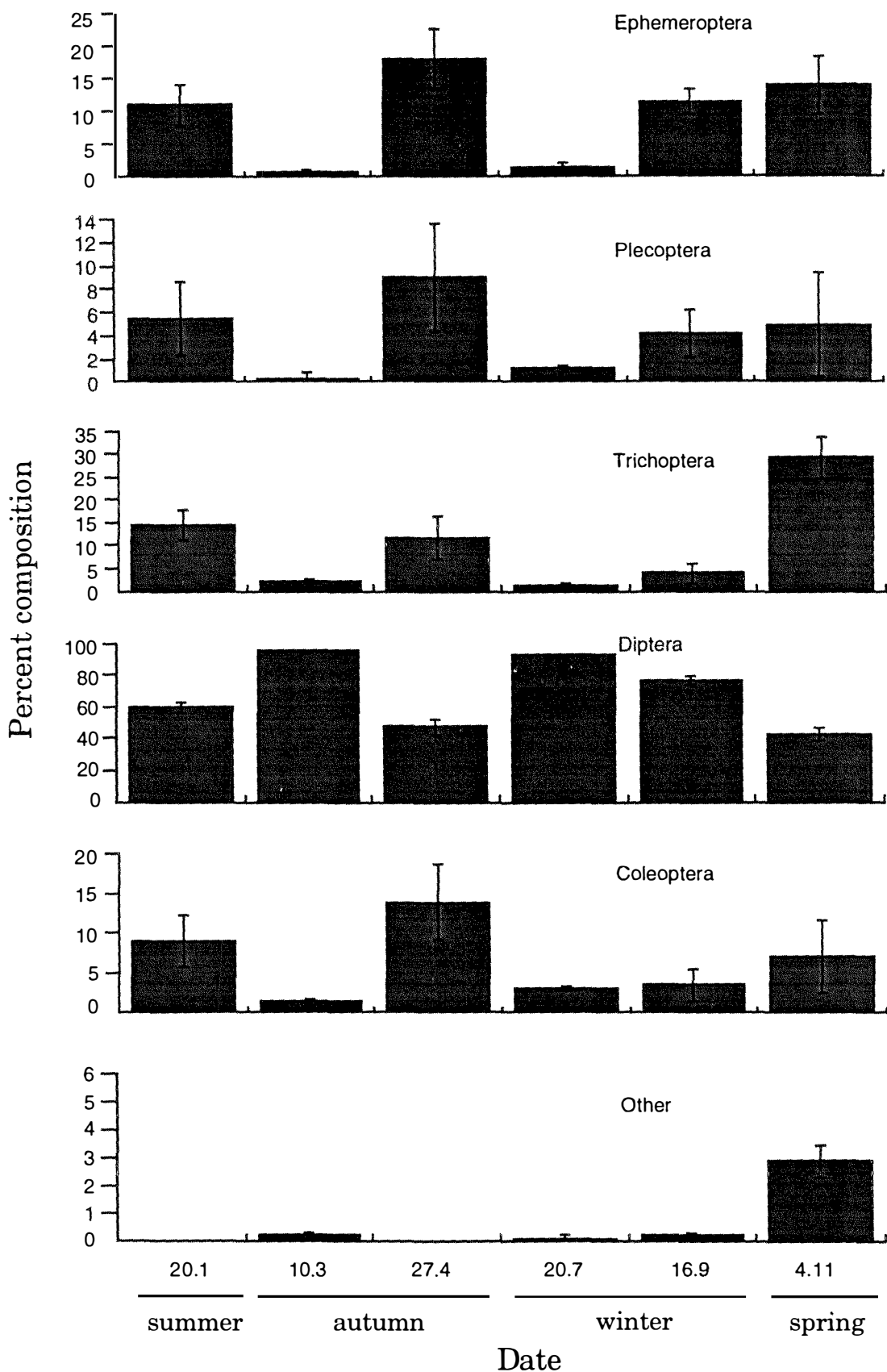


Fig. 3. 5 Mean (± 1 SE) relative numerical abundance of macroinvertebrate orders in samples collected from Tongariro River on sampling occasions (20.1 indicates 20 January). Note that scales on vertical axes vary between plots.

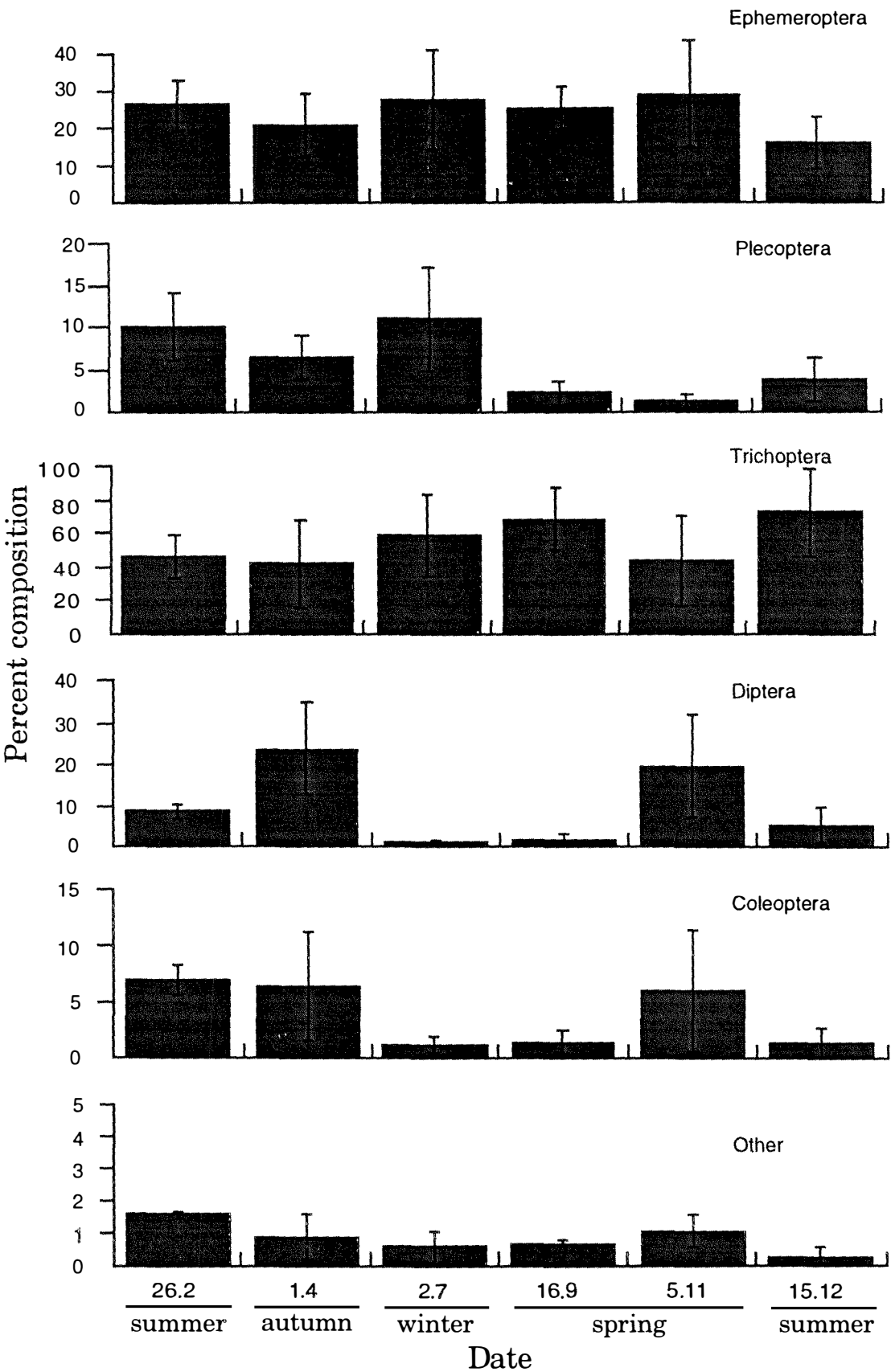


Fig. 3. 6 Mean (± 1 SE) relative abundances of macroinvertebrate orders in samples collected from Manganuiateao River on the sampling occasions (26.2 indicates 26 February). Note that scales on vertical axes vary between plots.

The size distributions of the macroinvertebrates collected from each river were examined. Mean size of all macroinvertebrates collected from Manganuiateao River was 4.6 ± 0.07 mm (median 3.3 mm) and 4.7 ± 0.05 mm (median 3.8 mm) from Tongariro River (Fig. 3.7).

3. 3. 2 Benthic macroinvertebrate fauna in Makaroro and Ikawetea Rivers

A total of 12,058 benthic macroinvertebrates was collected from Ikawetea River and 7,779 from Makaroro River. A total of 46 and 41 taxa was collected from Ikawetea and Makaroro Rivers respectively (Table 3.2). On both rivers all but one macroinvertebrate species recorded below the falls were also recorded above and *vice versa*. The exception was *Oniscigaster wakefieldi* which was collected only from sites below the Makaroro falls. Ephemeroptera, Plecoptera and Trichoptera dominated the macroinvertebrate communities of both rivers throughout the year above and below the waterfalls (Fig. 3.8 and 3.9). The community assemblages of both rivers were similar with *Deleatidium* sp. being the prominent Ephemeroptera, *Olinga feredayi* and *Beraeoptera roria* the most abundant Trichoptera, and *Zelandoperla* sp. the common Plecoptera. Diptera, particularly *Aphrophila neozelandica* and Chironomidae were collected from both rivers on all sampling occasions but only in small numbers (< 10% of sample).

Canonical discriminant analysis showed that the macroinvertebrate communities occurring above and below Ikawetea River waterfall did differ significantly ($p = 0.027$). The same pattern was not present for Makaroro River ($p = 0.528$). Examination of the discriminant analysis loading factors did however indicate that the predatory stonefly *Stenoperla prasina* was consistently more abundant above the falls on both rivers.

The distributions of macroinvertebrate body lengths obtained in the benthic samples above and below the waterfalls are presented in Fig. 3.10. The mean body lengths of macroinvertebrates collected above and below the two waterfalls are presented in Table 3.3. No significant differences were found to exist between the mean length of

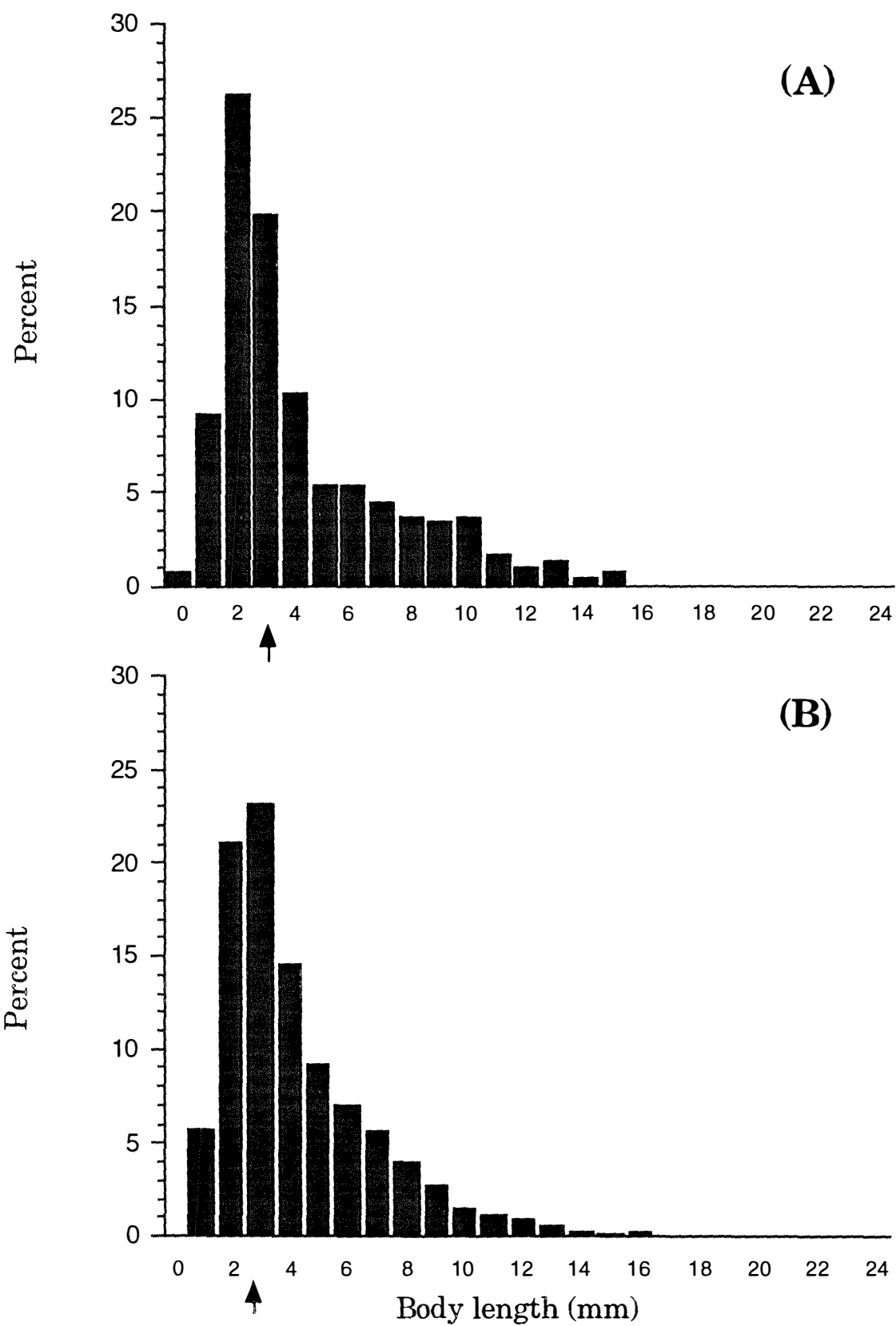


Fig. 3. 7 Body length distributions of macroinvertebrates collected from Manguiateao (A) and Tongariro Rivers (B). Arrows mark the median size value.

macroinvertebrates collected in each river above and below their waterfalls (Ikawetea: $t_{3926}=0.5097$ $p=0.554$; Makaroro: $t_{3868}=0.7601$ $p=0.447$).

Table 3. 3 Comparison of the mean body length (mm) of benthic macroinvertebrates collected from Ikawetea and Makaroro Rivers above and below their respective waterfalls.

River	Location	Mean length (mm)	± 1 SE
Ikawetea	Below waterfall	5.35	0.06
Ikawetea	Above waterfall	5.32	0.07
Makaroro	Below waterfall	5.64	0.07
Makaroro	Above waterfall	5.69	0.07

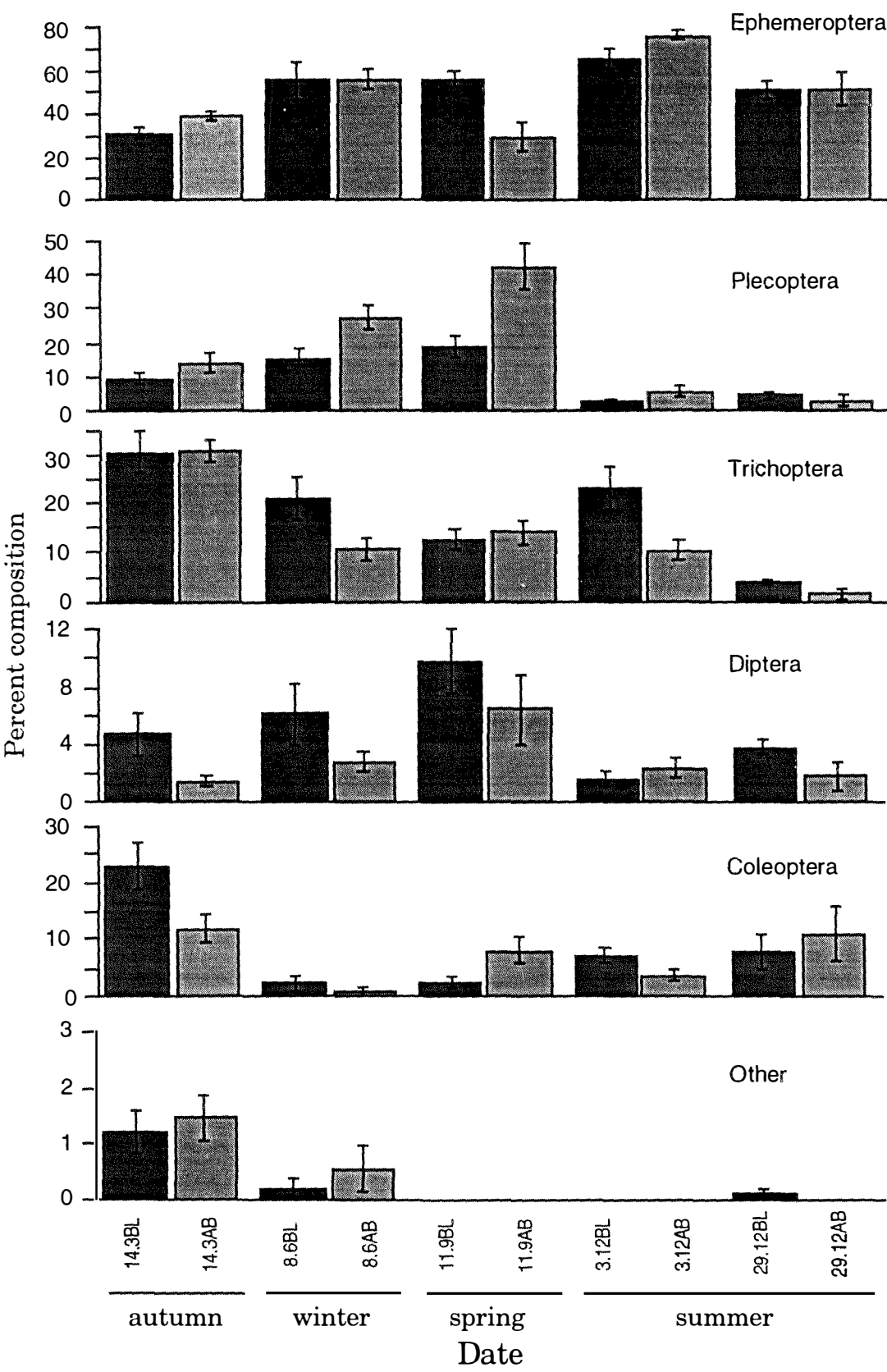


Fig. 3. 8 Mean (\pm SE) relative abundances of macroinvertebrate orders recorded in benthic samples collected from Ikawetea River on the sampling occasions. Below waterfall samples are indicated by BL while samples collected from sites above the falls are denoted by AB. Note that scales on vertical axes vary between plots.

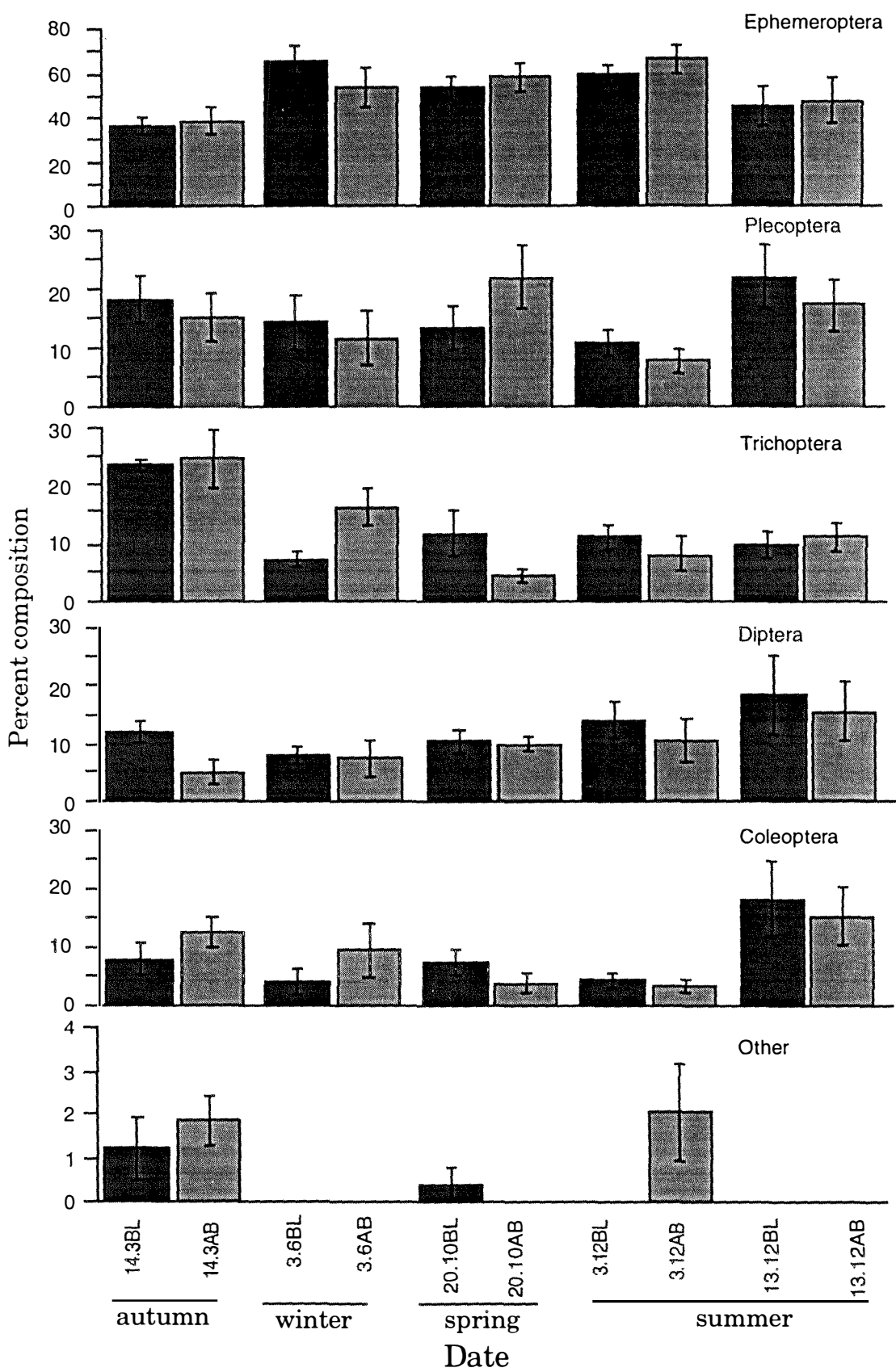


Fig. 3. 9 Mean (± 1 SE) relative numeric abundance of macroinvertebrate orders recorded in benthic samples collected from Makaroro River on the sampling occasions. Below waterfall samples are indicated by BL while samples collected from sites above the falls are denoted by AB. Note that scales on vertical axes vary between plots.

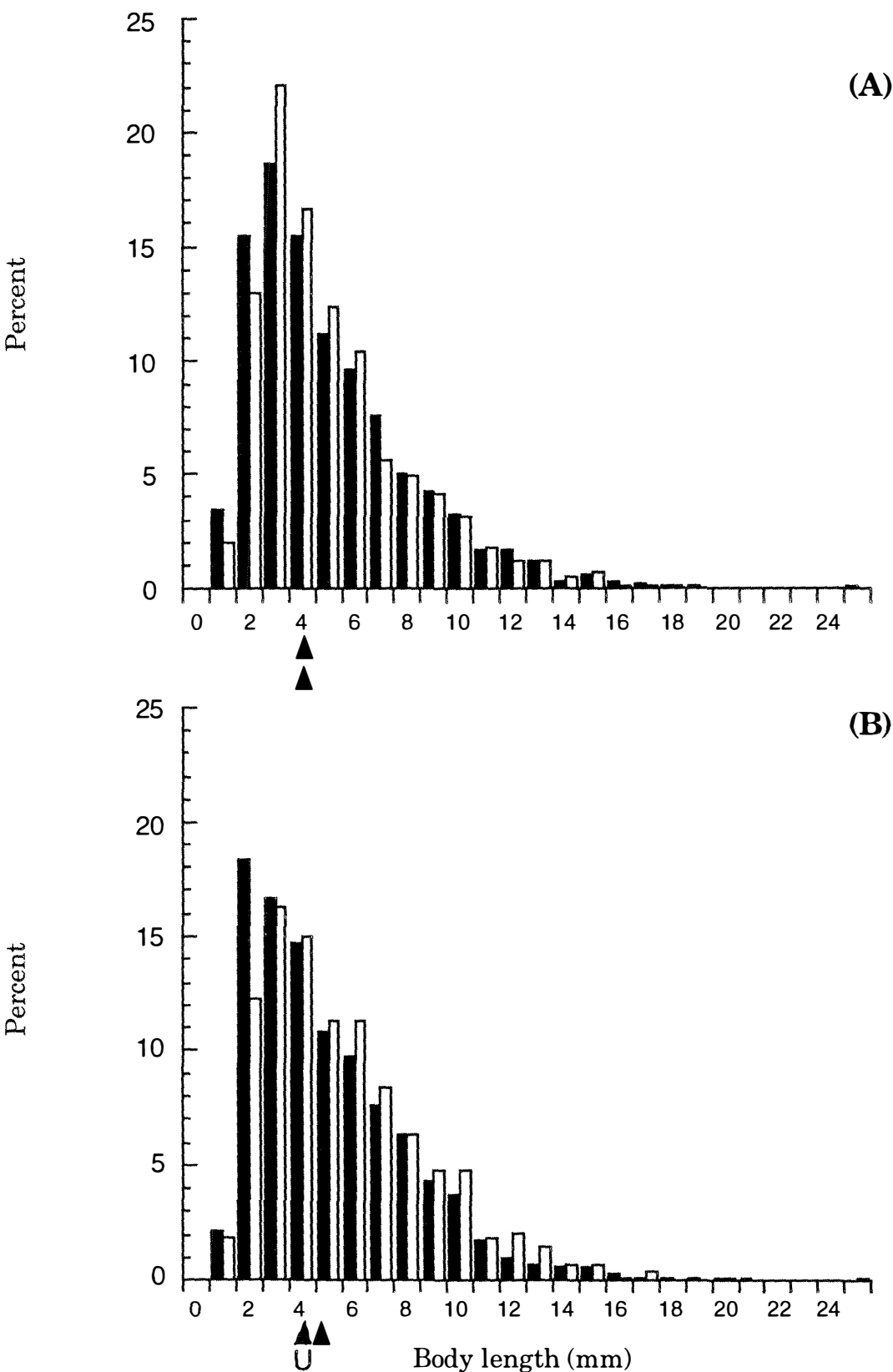


Fig. 3. 10 Body length distribution plots for macroinvertebrates collected from Ikaweteta (A) and Makaroro (B) Rivers. Shaded bars represent macroinvertebrate data for above the waterfalls while clear bars give below-waterfall data. Arrows (U = upstream of falls) indicate the median value.

3. 3. 3 Trout characteristics in Tongariro and Manganuiateao Rivers

Trout were collected from the Tongariro and Manganuiateao Rivers on all sampling occasions (Table 3.4). Only rainbow trout were collected from Tongariro River while both rainbow and brown trout were present in Manganuiateao River samples. The majority of the fish collected from both rivers were juvenile with most having clear parr markings along their flanks.

The mean fork length of the trout collected from Manganuiateao River was 90.4 ± 3.1 mm and 112.6 ± 6.9 mm from Tongariro River. A significant difference existed between the mean fork length of trout collected from the two rivers ($t_2=2.95$, $p = 0.004$). It was not possible to sex the trout as most were juvenile. The mean fork lengths of brown and rainbow trout collected from Manganuiateao River were similar (rainbow 90.6 ± 4.1 mm; brown 87.6 ± 5.6 mm).

Table 3. 4 Number of trout stomachs collected per season from Manganuiateao and Tongariro Rivers.

River	Season			
	Summer	Autumn	Winter	Spring
Manganuiateao	22	13	7	19
Tongariro	15	37	13	39

3. 3. 4 Trout diet in Tongariro and Manganuiateao Rivers

Stomach content analysis showed that aquatic macroinvertebrates formed a substantial proportion of the diet of trout inhabiting both rivers, although terrestrial insects and aquatic prey other than macroinvertebrates were also consumed. The number of prey in the trout stomachs varied from 0 to more than 100 items. The composition of trout diets on the different sampling occasions are presented in Appendix B1 in terms of both numbers eaten and the combined dry weight of the different prey groups.

Ephemeroptera, Trichoptera and Diptera accounted for a major proportion of the prey consumed by trout in both rivers. The most

abundant prey consumed by Tongariro River trout were *Deleatidium* sp. nymphs, the net-spinning Trichoptera *Aoteapsyche* sp. and to a lesser degree Hydrobiosidae (Appendix B1). The Plecoptera *Zelandoperla fenestrata* contributed substantially to the trout diet in July (numerically 21.4%; dry weight 22.4%) while Chironomidae were consumed in high numbers (30.6%) during November. However, due to the low dry weight of individual Chironomidae, they made up only 14.4% of the diet in terms of the dry weight proportion during this month. Terrestrial prey were found to be important in the diet of Tongariro River trout throughout the year, consistently comprising 10% or more of the total number of prey consumed.

Trichoptera were also important prey in the diet of Manganuiateao River trout, especially during the first half of the year (Appendix B2). At the latter three sampling occasions Ephemeroptera comprised in excess of 60% of the total number of prey consumed, reaching 88% in November. Unlike trout from Tongariro River, Manganuiateao River trout consumed much smaller numbers of terrestrial prey. Prey composition of the diet of Manganuiateao River trout was also different from that of the Tongariro River fish. Chironomidae along with the purse caddisflies *Oxyethira albiceps* and *Paraoxythira* sp. were consumed in large numbers throughout the year although the mayfly *Deleatidium* sp. dominated diet in terms of dry weight.

The body length distributions of the macroinvertebrates consumed by trout in each river were examined (Fig. 3.11). The mean body length of macroinvertebrates consumed by Tongariro River trout was 6.4 ± 0.3 mm (median 6.1 mm) and was similar to the mean body length of macroinvertebrates prey consumed by Manganuiateao River trout (6.6 ± 0.4 mm; median 7.8).

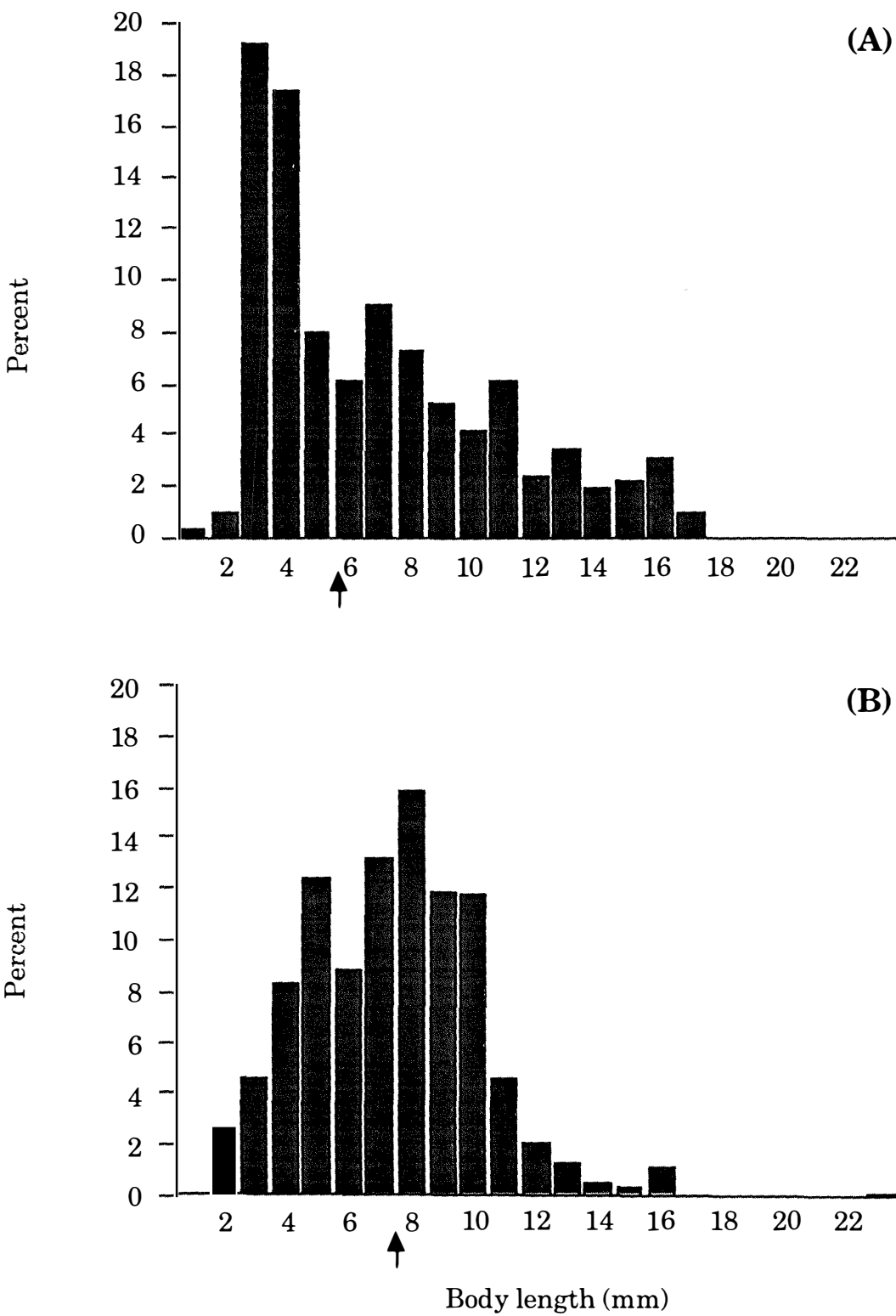


Fig. 3. 11 Frequency distribution of prey body length consumed by Tongariro (A) and Manganuiateao River (B) trout. Arrows indicate median prey body length.

3. 3. 5 Trout characteristics in Ikawetea and Makaroro Rivers

The numbers of trout stomachs collected from the Ikawetea and Makaroro Rivers are presented in Table 3.5. Samples from both rivers were composed of rainbow trout only. Significantly larger ($t_{39} = -13.22$, $p < 0.001$) trout were taken from the Ikawetea than the Makaroro (Ikawetea 547 ± 7.4 mm vs. 186 ± 26.3 mm). There were no significant differences in fork length between the sexes in either river.

Table. 3. 5 Number of trout stomachs collected per season from Makaroro and Ikawetea Rivers.

River	Season			
	Summer	Autumn	Winter	Spring
Makaroro	1	4	5	5
Ikawetea	9	0	1	15

3. 3. 6 Trout diets in Ikawetea and Makaroro Rivers

The stomachs collected from trout captured in both rivers contained between 68 and 1018 aquatic and terrestrial prey items.

The diet of trout taken from Ikawetea River was dominated by *Deleatidium* sp. in September and December while the cased Trichoptera *Olinga feredayi* dominated during March and June (Appendix B5). Other taxa such as the net-spinning Trichoptera, *Aoteapsyche* sp. and Plecoptera, *Zelandoperla* sp. were also abundant at times. With the exception of *Nesameletus* sp. in June, no other aquatic macroinvertebrate comprised more than 10% of the total number of prey consumed on any of the sampling occasions. Unlike the two large central North Island rivers, Chironomidae larvae did not occur in the diet of trout collected from Ikawetea River. Terrestrial prey were recorded in all trout stomachs and made up $73.7 \pm 13.0\%$ of all prey consumed by trout in March. Terrestrial vertebrate prey, namely mice and a gecko were also recorded in trout stomachs collected from the Ikawetea River.

Deleatidium sp. was the most abundant prey in trout from the Makaroro River (Appendix B6). The cased caddisflies *Olinga feredayi* and the Plecoptera *Zelandoperla fenestrata* were also prominent in the trout diet along with the Trichoptera *Beraeoptera roria* and *Pycnocentrodes* sp. However, due to the small dry weight of *Beraeoptera roria* and *Pycnocentrodes* sp. they did not contribute substantially to the dry weight of the diet. The exception was *Beraeoptera roria* in June when it constituted 35.3% .

The mean body length of prey consumed by trout in the two Ruahine rivers differed significantly ($t_{1184} = 8.15$, $p < 0.001$). with the larger Ikawetea trout consuming larger prey (Ikawetea: mean = 8.43 ± 0.18 mm; Makaroro: mean = 7.28 ± 0.13 mm) (Fig. 3.12).

3. 3. 7 Blue duck diets on Tongariro and Manganuiateao Rivers

Blue duck faeces collected from both rivers showed that the birds consumed a wide range of aquatic macroinvertebrates. A total of approximately 15,000 individual prey were identified from the faecal material collected from the two rivers, about 100 items per faecal sample.

The diet of blue ducks within the Tongariro River study area was numerically dominated by Chironomidae larvae (Diptera) on all sampling occasions except April, when the purse cased caddisflies *Oxyethira albiceps* and *Paroxyethira* sp. constituted the bulk of the diet (Appendix B3). Although Chironomidae larvae were numerically dominant for most of the year they did not dominate the diet in terms of dry weight due to their small individual dry weight. Nymphs of the Leptophlebiidae family contributed the greatest dry weight to the ducks' diet. *Aoteapsyche* sp. and *Pycnocentrodes* sp. also contributed substantially to the diet at different times of the year.

On five of the six sampling occasions (February, August, September, November and December) the droppings collected from the Manganuiateao River were dominated by Ephemeroptera and Trichoptera taxa both in terms of total prey eaten and dry weight (Appendix B4). The exception was April when Chironomidae were the most abundant prey in the diet (60%). *Beraeoptera roria* was the most

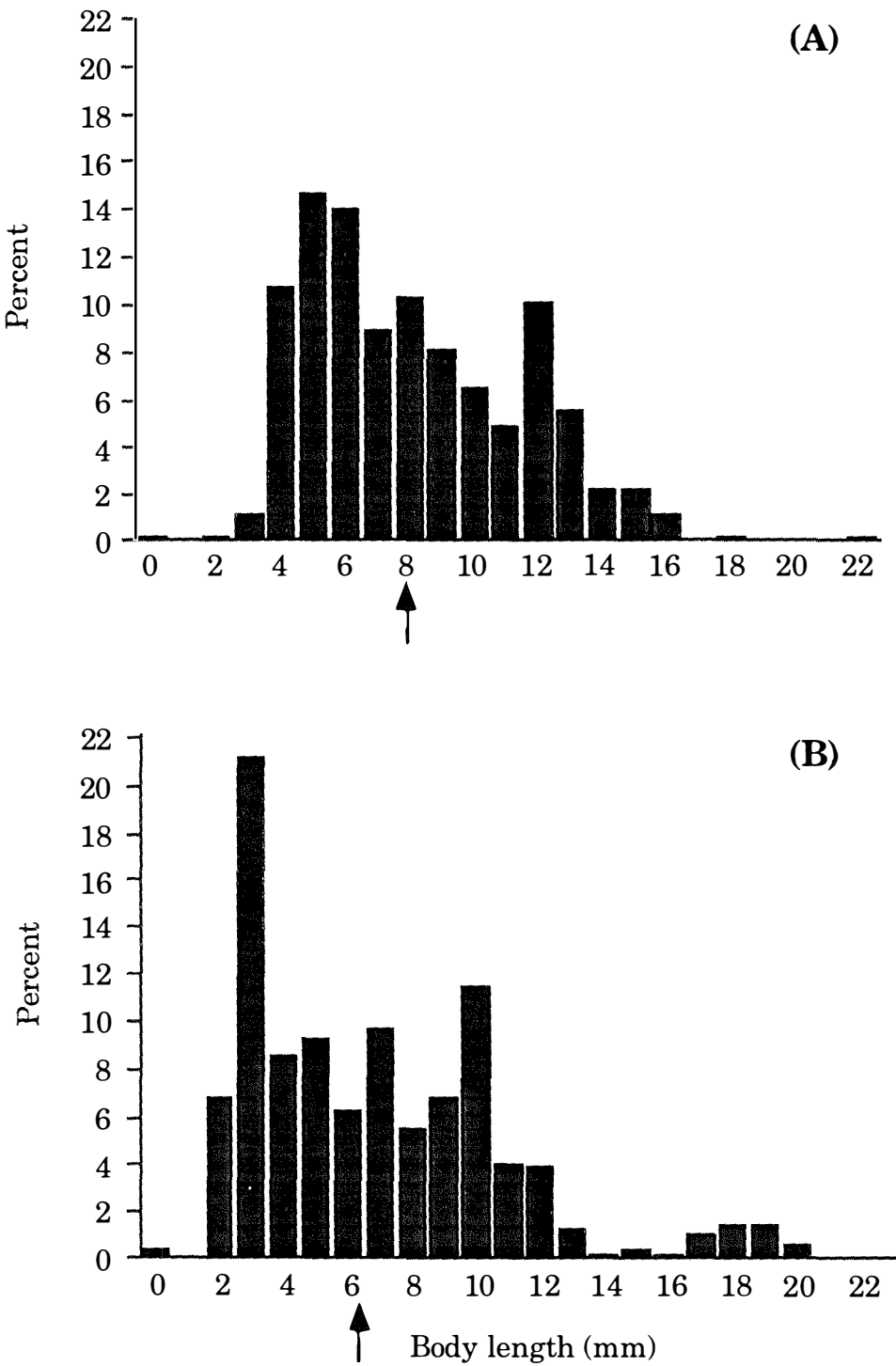


Fig. 3. 12 Frequency distributions of prey body lengths consumed by Ikawetea (A) and Makaroro River (B) trout. Arrows indicate median values.

abundant Trichoptera, but the Hydropsychidae, *Aoteapsyche* sp. and Hydrobiosidae were also abundant in the majority of droppings. In terms of the dry weight composition of the diet Leptophlebiidae larvae made up the largest proportion (34.4 - 57.7%) on all sampling occasions. Despite Chironomidae being numerically dominant in April, the small dry weight of individual Chironomidae meant that this taxon constituted only 18.7% of diet dry weight at that time. Throughout the rest of the year Chironomidae made up no more than 4.0% of diet dry weight.

Prey consumed on both rivers ranged in length from 1.0 to 11.0 mm (Fig. 3.13). The mean sizes of macroinvertebrates eaten by blue duck of Tongariro and Manganuiateao Rivers were 3.7 ± 0.08 mm and 3.8 ± 0.07 mm respectively.

3. 3. 8 Blue duck diets on Ikawetea and Makaroro Rivers

Approximately 8,500 aquatic macroinvertebrates were identified from the droppings collected from Ikawetea River during this study. The relative prey composition of the droppings collected from sections of Ikawetea River above and below the falls on each sampling occasion are presented in Appendix B7. Ephemeroptera belonging to the family Leptophlebiidae and the Trichoptera, *Beraeoptera roria* and *Olinga feredayi* dominated the diet of the birds both in terms of numbers of prey consumed and dry weight composition throughout the year both above and below the falls.

The mean body lengths of prey consumed by blue ducks above the falls was 4.90 ± 0.13 mm while below the mean prey body length was 3.76 ± 0.08 mm (Fig. 3.14). These mean values differed significantly ($t_{720} = -6.39$, $p < 0.001$).

Approximately 5,400 aquatic macroinvertebrates were identified from blue duck droppings collected from Makaroro River. The diet of ducks inhabiting Makaroro River was similar to those of Ikawetea birds, being dominated by Trichoptera both above and below the falls (Appendix B8). Throughout the year the cased caddisfly *Beraeoptera roria* was the most numerically common prey consumed. Both Ephemeroptera and Plecoptera taxa contributed to the diet on all occasions but never composed more than 50% of the total number of prey eaten. However,

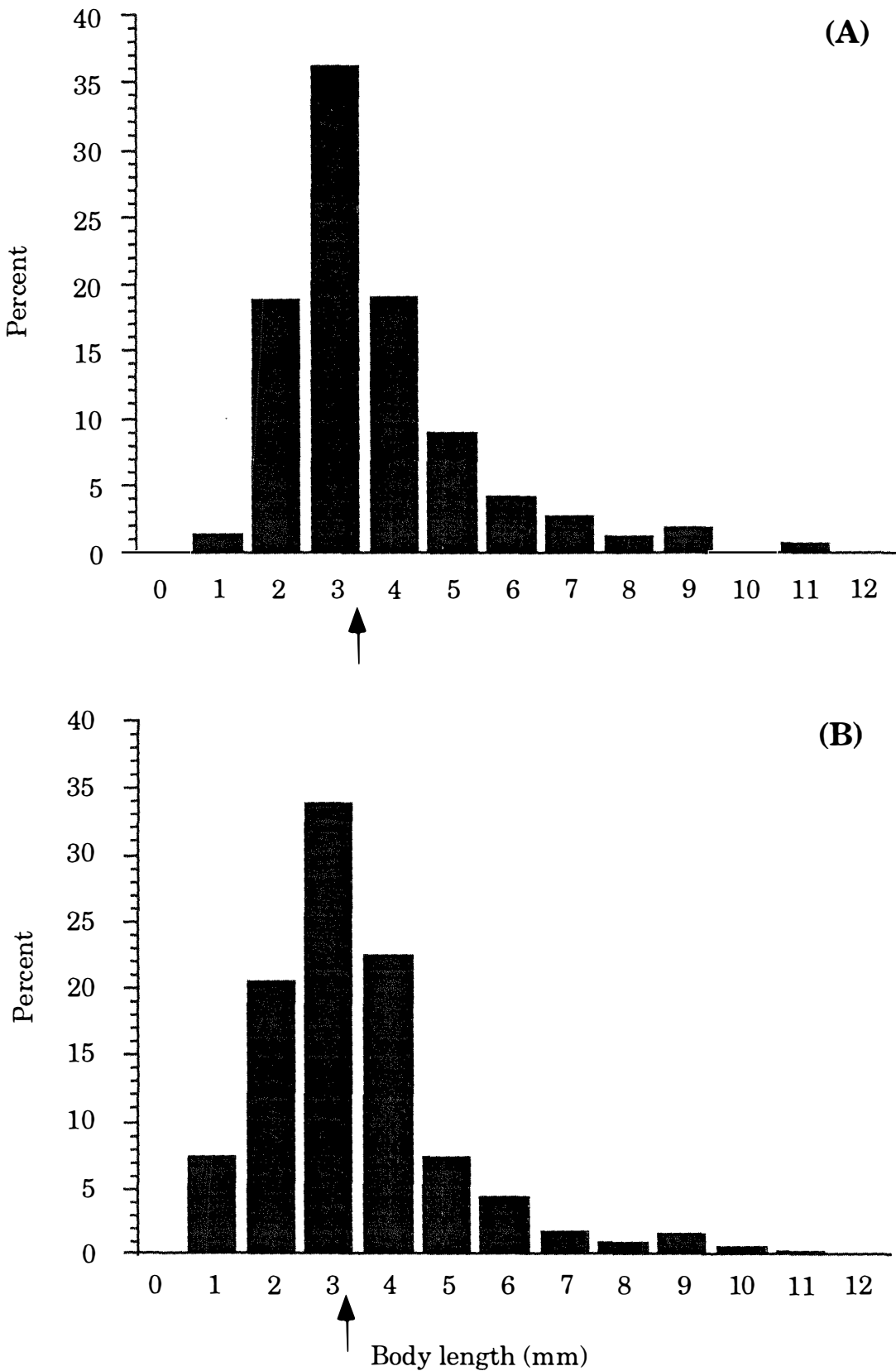


Fig. 3. 13 Frequency distributions of prey body lengths consumed by blue ducks inhabiting Tongariro (A) and Manganuiateao (A) Rivers. Arrows indicate median values.

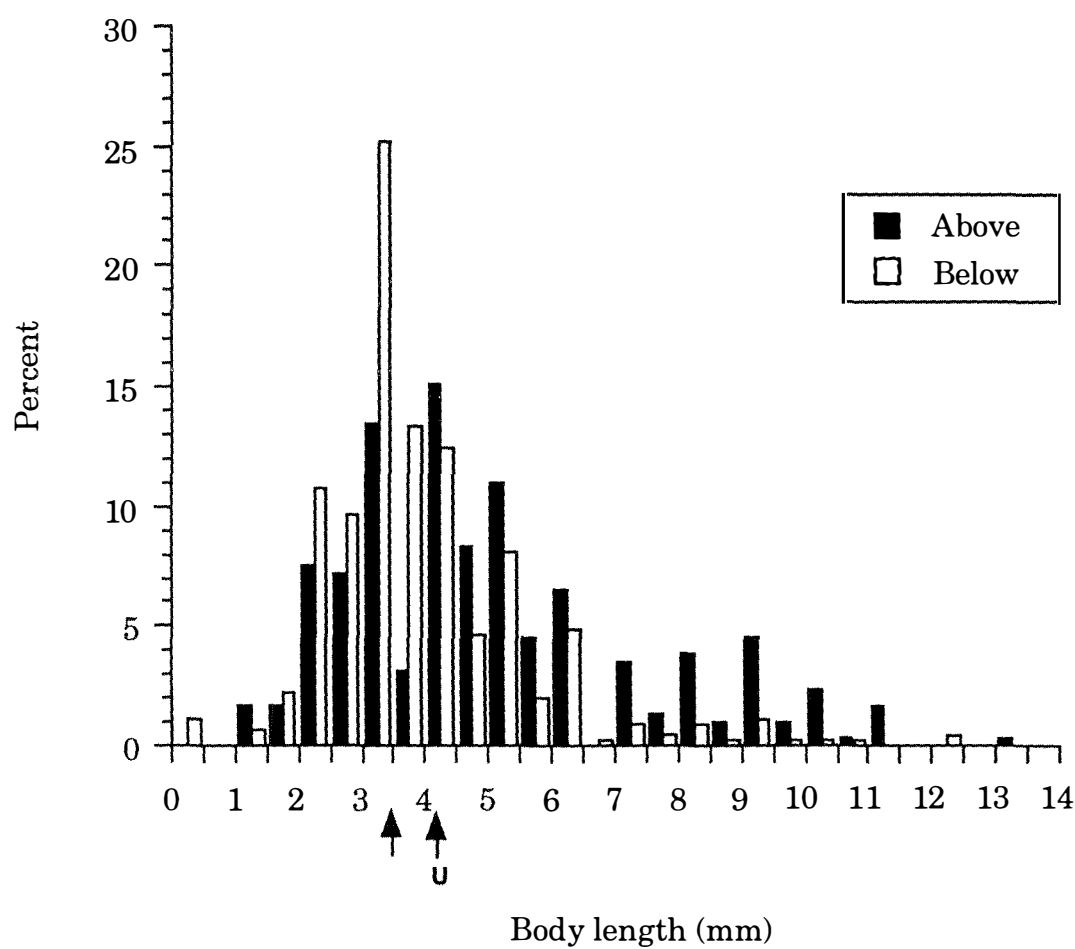


Fig. 3. 14 Distribution of prey body lengths consumed by blue ducks above and below the Ikawetea River waterfall. Arrow's indicate medians and "U" denotes upstream of falls value.

due to the high relative dry weight of these taxa, Ephemeroptera and Plecoptera dominated the diets in terms of dry weight throughout the year both above and below the waterfall. The only exception was in autumn when the Trichoptera *Beraeoptera roria* and Hydrobiosidae made up the largest proportion of diet dry weight.

Although the diets of Makaroro River birds above and below the waterfall were comprised of similar prey, significant ($t_{614}=4.90$, $p<0.001$) differences in the mean body length of macroinvertebrate consumed were noted. Mean macroinvertebrate body length in droppings collected from above the falls was 3.42 ± 0.11 mm compared with 4.14 ± 0.12 mm in droppings collected from below the falls (Fig. 3.15).

3. 3. 9 Comparison of trout and blue duck diets

Prey selection

Prey-selection indices calculated for the major macroinvertebrate orders consumed by trout and blue ducks from Manganuiateao and Tongariro Rivers are presented in Table 3. 6.

Blue ducks and trout from Tongariro River showed significant prey selection patterns ($F_{6,40}=18.32$ $p<0.001$) although no seasonal changes in selection were apparent ($F_{6,40}=0.78$ $p=0.71$). Both trout and blue ducks showed a similar pattern of selection. Both consumed relatively low proportions of Ephemeroptera and Trichoptera relative to those occurring in the benthos. Conversely, the proportions of Plecoptera in the diet of both predators were higher than that in the benthos. The only difference in prey selection between the blue ducks and trout on Tongariro River related to Diptera with trout showing positive selection for these insects while blue ducks appeared to avoid them.

Analysis also indicated significant ($F_{6,41}=5.55$ $p<0.001$) prey selection by Manganuiateao River trout and blue ducks. In addition, significant seasonality in prey selection was also recorded ($F_{6,41}=2.73$ $p=0.004$). As with Tongariro River trout and blue ducks, the Manganuiateao River predators displayed a similar pattern of prey selection albeit different from that of the Tongariro River predators. Ephemeroptera and to

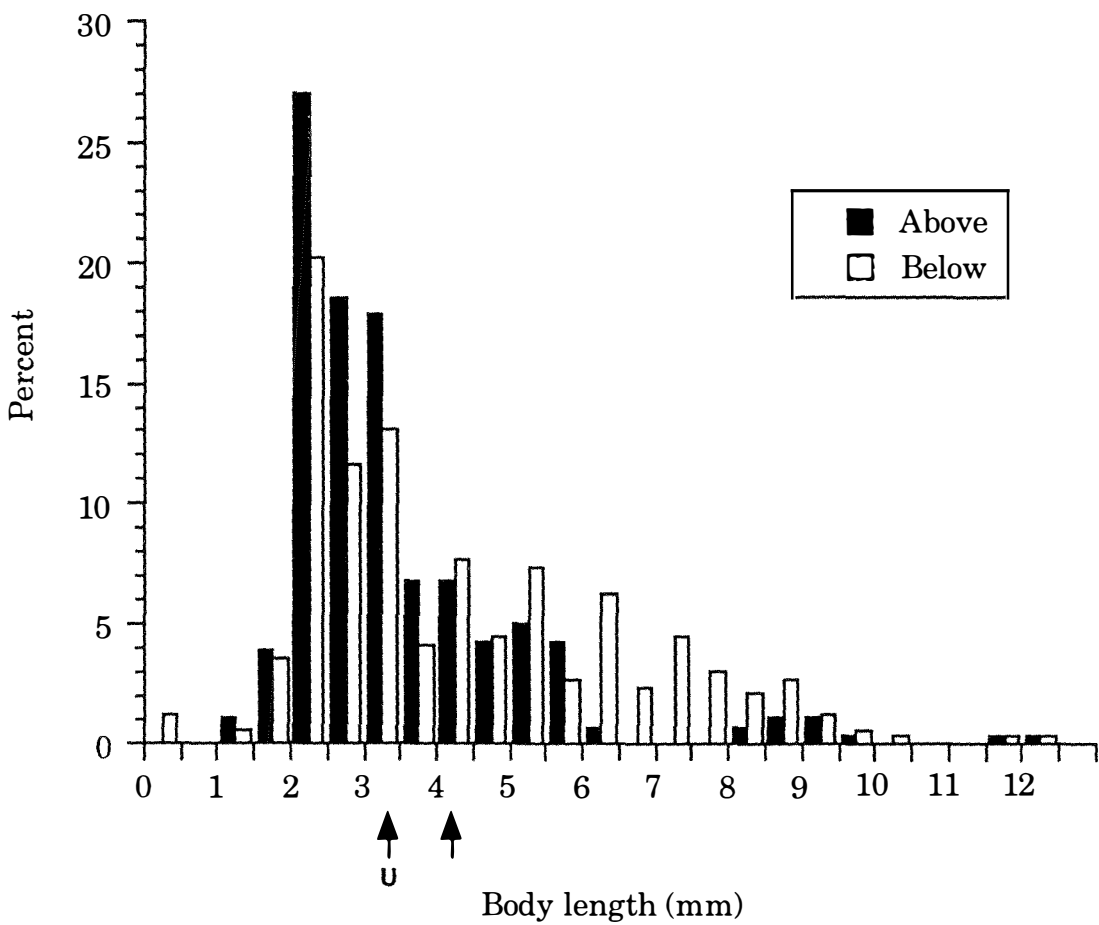


Fig. 3. 15 Distribution of prey body lengths consumed by blue ducks above and below the Makaroro River waterfall. Arrows indicate medians and "U" denotes upstream of falls value.

a lesser degree Diptera were both over-represented in the diets of Manganuiateao River trout and blue ducks. This was particularly so for Ephemeroptera during autumn. Plecoptera were substantially under-represented throughout the year but particularly so during autumn and winter. Trichoptera occurred in the diets of both trout and ducks in approximately the same proportion as that occurring in the benthos.

Blue ducks and trout on Ikawetea River showed significant (Blue duck $F_{6,36}=4.79$ $p=0.001$; Trout $F_{6,17}=4.79$ $p<0.001$) prey selection with both selectively depredating Ephemeroptera and Plecoptera (Table 3. 7). Trichoptera were substantially under-represented in the diets of both predators while Diptera and Coleoptera occurred in approximately the same proportion as that occurring in the benthos. The prey selectivity patterns of the two predators were similar ($F_{6,35}=1.05$ $p=0.410$) as was prey selectivity for blue ducks above and below the falls ($F_{6,36}=0.39$ $p=0.881$).

As with the Ikawetea predators, blue ducks and trout on Makaroro River illustrated a similar ($F_{4, 22}=1.72$ $p=0.181$) and significant pattern of prey selection (Blue ducks $F_{4,23}=4.77$ $p=0.006$; Trout $F_{4,11}=26.85$ $p<0.001$) (Table 3. 7). Ephemeroptera and Plecoptera were positively selected throughout the year but particularly in autumn and summer. Trichoptera were consistently over-represented in the diet of both trout and blue ducks on all sampling occasions but particularly so in autumn. As with the Ikawetea River blue ducks, Makaroro birds above and below the waterfall showed similar patterns of prey selection ($F_{4,23}=0.205$ $p=0.933$).

3. 3. 10 Relative importance of prey

Chironomidae and Ephemeroptera of the family Leptophlebiidae were of high relative importance in the diets of Tongariro River blue ducks and trout (Table 3.8). The Trichoptera *Pycnocentroides* sp. and *Aoteapsyche* sp. were also important prey to both predators. When the blue duck and trout prey IRIs were compared a significant correlation was found ($r_s = 0.834$ $p < 0.001$).

Table 3. 6 Prey-selection indices calculated from dry weight of macroinvertebrates in each of the major categories in the diets of trout and blue ducks from Tongariro and Manganuiateao Rivers in relation to that found in the benthos. Negative values indicate avoidance while positive values indicate selection. Values reflect the relative degree of selection or avoidance for prey by each predator.

Taxon	Tongariro		Manganuiateao	
	Trout	Duck	Trout	Duck
Ephemeroptera	-10.21	-18.13	3.79	15.93
Plecoptera	24.68	31.13	-20.66	-17.93
Trichoptera	-37.21	-13.95	0.22	-4.90
Diptera	16.19	-7.59	10.03	2.57
Coleoptera	6.15	7.49	2.45	0.09

Table 3. 7 Prey-selection indices calculated from dry weight of macroinvertebrates in each of the major categories in the diets of trout and blue ducks from Ikawetea and Makaroro Rivers in relation to that found in the benthos. Negative values indicate avoidance while positive values indicate selection. Values reflect the relative degree of selection or avoidance for prey by each predator. B and A denote below and above waterfall values respectively.

Taxon	Ikawetea				Makaroro			
	Trout		Duck		Trout		Duck	
	B	A	B	A	B	A	B	A
Ephemeroptera	-1.55	*	6.52	14.13	29.15	*	1.98	11.25
Plecoptera	-3.15	*	11.00	13.83	0.43	*	17.20	18.43
Trichoptera	-53.33	*	-26.28	-19.72	-44.88	*	-34.80	-27.10
Diptera	6.88	*	6.55	-1.38	9.38	*	9.37	10.23
Coleoptera	-1.38	*	1.32	2.38	5.88	*	5.88	9.68

* No trout above waterfalls.

Chironomidae were not of the same importance to Manganuiateao River birds (Table 3. 9). Instead, Leptophlebiidae were the most important prey followed by the Plecoptera, *Zelandoperla* sp. and several Trichoptera taxa. The diet of trout in Manganuiateao River was also dominated in terms of the relative importance of prey by Leptophlebiidae nymphs although the Trichoptera *Aoteapsyche* sp. was also important. The relative importance of the 19 prey groups to each predator was significantly correlated ($r_s = 0.662$ $p < 0.001$).

Examination of the relative importance of prey in the diet of blue ducks inhabiting sections above and below the Ikawetea River waterfall revealed that birds inhabiting both sections relied heavily on Leptophlebiidae nymphs and the Trichoptera *Beraeoptera* sp., *Aoteapsyche* sp. and *Pycnocentroides* sp. (Table 3.10). *Olinga feredayi* was also important in the diet of birds living above the falls. A significant correlation existed between the prey IRIs for ducks occurring above and below the Ikawetea waterfall ($r_s = 0.978$ $p < 0.001$).

Leptophlebiidae nymphs were also the most important in the diet of trout coexisting with blue duck below the Ikawetea waterfall. The Trichoptera *Olinga feredayi* and *Aoteapsyche* sp. were also important prey components. Plecoptera *Zelandoperla* sp. were of high relative importance in the trout diet. Despite this, the relative importance of the different prey was similar for trout and blue ducks in the lower reaches ($r_s = 0.786$ $p < 0.001$).

Leptophlebiidae nymphs dominated the diet of trout and blue ducks in both sections of Makaroro River in terms of relative importance (Table 3.11). The Trichoptera *Beraeoptera* sp. and the Plecoptera *Zelandoperla* sp. were important to blue ducks throughout the river while the cased caddisfly *Olinga feredayi* featured highly in the diet of trout living below the falls. As with Ikawetea River, the relative importance of different prey groups to blue ducks inhabiting reaches above and below the falls was very similar ($r_s = 0.981$ $p < 0.001$). Likewise, the relative importance of the different prey to trout and blue ducks in the lower reach was significantly correlated ($r_s = 0.661$ $p < 0.001$).

Table 3. 8 Indices of the relative importance (IRI) of common prey consumed by blue ducks and trout from Tongariro River.

Taxon	IRI Values		Taxon	IRI Values	
	Blue Duck	Trout		Blue Duck	Trout
Leptophlebiidae	3092	2980	<i>Aoteapsyche</i> sp.	1179	1172
<i>Coloburiscus</i> sp	60	58	Hydrobiosidae	273	1205
<i>Nesameletus</i> sp.	21	1	<i>Paroxyethira</i> sp.	323	158
<i>Zelandoperla</i> sp.	202	550	<i>Oxyethira</i> sp.	319	21
<i>Megaleptoperla</i> sp.	0.1	9	Other		
<i>Austroperla</i> sp.	0	6	Trichoptera	15	0.5
<i>Pycnocentroides</i> sp.	1355	349	Chironomidae	6612	1301
<i>Beraeoptera roria</i>	284	26	<i>Aphrophila</i> sp.	42	5
<i>Helicopsyche</i> sp.	46	27	<i>Archichauliodes</i> sp.	8	0
<i>Olinga</i> sp.	432	62	Elmidae	30	3

Table 3. 9 Indices of the relative importance (IRI) of common prey consumed by blue ducks and trout from Manganuiateao River.

Taxon	IRI Values		Taxon	IRI Values	
	Blue Ducks	Trout		Blue Ducks	Trout
Leptophlebiidae	6050	8234	<i>Aoteapsyche</i> sp.	1079	136
<i>Coloburiscus</i> sp	683	222	Hydrobiosidae	864	394
<i>Nesameletus</i> sp.	0.4	519	<i>Paroxyethira</i> sp.	0	1
<i>Zelandoperla</i> sp.	2018	1384	<i>Oxyethira</i> sp.	3	0
<i>Megaleptoperla</i> sp.	0	69	Other		
<i>Austroperla</i> sp.	0	66	Trichoptera	2	4
<i>Pycnocentroides</i> sp.	149	114	Chironomidae	780	310
<i>Beraeoptera roria</i>	3513	812	<i>Aphrophila</i> sp.	63	0.3
<i>Helicopsyche</i> sp.	7	92	<i>Archichauliodes</i> sp.	5	2
<i>Olinga</i> sp.	40	81	Elmidae	13	0

Table 3. 10 Indices of the relative importance (IRI) of common prey consumed by blue ducks and trout from Ikawetea River. A and B denote above and below falls.

Taxon	IRI Values			Taxon	IRI Values		
	Blue Ducks A	Blue Ducks B	Trout		Blue Ducks A	Blue Ducks B	Trout
Leptophlebiidae	3726	4637	5521	<i>Aoteapsyche</i> sp.	1231	1071	920
<i>Coloburiscus</i> sp	870	684	284	Hydrobiosidae	282	281	559
<i>Nesameletus</i> sp.	226	80	441	<i>Paroxyethira</i> sp.	0	0	0
<i>Zelandoperla</i> sp.	646	1068	1744	<i>Oxyethira</i> sp.	0	0	0
<i>Megaleptoperla</i> sp.	0	0	183	Other			
<i>Austroperla</i> sp.	0	0	40	Trichoptera	0.4	30	26
<i>Pycnocentroides</i> sp.	2318	2059	585	Chironomidae	171	48	0
<i>Beraeoptera roria</i>	3529	3712	264	<i>Aphrophila</i> sp.	38	34	194
<i>Helicopsyche</i> sp.	54	57	5	<i>Archichauliodes</i> sp.	109	66	114
<i>Olinga</i> sp.	1286	282	4872	Elmidae	34	3	0

Table 3. 11 Indices of the relative importance (IRI) of common prey consumed by blue ducks and trout from Makaroro River. A and B denote above and below falls.

Taxon	IRI Values			Taxon	IRI Values		
	Blue Ducks A	Blue Ducks B	Trout		Blue Ducks A	Blue Ducks B	Trout
Leptophlebiidae	6270	3815	6470	<i>Aoteapsyche</i> sp.	156	402	14
<i>Coloburiscus</i> sp	458	339	76	Hydrobiosidae	612	1371	66
<i>Nesameletus</i> sp.	10	18	140	<i>Paroxyethira</i> sp.	0	0	0
<i>Zelandoperla</i> sp.	1190	1792	1684	<i>Oxyethira</i> sp.	0	0	0
<i>Megaleptoperla</i> sp.	2	0	42	Other			
<i>Austroperla</i> sp.	0	0	22	Trichoptera	32	45	121
<i>Pycnocentroides</i> sp.	636	494	702	Chironomidae	0	0	0.5
<i>Beraeoptera roria</i>	5120	3499	879	<i>Aphrophila</i> sp.	34	348	160
<i>Helicopsyche</i> sp.	36	6	48	<i>Archichauliodes</i> sp.	0	88	59
<i>Olinga</i> sp.	170	18	2800	Elmidae	16	6	0

3. 3. 11 Comparison of prey size selection by blue ducks and trout

As well as comparing the prey types consumed by trout and blue ducks I also examined the body lengths of prey eaten by the two predators.

Trout in the two Central North Island rivers consumed prey of a significantly larger mean body length than that occurring in the benthos and than that consumed by blue ducks (Table 3.12). Blue ducks consumed prey of a significantly smaller body length than that occurring in the benthos. To test whether small trout consume small prey and hence are more likely to compete with blue ducks, an analysis of aquatic prey body length versus trout fork length was conducted on the combined data from all four rivers. A significant correlation was found to exist ($r_s = 0.49$ $p < 0.05$) with smaller trout selecting smaller prey. To test if smaller trout ($FL < 250$ mm) may overlap with blue ducks in respect to the size of prey consumed the prey mean body length occurring in the diets were compared. Small trout were found to take prey with a significantly ($t_{119} = -2.7476$ $p = 0.0069$) greater mean body length (6.42 ± 0.2 mm) than blue ducks (3.95 ± 0.2 mm).

No significant differences in the body lengths of benthic macroinvertebrates occurring above and below the Ikawetea or Makaroro River waterfalls were detected either when the data from each sampling event were combined or when they were examined individually (Table 3.13). Trout in all four rivers consumed benthic prey of significantly larger body length than that occurring in the benthos.

Blue ducks on Ikawetea and Makaroro Rivers consistently consumed prey of smaller mean body length than that occurring in the benthos. A comparison of the mean body length of prey consumed by blue ducks occurring above and below the Ikawetea River falls showed that the ducks above the falls consumed significantly larger prey than that eaten by blue ducks occurring below the falls. On Makaroro River blue ducks below the waterfall consumed the larger prey (Table 3.13).

Table 3.12 Mean body length of Manganuiateao and Tongariro River macroinvertebrates in the diet of trout and blue ducks, and in the benthos.

Comparison	Mean body lengths (mm)	P values from ANOVA
Tongariro River		
Trout vs Benthos	6.4 vs 4.7	0.001
Duck vs Benthos	3.7 vs 4.7	0.001
Duck vs Trout	3.7 vs 6.4	0.001
Manganuiateao River		
Trout vs Benthos	6.6 vs 4.6	0.001
Duck vs Benthos	3.8 vs 4.6	0.001
Duck vs Trout	3.8 vs 6.6	0.001

Table 3.13 Mean size of Ikawetea and Makaroro River macroinvertebrates in the diet of trout and blue ducks, and in the benthos. NS = Not Significant at 0.05.

Comparison	Mean body lengths (mm)	P values from ANOVA
Ikawetea River		
Trout vs Benthos _{below}	8.43 vs 5.32	0.001
Duck _{above} vs Benthos _{above}	4.90 vs 5.35	0.001
Duck _{below} vs Benthos _{below}	3.76 vs 5.32	0.001
Duck _{below} vs Trout	3.76 vs 8.43	0.001
Duck _{above} vs Duck _{below}	4.90 vs 3.76	0.001
Benthos _{above} vs Benthos _{below}	5.35 vs 5.32	NS
Makaroro River		
Trout vs Benthos _{below}	7.28 vs 5.64	0.001
Duck _{above} vs Benthos _{above}	3.42 vs 5.69	0.001
Duck _{below} vs Benthos _{below}	4.14 vs 5.64	0.001
Duck _{below} vs Trout	4.14 vs 7.28	0.001
Duck _{above} vs Duck _{below}	3.42 vs 4.14	0.001
Benthos _{above} vs Benthos _{below}	5.69 vs 5.64	NS

3. 3. 12 Blue duck and trout diet overlap

A low degree of overlap existed between trout and ducks throughout the year on Tongariro River (Table 3.14). Overlap values derived from numeric analysis of the diets had values of less than 0.6 in all months and a mean index of 0.35 ± 0.06 when all data were combined. The low degree of overlap was the result of trout consuming a substantial amount of terrestrial prey. This was illustrated by the higher overlap values derived from the dry weight data, which excluded terrestrial food from the analysis. However, with the exception of April and November, overlap on all sampling occasions were lower than 0.6. When the dry weight data were combined a mean overlap value of 0.52 ± 0.04 was obtained .

Analysis of diet overlap between blue ducks and trout inhabiting Manganuiateao River showed a higher degree of resource overlap throughout the year than that recorded for Tongariro (Table 3.14). Overlap values derived from prey numbers ranged from 0.26 to 0.69 and had a mean value when all seasonal data were combined of 0.50 ± 0.07 . As with the Tongariro River, the low degree of overlap between blue ducks and trout was in part the result of the terrestrial prey consumed by trout. This, as with the Tongariro River results, was shown by the overlap values derived from the dry weight data being greater than those calculated from numeric data. Only on two occasions were index values of less than 0.6 recorded for dry weight diet data and a mean overlap value of 0.68 ± 0.05 was derived when all seasonal data were considered jointly.

Diet overlap analysis based on the abundance of prey in the diet of trout and ducks inhabiting the Ikawetea River ranged from 0.21 to 0.53. A mean seasonal overlap value of 0.33 ± 0.07 (Table 3. 15) was obtained when data from all sampling events were combined. However, when terrestrial prey were removed and dry weight data considered, overlap between blue duck and trout increased and ranged between 0.30 to 0.64 with a mean value of 0.51 ± 0.07 .

Analysis of the diet overlap of trout and ducks inhabiting the Makaroro River showed a large range of values for both numerical and dry weight data (Table 3. 15). Overlap values based on numeric analysis of the diets

Table 3. 14 Diet overlap values for blue ducks and trout inhabiting Tongariro and Manganuiateao Rivers calculated by the Schoener (1970) proportional differences method. Overlap values are presented for the six sampling occasions and the combined numerical and dry weight data.

Date	Numerical	Dry weight*
Tongariro River		
20.1	0.23	0.53
10.3	0.26	0.45
27.4	0.53	0.63
20.7	0.24	0.40
16.9	0.51	0.52
4.11	0.33	0.61
mean ± SE	0.35 ± 0.06	0.52 ± 0.04
Manganuiateao River		
26.2	0.67	0.70
1.4	0.41	0.55
2.7	0.69	0.74
16.9	0.60	0.89
5.11	0.34	0.54
15.12	0.26	0.65
mean ± SE	0.50 ± 0.07	0.68 ± 0.05

* Dry weight estimates do not take into account the terrestrial component of the trout diet.

ranged from 0.04 to 0.66 while overlap indices based on dry weight analysis ranged from 0.22 to 0.75.

Diet overlap of birds above and below the Ikawetea falls was also examined by the determination of overlap values (Table 3. 16). All overlap values calculated from abundance and dry weight data, except summer samples, exceeded 0.60. The diets of ducks inhabiting both sections of the Makaroro River also showed a high degree of similarity with mean overlap values of 0.73 ± 0.06 and 0.66 ± 0.08 for prey abundance and dry weight data respectively (Table 3. 16).

Table 3. 15 Diet overlap values calculated by the Schoener (1970) proportional differences method between blue ducks and trout of Ikawetea and Makaroro Rivers. Overlap values are presented for the six sampling occasions for both abundance and dry weight data.

Date	Numerical	Dry Weight*
Ikawetea River		
14.3	0.21	0.62
8.6	0.21	0.30
11.9	0.45	0.64
3.12	0.53	0.60
29.12	0.27	0.40
mean ± SE	0.33 ± 0.07	0.51 ± 0.07
Makaroro River		
15.3	0.14	0.54
3.6	0.50	0.75
20.10	0.66	0.70
14.12	0.04	0.22
mean ± SE	0.34 ± 0.15	0.55 ± 0.12

* Dry weight estimates do not take into account the terrestrial component of the trout diet.

Table 3. 16 Diet overlap values calculated by the Schoener (1970) proportional differences method between blue ducks above and below the Ikawetea River waterfall. Overlap values are presented for the six sampling occasions for both abundance and dry weight data.

Date	Numerical	Dry Weight*
Ikawetea River		
14.3	0.69	0.72
8.6	0.76	0.70
11.9	0.84	0.85
3.12	0.66	0.78
29.12	0.50	0.65
mean ± SE	0.69 ± 0.06	0.74 ± 0.03
Makaroro River		
15.3	0.80	0.35
3.6	0.87	0.63
20.10	0.65	0.73
3.11	0.80	0.85
14.12	0.52	0.73
mean ± SE	0.73 ± 0.06	0.66 ± 0.08

* Dry weight estimates do not take into account the terrestrial component of the trout diet.

3. 4 Discussion

3. 4. 1 Composition of the benthic macroinvertebrate communities

The community composition of the Tongariro and Manganuiateao rivers were much the same as that reported in previous studies.

Dedual & Collier's (1995) recent study found Chironomidae larvae to be the most abundant organism in the Tongariro River's benthos. However, unlike my study Dedual & Collier (1995) did not report large numbers of the purse caddisflies *Paroxyethira* sp. and *Oxyethira albiceps* during the warmer summer months. Both these Trichoptera are algae piercers and occurred following the proliferation of algae in the river. Dedual & Collier (1995) do not report the status of the algal community during their investigation.

Collier & Wakelin (1992) collected 63 taxa from Manganuiateao River during their study of the macroinvertebrate drift patterns. This compares with the 47 taxa that I recorded, the difference being accounted for by the coarser taxonomic resolution used in my investigation with several taxa being identified to genus only. Past studies have found Chironomidae and Trichoptera larvae to be the most abundant macroinvertebrates in Manganuiateao River (Collier 1991, Veltman *et al.* 1995). I also found Trichoptera larvae to be abundant throughout the year however, Chironomidae larvae were not as numerous in my samples as previously found and at no time reached the 40% recorded by Collier (1991).

No previous data describing the benthic communities of Ikawetea and Makaroro Rivers exist. In terms of Quinn & Hickey's (1990) "100 River" study the core macroinvertebrate species recorded in the two Ruahine rivers (ie, mayflies, caddisflies and stoneflies) were typical of those common in "unmodified" New Zealand streams and rivers with catchments dominated by native bush.

3. 4. 2 Composition of trout diet

The composition of trout diet was generally consistent with the findings of earlier work. Allen (1952), in his much-cited Horokiwi study, found

cased caddisfly larvae to be of particular importance to trout with Ephemeroptera larvae also being consumed in great numbers. I found Trichoptera larvae, in particular *Olinga feredayi* and *Beraeoptera roria*, along with larvae of the mayfly *Deleatidium* sp. were of greatest importance in the diet of trout collected from all four rivers, both in numbers consumed and in terms of dry weight. Elliott (1973) found Trichoptera to have a high fat content in their body thus proving a high calorific return to predators. He suggested that this fact explained the high abundance of Trichoptera in trout diet.

McLennan and MacMillian (1984) studied the diet of rainbow and brown trout in Mohaka River and several other Hawkes Bay rivers. They found that mature trout of both species fed on drifting benthic larvae and terrestrial insects with mayflies dominating in summer and stoneflies in winter. This pattern was not as obvious in my study but trout in Manganuiateao and Tongariro Rivers did consume different prey in different proportions throughout the year.

Trout collected by Kusabs & Swales (1991) and Stephens (1989) from the upper reaches of the Tongariro River also contained high numbers of Chironomidae, (especially during summer), Ephemeroptera and caddisflies of the families Hydropsychidae and Hydropsychidae. However, the dry weight of Chironomidae prey in the diet was relatively low compared with the other common prey.

Experimentation with rainbow trout has shown they prefer large prey items (Angradi & Griffith 1990). Kusabs & Swales (1991) found juvenile rainbow trout in two tributaries of Lake Taupo fed extensively on large prey items. My study also found that the trout of all four rivers consumed benthic prey of a larger mean body length than that occurring in the benthos.

3. 4. 3 Effect of trout foraging on macroinvertebrate communities in Ikawetea and Makaroro Rivers

No consistent differences in the taxonomic composition of the benthic macroinvertebrate communities above and below the Ikawetea and Makaroro River waterfalls were found. The general lack of consistent difference in the composition of the benthic macroinvertebrate

communities indicated that foraging by trout is unlikely to be a major structuring agent on the taxonomic composition of the benthic communities in these rivers. Such a lack of trout effect on benthic macroinvertebrate populations has been widely reported in other studies (Thorp & Bergey 1981, Allan 1982, Reice 1983, Flecker & Allan 1984, Reice & Edwards 1986, Culp 1986, Reice 1991).

Interestingly discriminant analysis indicated, albeit at a non-significant level, that the predatory stonefly *Stenoperla prasina* was more abundant in the trout free reaches upstream of both waterfalls. The fact that *Stenoperla prasina* like trout preys upon aquatic macroinvertebrates raises the possibility that the apparent decline of this large insect in those sections of river containing trout could potentially be a result of competition with trout for prey.

Culp (1986) recorded no effect of coho fry (*Oncorhynchus kisutch*) on the composition of a North American creek macroinvertebrate community. Likewise, research conducted by Thorp & Bergey (1981) also found no evidence of a predatory fish impact on taxonomic richness. Several explanations for the lack of a predator effect have been advanced. Cummins & Hall (cited in Bechara *et al.* 1993) suggested that the productivity of benthic communities is usually well in excess of that required to compensate for fish predation and that foraging by fish simply removes the excess beyond the system's carrying capacity. Hence the impact of such foraging by fish is small and in most natural situations undetectable. Cooper *et al.* (1990) suggested that rapid macroinvertebrate recolonisation by downstream drift, masks the effect of predation. Collier & Wakelin (1992), in their study of macroinvertebrate drift patterns in Manganuiateao River found that the Trichoptera, *Beraeoptera roria* was one of the dominant macroinvertebrates in the drift. I found *Beraeoptera roria* to be consumed by trout in great numbers. If the drift of this Trichoptera was sufficient to compensate for those consumed by trout the effects of predation would go undetected. If similar patterns of drift as those documented by Collier & Wakelin (1992) occur in the two Ruahine rivers then the effects of trout foraging on the macroinvertebrate communities below the falls may be compensated for by macroinvertebrate drift from above the falls.

Both explanations for the lack of trout effect assume that fish density is below that threshold above which such compensation is exceeded. The trout densities in the Ikawetea and Makaroro Rivers are seasonal with fish moving into these systems following periods of high autumn river flow, to spawn. Following spawning the fish move back downstream out of the headwaters. For the rest of the year only a low density of resident adults inhabit these rivers (pers. observation). Thus, it seems likely that foraging by trout in these rivers does not exceed the ability of the macroinvertebrate communities to compensate.

Previous studies (Angradi & Griffith 1990, Kusabs & Swales 1991), have also shown that trout selectively prey on large benthic prey. However, despite such apparent selection by trout I did not find the mean body length of macroinvertebrates above and below the Ikawetea and Makaroro falls to differ significantly. Culp (1986) reported a similar lack of trout effect on macroinvertebrate size in a British Columbian stream. However, Bechara *et al.* (1993) found that brook trout significantly reduced the density of large to medium-sized macroinvertebrates in the benthos in artificial streams. They did however, find no such effect on macroinvertebrates occurring in the interstitial spaces and suggested that such refugia are important in reducing the impacts of trout predation. As blue ducks have the ability to extract their aquatic prey from such interstitial spaces this may impart an advantage to them. This is discussed in more detail in later sections and Chapter 6.

3. 4. 4 Composition of blue duck diet

Kear and Burton (1971) found Trichoptera, especially Conoesucidae (cased caddisflies) to be abundant in the diet of blue ducks on a number of rivers and streams. More recently Wakelin (1993) examined the contents of seven blue duck droppings collected from the Tongariro River in 1990. He found Chironomidae larvae dominated the samples numerically although Trichoptera and Ephemeroptera were also important in the diet.

Collier (1991) found that the diet of blue ducks on the Manganuiateao River contained large proportions of the cased caddisfly *Helicopsyche*, *Pycnocentroides* and *Beraeoptera roria*. I also found these taxa to be abundant in the diet of blue duck in my study area. In addition, Collier

(1991) found blue ducks consumed proportionally more cased caddisflies but fewer Chironomidae, *Coloburiscus humeralis* and Leptophlebiid mayfly larvae than that occurring in the benthos. The under representation of some mayflies in the diet of the blue ducks may arise from the difficulties associated with catching these agile prey. Fast swimming mayfly species might be expected to evade predation more easily than relatively sessile cased caddisfly larvae. However, the findings of Veltman *et al.* (1995) placed this conjecture in some doubt as they recorded a high proportion of the very agile mayfly *Nesameletus* sp. in the diet of blue duck on one occasion. My research also reports the presence of *Nesameletus* sp. and another fast swimming mayfly, *Oniscigaster* sp. in the diet of blue ducks from several of the study sites on more than one occasion.

Veltman *et al.* (1995) found evidence to support the hypothesis that blue ducks foraged selectively for preferred prey. During the course of their work on Manganuiateao River the diets of blue ducks were dominated by a number of different taxa, most of which were numerically abundant within the benthos. Collier (1991) examined the prey selectivity of blue ducks inhabiting Manganuiateao River and seven other North Island East Cape Rivers. He found that overall blue ducks consumed proportionately more cased caddisfly larvae and fewer Chironomidae, *Coloburiscus humeralis* and Leptophlebiid mayfly larvae than that occurring in the benthos, suggesting selective foraging. In addition to examining the blue duck diet in terms of the numbers of certain prey eaten, I also considered the diet in terms of the dry weight composition of different prey groups in the diet. Based on the premise that selectivity should be driven by energetic returns to the predator as optimal foraging theory predicts, I found that certain prey were either under- or over-represented in the blue ducks' diet relative to their occurrence in the benthos. However, the patterns were not consistent between rivers and in the case of the two Ruahine rivers no consistent patterns in the diets of birds above and below the falls were recorded. Collier (1991) also found that the occurrence of macroinvertebrate taxa in the blue duck faeces varied between rivers he studied, and even within pairs of birds and family groups on the same river. Collier (1991) suggested that this implies an element of chance or individuality in which prey taxa are

encountered and consumed rather than specific prey selection and avoidance.

3. 4. 5 Implications of the similarity in the diets of blue ducks and trout

As shown by my research the blue ducks and trout inhabiting the four rivers consumed similar prey with their diets showing a low to moderate degree of overlap on the majority of occasions. The relative importance of the different prey to both trout and blue duck also showed a high degree of similarity among rivers.

The effects of introduced trout on several of New Zealand's insectivorous native fish species has been well studied. Glova & Sagar (1991) studied the diet of the native fish and trout in Rangitata River, South Island. They found that diets of the two common trout species and the native galaxiid *Galaxias brevipinnis* overlapped considerably, 0.85 in terms of prey abundance and 0.60 in terms of dry weight. In spite of the general high degree of overlap found to exist between the fish species studied by Glova and Sagar (1991), they concluded that there appeared to be no apparent adverse effects on the species existence. They suggested that the intensity of competition was reduced by temporal differences in the diel feeding patterns of these fish. Sagar & Eldon (1983) studied the diet of native fish and trout in the lower Rakaia River. Despite recording a high degree of overlap between the native and exotic fish species they concluded that no significant degree of competition occurred. Sagar & Eldon (1983) attributed this lack of competition to interspecific difference in the feeding micro-habitats used by sympatric populations of galaxiids and Salmonidae.

Other examinations of coexisting populations of native fish and trout in New Zealand streams and rivers have found that where there is significant overlap, populations coexist as a result of differences in the spatial feeding habits, or by consuming different-sized prey items or by feeding in different micro-habitats thereby reducing the adverse effects (Sagar & Eldon 1983, Glova & Sagar 1991). Kusabs & Swales (1991) found that coexisting populations of trout and koaro (*Galaxias brevipinnis*) which consumed the same aquatic macroinvertebrate prey avoided adverse effects as a consequence of trout consuming terrestrial

prey. In my study, terrestrial prey were in the diets of trout from all four rivers and reduced the degree of overlap existing between the two predators. The consumption of terrestrial prey by trout may act as a mechanism to reduce the effects of diet overlap especially during periods of reduced aquatic prey availability. However, this would assume that during such periods trout shift their diet, selectively consuming greater proportions of terrestrial prey. If this was not the case blue ducks, which consume a smaller range of prey may suffer some adverse effect as they do not have the same dietary flexibility. There is one record of blue ducks eating berries (Harding 1990). If this behaviour was adopted by blue ducks during periods of resource limitation then, as with trout, blue ducks may also have a dietary refuge.

Sagar & Eldon (1983) suggested that the lack of adverse effect from diet overlap between coexisting populations of native fish and introduced trout was a result of each predator utilising different micro-habitats. Several studies (see Angradi & Griffith 1990) have concluded that trout obtain the majority of their food from the drift with only limited foraging of the benthos. Conversely, blue ducks obtain their prey by gleaning them from the substrate surface and interstitial spaces (Kear & Burton 1971, Collier 1991). Veltman *et al.* (1995) found the benthic fauna occurring on the top of boulders in the substrate differed from that inhabiting interstitial spaces. Therefore the difference in foraging micro-habitat may significantly reduce the impact of the overlap. Similar spatial resource partitioning has been reported to effectively reduce the degree of competition between resource users by Schoener (1970), Abrams *et al.* (1986) and James (1991).

Comparisons of the diets of trout and blue duck from all four rivers illustrated that the prey consumed by sympatric populations were similar. However, marked differences in the size of prey consumed were noted. Trout, particularly larger trout, consumed large prey items. However, despite the significant relationship between trout length and prey size reported here the mean body length of prey consumed by small trout was still significantly larger than that consumed by blue ducks. Glova and Sagar (1991) also reported that juvenile trout in New Zealand fed primarily on the larger size fraction of the available food resources. Size-selective predation of stream invertebrates by fish has also been

demonstrated in artificial (Bisson 1978, Ringler 1979), and natural streams (Metz 1974, Allan 1978, Bechara *et al.* 1993) elsewhere in the world.

Prey size selection has been demonstrated in other waterfowl. Common eiders, *Somateria mollossima*, feed on mussels with smaller mean shell lengths than that occurring in the mussel-bed on which they feed (Player 1971, Swennen 1976). Male tufted ducks (*Aythya fuligula*) have been found to select mussels ranging in size from 0.5 to 2.5 cm while female tufted ducks selected mussels in the size range 1.5 to 2.0 cm (Draulans 1982). The feeding of blue ducks on smaller prey may impart to the bird a competitive advantage if it gives the duck access to a more abundant food resource (ie, greater numbers of smaller early instar prey). Targeting this component of the resource maybe a particularly profitable strategy as smaller macroinvertebrates constitute the largest component of the community.

Several overseas research projects have examined the effects of significant diet overlap between birds and fish. Hunter *et al.* (1986) examined the similarity in the diets of brook trout (*Salvelinus fontinalis*) and black duck (*Anas rubripes*) populations in Maine, USA and derived overlap values in excess of 0.90 (Schoener's index). Their work found that fish reduced macroinvertebrate abundance, and ducklings raised on ponds containing high densities of fish grew at a reduced rate compared with those raised on fish-free waters. Hunter *et al.* (1986) concluded that the high degree of diet overlap found to exist between waterfowl and fish did result in adverse effects on the waterfowl population.

As with other studies Eadie & Keast (1982) found that goldeneye (*Bucephala clangula*) densities on ponds and lakes were negatively correlated with fish densities. An overlap value of 0.71 (Schoener's index) was obtained when they examined the degree of diet similarity existing between yellow perch (*Perca fluviatilis*) and goldeneye inhabiting three lakes in Timmiskaming County, Ontario, Canada. They also examined the prey size distributions consumed by the two insectivores and found no evidence of size selection.

It is clear from my results that coexisting populations of trout and blue ducks consume the same prey on each of the four rivers and as a result

resource overlap is moderately high. However, the foraging of trout appears to have little impact on prey availability in the Ikawetea and Makaroro Rivers. This lack of trout-effect on the benthic communities and the difference in mean body length of prey consumed by each predator documented here, combined with the difference in foraging micro-habitat shown elsewhere, indicates that competition for prey may not be intense.

Chapter Four

Field experiment to investigate responses of benthic macroinvertebrates to presence and absence of trout

4. 1 Introduction

The results presented in Chapter 3 showed that trout consumed the same aquatic macroinvertebrate prey as blue ducks, on the four North Island rivers I studied. Although no significant trout effects on the macroinvertebrate communities were detected in Chapter 3 other studies (Jacobi 1979, Culp 1986, Reice 1991, Bechara *et al.* 1993, Flecker & Townsend 1995) have reported substantial changes in benthic communities resulting from trout foraging. I further examined the potential of trout to modify macroinvertebrate abundance and / or macroinvertebrate community structure to establish if the presence of trout could lower the availability of blue duck prey.

The effect of trout on aquatic macroinvertebrate communities has been studied elsewhere by comparing the densities and biomass of benthic macroinvertebrates in the presence and absence of fish (Jacobi 1979, Allan 1982, Reice 1983, Flecker & Allen 1984, Culp 1986, Reice 1991, Bechara *et al.* 1993, Flecker & Townsend 1995). The results of such studies have differed markedly. On one hand, Jacobi (1979) found that a greater biomass of benthic animals existed above natural trout barriers in Raven Creek in the Yellowstone Lake watershed, USA. On the other hand Allan (1982) found no change in the community composition of the benthos after brook trout were removed from stretches of a Colorado stream, even after four years. Other studies recorded little or no effect of trout on macroinvertebrate abundance but instead documented significant reductions in the occurrence of larger macroinvertebrates. For example, Bechara *et al.* (1993) found that foraging by brook trout altered the size distribution of stream insects by removing many of the larger prey items in a small stream in Québec, Canada. Evaluating the impact

of predators like trout on macroinvertebrate biomass is made very difficult by the fact that each river differs in size, flow regime and fish and macroinvertebrate densities.

To overcome problems of interpretation, workers have developed the alternative approach of penning trout in enclosures in rivers and monitoring what happens to prey on the substrate within the enclosures (Forrester 1994). By varying trout density, it is possible in theory to relate changes in prey abundance to the known predator pressure. For example, in an experiment in a Pine River tributary in Canada, there was a 35% reduction in the density of the stonefly *Paragnetina media* when rainbow trout were penned in 13m² enclosures (Feltmate & Williams 1989). There is now convincing evidence from several such studies that fish do indeed lower the biomass and alter the community structure of their aquatic prey (Forrester 1994).

A similar trout effect has not been demonstrated under more-or-less natural conditions in New Zealand. I therefore designed and carried out an experiment on Tongariro River to test the hypothesis that trout foraging reduces aquatic macroinvertebrate biomass inside enclosed patches of substrate. In addition, I also tested the hypotheses that trout presence decreases taxonomic richness in the benthos and lowers the density of macroinvertebrates in the drift.

4. 2 Methods

4. 2. 1 Study site

The experiment was conducted immediately upstream of the Pillars of Hercules in a small braid of Tongariro River (S 39 09' 05", E 175 49' 02", elevation 620m asl) (Fig. 4.1). The braid was approximately 15m wide and 0.4m deep in its deepest point. The surrounding riparian vegetation was dominated by silver beech (*Nothofagus menziesii*) and toetoe (*Cortaderia toetoe*).

4. 2. 2 Experimental design

Macroinvertebrate communities were monitored in the presence or absence of trout in 9 plots of 6m². Each plot was triangular, 3m wide at

the base and 4m long (Fig. 4.2). Six of the 9 plots were enclosed with metal netting (18 mm aperture size) supported in each corner by metal stakes. The bottom 250 mm of netting was buried in the substrate to prevent trout from entering or leaving. The remaining 3 plots were delimited by 3 metal stakes only and acted as controls of a netting-effect. The plots were arranged in a 3 by 3 configuration with each downstream plot being offset by 3m from the plot directly upstream to minimise changes in flow caused by other plots. The triangular construction was adopted in an effort to reduce the build up of debris on the netting. I hoped that the oblique angle at which flow struck the netting would help remove debris periodically. However, it was necessary to occasionally remove debris from the netting. To stop large debris items (>100mm) from entering the study site a fence was constructed approximately 10m upstream of the first row of plots using 75 mm diamond netting .

The substrate ranged up to 300 mm in size. Maximum water velocities ranged from 0.44 to 0.77 ms⁻¹ and maximum water depths ranging from 300 to 455 mm were measured at the study site. Water temperature varied between 8.0 and 9.5°C over the duration of the experiment and no difference in temperature was detected between plots at any time. All plots were free of overhanging vegetation. Electrofishing suggested that rainbow trout were the only common fish in the study area.

Three treatments were allocated. In Treatment One, 3 enclosures were stocked with seven rainbow trout (1.2 individuals m² or 26.0 gm⁻²) collected from the Tongariro River. This stocking rate was based on earlier catch data obtained from downstream sites and was near the top end of the natural density range observed. Trout were size-matched among enclosures so that all 3 enclosures contained the same size range of fish. In Treatment Two all trout were removed from 3 enclosures. In Treatment Three, 3 plots were not enclosed by netting and these acted as "netting-effect" controls. This meant that aquatic macroinvertebrates in the unfenced control plots were exposed to natural levels of trout activity.

A stratified Latin square design was used in treatment allocation (Fig. 4.2, Plate 4.1).

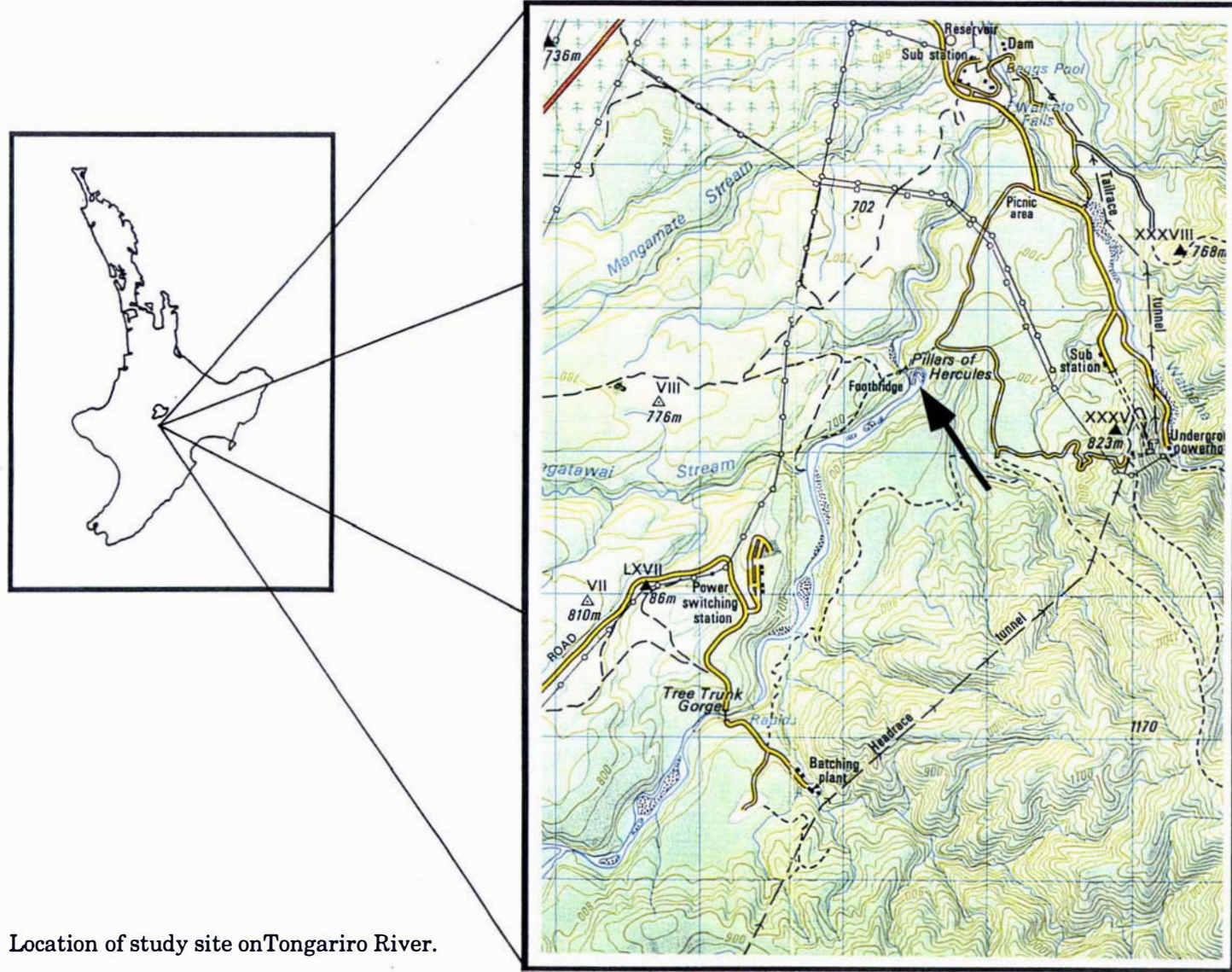


Fig. 4. 1 Location of study site on Tongariro River.

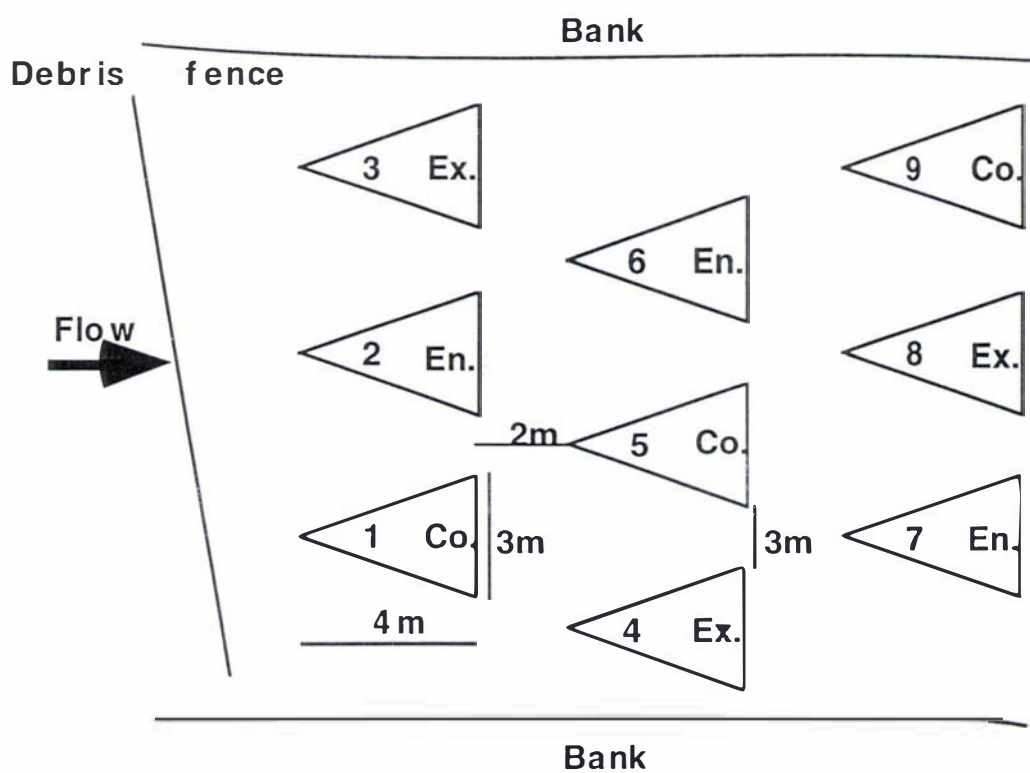


Fig. 4. 2 Experimental set-up showing position and relative dimensions of plots. Treatment allocation is denoted: En. = Trout enclosed; Ex. = Trout excluded; and Co. = Control. Numbers used to identify plots. Figure not to scale.



Plate 4. 1 View of experimental plots in Tongariro River.

4. 2. 3 Sampling

Sampling commenced on 21 April 1993 and concluded on 27 April 1993.

Two one-hour drift samples were collected from each plot at 0, 24, 72 and 144 hours after the start of the experiment. Samplers consisted of a rectangular "Marley" guttering sump (area = 0.0053m²) to which a 1m long net (0.5mm mesh) was attached. The guttering sump and attached net were supported by two metal stakes which were driven into the substrate (Field-Dodgson 1985). The sampler intake was positioned approximately half way between the water surface and river bed. Each sampler was placed directly behind its assigned plot in an area of maximum flow. Water velocity at the mouth of each sampler was measured using a velocity head rod at the commencement and completion of each sample. Sampling commenced at 0600 hrs on each occasion and terminated at 0700 hrs. This time frame was selected as it corresponds with the morning peak feeding time of blue ducks (Eldridge 1986, Veltman & Williams 1990). Captured insects were placed in 70% ethanol for later sorting and identification. Invertebrates were examined using a Zeiss stereoscopic microscope (mag. 10-40x) and identified using Winterbourn & Gregson (1989).

Two benthic macroinvertebrate samples were also collected from each plot in each sampling interval. Benthic samples were collected following the collection of drift samples using a 0.01m² Surber sampler. Sample sites were chosen at random within each plot. Two Surber samples equated to 0.3% of the total plot area and by the end of the study 1.3% of the substrate in each plot had been examined. No benthic samples were collected within 300 mm of the netting to avoid any edge effect caused by the netting (see Thorp & Bergey 1981). Benthic samples were processed in the same manner as drift samples.

After 144 hours the trout were removed from the Treatment One plots and their stomach contents examined.

4. 2. 4 Data analysis

Community-level responses to trout presence were evaluated by employing total abundance and/or biomass data. Biomass was calculated

for all aquatic macroinvertebrate prey consumed by trout and a representative proportion of each taxonomic group in the benthic samples using the length / dry-weight equations obtained in Chapter Two.

To test the hypothesis that trout foraged selectively, Ivlev's (1961) selectivity index was calculated at Order level. Ivlev's index compares the relative proportion of each prey item with the relative proportion initially available using the following equation

$$\text{Ivlev's index} = \frac{Ne/Se - N/S}{Ne/Se + N/S}$$

where Ne - is the proportion of type I prey eaten,

Se - the proportion of type I prey initially present in the foraging environment,

N - the proportions of type I, II, III,... initially present in the foraging environment,

S - the proportions of type I, II, III,... eaten.

The values of this index range from zero to minus one for increasing negative preference, and from zero to plus one for increasing positive preference. Ivlev's index is applied to both numerical and biomass data in selectivity assessment.

Analysis of Covariance (ANCOVA) was used to examine treatment effect over time. Due to large variations in insect numbers and to meet the assumptions of normality, testing was conducted on natural log + 1 transformed data. In all cases, statistical significance was set at $P < 0.05$.

Community diversity was calculated using Shannon's diversity index.

4.3 Results

4.3.1 Macroinvertebrate assemblages

Chironomidae larvae were present at very high densities at the time of conducting this experiment and dominated the benthos both in biomass and in numbers (Fig. 4.3). Trichoptera larvae were also relatively

numerous with the algae piercing *Oxythira albiceps* being the most common. Ephemeroptera and Plecoptera were not well represented in the benthos at the start of the experiment, together making up less than 10% of number and biomass.

Initially the macroinvertebrate community present in all treatments was similar although Treatment Two (trout excluded) plots contained slightly higher numbers of Trichoptera. At this time the density of macroinvertebrates in all plots was in the order of 1000s per m².

4. 3. 2 Trout diet

Trout consumed both benthic and terrestrial macroinvertebrates, but benthic macroinvertebrates dominated trout diets. Fifteen categories of benthic macroinvertebrates were discriminated (Fig. 4. 4). Trichoptera made up the greatest proportion of the diet in both numerical and biomass terms (Fig. 4. 4) with Hydrobiosidae being the most frequently consumed Trichoptera. Ephemeroptera, Plecoptera and Trichoptera proportions in trout stomachs exceeded their relative proportions in the benthos, indicating high preference by trout for these items. Chironomidae (Diptera), which composed the vast majority of the benthos both numerically and in terms of biomass were greatly under-represented in trout diet and consequently had a high negative selectivity index (Fig. 4. 3).

4. 3. 3 Trout effect

Following 144 hrs no significant difference in total macroinvertebrate abundance was detected between treatments ($F_{2, 33} = 0.081$ $P = 0.923$). However, diversity was significantly modified in the presence of trout with epibenthic fauna diversity being greater in plots from which trout were excluded ($F_{2, 33} = 4.901$ $P = 0.014$). Further examination of this disparity illustrated that the density of Ephemeroptera and Plecoptera larvae in those plots free of trout was significantly higher than in the other two treatments ($F_{2, 33} = 8.627$ $P = 0.001$). Likewise, the total numerical abundance of Trichoptera significantly declined in the three enclosures containing rainbow trout ($F_{2, 33} = 3.615$ $P = 0.038$) (Fig. 4. 5).

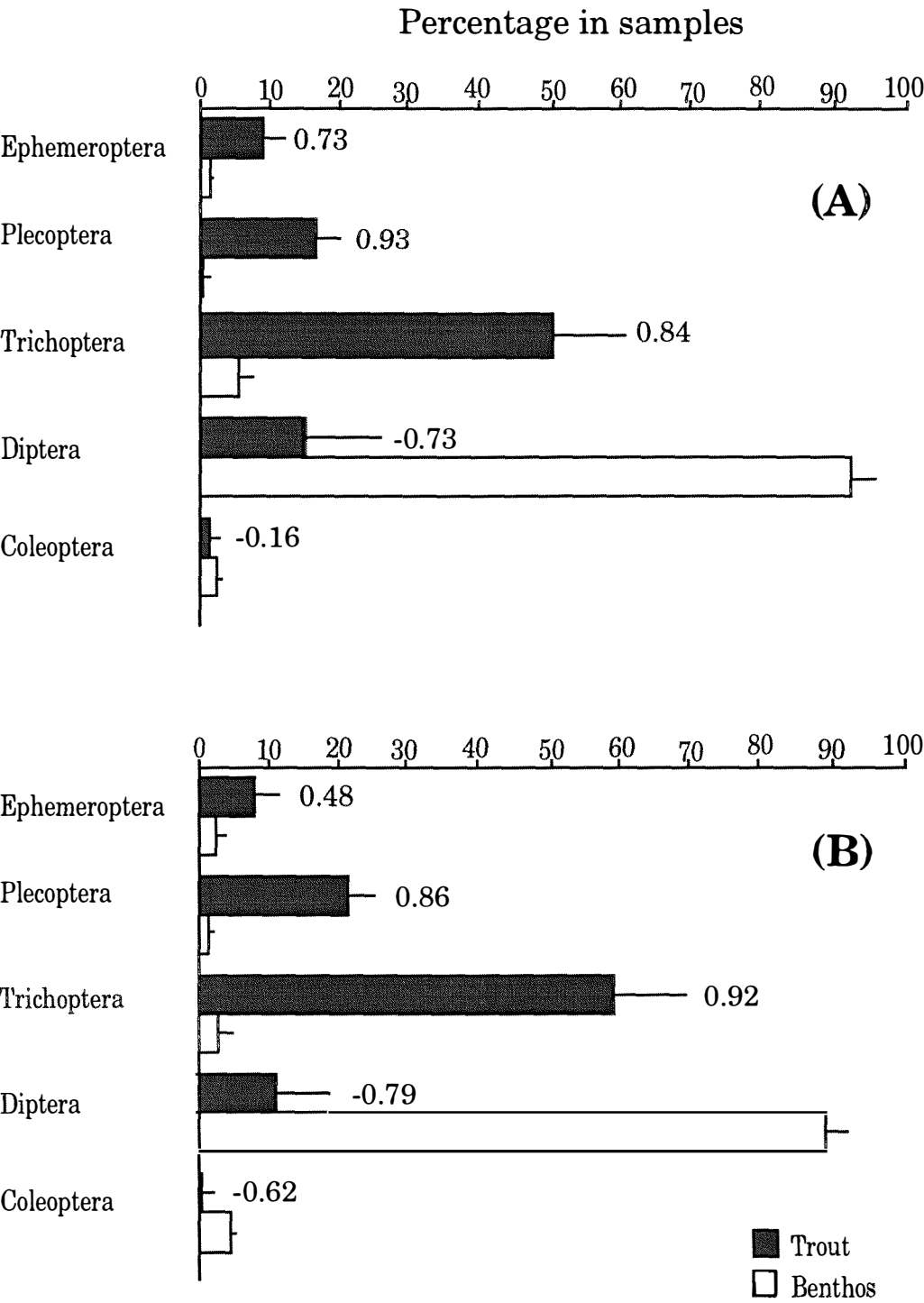


Fig. 4. 3 Relative numerical (A) and biomass (B) composition of the macroinvertebrate community in the benthos and the diet of trout inhabiting and taken from Treatment One enclosures at the end of 144 hours. The numbers are selectivity indices for each Order. Bars represent ± 1 S.E.

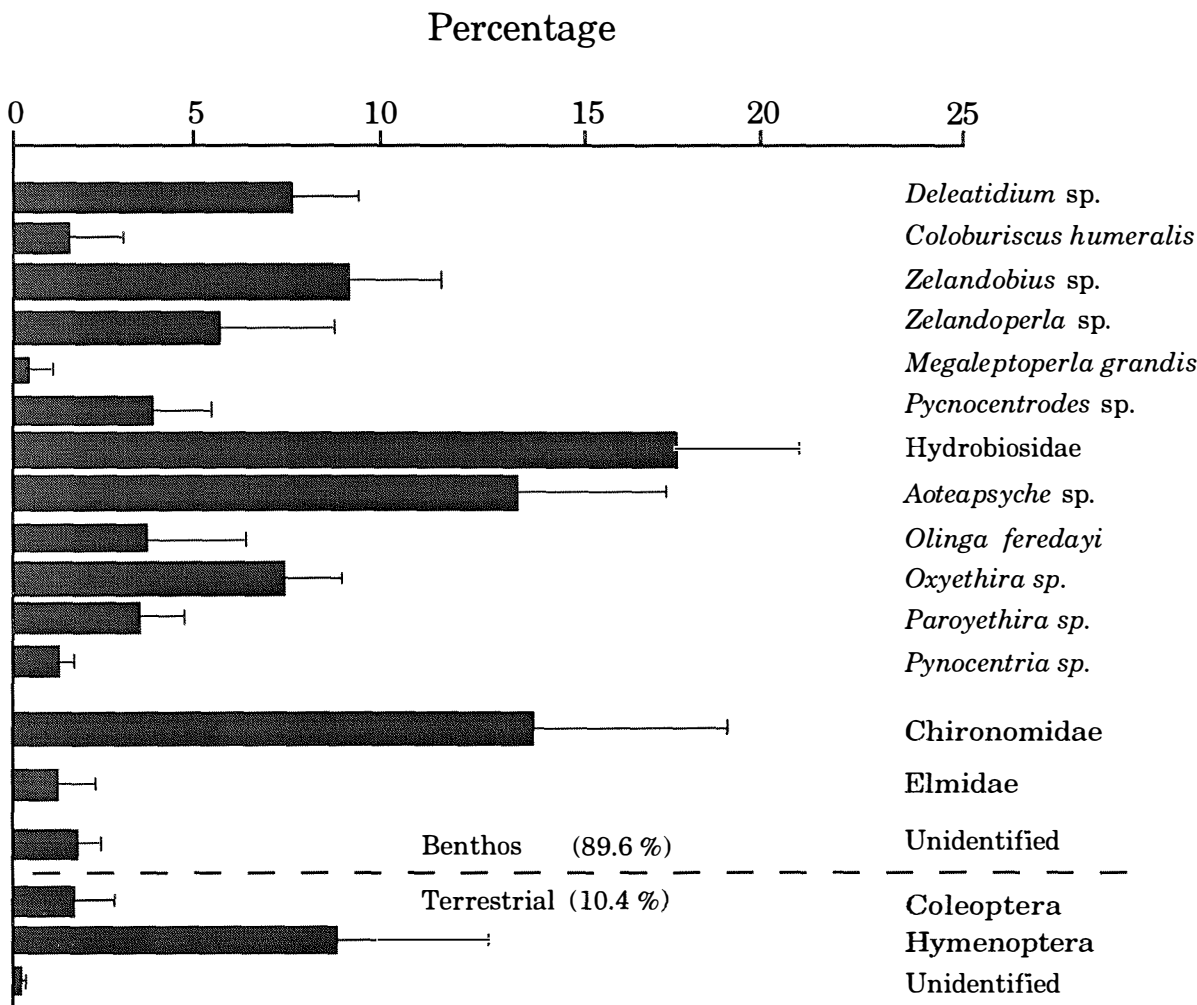


Fig. 4. 4 Relative abundance (\pm 1SE) of the different prey items in the diet of trout removed from enclosures (Treatment One).

Drifting insect densities ranged from 8.4 to 74.3 animals per 10m³ of water sampled. Drift, like the benthos, was dominated by Chironomidae larvae. Trichoptera also illustrated a propensity to drift composing 10 to 30% of drift at each sampling (Fig. 4.6).

In plots with no trout the total number of insects entering the drift was less than that from the other treatments ($F_{2, 33} = 3.121$ $P = 0.057$). Where trout had access to benthic insects, drift rates remained constant over the duration of the experiment. At Order level no treatment effect was detected for either the number of drifting Diptera ($F_{2, 33} = 2.409$ $P = 0.106$) or Trichoptera ($F_{2, 33} = 1.271$ $P = 0.294$). However, a significant treatment effect was detected for the number of drifting Ephemeroptera ($F_{2, 33} = 10.188$ $P < 0.001$) with approximately three times as many Ephemeroptera drifting from Treatment Three (no netting control) as from either of the other two treatments.

To explore the effect of trout predation further, the sizes of macroinvertebrates present at 0 and 144 hours in the trout-free and trout-present plots were compared. Owing to the low numbers of specimens of the larger sizes, data were pooled for each treatment for each sampling interval. The size structure of the benthic macroinvertebrate communities at 0 hours was similar in all plots. A skew in size distribution towards smaller size categories was primarily a result of the predominance of Chironomidae (Fig. 4.7A). At the community level, changes in insect size-distribution between treatments were detected at 144 hours. Large insects (>7.1 mm) were absent from the benthos in those plots containing trout at the end of the experiment whereas, the relative abundance of such large insects was higher at the end of the experiment in the trout-free plots than at the start (Fig. 4.7B).

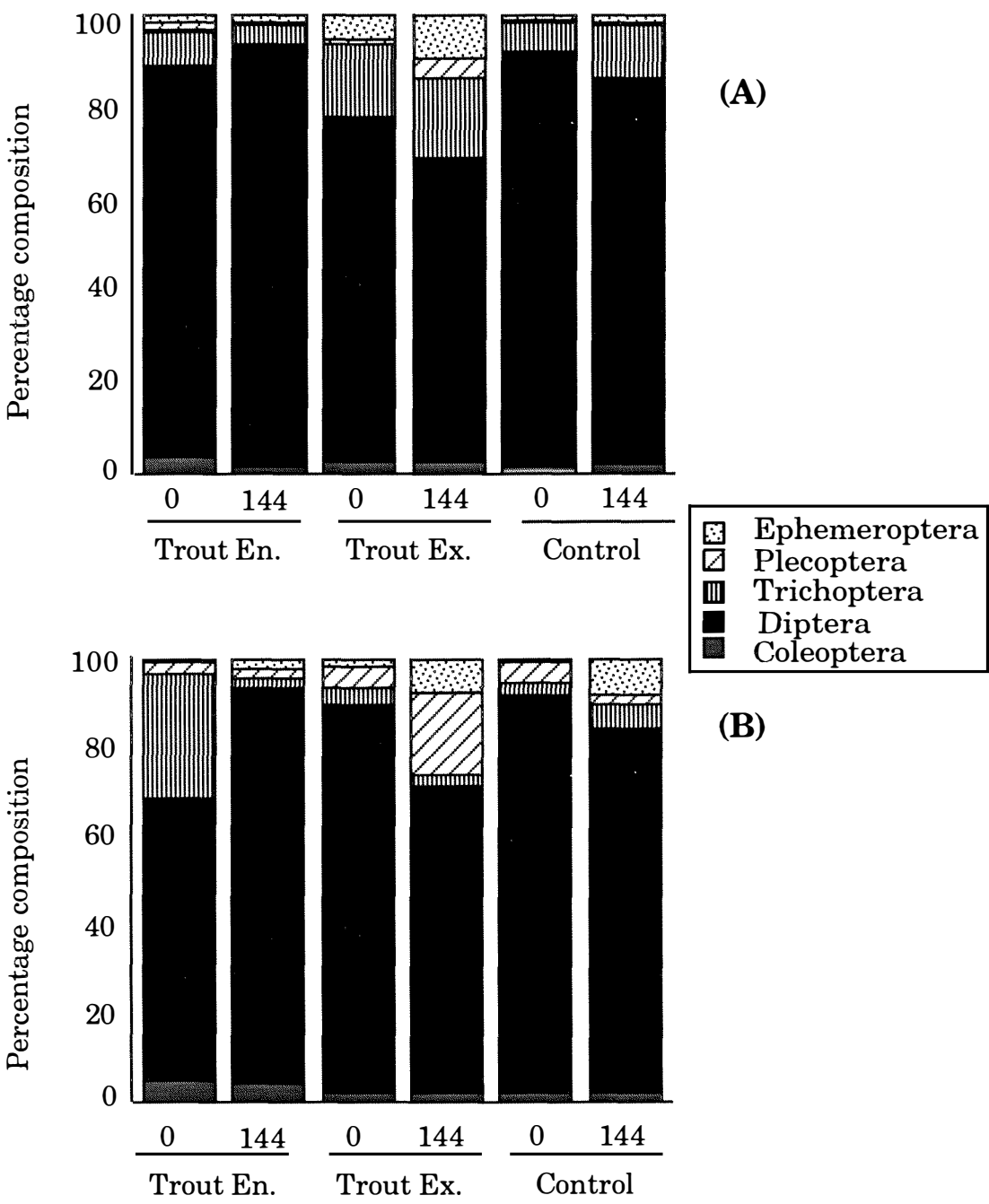


Fig. 4. 5 Relative numerical (A) and biomass (B) composition of the epibenthic macroinvertebrate communities present in each of the three treatments at 0 and 144 hours.

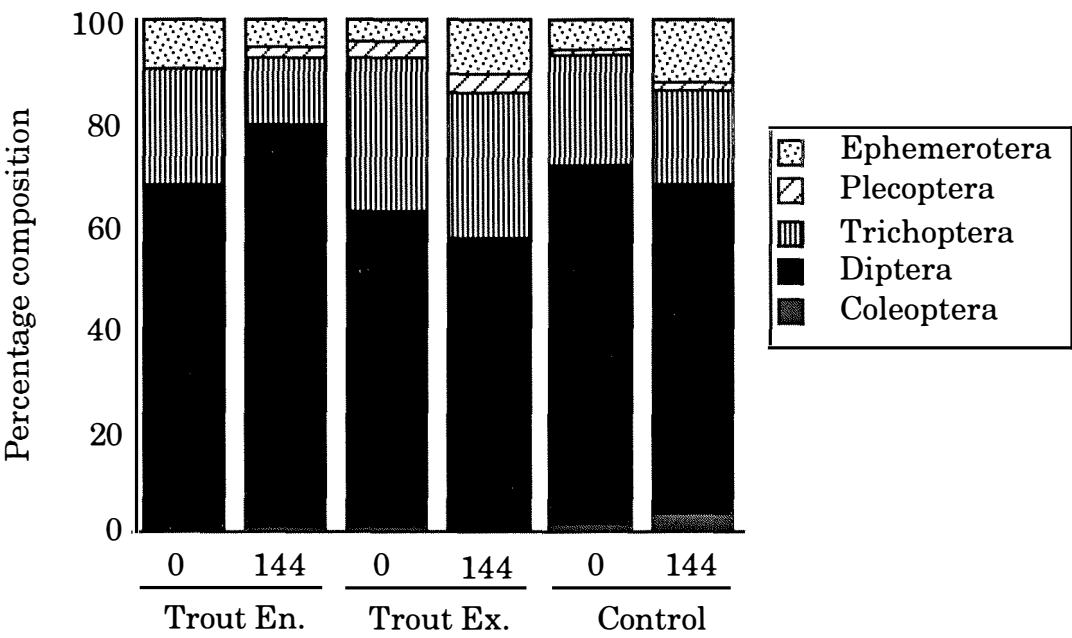


Fig. 4. 6 Percentage composition of drift based on numerical data for each treatment at 0 and 144 hours.

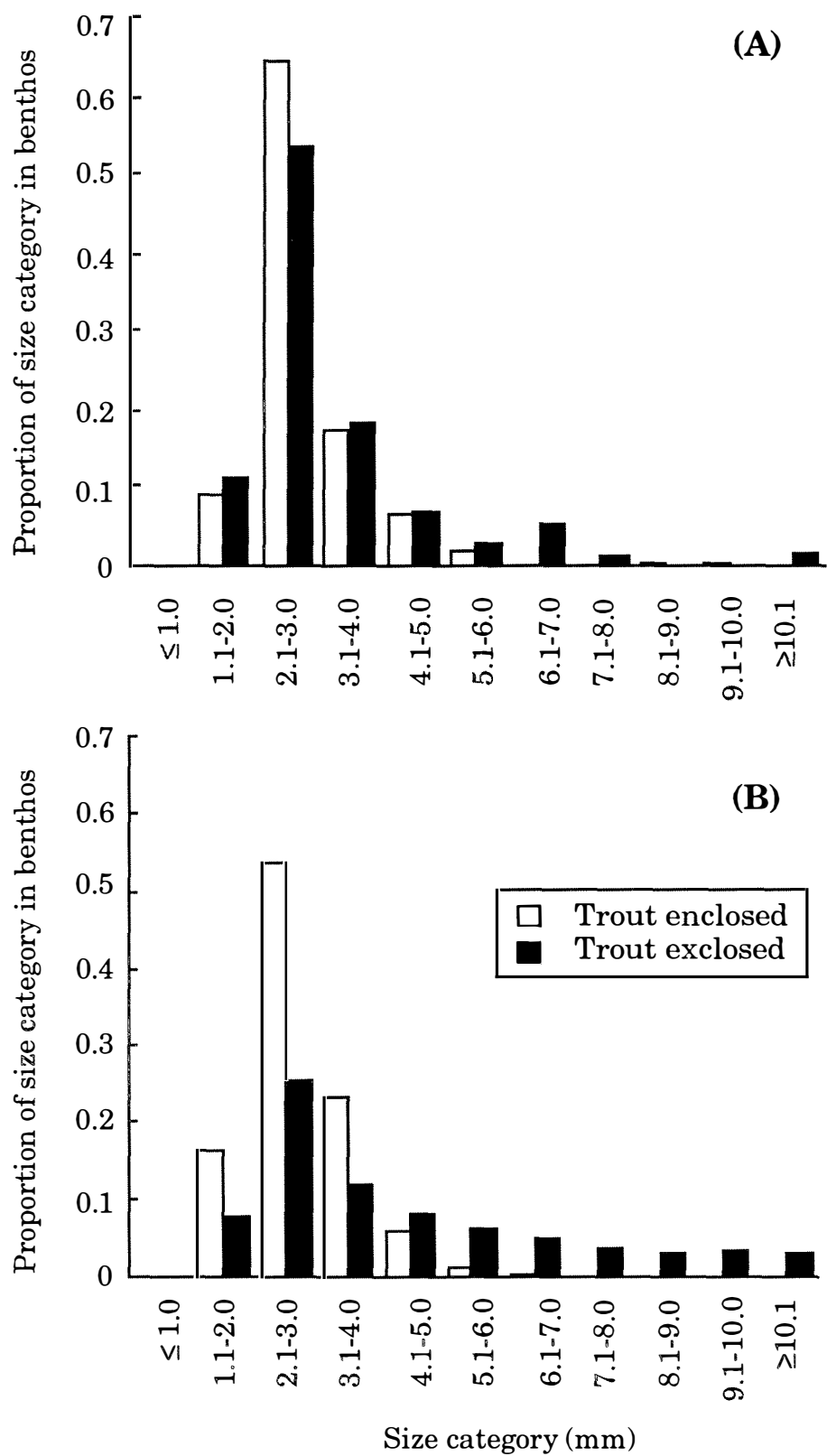


Fig. 4. 7 Size composition of the benthic macroinvertebrate community at 0 (A) and 144 (B) hours in trout enclosures and trout exclosures respectively.

4. 4 Discussion

The macroinvertebrate community found in Tongariro River at the time of conducting this experiment was typical of that common to New Zealand stony rivers with high water quality (Quinn & Hickey 1990). During the experimental period, Diptera dominated the benthos both in terms of numbers and biomass. Work conducted by Dedual & Collier (1995) on the same river in December 1992 found a similar community. However, despite this dominance, Chironomidae were significantly unrepresented in the diet of trout removed from the enclosures, representing less than 18% both by numbers and by biomass. This low incidence of Diptera in the diet of trout inhabiting Tongariro River has also been reported by Dedual & Collier (1995) and Stephens (1989). Stomach contents of the trout removed from Treatment One plots in my experiment, showed Trichoptera larvae to be the major prey item consumed with trout showing a high preference. Ephemeroptera and Plecoptera were also positively selected for. This pattern of trout predation has been reported by several other studies (Egglishaw 1967, Bisson 1978, Peddley & Jones 1978, Glova & Sagar 1991, Kusabs & Swales 1991). It has been suggested (Dedual & Collier 1995) that this negative preference illustrated by trout for Diptera relates to the small relative size of these prey. As trout rely heavily on their vision when foraging, these smaller prey items may be less obvious relative to the more easily identified larger prey.

The results presented here support the hypothesis that trout can influence the structure of benthic macroinvertebrate communities. At the end of this experiment trout had significantly reduced the densities of Ephemeroptera and Plecoptera larvae and lowered the diversity of the benthic macroinvertebrate communities. However, despite these declines, no trout-induced reduction in the combined total density of benthic macroinvertebrates was detected. This finding conflicts with several similar studies that reported significant trout-induced reductions in total macroinvertebrate density (Schofield *et al.* 1988, Dudgeon 1991, Bechara *et al.* 1993, Flecker & Townsend 1995). However, Bechara *et al.* (1993), who conducted an experiment in a pebble-bottomed forest stream in Canada, reported that trout foraging reduced the density of certain prey groups without significantly affecting the total macroinvertebrate

density. Their data suggested that only a large change in the total macroinvertebrate density could be detected, while only relative small changes in the densities of each individual prey group were necessary to yield significant results. This may in part explain the absence of any significant trout effect on the total density of benthic macroinvertebrates in plots containing trout. The very high densities of Diptera relative to other taxa likely countered the decline in the other less well represented taxa.

Bechara *et al.* (1993) also suggested that the lack of significant trout-induced reductions in the overall density of macroinvertebrates, could arise from a corresponding increase in smaller-sized taxa, such as Chironomidae. Like all biological systems, aquatic communities are dynamic and are composed of multiple trophic levels. If trout remove predatory insects this may result in flow-on effects which lead to higher densities of insects at lower trophic levels. In Bechara's *et al.* (1993) experiment, Chironomidae abundance increased as a result of decreased competition and predation. In contrast my experiment did not record a similar significant increase in the numbers of Chironomidae, perhaps because the short duration of my experiment did not allow sufficient time for Chironomidae to significantly increase their densities.

Ephemeroptera and Plecoptera responded rapidly to the different treatments, with densities of these insects being significantly higher in plots free of trout. A similar finding was reported by Schofield *et al.* (1988) who found that caddis larvae *Plectrocnemia conspersa* quickly colonised and reached high numbers in fishless enclosures while populations of the same insect remained relatively low in enclosures containing brown trout. Mayfly and stonefly taxa are highly mobile and disperse by crawling through the substrate or drifting downstream in the current. Potentially, this mobility allows these animals to respond quickly to changes in their environment, giving them the opportunity to reside in the most favourable microhabitats. Such an ability to quickly respond to external pressures is likely to be an important attribute for survival in lotic environments which experience major stochastic events and temporal uncertainty like flooding.

At the termination of my experiment (6 days) it was apparent that trout preferentially fed on larger sized prey, a result that I also showed in

Chapter 3. Size and prey-selective visual feeding by trout has been described by Ware (1971, 1972), McLennan & MacMillan (1984), Newman & Waters (1984), and Kusabs & Swales (1991). Schofield *et al.* (1988) suggested that brown trout preferred to take large *Plectrocnemia conspersa* while data presented by Bisson (1978) showed that diet selectivity in juvenile rainbow trout was positively correlated to prey size. Bechara *et al.* (1993) found that foraging brook trout significantly reduced the density of large to medium-sized benthic insects. The decline in the abundance of Ephemeroptera and Plecoptera in those plots containing trout is consistent with a trout preference for larger prey as these taxa composed the majority of the larger macroinvertebrate size classes. Similarly, the low trout preference for Chironomidae larvae, which dominated the smaller size classes is also consistent with general size-selection behaviour.

Drift densities recorded at the commencement of the experiment were consistent with those documented by Dedual & Collier (1995) for the Tongariro River. The similar taxonomic composition of the drift and benthos suggested that most taxa were drifting in proportion to their abundance. No differences in the drift densities arising from plots with and without trout were observed. Research by McIntosh *et al.* (1994) on *Nesameletus* sp. (Ephemeroptera) collected from sites within New Zealand illustrated that this mayfly has an increased propensity to drift in the presence of introduced brown trout. McIntosh *et al.* (1994) suggested that this behaviour may be adopted by the mayfly in an attempt to avoid trout predation by drifting from areas of trout presence. My results and McIntosh *et al.* (1994) differ from the findings of Bechara *et al.* (1993) who reported a significant decline in the density of drifting macroinvertebrates, in particular Ephemeroptera nymphs in the presence of brook trout. They suggested that in the presence of trout, nymphs tend to remain in the substrate to reduce the risk of predation. Both explanations are however, in keeping with the increasing evidence that aquatic insects can detect fish presence using chemical and/or physical cues and thereby modify their behaviour to minimise risk (Williams & Moore 1985, Anderson *et al.* 1986, Kohler & McPeck 1989).

The results of my study indicate that biotic factors in the form of trout can be an important structuring agent during periods of stability in lotic environments, even if such effects are undetectable on a larger scale (Chapter 3).

Chapter Five

Foraging by blue ducks in artificial streams stocked with trout

5.1 Introduction

The field experiment presented in Chapter 4 showed that introduced rainbow trout altered the aquatic macroinvertebrate communities within enclosures in a river. Macroinvertebrates found in Chapter 3 to be prominent in the diet of blue ducks declined in abundance in enclosures containing trout.

High fish densities have caused larger foraging ranges and durations in waterfowl populations (Pehrsson 1984, Des Granges & Rodrigue 1986, Hill *et al.* 1986, Hunter *et al.* 1986), and low duckling survival (Phillips & Wright 1993, Hill *et al.* 1986). Several other studies have shown waterfowl to prefer rivers and lakes containing low densities of insectivorous fish (Eriksson 1979, Pehrsson 1984, Phillips 1992). Phillips & Traill-Stevenson (1988) analysed waterfowl census data following fish removal from Main Lake, Linford, England. They recorded a significant increase in aquatic insect numbers and consequently, waterfowl densities following the eradication of fish. Such findings indicate an ability of birds to detect and react to alterations in food resources thereby maximising the net rate of food intake (Eriksson 1979, Phillips 1992).

If blue ducks react in much the same way as the waterfowl studied by Phillips & Traill-Stevenson (1988) then, to maximise the net rate of food intake, blue ducks may leave stretches of river where trout presence has reduced macroinvertebrate resources and raised the energetic costs to blue ducks of feeding. If blue ducks detect and respond negatively to trout-induced changes to macroinvertebrate communities, or if the energetic costs in relation to returns become too great, then the density of ducks on a river may decline as birds leave for better feeding areas.

To examine trout-duck trophic interactions I sought to test the hypothesis that blue ducks perceive and respond to trout-induced alterations of stream macroinvertebrate communities. I predicted that blue ducks would spend more time and forage more often in patches free of trout influence.

To achieve this I designed an experiment consisting of two identical artificial streams housed in an aviary. Trout were introduced to one of the two channels where they fed on stocked benthic macroinvertebrates. One blue duck was then liberated into the aviary and its foraging pattern recorded. The foraging behaviour of four different birds was examined twice to assess if they chose to feed in the trout-free channel where trout had not altered the amount or type of food available.

At a theoretical level the experiment tests some of MacArthur & Pianka (1966) and Charnov's (1976) optimal foraging model predictions. Their model was based on the premise that a forager employs a strategy that maximises its net rate of food intake. Such early or first generation models were deterministic in nature (Kamil *et al.* 1987), assuming environmental factors such as prey density were constant throughout time. However this is seldom the case in natural environments where foragers must deal with spatial and temporal unpredictability. Such environmental stochasticity may greatly influence the way a forager allocates its efforts. This experiment therefore adds empirical data about patch use in an environment where the forager must deal with changing patch quality.

5.2 Methods

5.2.1 Experimental system

Experiments were conducted in an aviary at Staglands in the Akatarawa Valley (175° 07' 6" E 40° 59' 7" S), approximately 30 km north of Wellington. The aviary measured 2 x 4 x 2 m. Two identical flow-through channels measuring 4 x 0.5 x 0.3 m were constructed within the enclosure. Each channel was built using 300 x 25 mm tannalised timber and lined with 250 µm clear plastic sheeting. Water from a first order stream was gravity fed into the channels via ethylene piping (Fig. 5. 1). The flow in each channel was monitored by separate v-notch weirs and

maintained at approximately 0.22 l s^{-1} by adjusting taps located on the inflow pipes. To equalise the flow over the width of the channel, water entered each channel near the bottom at one end via a diffusing nozzle (Plate 5. 1) The outflow from each channel was covered with 0.5mm mesh to stop macroinvertebrates drifting out of the system.

The bottom of each channel was filled with cobble-sized stones collected from Akatarawa River. All cobbles were cleaned of aquatic macroinvertebrates, but not periphyton, before being placed in the channels. Four clay pipes were positioned equi-distant along the channel length to act as refuges for trout (Plate 5.1).

Water temperature ranged from 9° to 11° C during the duration of the experiment and at no time did water temperature differ between channels.

5. 2. 2 Macroinvertebrate prey

Aquatic macroinvertebrates were collected from Akatarawa River. For each trial, 44 kick samples of 20 seconds duration were collected. Twenty-two samples were randomly assigned to each channel establishing a mean ($\pm 1\text{SE}$) macroinvertebrate density of $4806 \pm 1201 \text{ m}^{-2}$. This represented an macroinvertebrate density in the range recorded by Veltman *et al.* (1995) and Collier & Wakelin (1992) for rivers sustaining blue duck populations. Subsequent sampling of aquatic macroinvertebrates was facilitated by four 0.053m^2 metal trays placed equi-distant along the length of each channel. Each tray was embedded in the cobbles on the channel floor. Insect sampling was conducted by lifting each tray and counting its contents. The tray and its contents was then returned to its original location.

5. 2. 3 Trout

Hatchery-reared rainbow trout with fork lengths ranging from 70 to 80 mm were used in this experiment. Trout biomass in those channels to which trout were assigned was approximately 52.5 gm^{-2} (7.5 individuals m^{-2}). This was achieved by placing 15 trout in each channel. At the end of each trial, trout not used for diet examination were held in Stagland's trout pools.

5. 2. 4 Blue ducks

Four captive-reared male blue ducks of similar age (approximately 1 year) were used in the experiment with each bird being used in two trials. These birds originated from the Ducks Unlimited's captive breeding programme. Blue duck foraging was recorded using a purpose-built infra-red beam system. Separate beams were directed down the length of each channel as shown in Figure 5. 1 and worked in much the same way as those common at shop entrances. When the foraging bird interrupted a beam, the incident and length of foraging activity was plotted on a chart recorder for later analysis (Plate 5. 2).

5. 2. 5 Experimental design

Experimentation commenced on the 12 of April, 1994 and concluded on the 14 of July 1994. The first component of the experiment was to check that neither channel had a greater rate of macroinvertebrate mortality and to determine the mortality in the absence of predators. This was achieved by stocking both channels with macroinvertebrates and sampling macroinvertebrate numbers in both channels 24, 48, 96 and 144 hrs later to check the rate of mortality. This comparison was replicated twice.

The second component of the experiment involved the recording of blue duck foraging. Treatments assigned for each experimental trial involving blue ducks are summarised in Table 5. 1. Insects and trout were introduced to channels 96 hours preceding the introduction of a duck. This lead to a trout-induced difference in macroinvertebrate density between the channels. After 96 hours a blue duck was introduced and his foraging activity recorded over the next 72 hours. Macroinvertebrate samples were collected at 96, 144 and 168 hrs during each trial. Duck faeces and the stomach contents of 3 trout were collected at the termination of each trial to measure diet composition.

Table 5. 1 Treatment allocation for the eight trials involving blue ducks. T= trout introduced to channel, N= no trout introduced to channel.

Trial	Bird number	Channel	
		A	B
1	1	T	N
2	2	N	T
3	1	N	T
4	2	T	N
5	3	T	N
6	4	N	T
7	3	N	T
8	4	T	N

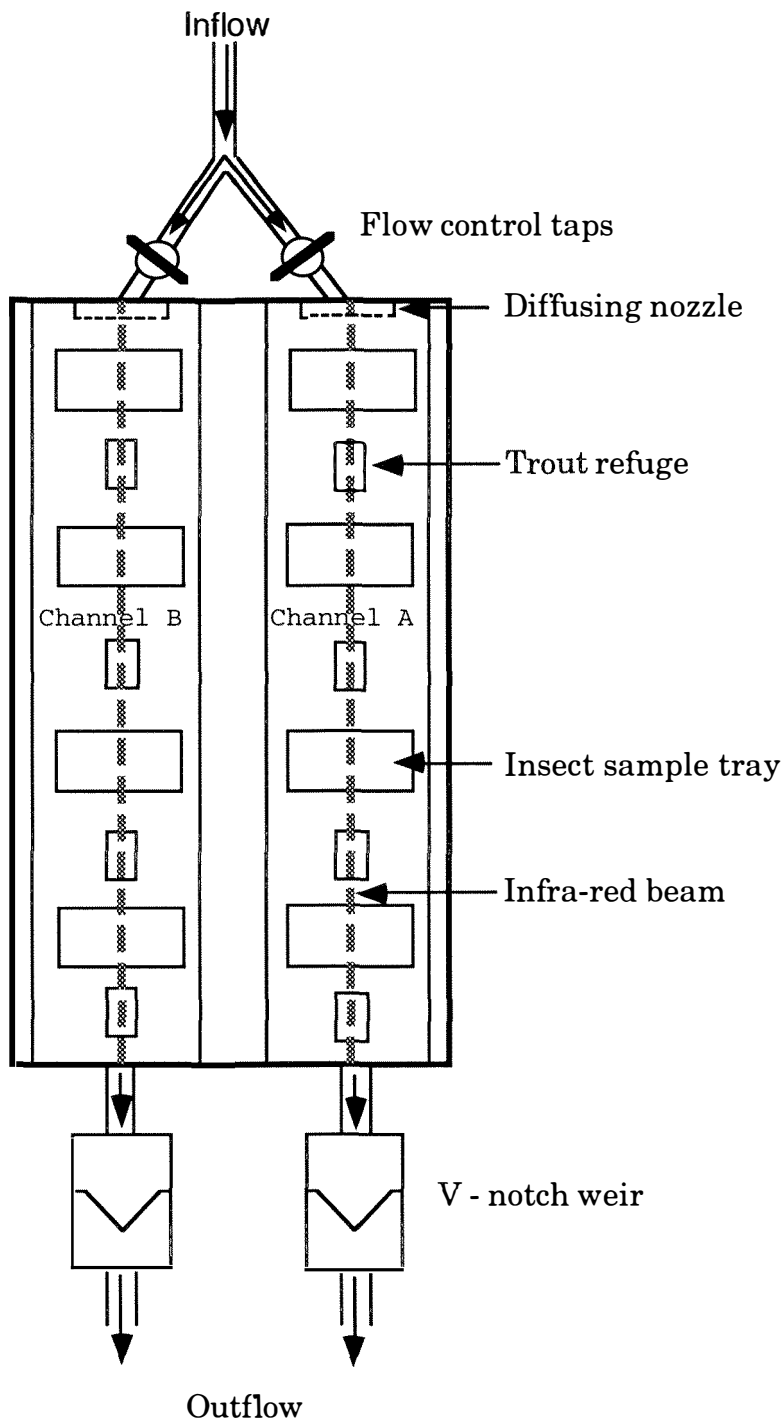


Fig. 5. 1 Diagram of experimental system. Aviary not shown and not to scale.



Plate 5. 1 Experimental channel. Note nozzle on inflow designed to produce even flow over the width of the channel. The clay pipes on the channel bed provided cover for trout. The metal macroinvertebrate sampling trays can also be seen.

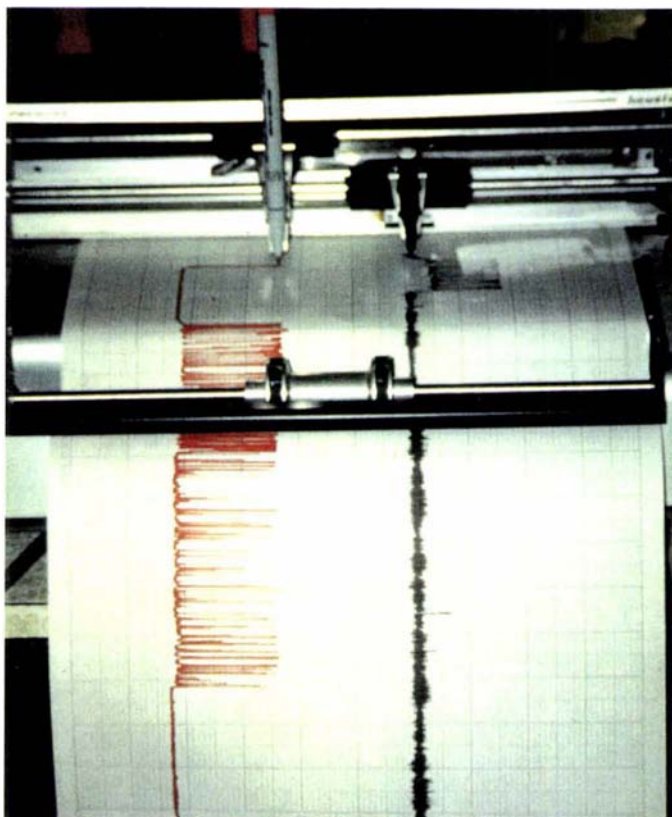


Plate 5. 2 Chart recorder and print out registering foraging activity (spikes) on the two channels.

5.3 Results

5.3.1 Prey mortality

Prey mortality rates were highest during the first 24 hrs in both trials (Fig. 5. 2a, b). Losses of 54.9% and 55.3% were recorded for channels A and B respectively during trial one and 52.7% for channel A and 43.0% for channel B in trial two. Pooled mortality rates gave a mean value of $51.5 \pm 2.5\%$ for the first 24 hours. After this initial period of high loss, mortality among the aquatic macroinvertebrates decreased. Over the last 48 hrs a mean mortality rate of $24.8 \pm 9.1\%$ was recorded.

There was a high degree of similarity between channels in mortality rates for both trials (Fig. 5.2). No significant differences between the two slopes in either trial was detected (trial 1: $t_6 = 0.02$ $P > 0.05$; trial 2: $t_6 = 0.07$ $P > 0.05$). To compare the mortality rates between trials the two mortality rates recorded for channel A and B in each trial were pooled (Fig. 5. 3). The regression slopes were not significantly different ($t_{16} = 0.07$ $P > 0.05$).

To determine which macroinvertebrate taxa experienced greatest mortality during the first 24 hrs after introduction to the channels, I calculated relative mortality rates by comparing the percentage represented by a taxon in the community after 24 hrs with that at 0 hrs using the following formula:

$$RM = \frac{T_{24} - T_0}{T_0}$$

where

- RM = relative mortality,
- T_0 = percentage of taxon in community at 0 hrs,
- T_{24} = percentage of taxon in community at 24 hrs.

This index produces both positive and negative values which can be directly compared between taxa. Positive values indicate an increase in the relative proportion of a taxon over the time period while a negative value indicates that the taxon has experienced mortality resulting in a decline in its abundance (Table 5. 2).

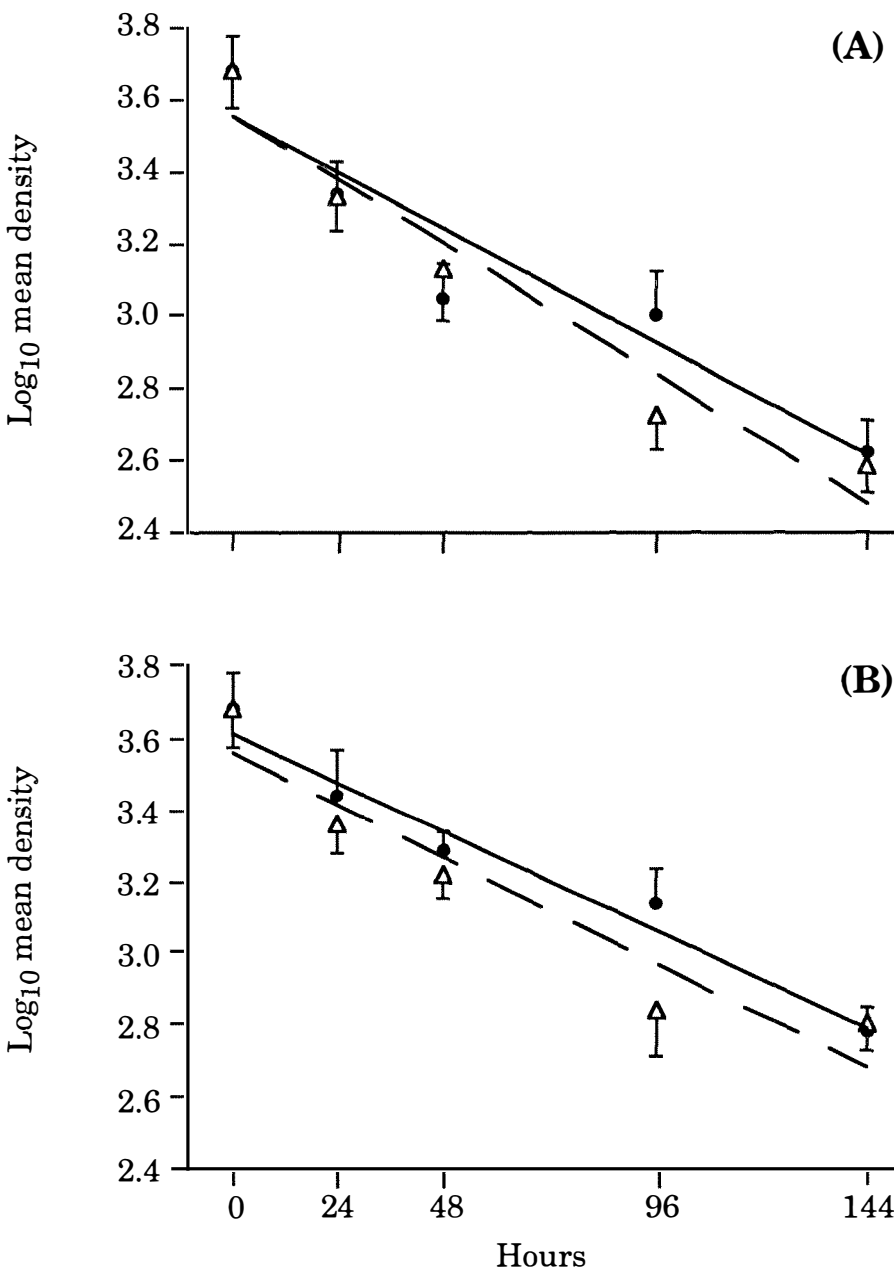


Fig. 5. 2 Plots of \log_{10} mean macroinvertebrate density (m²) over time; (A) trial 1, (B) trial 2. Channel A denoted by —●— and channel B denoted by —Δ—. S.E. bars shown.

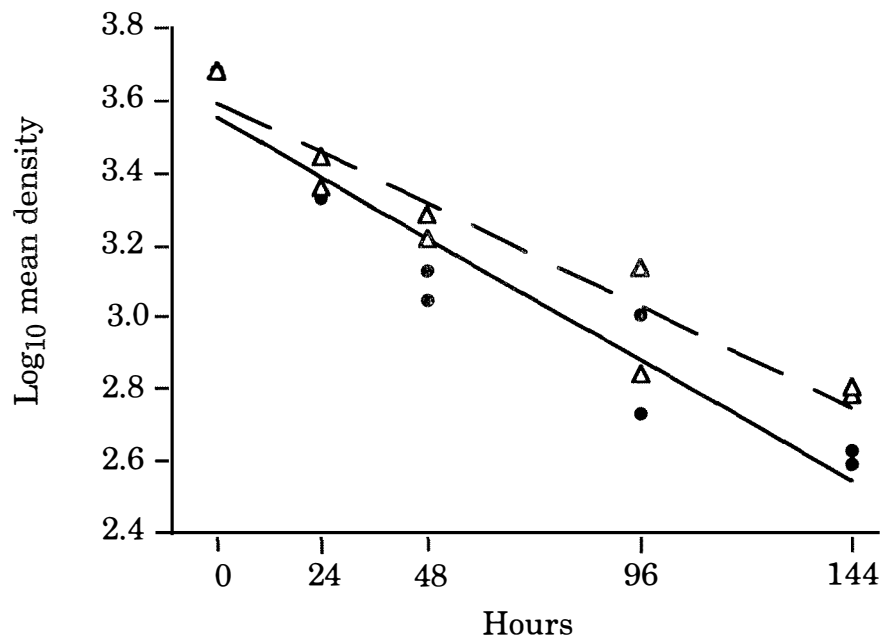


Fig. 5.3 Plot of log₁₀ mean macroinvertebrates density over time for combined data from trials 1 and 2. Trial 1 denoted by —●— (bottom line), $r^2=91.7$, trial 2 denoted by -Δ- (top line), $r^2=91.7$.

Table 5. 2 Percentage composition at 0 and 24 hrs, and relative mortality (RM) rates for taxa in experimental channels. Those taxa absent from the 24 hr samples are denoted by an "a" while "*" denotes those taxa with abundances of less than 0.1 %.

Taxon	% 0 hrs	% 24 hrs	RM
Ephemeroptera			
<i>Deleatidium</i> sp.	14.8	37.8	1.6
<i>Coloburiscus humeralis</i>	3.3	3.8	0.2
<i>Nesameletus</i> sp.	1.1	1.5	0.4
<i>Ameletopsis percitus</i>	0.1	a	
<i>Zephlebia</i> sp.	0.1	0.2	1.0
<i>Oniscigaster wakefieldi</i>	*	a	
<i>Neozephlebia</i> sp.	*	a	
<i>Acanthophlebia</i> sp.	0.2	0.4	1.0
<i>Ichthybotus</i> sp.	*	a	
<i>Mauiulus</i> sp.	*	a	
combined <0.1%	0.3	a	
Plecoptera			
<i>Zelandoperla</i> sp.	3.8	2.3	-0.4
<i>Stenoperla prasina</i>	1.0	0.6	-0.4
<i>Austroperla cyrene</i>	0.3	0.4	0.3
<i>Zelandobius</i> sp.	0.4	a	
<i>Megaleptoperla grandis</i>	0.1	a	
Trichoptera			
<i>Olinga feredayi</i>	41.4	35.8	-0.2
<i>Helicopsyche</i> sp.	3.8	1.8	-0.5
<i>Aoteapsyche</i> sp.	4.0	0.7	-0.8
Hydrobiosidae	1.1	0.6	-0.5
<i>Orthopsyche</i> sp.	*	a	
<i>Diplectronea</i> sp.	*	a	
<i>Beraeoptera roria</i>	12.8	7.4	-0.4
<i>Pycnocentrodes</i> sp.	0.2	1.2	5.0
<i>Oeconesus maori</i>	*	a	
<i>Philorheithrus</i> sp.	*	a	
<i>Pycnocentrella eruensis</i>	*	a	
combined <0.1%	0.5	a	
Diptera			
<i>Aphrophila neozelandica</i>	0.5	0.3	-0.4
Chironomidae	0.2	a	
<i>Eriopterini</i> sp.	0.2	a	
Blephariceridae	*	a	
combined <0.1%	0.02	a	
Coleoptera			
Elmidae (larvae)	7.6	3.4	-0.6
Hydraenidae (adult)	0.2	a	
Gastropoda			
<i>Potamopyrgus antipodarum</i>	0.2	a	
Megaloptera			
<i>Archichauliodes diversus</i>	2.0	1.7	-0.2

5. 3. 2 Effects of trout on benthic macroinvertebrates

All trout stomachs examined during the experiment contained aquatic macroinvertebrates. Trout exploited *Olinga feredayi* (45.7%) and *Beraeoptera roria* (25.6%) (Trichoptera) intensely (Table 5. 3). Ephemeroptera and Trichoptera comprised 91.4% of the total number of the prey consumed by trout.

Significant reductions in macroinvertebrate density and diversity (richness) were observed in 3 of the 8 trials in which trout were present. In trial 3, trout significantly reduced macroinvertebrate density but not number of taxa while in trial 8, the number of taxa was significantly reduced but not macroinvertebrate density. After 96 hours macroinvertebrate density was higher, although not significantly ($p = 0.075$) in the trout treatment than in the trout-free treatment for trial 2 (Table 5. 4).

Table 5. 3 Diet composition of trout stomachs (n = 24).

Taxon	%	Taxon	%
Ephemeroptera		Plecoptera	
<i>Deleatidium</i> sp.	4.2	<i>Zelandoperla</i> sp.	2.6
<i>Coloburiscus humeralis</i>	5.1	<i>Stenoperla prasina</i>	0.6
<i>Nesameletus</i> sp.	0.3	<i>Zelandobius</i> sp.	0.3
<i>Ameletopsis percitus</i>	0.3	<i>Megaleptoperla grandis</i>	0.3
Trichoptera		Diptera	
<i>Olinga feredayi</i>	45.7	<i>Aphrophila neozelandica</i>	0.6
<i>Helicopsyche</i> sp.	8.6	Gastropoda	
<i>Aoteapsyche</i> sp.	0.3	<i>Potamopyrgus antipodarum</i>	0.3
Hydrobiosidae	0.3	Megaloptera	
<i>Beraeoptera roria</i>	25.6	<i>Archichauliodes diversus</i>	0.6
<i>Pycnocentrodes</i> sp.	1.0	Terrestrial Prey	
		Coleoptera	2.2
		Arachnida	0.3
		Amphipoda	0.6

Table 5. 4 Mean macroinvertebrate densities and numbers of taxa (± 1 SE) after 96 hrs. Means derived from sampling trays located in each channel. Differences in mean macroinvertebrate densities in each channel were examined using Students t-test (logged density data). † denotes trout in channel.

Trial	Channel			P
		A	B	
1	Density	21.50 ± 0.75 †	64.75 ± 5.45	0.010
	Taxa	4.75 ± 0.41	8.25 ± 0.22	0.009
2	Density	57.75 ± 19.49	85.0 ± 15.24 †	0.075
	Taxa	7.25 ± 1.39	8.25 ± 0.41	0.122
3	Density	112.5 ± 13.60	59.75 ± 22.0 †	0.042
	Taxa	10.25 ± 1.14	7.75 ± 1.56	0.095
4	Density	19.0 ± 3.8 †	112.75 ± 23.4	0.042
	Taxa	6.5 ± 1.0	8.50 ± 1.0	0.041
5	Density	9.25 ± 2.5 †	19.0 ± 3.8	0.010
	Taxa	4.75 ± 0.5	6.50 ± 1.0	0.027
6	Density	39.50 ± 7.79	29.0 ± 10.76 †	0.193
	Taxa	8.75 ± 0.74	4.00 ± 1.35	0.075
7	Density	44.75 ± 8.83	38.75 ± 9.85 †	0.282
	Taxa	8.50 ± 1.52	6.25 ± 1.29	0.155
8	Density	25.25 ± 6.41 †	35.5 ± 9.63	0.282
	Taxa	4.00 ± 0.61	8.00 ± 0.79	0.010

5. 3. 3 Blue duck foraging behaviour

The ducks foraged throughout their 72 hour containment (Plate 5. 3). Aquatic macroinvertebrate fragments were recorded in all faecal samples collected at the completion of each trial.

The division of foraging visits per channel was examined (Table 5. 5). There was no significant ($\chi^2 = 0.217$, $p < 0.05$) deviation from an equal number of foraging visits in the two channels when the data from the eight trials were examined. However, a significant correlation between prey density and number of foraging visits ($r_s = 0.738$, $p < 0.05$) was found to exist. A significant correlation was also found between the proportion of total foraging time spent in a channel and the proportion of total macroinvertebrate numbers in a channel ($r_s = 0.833$, $p < 0.05$).

If blue ducks were foraging in an optimal way, they should allocate their foraging activity evenly between the channels when both channels

contain the same amount of food as there was no major cost of travelling between channels. To examine this hypothesis foraging effort, as expressed by "proportion of foraging visits" and "total time spent foraging", was examined in relation to food availability in the two channels. Theoretically when the two channels contain the same amount of food the "proportion of foraging visits" and "total time spent foraging" should be even (ie the regression should have an intercept of 0.5). However, when the "proportion of foraging visits" and "total time spent foraging" against differing food availabilities was examined for all 8 experiment trials, intercepts approximated 0.4. When trial seven was removed from the analysis the intercepts for both dependent variables more closely approximated 0.5 (Fig. 5. 4).

Trial seven deviated markedly from the general trends of the other seven trials. Although the trout-free channel contained a greater density of macroinvertebrates than the trout channel, duck 3 visited the "poor" channel significantly more ($\chi^2 = 12.5$ $p < 0.05$).

Table 5. 5 Number of foraging visits made by blue duck to "Trout" and "No trout" channels during each trial.

Trial	Foraging visits	
	No trout	Trout
1	14	7
2	39	44
3	49	45
4	52	38
5	31	14
6	88	81
7	25	57
8	90	74
Total	388	360

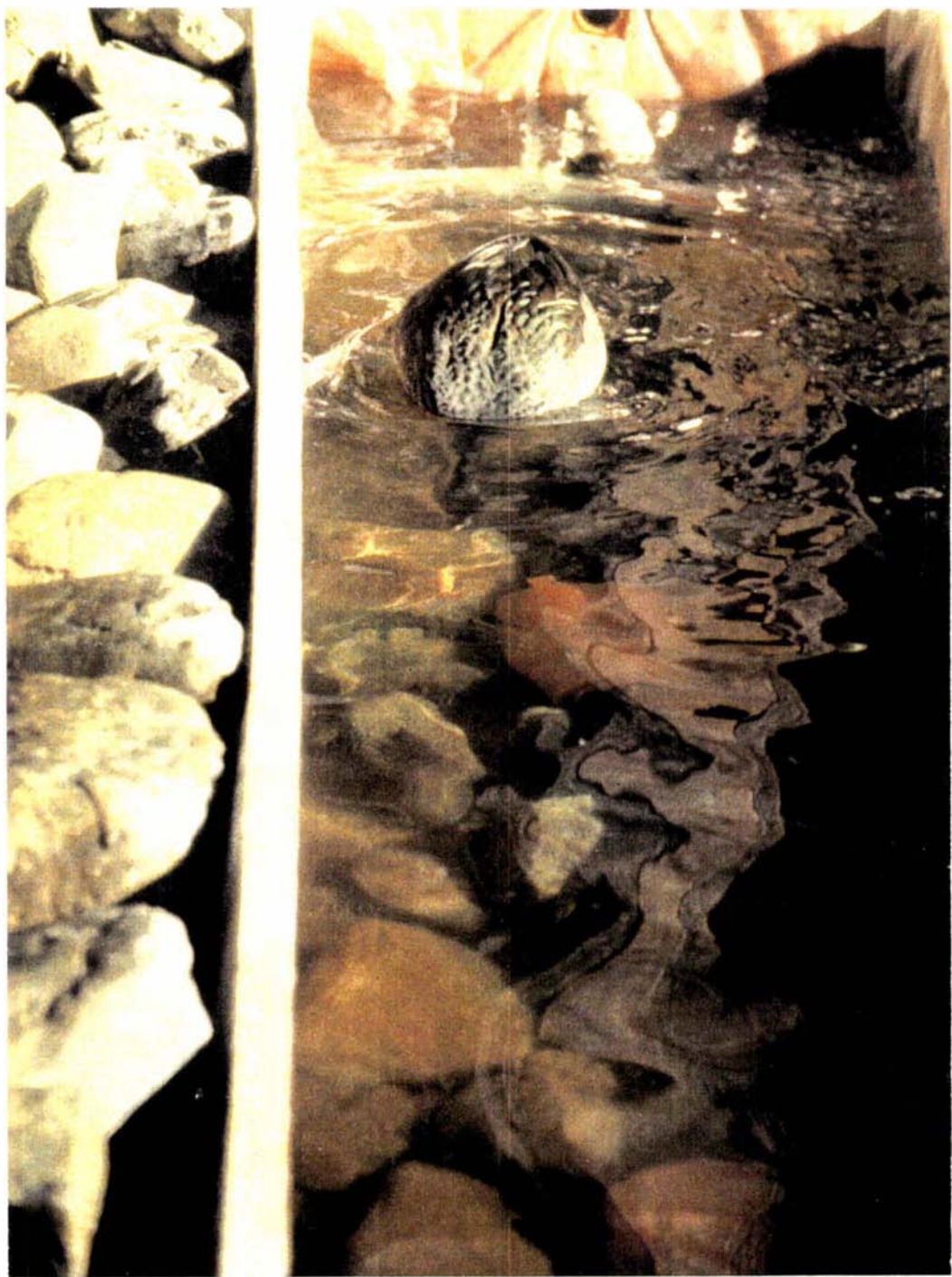


Plate 5. 3 Blue duck foraging upon aquatic macroinvertebrates in an experimental channel.

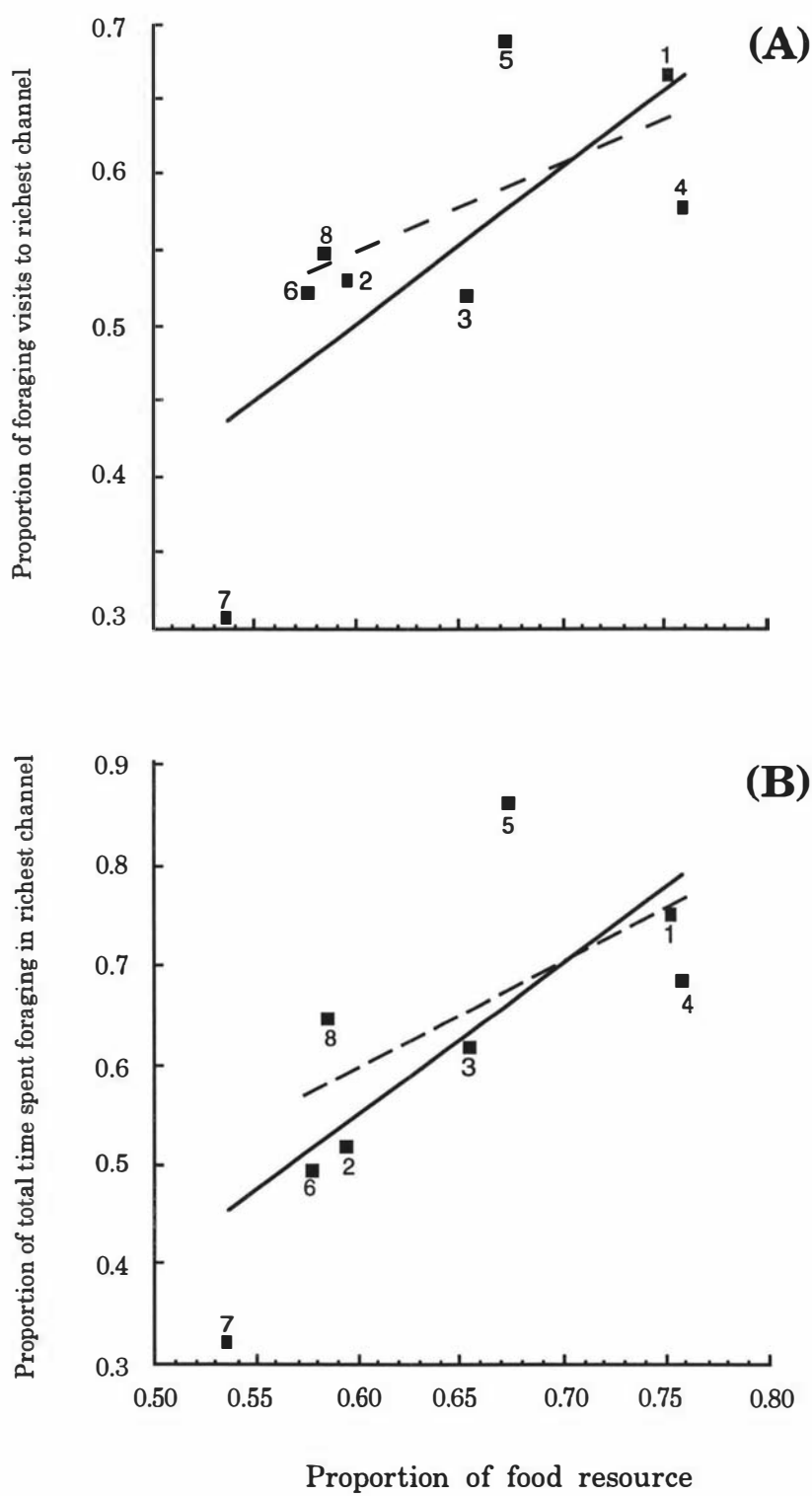


Fig. 5. 4 Proportion of foraging visits to the richest channel (channel with most food) versus the proportion of food in that channel, for all 8 trials (A). Plot (B) regresses the total time spent foraging in the richest channel against the proportion of food resource, for all 8 trials. Numbers denote trial. The regression line for all eight trials is shown (—) along with that excluding trial seven (---).

Blue ducks allocated foraging visits and total foraging time in relation to macroinvertebrate density independent of trout presence/absence. In trial 2, for example, macroinvertebrate density was higher in the channel containing trout when the duck was initially introduced. Despite trout presence the duck allocated more of its foraging effort to the richer channel (Table 5. 5). When the foraging activity during the last 24 hours was examined in four trials, the birds utilised the richer channel to a greater extent. This is of importance as in rivers and streams that contain trout it would seem that as long as sufficient food is available trout presence *per se* will not discourage blue ducks.

5. 3. 4 Patch use in a depleting environment

To assess blue duck patch use in a depleting environment I tested the null hypothesis that blue ducks reduce their use of patches in relation to declines in prey availability by examining macroinvertebrate densities and foraging activity in the first and last 24 hr periods of the experiment. The comparison was made between these two periods because the relative difference in macroinvertebrate density was most pronounced at those times (Table 5. 6).

Table 5. 6 Proportion of food resource (based on macroinvertebrate density) in channel A and B for the eight trials. Trout presence in a channel is indicated by *.

Trial	1		2		3		4		5		6		7		8	
CHAN	A*	B	A	B*	A	B*	A*	B	A*	B	A	B*	A	B*	A*	B
1st 24 hrs	0.249	0.751	0.405	0.595	0.653	0.347	0.241	0.759	0.327	0.673	0.577	0.423	0.536	0.464	0.416	0.584
Last 24 hrs	0.507	0.493	0.457	0.543	0.554	0.446	0.528	0.472	0.087	0.913	0.627	0.373	0.541	0.459	0.515	0.485

Linear regression analysis of the proportion of visits in relation to proportion of food available during the first and last 24 hour periods showed a tendency for ducks to use the richest patches. However the relationship was not significant for either period (1st 24 hr $p = 0.098$, last 14 hr $p = 0.077$) (Fig. 5. 5A). The proportion of total time spent foraging in each of the two channels was also found to relate to macroinvertebrate density during both periods, although again the relationship was not statistically significant (1st 24 hr $p = 0.099$, last 14 hr $p = 0.118$) (Fig. 5. 5B).

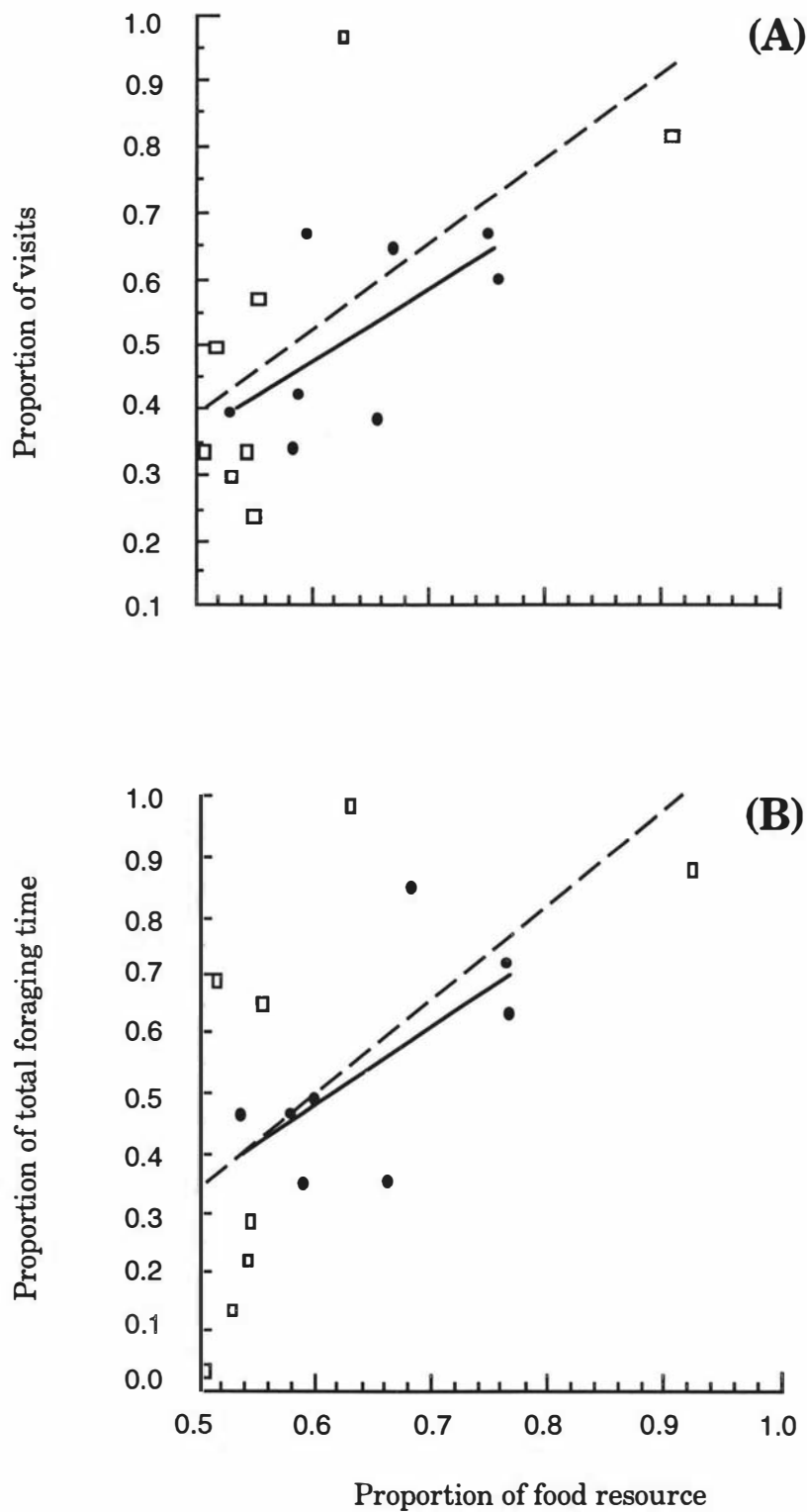


Fig. 5. 5 Proportion of visits (A) and foraging time (B) in relation to food availability during the first and last 24 hour periods (—●— first 24 hrs, ---- last 24 hrs,). Coefficient of determination for A, first 24 hrs $r^2=39.0$, last 24 hrs $r^2=43.1$; B, first 24 hrs $r^2=38.8$, last 24 hrs $r^2=35.7$.

5. 4 Discussion

5. 4. 1 Macroinvertebrate mortality

Substantial mortality was recorded for all macroinvertebrate orders following liberation into the channels. Relative mortality rates showed however that the Ephemeroptera sustained relatively less mortality than the other macroinvertebrate taxa. The high macroinvertebrate mortality recorded during the first 24 hours in the channels is probably in part the result of injury sustained during collection. Sagar (1986) suggested that reductions in macroinvertebrate densities following large flood events was, to some degree the result of physical damage caused by mass substrate movement. The relative robustness of the Ephemeroptera taxa was surprising in view of their apparent delicate morphology. Kick sampling, the technique employed to collect aquatic macroinvertebrates involves the violent agitation of the stream substrate. The delicate external gills of the Ephemeroptera would seem to be highly prone to damage during collection. Studies by Sagar (1986) and Scrimgeour & Winterbourn (1987) however, indicate that larval *Deleatidium* (Ephemeroptera) are well adapted to surviving frequent and unpredictable flood events where substantial bed movement occurs.

5. 4. 2 Trout foraging

Trout were obtained from a local trout hatchery where they were fed commercial rearing pellets. Experiments have shown that hatchery-reared trout learn to exploit natural but unfamiliar food items quickly (Ware 1971, Strameyer & Thorpe 1987), as happened in this experiment.

The diet of those trout removed from the artificial channels were similar to the trout diets detailed in Chapters 3 and 4. Likewise, other studies of juvenile trout diet obtained from natural sources have also recorded similar diet composition. Kusabs and Swales (1991) found that juvenile trout relied heavily on Ephemeroptera, Trichoptera, Plecoptera and Diptera larvae. Stephens (1989) showed that rainbow trout fingerlings (<50 mm F.L.) collected from the Tongariro river fed predominantly on Trichoptera nymphs over the winter months. Similar heavy cropping of Trichoptera has been recorded among adult rainbow trout (McLennan and MacMillan 1984).

5. 4. 3 Foraging by blue duck and optimal foraging theory

Optimal foraging theory predicts that animals try to maximise their net rate of energy intake (Charnov 1976). To achieve this goal, a forager should forage in those places and in those ways that maximise returns while minimising cost. In the natural world food is rarely spread homogenously throughout the environment but rather is aggregated in patches of differing quality. Where such resource patches are not significantly depleted by foraging or where the exploited resource renews at a rate equal or near equal to the rate of depletion the forager has only to identify the patches of best quality and forage within them to maximise net returns. However, non-depleting patches rarely occur in nature as such "super rich" patches quickly attract many foragers, which in turn promptly erode patch quality Biebach *et al.* (1994). More commonly, foragers find themselves in a stochastic world where they face both temporal and spatial unpredictability in patch quality. This is particularly true for blue ducks that live in an environment prone to floods which markedly alter rivers and streams.

Owing to depletion of prey, the capture rate within a patch is likely to be a decreasing function of the time spent there (Charnov 1976). As patches degrade, at some point patch quality will reach a level where it becomes inferior to others and therefore a decision must be made to move to a new location. However in my study blue ducks had only to choose between two patches separated by negligible distance. The design therefore allowed me to measure how blue ducks respond to differences in patch quality without the complication of travel costs.

Blue ducks, by preferring those channels containing higher densities of macroinvertebrates, behaved as predicted by optimal foraging theory. The blue ducks used in this experiment showed a graded response in respect to relative food availability with more visits to and greater time spent in channels containing higher macroinvertebrate densities. Smith & Sweatman (1974) examined the food-searching behaviour of titmice (*Parus major*). When the birds were presented with multiple patches containing differing densities of prey the birds concentrated their foraging efforts in the high density patches. Although no significant correlation was recorded between search effort and prey density for the titmice initially, a positive trend between the two was apparent following a

period of acclimatisation by the birds to the experimental situation.

Predation of aquatic macroinvertebrates by ducks and trout, combined with natural losses by mortality and emergence, led to temporal variation in patch quality in the aviary. Despite this, blue ducks behaved in a way consistent with optimisation in a changing foraging environment. However, the relationships between foraging visits, foraging time and food availability did deviate (the relationships were not significant) from what theory would predict if foraging was truly optimal, ie. forage only in the best patch. This deviation may reflect a "smart" approach by the blue duck with it intermittently checking previously lower quality patches to assess their present and relative quality. Smith & Sweatman (1974) made the point that if the quality of available patches varied over time, the optimal strategy may not be to allocate all available time to one high quality patch, but rather allocate some time to sampling a variety of patches. By sampling the environment, they suggested that foragers may obtain necessary information for subsequent foraging decisions thus maximising future returns.

In the natural environment, deviations from optimisation might be expected. While food-related considerations are very important in ecological terms, confounding factors may lead to deviations from theoretical predictions. Royama (1970) pointed out that such deviation may arise as a result of two confounding types of limiting factors. First, an individual's inherent limitations in assessing the environment around it correctly and optimally, and second, as a result of conflicting environmental pressures, for example the risk of predation that a particular forager itself may face. This being the case the existence of truly optimal foraging would seem unlikely to be common in the natural environment.

5. 4. 4 Optimal foraging theory and its ecological relevance for blue ducks

The fact that foragers deplete resource patches rather than consume them, as they do in terms of prey items, provides a general rationale for the set of predictions now referred to as "the compression hypothesis" (Schoener 1987). This hypothesis examines a new species' impact when invading the range of a pre-existing species. When individuals of a competing taxon invade they lower the food availability within the

environment. Schoener (1987) suggested that this could happen at two levels. First, certain prey within a patch could become rare, and second, the quality of certain kinds of patches could be decreased. If patch quality declines below that required by the resident species it could easily cause a patch type to be dropped from the resident's patch repertoire. If other patch types are not added, an overall narrowing of the niche breadth would result, and in any event the two species patch types would be "compressed" away from one another. In other words the two species are forced to utilise resources not used by the other more intensely. If this is not possible for one or both of the species concerned then one species may be displaced or both species will be held at sub-optimum levels.

Aquatic macroinvertebrates upon which blue ducks feed are not spread homogeneously throughout the lotic environment but are rather aggregated in response to physical factors like flow, temperature, depth and substrate (Rabeni & Minshall 1977, Winterbourn *et al.* 1981, Jowett & Richardson 1994). Therefore the food of blue duck is distributed in semi-discrete patches of differing quality throughout the lotic environment. In Chapter 4 it was established that rainbow trout can alter the community structure and composition of aquatic benthic macroinvertebrates, a finding supported by other studies (Bechara *et al.* 1993, Flecker and Townsend 1995). Therefore, the question of ecological importance is "can trout reduce the value of those patches important to blue ducks to a level where blue duck are excluded from them?"

The fact that blue ducks detected the decline in macroinvertebrate densities induced by trout and responded by moving to a richer patch in the present experiment indicates that if trout can have this effect on a large scale in the streams and rivers where blue duck live the potential exists for trout to displace blue ducks. Several studies have found that certain species of waterfowl leave lakes and rivers that have high densities of fish for other sites with low fish presence. Pehrsson (1984) recorded higher densities of mallards on small lakes lacking fish than that on lakes containing high densities in Sweden. Similar aversion to lakes containing high densities of insectivorous fish by waterfowl has also been noted by Eriksson (1979).

Chapter Six

General Discussion

6.1 Review of field and experimental work

As reported in Chapter 3, the diets of blue ducks and trout were much the same as those reported in previous studies and there was moderately high overlap. However, the degree of overlap was reduced as a result of trout consuming prey other than aquatic macroinvertebrates.

Trout in all four rivers showed a consistent trend to choose prey of a larger body length than the average occurring in the benthos. However, despite this size-selective feeding no significant difference in the mean body length of benthic macroinvertebrates above and below the Ikawetea and Makaroro waterfalls were detected. This finding is consistent with the results reported by several similar investigations. Newman & Waters (1984) did not find any effect of rainbow trout predation on benthic communities in a tributary of the St. Croix in Minnesota, U.S.A. Likewise, Allan (1982) reported no change in the aquatic macroinvertebrate community following the removal of trout from a Colorado stream. Culp (1986) suggested that often in natural systems fish densities do not reach that level required to exceed the ability of the macroinvertebrate community to compensate for predation induced loss and therefore the probability of detecting any trout effect is low. Based on this, Culp (1986) suggested the best method to assess the impacts of such predation was to conduct an enclosure experiment to control as many of the confounding variables as possible.

Even though I detected no differences in the macroinvertebrate communities existing above and below the waterfalls other researchers (Schofield *et al.* 1988, Flecker & Townsend 1995) have recorded marked changes in a number of community parameters as a result of trout foraging. In light of Culp's suggestion and the findings of Schofield *et al.* (1988) and Flecker & Townsend (1995) I conducted the enclosure / exclosure experiment described in Chapter 4.

My experiment showed that trout predation of macroinvertebrates can in a relatively short time period result in marked alterations to the structure of the invertebrate communities. Changes in the relative abundance of Ephemeroptera and Plecoptera were of particular interest as these taxa were found to be an important component of the diet of blue ducks in my study area and elsewhere. In addition, in those enclosures containing trout the occurrence of large invertebrate specimens declined. Schofield *et al.* (1988) found that brown trout foraging reduced the density of certain aquatic macroinvertebrates inhabiting a stream in the Ashdown Forest in southern England. In New Zealand, experimental work by Flecker & Townsend (1995) illustrated that the presence of brown trout significantly altered the density of benthic macroinvertebrates. However, as has been shown in Chapter 3, blue ducks took smaller macroinvertebrates than trout and thus a decline in the occurrence of larger prey items in the benthos may have little direct detrimental effect on the ducks.

The apparent contradiction in the findings arising from my above and below waterfall observations (Chapter 3) and enclosure / enclosure data (Chapter 4) with respect to the effects of trout on benthic macroinvertebrate communities are not dissimilar from those reported in the literature (see Bechara *et al.* 1993). Several explanations have been advanced to account for such disparity. Culp (1986) suggested that the lack of difference in benthic community composition between sections of stream with and without trout was a result of trout densities being well below that required to produce an effect. Trout biomass used in my enclosures on Tongariro River was 26 gm^{-2} and although trout biomass was not quantified below the two waterfalls trout count data would indicate the trout biomass was below this figure in both rivers (approximately 7.0 gm^{-2} Ikawetea River; 2.5 gm^{-2} Makaroro River). The difference in trout densities used in my experiment and occurring in the two rivers may explain the contrary findings about a trout effect on the macroinvertebrate communities.

It has been suggested that predators that forage within the substrate interstices have a greater potential for influencing the distribution and abundance of benthic macroinvertebrates than predators that feed on substrate surfaces or on the drift (Culp 1986). The trout used in the enclosure experiment were of a shorter fork-length than those occurring

in Makaroro and Ikawetea Rivers and thus may have extracted prey from the interstices during their confinement when food resources became limited. Larger trout, like those occurring below the two waterfalls predominantly captured prey from the drift and usually do not feed to any great extent on macroinvertebrates in the benthos itself (Mills 1971). This difference in feeding behaviour is likely to have lessened trout impact on the macroinvertebrate communities occurring below the two waterfalls.

As a result of my findings from the enclosure / exclosure experiment a second experiment was conducted, to test the response of blue ducks to alterations in food availability induced by trout predation (Chapter 5). This experiment showed that blue ducks were sensitive to food availability preferring to forage at those sites containing the richest supply of macroinvertebrates. Similar research conducted in Canada by Eadie & Keast (1982) and Phillips (1992) in England, also showed that waterfowl respond to fish-induced changes in the availability of invertebrate food. In both cases waterfowl used waters containing high densities of fish significantly less than waters with low fish densities.

The implications of my findings are discussed below in relation to competition theory and blue duck conservation strategy.

6. 2 Diet overlap and its relationship with competition

An underlying principle of competition theory is the greater the overlap in the use of resources, then all other things being equal, the greater the intensity of the resulting competition. However, this premise has been challenged by many ecologists (see Schoener 1982) who have argued that overlap and competition need not be related. Schoener (1982) advanced several conditions where substantial overlap between organisms may not result in significant competition and hence the occurrence of adverse effects.

In communities, predation often holds population growth and size below the theoretical carrying capacity of the environment. Colwell & Futuyama (1971) suggested that predation often maintains the population size of potential competitors well below that level where resource limitation and hence competition occurs. Roughgarden & Feldman (1975) also suggested that predation may allow coexisting

species to make similar demands on resources and went on to speculate that predation increases the diversity of organisms an environment can support. Several field studies (see Pontin 1982) have provided supporting evidence for the role of predation in reducing the occurrence and intensity of competition. Dodson (1974) found that the aquatic pond macroinvertebrates *Diaptomus* sp. and *Chaoborus* sp. only coexisted where fish that consumed *Diaptomus* sp. occurred. In ponds where fish density dropped, *Diaptomus* sp. numbers increased and *Chaoborus* sp. was quickly excluded as a result of food competition.

A similar mechanism for reducing the occurrence and / or intensity of competition could operate in harsh environments where population sizes of potential competitors are maintained at low levels by mortality associated with abiotic factors. Although no data are available, the nature of rivers and streams (ie, sporadic flooding) may maintain trout and blue duck numbers below levels required for competition to occur thus allowing coexistence in much the same way as that described for predation.

The ways in which resources are exploited by coexisting species and the effects of such differences on competition have received considerable attention in recent years (see Keddy 1989). Resource partitioning, as it is popularly referred to has been found to reduce the occurrence and magnitude of competition and the adverse effects associated with it. Kusabs & Swales (1991) found that koaro (*Galaxias brevipinnis*) and juvenile rainbow trout in certain Lake Taupo tributaries overlapped greatly in the prey consumed. However, these species were able to coexist due to both temporal and spatial partitioning of food resources. This resulted from juvenile trout feeding diurnally on the drift occurring in the middle zone of the water column, while koaro fed nocturnally, actively taking invertebrates from the benthos. The exploitation of micro-habitats has been found to reduce the effects of significant diet overlap (Sagar & Eldon 1983, Kusabs & Swales 1991). Blue ducks collect their macroinvertebrate prey by using their sensitive bill to glean animals from the substrate (Kear & Burton 1971) while trout obtain a significant proportion of the prey items from the drift (Mills 1971). These differences in the method of prey capture and the micro-habitat from which the two insectivores collect their prey may, as with the fish species described, help to alleviate the occurrence of competition.

Sagar & Eldon (1983) recorded high levels of diet overlap between juvenile brown trout and various native fish species in the Rakaia River. Likewise, Kusabs & Swales (1991) found that competition appeared to be reduced by differences in spatial and temporal feeding habits, but also by the consumption of different-sized prey items. I found blue ducks consumed prey of significantly smaller body length than that consumed by coexisting trout. This segregation in the use of the resource is likely to, as described by Kusabs & Swales (1991), reduce competition.

Although macroinvertebrate densities were not measured in my study there is some evidence that macroinvertebrate availability is not limiting at times of stable flow. Veltman *et al.* (1991) in their study of the Manganuiateao River blue duck population concluded that the territorial behaviour displayed by resident blue ducks was not related to the defence of nutritional resources as the birds could meet their daily requirements by consuming the macroinvertebrates inhabiting approximately 2 m² of substrate. The other three rivers from which I collected data appeared to contain similar densities of macroinvertebrates and thus on the basis of density alone macroinvertebrate densities in all four rivers would appear to be in excess of that required to meet blue duck demands within average sized territories.

6. 3 Conservation biology and competition theory: The role of introduced species

Simberloff (1981) reviewed numerous papers dealing with the effects of introduced species on "pristine" systems. He concluded, "The most striking result is that in so many instances (678 of 854), an introduced species has no effect whatever on species in the resident community, or on the structure and function of the community". This also appears to be the case for several species of New Zealand's avifauna which seem to be unaffected by competition with exotic bird species (Diamond & Veitch 1981). Simberloff (1981) attributed this lack of introduced species impact to the fact that most communities have numerous vacant niches which are exploited by successful invading species. Herbold & Moyle (1986) however, disagreed with Simberloff's findings and presented evidence demonstrating that introduced species had significant effects on the receiving environment. Herbold & Moyle (1986) specifically disagreed with Simberloff's vacant niche concept instead suggesting that

Simberloff's so called vacant niches occurred in highly disturbed communities from which species had been removed. They instead agreed with Elton (1958) suggesting that in undisturbed habitats introductions usually displaced native species, often through competition.

The role of species invasions on native communities is currently receiving considerable attention again. This more recent research has to some extent moved away from species level examination instead considering the consequence of species introduction at community level. While Pimms (1991) presented examples where invaders have substantially modified communities, Simberloff (1981) argued that in the vast majority of cases natural communities are resistant to invasions. In those situations where a new organism enters a community Simberloff (1981) suggests that the arrival of the vagrant species only adds to the diversity of the community rather than subtracting from it.

New Zealand has had a long history of introducing exotic animals (King 1984) and while the introduction of certain organisms such as mustelids has had a dramatic effect on the country's native species the effects of other exotic organisms have not been so conspicuous or are less well studied. Both rainbow and brown trout were introduced into New Zealand rivers and lakes over a period of twenty years following the 1870s, and today, as a result of repeated liberations and natural dispersal few suitable lotic environments remain free of these salmonids. Even at the time of trout introduction some concern was expressed to the effects of the exotic on the native fauna (Hutton 1873). Since the introduction of trout into New Zealand there has been a great deal of speculation and some data to show that the decline in the country's native trout fishery has been in part due to direct predation or competition for resources (Allen 1961, McDowall 1990, Townsend & Crowl 1991). Substantial proof of the detrimental effects of invading fish species have been reported elsewhere for both lotic and lentic systems (see McDowall 1990). Examples of introduced fish substantially altering native communities include the introduction of Nile perch (*Lates calcarifer*) to Lake Victoria. Following the introduction of this fish to the lake, the lake's native fishery was almost decimated. The introduction of rainbow trout into Lake Titicaca in Peru in the 1940s also led to a dramatic decline in the abundance of the lake's native fish population with some of the native

species being totally eliminated from the system (Campbell 1976; cited McDowall 1990).

Because trout and blue ducks have evolved in isolation from one another and as they make similar demands on the environment, they are potential competitors for food resources. However, as has been shown the two insectivores do differ in the component of the resource they select and, as has been shown elsewhere in species-specific research, each collects prey from different micro-habitats (Mills 1971, Sagar & Eldon 1983, Collier & Lyon 1991). In similar studies this resource partitioning has been considered important in reducing the degree of competition. In the Rytton River, New Zealand, Glova & Sagar (1991) found that even though trout and native fish overlapped substantially in their use of aquatic invertebrate prey, competition was reduced as a result of each exploiting the resource in a slightly different manner.

Never-the-less blue ducks have declined over the last hundred years (Williams 1988). To conserve and ensure the future of a threatened species the "agent-of-decline" must be identified and action taken to remove or minimise its effect (Caughley 1994). Diamond (1984, 1989) attributed recent species extinctions and reductions to four agents-of-decline (i) overkill, (ii) habitat destruction and fragmentation, (iii) impact of introduced species and (iv) chains of extinction. These he termed "the evil quartet".

The introduction of exotic species into regions where they did not previously exist has been reported to have caused severe damage and modification to 'native' species and communities (Pimms 1991). Despite Diamond & Veitch's (1981) finding that several species of New Zealand's avifauna which seem to be unaffected by the introduction of exotic bird species, Atkinson (1989) attributed 74% of bird extinctions or near extinctions in New Zealand to the liberation of alien species. Elton (1958) suggested that in undisturbed habitats introductions usually displaced native species, often through competition. Therefore, the role of competition in the decline of a native population following the introduction of an exotic species needs special consideration. However, the identification and measurement of competition is not an easy task in most environments. What makes competition particularly difficult to quantify and assess is that its magnitude is dictated by interacting

variables such as resource availability and population density and hence its occurrence at a measurable level is likely to be sporadic.

Because of this, competition, as an agent of species decline, is likely to go undetected for the majority of time. However, during periods of limited resource availability, competition may reach sufficient intensity to, if not totally exclude one organism, then reduce numbers to levels where the population enters the 'extinction vortex' and other agents of decline related to low numbers establish (ie, inbreeding depression, environmental instability). These agents may then drive population numbers down further and in doing so obscure the original role of competition. If efforts to determine the cause of population decline are conducted following the initial drop in population size those factors associated with the 'extinction vortex' (Caughley 1994) may wrongly be identified as the agent-of-decline and attempts to address them may not ease the limitation imposed by interspecific competition with the introduced species.

This scenario may be of particular importance during times of environmental stress (ie, during a severe winter) when competition levels that at other times may be tolerated by a particular species, may act in an additive sense with other adverse elements and reduce population size to such a level exposing it to extinction. Schoener (1982) examined 30 studies of overlap amongst coexisting species and reported that during lean times, resource overlap between species declined hence reducing the intensity of competition. However, recent work has questioned this "snap-shot" approach. Jaksic *et al.* (cited Wiens 1993) studied the feeding habits of predatory birds in Chile and found that diet overlap stayed relatively constant throughout their four-year study despite food availability varying. This suggests that competition intensity may become significant during periods of low resource availability. This conclusion was reiterated in Wiens (1993) paper which reviewed competition during "fat times and lean times". Thus when endeavouring to identify the agent-of-decline the assessment of competition is likely to be most precise during such periods of stress.

Some researchers have hypothesised that most organisms are held for the majority of the time at such low population densities that competition rarely occurs (Connell 1975) and hence seldom if ever constitutes an

active agent-of-decline. Where this is the case, the potential role of competition as an agent-of-decline may be shrouded by other community forces such as predation which may act to hold the population density of an introduced species below that required to have an adverse effect on the native organisms. In these situations, competition may not be identified as constituting a potential threat. However, during times when predator abundance falls and the abundance of the invader correspondingly increases, then density may reach that level where competition becomes intense and in turn drives down the density of the native species.

Of course interspecific competition between an exotic and native species does not invariably lead to the exclusion of one or the other. A significant underlying premise of competition theory in terms of species conservation is that competing species occurring in stable environments are for the most in a state of equilibrium with both populations being maintained at levels below that, that they would reach in the absence of competition. This does have important ramifications for conservation because smaller populations have been shown to be at greatest risk from extinction (Terborgh & Winter 1980, Diamond 1984). If competition confines a threatened species population to low numbers this will expose the species to a greater risk of being wiped out by a catastrophic event.

Despite the potential for an introduced species to have a detrimental impact, care must be taken if its exact role is to be determined. In several cases where the introduction of an exotic organism has been credited with the competitive displacement of a native, closer examination has found competition not to be the primary agent-of-decline. Diamond & Veitch (1981) found that exotic birds that were thought to have competitively excluded several native bird species on Cuvier Island, New Zealand, were themselves displaced by other native species following the elimination of introduced mammalian predators from the island. Based on this observation Diamond & Veitch (1981) suggested that the extinction of the native species was not in fact due to competition but instead resulted from predation and that it was only following the decimation of the native species by the introduced predators that the exotic avian species were able to established.

6. 4 Implications for blue duck conservation strategies

A challenge faced by those who endeavour to conserve threatened species is to understand the role of introduced organisms in the decline of that they strive to protect (Coblentz 1990, Soulé 1990, Pimms 1991, Flecker & Townsend 1995). This is particularly so when endeavouring to determine and address the primary "agent-of-decline" (Caughley 1994). Competition for food resources following the introduction of an exotic species into a community has been implicated in the decline of several organisms. In New Zealand Leathwick *et al.* (1983) examined the influence of introduced browsing mammals on the decline of North Island Kokako (*Callaeas cinerea wilsons*). They suggested that the overlap in the diets was such as to indicate that the reduction in the abundance of the more palatable food species by possums was likely to constitute the primary agent-of decline for this bird. Likewise, other New Zealand avifauna has been found to have suffered as a result of diet competition with introduced animals (Mills & Mark 1977). In each case, efforts to conserve the "threatened" species has involved removing or at least reducing the abundance of the coexisting exotic species within the ecosystem.

As with the Kokako, blue ducks have declined in both numbers (Williams 1988) and range (King 1984) over the last hundred years and today an effort is being made to conserve this unique waterfowl.

My research was conducted to assess the role of trout as a possible agent-of-decline and thus to what extent future conservation efforts need to focus on trout. As detailed in Chapter 3 and in section 6.1 trout and blue ducks do utilise the same food resource and hence overlap to a moderate to relatively high degree. However, no effects of trout foraging were detected where blue duck and trout coexisted naturally although trout altered the benthic community under experimental conditions. Further experimentation showed that where trout altered the composition of the benthos blue ducks foraged in those patches richest in food reserves and readily responded to trout induced reduction in patch quality.

As discussed in section 6. 3 those entrusted with species conservation are faced with two options; remove or minimise the effects of the agent-of-decline within the habitat of the threatened species or conversely if the agent can not be removed or minimised then the translocation of the

threatened species to a new environment where the agent is absent or does not exert the same pressure.

The first of these two approaches as applied to blue duck conservation strategy would involve the removal of trout, or at least the control of their density in those rivers and streams set aside for this waterfowl. However, the degree of resource partitioning detected by my research indicates that such a measure is not appropriate as adverse effects on blue duck resulting from competition for resources is likely to be minimal. The fact that blue ducks can and do react to alterations in food availability, as shown in Chapter 5 suggests that where the two animals presently coexist in a relatively stable state such partitioning in resource utilisation may be sufficient to rule out the occurrence of adverse competition. Hynes (1970) suggested that similarity of diet in two coexisting species indicates that "however else they may be competing, they are not competing for food" and that close examination usually illustrates significant differences in resource utilisation. It appears from my data that this may also be the case for coexisting populations of trout and blue ducks.

A second, often used strategy in species conservation is the establishment of new populations either away from their present indigenous environment or reintroduction into a previously occupied habitat. Such an approach has been extensively used in New Zealand with many avian populations being transported to off-shore islands free of the agent-of-decline encountered on the mainland. Often where the agent is acute and can not be readily addressed the complete re-location of an endangered population occurs. A prime example of such an undertaking was the removal of black robins (*Petroica traversi*) from Little Mangere Island to the larger Mangere Island in the early 1980's (Butler & Merton 1992). Although the complete relocation of populations occurs from time to time more often "satellite" populations are established to ensure that while efforts to identify and address the agent-of-decline in the indigenous habitat are proceeding, individuals and hence genetic material are maintained in relative safety. The translocation and establishment of a satellite population of New Zealand stitchbirds (*Notiomystis cincta*) to Kapiti Island off the coast of New Zealand's North Island is one such example.

Blue ducks were once common on much of the country's riverine habitat and although a great deal of it has been substantially modified considerable scope for reintroduction and the establishment of satellite populations would appear to exist. However, efforts to establish new blue duck populations should focus on that habitat best suited to the requirements of the bird. To assess habitat quality the collection of precise data is essential. Little, of course would be gained by reintroducing birds into areas where they no longer exist as a result of competition.

Any conservation strategy designed to conserve blue duck populations must consider the possibility that trout may have an impact on habitat utilisation by blue duck. However the apparent resource partitioning documented in my research and the obvious abundance of macroinvertebrates relative to that required to meet blue duck and trout nutritional requirements detailed in other work (Veltman *et al.* 1995) would suggest that in regions where both predators coexist in a relatively stable state, competition for food may not be the prime agent-of-decline.

6.5 Summary

My study has demonstrated that introduced trout and New Zealand's endemic blue duck occupy relatively similar dietary niches and at times display considerable overlap in the composition of their diets. However, despite such overlap it appears that both predators exploit different components of the resource. Such resource partitioning has been reported to significantly reduce the magnitude of interspecific competition in other studies and this may well be the case with coexisting populations of blue ducks and trout.

Experimental examination of the effect of trout foraging on Tongariro Rivers benthic macroinvertebrate community showed that intensive foraging by trout results in significant changes in the occurrence of certain macroinvertebrate taxa and size-classes. Further experimentation designed to assess the responses of blue ducks to such alterations showed that blue ducks can detect and respond to such trout induced modification to food availability.

For those endeavouring to develop strategy to ensure the long term survival of this unique waterfowl my research indicates that where trout

and blue duck populations coexist resource partitioning may result in little interspecific competition occurring. This coupled with the abundance of benthic macroinvertebrates in most relatively unmodified catchments, indicates that interspecific competition between blue ducks and trout for aquatic prey is unlikely to be a principle agent-of-decline in the reduction of this unique waterfowl.

Appendix A

Reprint of:

Predicting dry weight of New Zealand aquatic macroinvertebrates from linear dimensions.

Appendix B

Relative composition (%) of the major aquatic food categories in the diets of trout and blue ducks inhabitiing the four study areas.

Appendix B1. Relative composition (%) of major aquatic food categories in trout diets collected from Tongariro River as determined by numerical, dry weight and incidence-of-occurrence analyses. Numbers in parentheses represent standard error of mean.

Date	Numerical						Dry Weight						Occurrence					
	20.1	10.3	27.4	20.7	16.9	4.11	20.1	10.3	27.4	20.7	16.9	4.11	20.1	10.3	27.4	20.7	16.9	4.11
Taxon																		
Leptophlebiidae	21.4 (5.8)	24.8 (5.5)	8.8 (3.2)	11.5 (4.4)	4.6 (2.3)	29.1 (6.3)	26.8	16.9	7.3	28.9	14.0	35.1	100	100	81.8	38.5	60.0	92.0
Coloburiscus sp.	0.6 (0.6)	0.90 (0.7)	1.1 (0.7)	2.5 (2.5)	0	1.4 (0.9)	1.0	4.6	5.2	5.0	0	3.8	13.3	19.2	18.2	7.7	0	20.8
Nesameletus sp.	0.6 (0.6)	0.3 (0.3)	0	0	0	0	1.0	<0.1	0	0	0	0	6.7	7.7	0	0	0	0
Zelandoperla sp.	3.5 (2.5)	1.4 (0.8)	7.5 (2.0)	21.4 (5.7)	8.2 (6.2)	4.2 (1.2)	3.5	1.8	8.9	22.4	15.1	6.1	33.3	11.5	9.1	69.2	30.0	37.5
Zelandobius sp.	0	0	0	18.9 (7.4)	0	0	0	0	0	10.0	0	0	0	0	0	46.2	0	0
Megaleptoperla sp.	0	0.5 (0.5)	0.2 (0.2)	1.0 (0.1)	0	0	0	1.2	0.9	2.5	0	0	0	11.5	27.3	7.7	0	0
Austroperla sp.	0	0	0	0	4.7 (3.3)	0.4 (0.4)	0	0	0	0	5.0	1.1	0	0	0	0	10	8.3
Pycnocentroides sp.	3.5 (1.7)	0	3.3 (2.2)	0	8.4 (3.6)	18.0 (5.2)	6.5	0	6.0	0	11.2	12.1	40.0	0	36.4	0	50.0	33.3
Beraeoptera sp.	3.5 (1.7)	0	0	0	3.5 (2.5)	2.0 (1.2)	1.9	0	0	0	0.9	2.0	40.0	0	0	0	20.0	8.3
Helicopsyche sp.	0	0	0	0.5 (0.5)	3.2 (3.2)	0.8 (0.7)	0	0	0	0.7	0.4	1.2	0	0	0	7.7	0	12.5
Olinga sp.	3.7 (0.2)	0.1 (0.1)	3.7 (3.3)	0.5 (0.5)	1.9 (1.6)	2.5 (1.2)	1.6	2.1	1.8	2.7	3.2	3.6	13.3	3.8	27.3	7.7	20.0	8.3
Aoteapsyche sp.	2.2 (0.9)	1.4 (0.8)	25.9 (12.0)	20.2 (9.1)	2.3 (1.5)	2.3 (1.3)	28.9	34.3	32.3	30.6	3.2	10.8	33.3	23.1	81.8	38.5	30.0	33.3
Hydrobiosidae	7.6 (2.4)	11.5 (3.1)	17.4 (6.2)	0	5.1 (2.2)	11.2 (3.0)	17.0	15.8	23.3	0	9.8	16.8	66.6	84.6	90.9	0	10.0	75.0
Paroxyethira sp.	1.2 (1.0)	4.9 (1.3)	7.5 (4.1)	1.0 (0.5)	1.7 (1.7)	4.2 (1.9)	0.9	2.0	8.1	1.0	6.3	5.2	13.3	42.3	27.3	7.7	10.0	29.2
Oxyethira sp.	3.7 (2.3)	5.7 (5.3)	0	0	0	0	1.0	2.0	0	0	0	0	13.3	46.2	0	0	0	0
Other Trichoptera	0.6 (0.6)	0.1 (0.1)	0	0	0	0	0.5	0.4	0	0	0	0	6.7	3.8	0	0	0	0
Chironomidae	5.7 (2.8)	13.8 (2.5)	7.1 (2.4)	8.2 (3.7)	30.6 (9.9)	5.1 (1.7)	2.8	15.9	5.2	6.2	14.4	2.2	53.3	92.3	45.5	30.8	80.0	54.2
Aphrophila sp.	1.7 (0.8)	0.1 (0.1)	0	0	0	0	3.3	0.3	0	0	0	0	26.7	3.8	0	0	0	0
Elmidae	0	0.2 (0.2)	0.9 (0.9)	0	0	0.4 (0.4)	0	0.8	1.0	0	0	0.6	0	3.8	18.9	0	0	8.3
Terrestrial	41.4 (6.6)	26.7 (7.7)	14.4 (10.9)	12.6 (7.9)	21.9 (6.0)	12.0 (4.4)	*	*	*	*	*	*	100	96.2	81.8	30.8	90.0	92.0

* Dry weight figure could not be calculated due to the lack of appropriate conversion equations.

Appendix B2. Relative composition (%) of major aquatic food categories in trout diets collected from Manganuiateao River as determined by numerical, dry weight and incidence-of-occurrence analyses. Numbers in parentheses represent standard error of mean.

Date	Numerical						Dry weight						Occurrence					
	26.2	1.4	2.7	16.9	5.11	15.12	26.2	1.4	2.7	16.9	5.11	15.12	26.2	1.4	2.7	16.9	5.11	15.12
Taxon																		
Leptophlebiidae	10.5 (6.1)	17.7 (2.7)	24.6 (8.3)	52.5 (8.8)	64.6 (13.2)	71.2 (6.1)	19.5	31.7	37.1	58.0	71.3	78.3	50.0	100	100	100	100	100
Coloburiscus sp	0	4.2 (1.2)	4.8 (2.9)	4.1 (1.5)	0	3.4 (1.4)	0	0	6.2	5.8	0	4.1	0	76.9	71.4	54.5	0	42.9
Nesameletus sp.	0.4 (0.4)	2.6 (2.6)	2.2 (1.2)	1.3 (0.6)	11.5 (9.3)	4.7 (1.8)	1.1	7.4	5.1	4.7	18.1	7.7	12.5	76.9	42.9	45.5	37.5	64.3
Zelandoperla sp.	12.5 (7.6)	15.5 (3.3)	21.2 (7.7)	3.1 (1.3)	4.4 (2.3)	0.6 (0.3)	22.8	27.7	29.6	5.9	4.9	1.4	37.5	100	100	54.5	12.5	28.6
Zelandobius sp.	0	0	0	0	3.3 (3.1)	0.2 (0.2)	0	0	0	0	4.0	0.9	0	0	0	0	25.0	7.1
Megaleptoperla sp.	0	1.1 (0.4)	2.4 (0.8)	0.8 (0.5)	0	0.3 (0.3)	0	3.1	4.1	1.2	0	0.7	0	69.2	71.4	36.4	0	7.1
Austroperla sp.	3.8 (2.5)	1.9 (0.4)	0	0.9 (0.9)	0	0	6.7	2.9	0	1.7	0	0	37.5	69.2	0	27.3	0	0
Pycnocentrodes sp.	5.3 (1.9)	1.9 (0.7)	0.6 (0.6)	4.2 (2.8)	0	1.0 (0.9)	5.3	1.1	0.3	2.1	0	0.2	75.0	53.8	14.3	27.3	0	14.3
Beraeoptera sp.	9.3 (5.0)	16.7 (3.3)	22.4 (8.6)	13.4 (5.8)	0	6.3 (5.5)	7.2	8.7	7.1	6.4	0	2.1	37.5	92.3	71.4	63.6	0	28.6
Helicopsyche sp.	4.7 (4.7)	7.7 (1.8)	4.2 (3.5)	3.6 (1.1)	0	0.8 (0.6)	0.8	2.9	0.3	0.9	0	<0.1	12.5	71.9	28.6	9.1	0	7.1
Olinga sp.	1.6 (1.6)	5.7 (1.5)	2.7 (1.4)	0	0	0	2.8	4.9	2.0	0	0	0	12.5	76.9	57.1	0	0	0
Aoteapsyche sp.	8.0 (6.1)	0.5 (0.5)	1.1 (1.1)	2.9 (1.1)	0	0.8 (0.6)	12.9	1.0	3.6	4.2	0	1.3	37.5	7.7	14.3	54.5	0	21.4
Hydrobiosidae	7.1 (3.2)	5.2 (1.6)	1.4 (0.7)	3.6 (1.1)	0.3 (0.3)	3.2 (1.0)	8.9	4.8	3.2	4.9	1.0	4.5	50.0	69.2	42.9	63.6	12.5	57.1
Paroxyethira sp.	2.5 (2.5)	0	0	0	0	0	0.4	0	0	0	0	0	12.5	0	0	0	0	0
Oxyethira sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Other Trichoptera	0.4 (0.4)	0.2 (0.2)	0.8 (0.8)	0	0	0	0.4	2.1	0.7	0	0	0	12.5	7.7	14.3	0	0	0
Chironomidae	22.7 (8.4)	3.7 (2.2)	0	5.2 (2.2)	2.5 (2.5)	2.2 (1.2)	10.6	0.5	0	3.1	1.1	0.4	62.5	38.5	0	72.7	12.5	28.6
Aphrophila sp.	0	0	0	0.3 (0.3)	0	0	0	0	0	1.1	0	0	0	0	0	9.1	0	0
Archichauliodes sp.	0	0.7 (0.3)	0.8 (0.8)	0	0	0	0	2.1	1.5	0	0	0	0	30.8	14.3	0	0	0
Elmidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Terrestrial	11.2 (5.0)	10.9 (2.4)	9.8 (4.8)	3.4 (1.5)	11.7 (2.8)	1.5 (0.7)	*	*	*	*	*	*	62.5	76.9	28.6	45.5	12.5	7.1

* Dry weight figure could not be calculated due to the lack of appropriate conversion equations.

Appendix B3. Relative composition (%) of major aquatic food categories in the diet of blue ducks resident within Tongariro River study area as determined by numerical, dry weight and incidence-of-occurrence analyses. Numbers in parentheses represent standard error of mean.

[illegible]

Appendix B5. Relative composition (%) of major aquatic food categories in trout diets collected from Ikawetea River as determined by numerical, dry weight and incidence-of-occurrence analyses. Figures in parentheses represent standard error of means.

Date	Numerical					Dry weight					Occurrence				
	14.3	8.6	11.9	3.12	29.12	14.3	8.6	11.9	3.12	29.12	14.3	8.6	11.9	3.12	29.12
Taxon															
Leptophlebiidae	8.8 (7.4)	2.7	40.9 (3.9)	45.4 (10.5)	26.3 (9.6)	36.1	3.4	47.3	58.3	37.5	50.0	100	100	100	100
Coloburiscus sp.	0.7 (0.4)	0.2	1.6 (0.4)	1.4 (0.4)	0.9 (0.1)	3.7	1.2	3.2	1.2	3.1	50.0	100	83.3	80.0	100
Nesameletus sp.	0	11.2	1.4 (0.5)	1.7 (1.3)	0.7 (0.5)	0	13.2	3.1	2.1	1.2	25.0	100	83.3	60.0	50.0
Zelandoperla sp.	0.5 (0.3)	9.8	16.7 (3.5)	17.6 (2.2)	1.3 (0.9)	2.1	11.2	20.4	21.1	1.9	50.0	100	100	100	75.0
Zelandobius sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Megaleptoperla sp.	1.6 (1.3)	0	1.1 (0.2)	0.4 (0.2)	1.1 (0.7)	7.5	0	1.1	0.7	2.8	50.0	0	100	80.0	50.0
Austroperla sp.	0.2 (0.2)	0.2	0.4 (0.3)	0 (0.1)	0.1 (0.1)	1.0	0.8	1.0	0	0.9	25.0	100	66.7	0	25.0
Pycnocentroides sp.	0.5 (0.5)	3.0	13.5 (5.8)	0.5 (0.5)	4.4 (1.6)	1.1	2.1	7.1	1.0	1.2	25.0	100	100	100	100
Beraeoptera sp.	0	0.1	3.6 (1.1)	2.2 (0.4)	6.4 (3.3)	0	0.1	1.8	0.9	2.5	0	100	100	100	75.0
Helicopsyche sp.	0	0	0.3 (0.2)	0.3 (0.1)	0	0	0	0.1	0.1	0	0	0	66.7	80.0	0
Olinga sp.	6.6 (3.2)	53.8	13.2 (5.6)	5.0 (2.2)	53.9 (10.2)	23.1	46.7	7.6	4.5	42.0	75.0	100	100	100	100
Aoteapsyche sp.	2.9 (0.9)	9.1	1.7 (0.3)	2.6 (0.5)	1.0 (0.2)	11.2	11.3	3.2	3.2	1.4	100	100	83.3	100	100
Hydrobiosidae	1.9 (1.3)	2.7	2.1 (0.8)	4.9 (1.1)	4.9 (1.1)	6.3	3.6	4.2	5.2	3.2	50.0	100	83.3	100	25
Paroxyethira sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxyethira sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Other Trichoptera	0	0.9	0.1 (0.1)	0.2 (0.1)	0.1 (0.1)	0	1.1	0.2	0.1	< 0.1	0	100	50.0	60.0	25.0
Chironomidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Muscidae	0	0.2	0	0	0	0	0.7	0	0	0	0	100	0	0	0
Aphrophila sp.	0.8 (0.5)	1.2	0.3 (0.1)	0.6 (0.2)	1.1 (1.0)	3.6	2.1	1.1	0.9	2.3	50.0	100	66.7	80.0	50.0
Archichauliodes sp.	1.1 (0.9)	2.0	0.1 (0.1)	0.1 (0.1)	0	6.1	3.2	0.7	0.7	0	50.0	100	33.3	20.0	0
Elmidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Uniden.	0	2.1	0	0	0	0	1.2	0	0	0	0	100	0	0	0
Terrestrial	73.7 (13.0)	1.0	3.1 (1.0)	6.1 (2.8)	2.7 (0.2)	*	*	*	*	*	100	100	100	100	100

* Dry weight of terrestrial prey could not be calculated due to lack of conversion equations.

Appendix B6. Relative composition (%) of major aquatic food categories in trout diets collected from Makaroro River as determined by numerical, gravimetric and incidence-of-occurrence analyses. Figures in parentheses represent standard error of means. † no trout captured.

Date	Numerical					Dry weight					Occurrence				
	15.3	3.6	20.10	3.11 [†]	13.12	15.3	3.6	20.10	3.11 [†]	13.12	15.3	3.6	20.10	3.11 [†]	13.12
Taxon															
Leptophlebiidae	46.2 (4.1)	33.8 (5.2)	25.5 (4.3)		0.2	58.9	40.8	42.5		11.0	100	100	100		100
Coloburiscus sp.	0	0.7 (0.4)	2.5 (1.8)		0	0	1.8	7.3		0	0	40.0	80.0		0
Nesameletus sp.	2.2 (0.8)	0.9 (0.7)	0.5 (0.4)		0	5.2	2.1	1.9		0	75.0	60.0	40.0		0
Zelandoperla sp.	12.2 (7.1)	19.7 (6.9)	10.8 (3.3)		0	17.9	27.2	17.5		0	75.0	100	80.0		0
Zelandobius sp.	0	0	0		0	0	0	0		0	0	0	0		0
Megaleptoperla sp.	0.1 (0.1)	0.2 (0.2)	1.0 (0.8)		0	0.9	1.0	3.1		0	25.0	40.0	40.0		0
Austroperla sp.	1.3 (1.3)	0.2 (0.2)	0		0	3.1	0.9	0		0	25.0	40.0	0		0
Pycnocentroides sp.	5.4 (0.7)	2.2 (1.4)	1.4 (1.0)		4.0	2.3	2.0	0.6		24.9	100	40.0	20.0		100
Beraeoptera sp.	4.9 (2.3)	11.8 (6.6)	8.0 (1.7)		0.2	3.1	7.2	0.5		3.8	75.0	80.0	100		100
Helicopsyche sp.	2.4 (0.8)	2.0 (1.0)	0		0	0.2	0.3	0		0	75.0	80.0	0		0
Olinga sp.	6.4 (2.4)	10.6 (3.8)	28.7 (2.8)		4.0	1.8	8.4	16.1		36.2	100	100	100		100
Aoteapsyche sp.	0	0.5 (0.3)	0.2 (0.2)		0	0	1.3	1.7		0	0	40.0	20.0		0
Hydrobiosidae	0.2 (0.2)	1.1 (0.5)	1.2 (0.6)		0	0.9	1.7	2.1		0	25.0	60.0	60.0		0
Paroxyethira sp.	0	0	0		0	0	0	0		0	0	0	0		0
Oxyethira sp.	0	0	0		0	0	0	0		0	0	0	0		0
Other Trichoptera	0.2 (0.2)	0.2 (0.2)	0.3 (0.3)		3.6	0.1	0.1	0.8		24.1	25.0	20.0	20.0		0
Chironomidae	0	0.2 (0.2)	0		0	0	<0.1	0		0	0	0	0		0
Muscidae	0	0	0		0	0	0	0		0	0	0	0		0
Aphrophila sp.	0.8 (0.1)	1.3 (0.7)	1.4 (0.9)		0	2.1	3.4	2.8		0	75.0	80.0	60.0		0
Archichauliodes sp.	0.2 (0.2)	0.1 (0.1)	0.7 (0.5)		0	3.1	1.8	3.1		0	25.0	40.0	40.0		0
Elmidae	0	0	0		0	0	0	0		0	0	0	0		0
indet.	0	0	0		0	0	0	0		0	0	0	0		0
Terrestrial	17.0 (2.2)	14.7 (7.7)	17.1 (6.7)		88.0	*	*	*		*	100	100	100		100

* Dry weight of terrestrial prey could not be calculated due to lack of conversion equations.

Appendix B7. Relative composition (%) of major aquatic food categories in blue duck diets collected above and below the falls from Ikawetea River as determined by numerical, dry weight and incidence-of-occurrence analyses. Figures in parentheses represent the mean standard error. A denotes data collected from above the falls while B denotes data collected from below.

Date	Numerical										Dry Weight										Occurrence									
	14.3		8.6		11.9		3.12		29.12		14.3		8.6		11.9		3.12		29.12		14.3		8.6		20.10		3.11		13.12	
Taxon	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A
<i>Leptophlebiidae</i>	25.3 (3.7)	23.6 (4.6)	13.3 (5.6)	11.3 (3.2)	27.0 (13.9)	14.4 (5.9)	16.3 (1.3)	5.7 (1.7)	13.0 (4.1)	12.3 (3.9)	34.2	30.2	30.5	33.7	37.3	32.9	25.3	17.2	27.4	21.4	100	100	100	80	100	100	80	100	80	80
<i>Coloburiscus</i> sp.	11.0 (3.1)	6.0 (2.6)	3.3 (0.9)	6.3 (2.4)	3.8 (0.8)	6.7 (3.6)	0 (0.1)	0.1 (0.9)	1.5 (1.8)	6.1 (1.8)	17.2	8.2	6.9	13.7	7.9	10.7	0	1.2	5.7	9.2	100	40	60	60	100	100	0	40	40	80
<i>Nesameletus</i> sp.	5.3 (1.7)	3.5 (1.4)	1.4 (1.0)	0 (1.0)	0 (1.2)	2.0 (1.2)	0 (1.3)	2.1 (1.3)	0 (0.4)	0.4 (0.4)	7.6	5.6	5.9	0	0	5.1	0	7.8	0	1.7	80	100	20	0	0	80	0	20	60	0
<i>Zelandoperla</i> sp.	4.0 (1.3)	0.1 (0.1)	9.2 (3.3)	0 (3.3)	6.3 (2.1)	3.8 (1.6)	13.1 (8.7)	9.7 (5.1)	1.7 (0.7)	5.7 (1.7)	1.3	0.3	20.1	0	11.7	6.9	19.1	16.3	2.4	7/5	80	20	0	60	80	60	80	100	60	80
<i>Zelandobius</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Megaleptoperla</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Austroperla</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pycnocentroides</i> sp.	9.1 (2.3)	17.5 (4.5)	11.0 (3.5)	20.6 (3.4)	5.2 (3.0)	9.4 (3.7)	11.3 (4.7)	18.3 (4.7)	25.6 (6.6)	14.0 (2.8)	5.2	7.0	5.2	9.2	3.2	6.4	6.3	14.2	35.2	21.3	100	80	100	100	40	40	100	100	100	100
<i>Beraeoptera</i> sp.	15.2 (5.7)	25.0 (3.2)	55.2 (11.2)	45.4 (7.4)	43.9 (13.3)	43.0 (11.7)	7.1 (2.1)	8.9 (2.2)	37.1 (8.7)	12.0 (3.2)	7.1	12.3	23.7	21.8	27.1	23.1	3.1	3.2	12.3	5.8	60	100	100	100	60	40	80	100	100	100
<i>Helicopsyche</i> sp.	1.0 (0.6)	1.2 (0.7)	0.6 (0.6)	0 (0.6)	0 (0.4)	0.7 (2.1)	5.6 (0.3)	0.8 (0.3)	0 (1.8)	3.5 (1.8)	<0.1	0.1	0.2	0	0	0.1	1.6	0.1	0	1.2	40	20	20	0	0	40	100	60	0	60
<i>Olinga</i> sp.	3.5 (1.8)	18.5 (5.7)	2.0 (0.8)	5.1 (2.5)	1.5 (0.8)	1.5 (0.9)	6.2 (2.6)	7.0 (4.9)	0.9 (0.6)	32.2 (10.9)	2.1	9.1	1.0	4.8	1.3	1.7	5.1	5.8	0.2	14.5	60	100	80	40	60	60	80	20	20	100
<i>Aoteapsyche</i> sp.	6.5 (1.5)	15.6 (2.4)	1.3 (0.9)	7.3 (2.3)	1.3 (1.1)	2.1 (0.8)	15.5 (3.0)	5.7 (1.7)	8.6 (3.4)	0	7.4	20.8	2.1	11.2	4.7	5.7	19.3	12.9	3.8	0	80	60	80	80	60	80	100	100	60	60
Hydrobiosidae	3.9 (1.7)	2.2 (1.2)	2.7 (1.0)	0 (0.8)	1.5 (0.8)	1.8 (0.8)	15.0 (1.2)	5.8 (2.0)	0 (2.3)	3.2	4.9	4.2	3.6	0	2.1	2.9	12.6	9.9	0	8.9	60	40	20	0	40	80	100	80	0	60
<i>Paroxyethira</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Oxyethira</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Other Trichoptera	3.1 (1.8)	0.3 (0.3)	0	0	0	0	0	0	2.4 (1.3)	0	2.1	<0.1	0	0	0	0	0	0	0.1	0	40	20	20	0	0	0	0	0	40	0
Chironomidae	0.3 (0.3)	0	0	0	9.4 (5.5)	14.4 (4.1)	0	6.0 (2.3)	1.8 (1.6)	2.9 (2.0)	<0.1	0	0	0	2.3	3.6	0	2.1	0.9	1.1	0	0	0	0	60	80	0	20	20	40
Muscidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Aphrophila</i> sp.	3.2 (1.0)	0	0	0	0	0.2 (0.2)	0	0	1.3 (0.6)	3.6 (1.1)	5.7	0	0	0	0	0.9	0	0	3.8	4.5	0	0	0	0	0	20	0	0	60	80
<i>Archichauliodes</i> sp.	0 (1.1)	1.1 (1.1)	0	0	0.1 (0.1)	0	2.9 (2.9)	2.9 (1.2)	0.6 (0.3)	1.6 (1.0)	0	3.2	0	0	1.2	0	5.4	5.7	6.5	4.9	0	20	0	0	40	0	40	80	20	40
Elmidae	0	0	0	2.0 (0.8)	0	0	5.8 (4.7)	0 (0.5)	0.5 (0.5)	0	0	0	0	1.5	0	0	2.1	0	1.7	0	0	0	0	20	0	0	20	0	60	0
Uniden.	0	0	0	0	0	0	0.1 (0.1)	0	0	0	0	0	0	0	0	0	<0.1	0	0	0	0	0	0	0	0	0	20	0	0	0

Appendix B8. Relative composition (%) of major aquatic food categories in blue duck diets collected above and below the falls from Makaroro River as determined by numerical, dry weight and incidence-of-occurrence analyses. Figures in parentheses represent the standard error.

Date	Numerical										Dry weight										Occurrence									
	15.3		3.6		20.10		3.11		13.12		15.3		3.6		20.10		3.11		13.12		15.3		3.6		20.10		3.11		13.12	
Taxon	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A
Leptophlebiidae	4.0 (2.2)	0	15.0 (5.5)	1.7 (1.1)	25.2 (3.1)	26.9 (4.9)	16.7 (2.7)	26.7 (1.8)	27.6 (2.9)	48.3 (9.5)	27.2	0	32.1	8.5	56.9	32.3	49.8	55.4	56.9	51.2	100	0	100	100	100	100	100	80	100	100
Coloburiscus sp.	0	0	2.0 (0.8)	0	7.2 (5.5)	6.6 (4.0)	3.8 (2.2)	1.5 (1.5)	3.8 (1.9)	12.7 (3.8)	0	0	4.4	0	11.7	11.3	9.9	5.9	8.9	14.7	0	0	80	0	20	60	60	20	60	80
Nesameletus sp.	0	0	0.8 (0.5)	0	0	0	0	0	0	3.8 (2.4)	0	0	2.8	9	0	0	0	0	0	7.3	0	0	60	0	0	0	0	0	0	40
Zelandoperla sp.	2.8 (1.4)	0	12.1 (4.7)	18.7 (8.4)	6.3 (2.9)	18.4 (10.3)	5.0 (2.0)	7.8 (2.5)	0	10.3 (4.0)	18.3	0	22.7	37.8	9.7	22.3	16.4	12.7	0	12.0	60	0	100	60	80	100	80	80	0	80
Zelandobius sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Megaleptoperla sp.	0	0	0	0	0.8 (0.8)	0	0	0	0	0	0	0	0	0	1.7	0	0	0	0	0	0	0	0	0	20	0	0	0	0	0
Austroperla sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Pycnocentrodes sp.	17.1 (5.3)	0	2.3 (1.3)	13.4 (3.8)	0	10.3 (4.5)	0	0	15.9 (4.8)	10.8 (4.3)	8.9	0	1.7	7.8	0	4.2	0	0	6.8	5.2	100	0	100	100	0	60	0	0	100	80
Beraeoptera sp.	63.5 (7.1)	81.3	54.0 (11.3)	53.2 (10.0)	29.2 (3.8)	16.3 (6.7)	25.2 (5.8)	18.6 (10.5)	12.3 (5.7)	0	23.1	35.3	21.1	19.8	9.2	6.3	13.2	12.1	5.3	0	100	100	100	100	100	60	100	100	100	0
Helicopsyche sp.	1.3 (1.2)	0	0	0	1.2 (1.2)	5.9 (5.8)	3.0 (1.5)	0	0.3 (0.3)	0	0.2	0	0	0	<0.1	1.2	1.1	0	<0.1	0	60	0	0	0	20	20	20	0	20	0
Olinga sp.	0	0	2.3 (1.3)	2.3 (1.2)	21.8 (9.0)	1.9 (1.2)	0	0	0	0	0	0	1.7	1.4	9.9	0.3	0	0	0	0	0	0	60	60	60	20	0	0	0	0
Aoteapsyche sp.	4.0 (3.1)	0	1.0 (0.5)	3.2 (0.5)	1.3 (0.7)	0.7 (0.7)	0	4.1 (0.6)	3.5 (0.3)	4.9 (2.0)	9.2	0	3.3	6.9	2.1	1.5	0	6.9	9.5	5.3	100	0	80	100	60	20	0	100	100	80
Hydrobiosidae	4.5 (2.4)	1.9	2.5 (1.1)	1.3 (0.7)	2.2 (1.6)	8.6 (2.5)	2.4 (0.6)	3.9 (1.9)	1.6 (1.3)	5.5 (1.6)	8.2	23.6	3.8	4.2	4.6	14.3	9.6	4.8	3.5	6.4	100	100	80	80	40	100	100	100	40	80
Paroxyethira sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxyethira sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Other Trichoptera	0.4 (0.4)	0	0	5.4 (1.7)	0	0.3 (0.3)	0	0.5 (0.5)	0	0	0.9	0	0	7.2	5.9	0.1	0	0.8	0	0	60	0	0	40	0	20	0	20	0	0
Chironomidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Muscidae	0	0	0	0.1 (0.1)	0	0.6 (0.6)	0	0	0	0	0	0	0	0.2	0	1.2	0	0	0	0	0	0	0	20	0	20	0	0	0	0
Aphrophila sp.	0.7 (0.5)	1.9	0.8 (0.3)	0.7 (0.4)	0	3.4 (1.0)	0	0.7 (0.6)	0	0.5 (0.5)	2.1	15.8	2.5	4.2	0	5.8	0	1.4	0	1.1	60	100	80	60	0	80	0	40	0	20
Blepherciidae	0	0	0	0	0	0	0	0	35.0 (4.1)	0	0	0	0	0	0	0	0	0	9.1†	0	0	0	0	0	0	0	0	0	80	0
Archichauliodes sp.	0	1.9	0	0	0	0	0	0	0	0	0	20.0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0
Elmidae	1.7 (0.9)	0	0	0	0	0.1 (0.1)	0	0	0	0	1.0	5.3	3.9	0	0	<0.1	0	0	0	0	60	0	0	0	0	20	0	0	0	0
Uniden.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

† General Diptera BL-DW conversion equation applied

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