# The Fluvial Biology of Lake Taupo Rainbow Trout

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Doctor of Philosophy
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by
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Rainbow trout--9 pounds

Waddell's Pool, Tongariro River--June 1989

To my father,

A.G. Rosenau

1 March 1933  26 March 1981

## ABSTRACT

The riverine biology of adfluvial-lacustrine rainbow trout (Oncorhynchus mykiss, previously Salmo gairdneri) from the Waimarino, Tokaanu, and Hinemaiaia Rivers was investigated. These three streams are important spawning and rearing habitats for rainbow trout recruiting to an economically important sport fishery in Lake Taupo, New Zealand, yet each has very different bio-physical characteristics; the Waimarino River is an unregulated stream with seasonally varying flow and temperature regimes; the Hinemaiaia River is an hydro-electric flow-controlled stream having a seasonally varying temperature regime and daily flow fluctuations; the Tokaanu River is an unregulated groundwater-fed stream with stable flows and temperatures. Nutrient concentrations and spawning and rearing habitats also vary considerably among these streams.

Scales were taken from adult rainbow trout from these streams and examined; they showed both widely-spaced outer, and narrowly-spaced inner, circulus zones. While there were no among-population differences in average circulus-spacing in the outer-growth zone, there were significant among-population differences in the inner zone; these two zones are suggested to represent (common) lake and natal stream rearing, respectively. The back-calculated minimum and average lengths at migration of juveniles from stream to lake was similar for all three populations (ca. 94 mm and ca. 140 mm, respectively) but there were significant among-population differences in age at emigration. The scale patterns and stream sampling suggested that most Hinemaiaia River rainbow trout left the river within the first year of growth (64%) whilst much higher proportions of juveniles surviving to adulthood in the other two streams overwintered before emigrating in their second year (up to 70%).

Scales were also taken from juvenile rainbow trout captured from the Waimarino and Tokaanu Rivers. The patterns on these scales corresponded closely with the features seen on the inner-growth zone of the adult scales. This further strengthened the assertion that the inner-growth zone on the adult scales reflects a period of juvenile natal-stream growth before the fish go to Lake Taupo.

The utilization of fluvial habitat by juvenile rainbow trout, common bullies and koaro in the Waimarino River was examined using minnow trapping as a methodology. There was segregation of habitat by these three species with regards to one or more of the following variables: 1) water depth, 2) water velocity, 3) substrate size, and 4) instream cover. Except in winter when the habitat choices by fingerlings (45-93 mm fork length) and smolts (>93 mm fork length) overlapped, there was also a segregation of habitat by the various size classes of juvenile trout, including fry (<45 mm fork length). Furthermore, there were ontogenetic trends and larger juvenile trout choose habitats with faster and deeper water and having substrates with larger diameters than did the smaller size classes of fish; larger juvenile trout were also more closely associated with instream cover. Woody and herbaceous cover were generally important for all species and size classes of fish in the Waimarino River.

The distributions of juvenile trout and koaro and common bullies in the Waimarino, Tokaanu and Hinemaiaia Rivers was investigated. The species composition varied considerably among seasons, study sites and rivers. More bullies were found in the downstream reaches of these streams and this appeared to be positively related to water column depths and inversely related to velocities. There was a negative relationship between the catch rates of rainbow trout juveniles and koaro. The hydro-electric dam overflow channel on the Hinemaiaia River contained exceptional numbers of koaro.

I also examined the inherited variability in parr mark numbers in juvenile rainbow trout from the Tokaanu and Waimarino Rivers. Ripe male and ovulated female trout were obtained from each of the study streams and reciprocal and pure crosses were made from the pooled gametes. The resulting juveniles were reared to fingerling size in separate tanks under similar conditions. The parr marks bisecting the lateral line on the left side of the fish were counted and there were significant differences between the two pure crosses; the reciprocal hybrid crosses were intermediate in number. This suggests that there was a genetic difference controlling parr-mark number in these fish. The parr marks of wild-caught fingerling rainbow trout from the two study populations were also counted and there were no significant differences in number between these groups but the wild caught fish had intermediate numbers of parr marks compared to the laboratory fish. This suggests that either 1) there were genetic differences controlling parr-mark number between the laboratory and the wild fish with regards to the genetic control of parr mark number in these groups, or 2) population-specific environmental influences (e.g., temperature) were modifying the parr-mark number of the genetically different wild juvenile trout, during their embryonic development in their respective natal streams, to produce a similar parr-mark number in these stocks of fish.

Genetic differences in agonistic behaviour were also investigated in laboratory-incubated juvenile rainbow trout from the Waimarino and Tokaanu Rivers. Because of the small sample sizes involved in this experiment, the results are considered to be only preliminary. However, if the observations reflect the behaviours in the wild populations, this genetic difference is likely to be adaptive and have evolved in response to the very different conditions in these two rearing streams.

Finally, embryo and alevin development and survival rates were examined for fish from the Waimarino and Tokaanu Rivers. Two pure and two reciprocal-hybrid crosses were made and the resulting groups were incubated at the same time and under identical conditions at target temperatures of either 12 or 7°C. Within temperatures, the hatching date was the same for all crosses (12°C, 27 d; 7°C, 51 d). However, there were significant among-cross differences, within temperatures, with respect to emergence date; these differences were a result of phenotypic (egg size) and genotypic variability. Alevins from smaller eggs emerged earlier than equivalent crosses from larger eggs; alevins sired by Tokaanu River males emerged earlier than equivalent crosses of Waimarino River males. Samples of eggs were also taken ovulated rainbow trout from each population and the Tokaanu rainbow trout had lower egg weights at standard female lengths. These population differences in egg-size and rates of development are thought to be adaptive and to have evolved in response to conditions encountered by the incubating fish in their respective natal streams. The

Tokaanu river has an inferior spawning environment, with lower intra-redd dissolved oxygen levels and poorer quality gravel; thus, selection has produced a population of rainbow trout having small eggs, fast developing alevins in order to maximize survival under adverse incubation conditions. Survival rates from fertilization to hatch in the experimental crosses were above 90% for all groups at both 7 and 12°C; however, embryos of larger eggs had slightly, but consistently, lower survival rates than embryos from smaller eggs, at both temperatures. Likewise, survival from hatch to emergence was also above 90% for all crosses at 12°C; however, there were substantial among-cross differences in alevin survival rates at 7°C and this was the result of phenotypic (egg size) and genotypic (population) effects. These differences are also thought to be adaptive and appear to reflect selection resulting from water temperature differences that these alevins would normally encounter under natural conditions in their respective natal streams.

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# SECTION I--STUDY BACKGROUND

## Chapter 1.--INTRODUCTION

The rainbow trout (**Oncorhynchus mykiss** Richardson) has been introduced into areas world wide, well beyond its indigenous range. Although fresh waters on both the Asiatic and North American sides of the north Pacific Ocean comprise its native distribution (McPhail and Lindsay 1970; Lee et al. 1980; Okazaki 1984; see also, Kendall 1988), self-sustaining populations are now found on all continents except Antarctica (MacCrimmon 1971). The anthropogenic-range extension of rainbow trout includes many New Zealand streams and lakes (McDowall 1990) and most of these fish are progeny arising from introductions occurring in the latter half of the 19th century (Scott et al. 1978).

Various reasons have been given to explain the spectacular success of rainbow trout in adapting and acclimatizing to its new environments. Allendorf and Utter (1979) suggested that the key is the high average genetic heterozygosity found in rainbow trout and that adaptation through selection can occur very rapidly (e.g., Reisenbichler and Phelps 1989). Among-population variation in rainbow trout has been demonstrated for a number of character traits including allozymes (Utter et al. 1980; Parkinson 1984), meristics (Smith 1969), morphology (Tully 1989), growth and survival rates (Reisenbichler and McIntyre 1977), and time of spawning (Smith 1969) and these examples are each thought to have a largely inherited component.

Nevertheless, not all aspects of rainbow trout biology are rigidly entrained by the genetic constitution of the species and individuals within a population can often acclimatise well under a variety of conditions. Scott and Crossman (1973) have described rainbow trout as generalists with fairly plastic life-history traits. As an example, rainbow trout often shift with relative impunity from fluvial to lacustrine, and freshwater to marine, environments.

One facet of rainbow trout biology that is, however, very consistent is the importance of the fluvial environment. Virtually all populations use streams for reproduction and the fish of many stocks live out their entire lives in a riverine environment, rarely moving in location more than a few metres from birth to death (Gerking 1959). In contrast, other populations emigrate from their natal streams and travel hundreds or thousands of kilometres to feeding grounds in lakes or the ocean, although they may first undergo extensive fluvial rearing before emigration (Scott and Crossman 1973). However, and again demonstrating the plasticity of life-history traits in this species, an extended period of fluvial rearing is not present in all migratory lacustrine populations (Hayes 1988a,b). Nevertheless, whether the population is migratory or sedentary, individuals return to their natal streams, usually with great fidelity, to spawn and repeat the life cycle.

While the functional utility of streams to rainbow trout is unequivocal, varying physical and biological conditions therein will affect their growth and survival. These conditions include: species composition and densities of competitors and predators (Fausch 1984; Hayes 1987; 1989), nutrients levels (Scarnecchia and Bergersen 1987), range and variability of water temperature (Hokanson et al. 1977), structure and quality of rearing habitat (Ward and Slaney 1981; Shirvell 1990), flow (Bovee 1982; Binns 1982), levels of dissolved gases (Chapman 1988), and spawning-substrate quality (Sheppard and Johnson 1985; Chapman 1988).

In New Zealand, rainbow trout are completely freshwater although most stocks arose from a donor population of anadromous steelhead trout (Scott et al. 1978). While some populations are solely riverine, most New Zealand stocks are lake-migratory, or adfluvial-lacustrine (McDowall 1990); that is, the fish spawn in a stream and the young go to a lake for further rearing. However, the amount of stream rearing by migratory juveniles, before emigration, can vary considerably among New Zealand populations of rainbow trout (c.f., Hayes 1988a,b; Stephens 1989).

The majority of rainbow trout in New Zealand are found in the lakes of the

Volcanic Plateau of the central North Island (McDowall 1990) with the single greatest concentration in the Lake Taupo watershed (Scott 1987). Both brown (**Salmo trutta**) and rainbow trout were introduced into Lake Taupo at the end of the 19th century and by the first decade of the 20th it had became the site of an internationally renowned sport fishery (Burstall 1983). Lake Taupo's rainbow trout utilize many of its inlet streams for spawning and rearing and because of the unique and varied geological conditions in this geographic area, these streams often differ considerably in their flow characteristics, water chemistry, temperature regimes, and water sources (Schouten et al. 1981). Nevertheless, the production of rainbow trout by these streams is considerable compared to populations elsewhere in the world (Cryer 1991) and this watershed provides the basis for a multi-million dollar industry in this area of New Zealand (Shaw et al. 1985).

Despite world-wide interest and an importance to the local economy, only recently has there has been any fisheries research conducted on the fluvial biology of fishes in the Lake Taupo watershed. Tully (1989), examining rainbow trout reproduction in three Lake Taupo tributaries, showed that there was considerable among-stream variability in the physical characteristics (water depths and velocities, substrate composition, dissolved gases) of the spawning habitats in these streams. He suggested that there was significant inter-population differences in morphology and fecundity of the rainbow trout in these streams and that this was the result of adaptation to their respective and differing spawning environments.

Other studies have also provided preliminary evidence that an extended stream-rearing period by juvenile rainbow trout, prior to emigration to Lake Taupo, may be an important to the production of fish in this watershed (Stephens 1984, 1989; Kusabs 1989; Pitkethley 1990). Nevertheless, large gaps still remain in our understanding of the biological processes contributing to the survival and growth of fish in these waters.

Hence, this study was conducted to further our understanding the fluvial biology of rainbow trout in Lake Taupo. The main objective was to determine how the riverine environment, interacting with the unique biology of rainbow trout, has contributed to the extraordinary success of this species in Lake Taupo. Specifically, the following points were to be addressed:

### Stream rearing

1) Is stream rearing by juveniles, prior to emigration, an important component of the survival of Lake Taupo rainbow trout? If so, how long do the fish stay in the stream before going to the lake and what size are they when they emigrate? Do populations living in streams having differing flow, water chemistry and temperature characteristics have differing growth rates and do they migrate at varying sizes or ages?

2) If stream rearing by young rainbow trout is important, what constitutes fluvial habitat for juveniles? Does the habitat usage vary amongst rearing streams? From a fishery management perspective, is it important to protect particular habitat types?

3) Are juvenile rainbow trout in the Lake Taupo watershed adapted to their natal stream environments with respect to agonistic behaviour or body characteristics (meristics) ? That is, are there any inherited between-population differences with regards to these character traits?

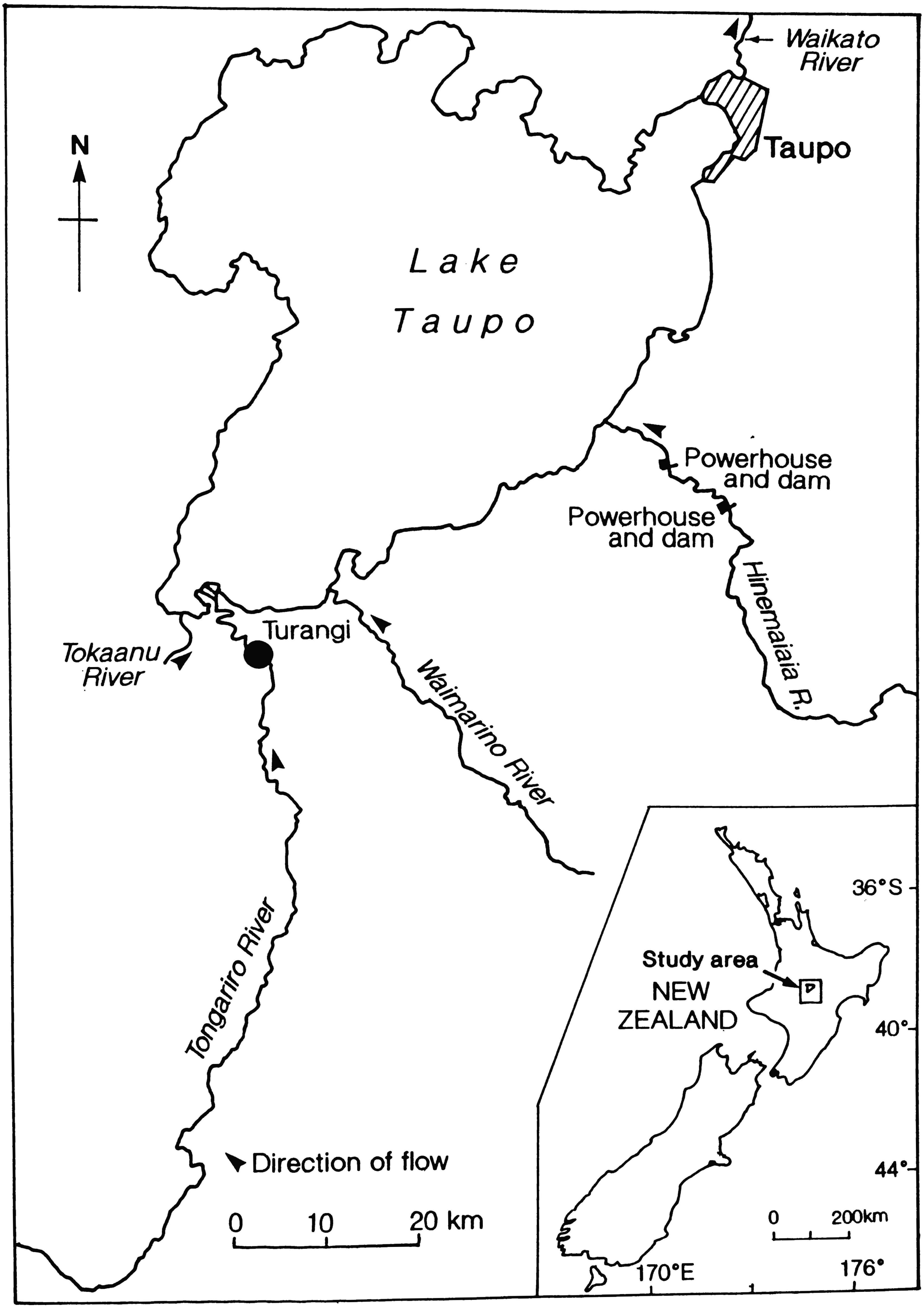
### Reproduction

1) Given that the spawning and incubation conditions in Lake Taupo spawning tributaries vary so considerably, is there any among-population differentiation in rainbow trout incubation or survival rates? Can any observed genetically-mediated differences then be correlated to habitat characteristics of the particular natal

stream?

2) Tully's (1989) data suggested that rainbow trout fecundity varied among his three study streams. If this is so, then I hypothesize that egg size should also vary among these populations. Fecundity and egg size variation among populations is thought to often have a strongly inherited component in salmonids (Brannon 1987). Therefore, I decided to investigate the functional significance of any between-population variation in this character trait in these Lake Taupo populations of rainbow trout.

Figure 1.1.--Location of the study streams flowing into Lake Taupo.


Waikato River
Taupo
N
Lake Taupo
Powerhouse and dam
Powerhouse and dam
Hinemaiaia R.
Turangi
Tokaanu River
Waimarino River
Tongariro River
Direction of flow
0
10
20 km
36°S
Study area
NEW ZEALAND
40°
44°
0
200km
170°E
176°

# Chapter 2.--RAINBOW TROUT IN LAKE TAUPO

## 2.0 INTRODUCTION OF TROUT TO LAKE TAUPO

Perhaps nowhere on earth has man changed the biota of a land as extensively and in so short a period of time as in New Zealand (Druett 1983). Part of the reshaping of the fauna has been the introduction of non-indigenous species of freshwater and anadromous fishes (McDowall 1990). The most well received species were of the family Salmonidae including the quinnat salmon (**Oncorhynchus tshawytscha**) and the rainbow and brown trouts. Lake charr (**Salvelinus namaycush**), brook charr (**S. fontinalis**), sockeye salmon (**O. nerka**) and Atlantic salmon (**Salmo salar**) were also introduced but with more limited success. Nevertheless, there is some debate as to the desirability of any of these fish species in New Zealand. McDowall (1990) speculates that incalculable damage may have been done to native fishes as a result of the acclimatization of these non-indigenous animals.

The first rainbow trout to survive in this country seem to have arrived in New Zealand in 1883 (Scott et al. 1978) and most of the extant populations seem to have been derived from this group. These fish were from a California, USA, anadromous steelhead stock of rainbow trout although there are no known sea-going populations in New Zealand waters (Scott et al. 1978). Because of the genetic likeness and similar life-history patterns in their fluvial environments, "rainbow trout" and "steelhead" will be regarded as equivalents in this study.

By 1900, rainbow trout were well entrenched in New Zealand and, by all accounts, the earliest sport fishing for these fish in was spectacular (Burstall 1983). Rainbow trout were first introduced into Lake Taupo in 1899 (Ashby 1967) and by 1911 a major fishery had sprung up in the area which catered to anglers coming world wide for trout that were both large and plentiful (Burstall 1983). Nevertheless, soon after the introduction of trout, the native fish populations in the lake began to disappear and there was a severe reduction in the numbers of koaro (**Galaxias brevipinnis**). Rainbow trout responded to the lower numbers of these forage fish and there was a drop in body size and numbers of catchable-sized fish (Burstall 1983). Subsequently, the common smelt (**Retropinna retropinna**) was introduced into Lake Taupo to act as a forage-fish base, in the 1930's, and the trout stocks and the fishery rebounded. To this day this watershed is an important destination for many sports anglers.

The economic benefits of the Lake Taupo trout fishery are considerable. Shaw et al. (1985) estimated that the number of anglers utilizing this watershed exceeded 45,000 per annum and almost $17 million dollars were spent on consumer goods related to fishing. These values have undoubtedly increased substantially since the time of their study given the steady increase in the number of anglers in recent years (Cryer 1991). Consequently, any detrimental impacts on the rainbow trout populations in this lake are of major concern to fisheries managers.

## 2.1 IMPACTS ON THE TROUT POPULATIONS

Exploitation by angling appears to be the greatest anthropogenic impact on rainbow trout in Lake Taupo at present. Cryer (1991) estimated that the total yearly harvest of fish was about 130,000 fish (approximately 180 tonnes) and this was between 30 and 50% of the total production of trout in the lake. Cryer's estimate of harvest is about 1/3 that given by Shaw et al. (1985) but it appears that the later study provides a much more accurate picture. Recent reductions in angler bag limits were implemented to protect this socially and economically important fishery.

Despite the considerable effects by angler exploitation, changes to habitat have the greatest potential to have permanent and insidious impacts on Lake Taupo trout. For example, in the 1950's it was realized that the Tongariro River could be used to generate large amounts of electricity. This was of much concern to anglers as the

Tongariro River watershed has the largest escapements of brown and rainbow trout of any stream flowing into Lake Taupo. Nevertheless, a scheme was initiated in 1964 which was to divert substantial amounts of water from the Tongariro River and into power generating turbines at Tokaanu; this program was finally completed in 1984. As part of the scheme, water from two other southerly flowing systems--the Moawhango/Whangaehu and the Wanganui/Whakapapa River watersheds--were also diverted into Lake Taupo and, hence, down the Waikato River. Despite the substantial changes in flow regime, the long-term effects of this power project on the trout populations in Lake Taupo and the Tongariro River do not seem to be significant (Stephens 1989).

Other smaller streams in the Lake Taupo watershed have also been impounded for electric generation including the Kuratau and Hinemaiaia Rivers. After the Tongariro, the Hinemaiaia River is the next most important trout-producing stream affected by hydro-electric dams. Again, while the effects of the altered flow regimes on trout production in this stream are unknown, concern is great enough that studies are now being undertaken to evaluate the impacts of the power scheme on the rainbow trout populations in the Hinemaiaia River (B. Hicks, Ministry of Agriculture and Fisheries, Rotorua, New Zealand, pers. comm.).

Other potential effects on trout rearing habitat in the Lake Taupo watershed include increases of fertilizer and sewerage nutrients into the lake and its streams through forestry and farming practices as well as urbanization (Forsyth and Howard-Williams 1983). Direct physical impacts to trout production may also be occurring through changes in riparian and instream habitat resulting from the clearing of land for silviculture and agriculture in addition to providing anglers with more access to fishing waters.

## 2.2 OTHER STUDIES

Stephens' (1984) thesis on smelt dynamics and their predation by rainbow trout was the first major formal study on Lake Taupo rainbow trout, although some unpublished research had been carried out by the Department of Internal Affairs and the Marine Department prior to his work (Burstall 1983). Subsequent to this, further research includes: 1) the migration and reproductive biology of adult rainbow trout in the Hinemaiaia, Waimarino and Tokaanu Rivers (Tully 1989), 2) interactions between juvenile trout and koaro in small Lake Taupo tributary streams (Kusabs 1989), 3) the population dynamics of juvenile trout in two small Tongariro River tributary streams (Pitkethley 1990), and 4) an electrophoretic analysis of four Lake Taupo tributary populations (Snowdon, in prep.).

Stephens (1989) considered the effects of the Tongariro hydro-electric scheme on the trout fishery in the Tongariro River and found that there were no apparent effects on trout spawning, rearing and angling by this project. A recent four year study, carried out by Cryer (1991), investigated the population dynamics of trout and smelt as well as the harvest levels of trout by anglers in this watershed. Cryer suggested that the fishery is now close to Maximum Sustained Yield and recommended that the harvest be curtailed.

# Chapter 3.--STUDY AREA

Lake Taupo is located in the central North Island of New Zealand (Fig. 1.1) and is the largest freshwater lake in Australasia. It has a surface area of just over 600 km$^2$ with average and maximum depths of 100 and 185 m, respectively (Cryer 1991). The Tongariro River is the largest tributary flowing into this lake and enters the southern end at Turangi. There are a total of 28 named streams draining into Lake Taupo and they have average discharges ranging from 0.09 to 31 m$^3$s$^{-1}$ (Timperley 1983). The Waikato River, New Zealand's longest stream, drains the lake at the northerly end, near Taupo. Other aspects of the lake's hydro-geology, limnology and fisheries biology have been well described in Forsyth and Howard-Williams (1983).

The three tributary streams investigated in this study were the Waimarino (Plate 3.1), Tokaanu (Plate 3.2), and Hinemaiaia (Plate 3.3) Rivers. These streams differ considerably in their bio-physical characteristics (Table 3.1) yet, historically, each has supported large spawning runs of migratory rainbow trout which are thought to contribute significantly to the Lake Taupo sport fishery (R.T.T. Stephens, Department of Conservation, Hamilton, New Zealand, pers. comm.). These streams are approximately similar in the mean annual discharges (less than one-half an order of magnitude difference) with the Tokaanu River having stable flows which are a result of its groundwater sources whereas the Waimarino and Hinemaiaia Rivers have seasonally variable flows (Fig. 3.1). The Tokaanu River also has relatively more stable temperatures (Fig. 3.2) and considerably higher levels of phosphorus and nitrogen than the other two streams (Table 3.1).

The Tokaanu River is the shortest of the three streams arising from groundwater vents at the base of Mt Pihanga near the town of Turangi (Fig. 1.1). A cross-stream fish fence, operated by the New Zealand Department of Conservation, is located 2 km from its upstream source; the fence is used to monitor escapement of spawning rainbow trout. The numbers of mature trout migrating through the fence averaged 1374 fish from 1985 to 1989 and these values appear to be the lowest since escapements were first monitored in the Tokaanu River (G. MacLean, Department of Conservation, Turangi, New Zealand, pers. comm.). Spawning area in the Tokaanu River is limited to about 1 km in its upper reaches and redd superimposition is common in this stream (Tully 1989; my observations). Juvenile and adult rainbow trout (Plates 3.4, 3.5) are the predominant fish species in the upper areas of this stream while the common bully (**Gobiomorphus cotidianus**) (Plate 3.6) are numerically the most abundant in the downstream reaches. A few koaro (Plate 3.7) are also found in the Tokaanu River.

The Waimarino River also flows into the southern end of Lake Taupo east of the village of Turangi (Fig. 1.1). About 9 km upstream from Lake Taupo there is a major falls which restricts the upstream migration of fish. Rainbow trout redd superimposition is not common in the Waimarino River (Tully 1989; my observations). Adult and juvenile rainbow trout are numerically the dominant species upstream of the State Highway 1 bridge and Tully (1989) had an escapement estimate of 14,676 adult spawners for 1988. The common bully and koaro also are also present in parts of this stream.

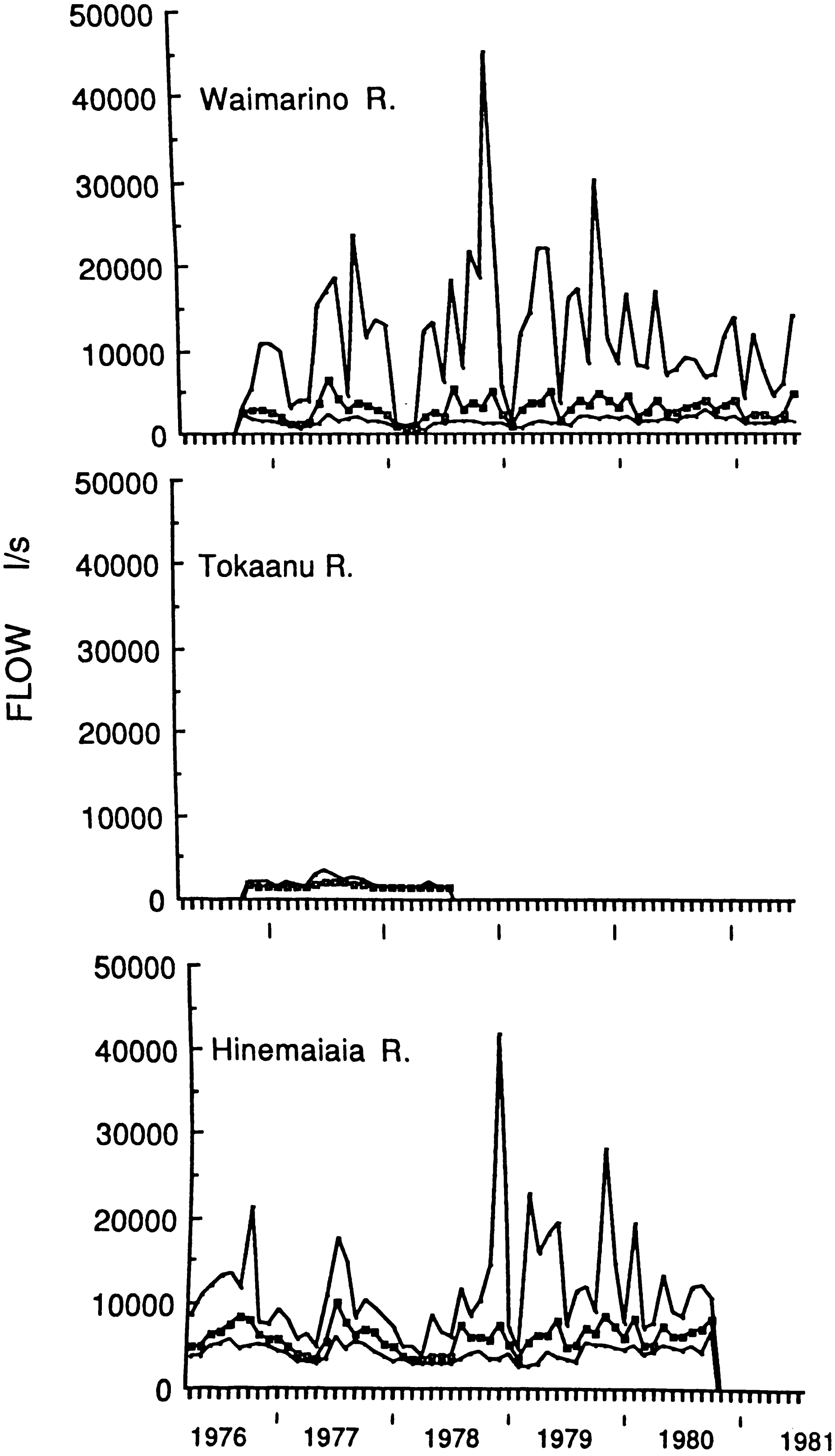
The Hinemaiaia River is located approximately half way between the villages of Taupo and Turangi (Fig. 1.1). It is a flow-controlled stream with the downstream hydroelectric-power dam located 7 km upstream of Lake Taupo. This dam acts as a complete barrier to the upstream migration of all fish. Three dams are situated on this stream and the downstream flows fluctuate considerably within a 24 hour period as a function of hydro-electric power generation (Fig. 3.3). Adult trout are most abundant in the winter (July 1988 -- 5556 fish; Tully 1989) while juvenile rainbow trout are very common during spring with their peak emergence occurring before mid-November (B. Hicks, Ministry of Agriculture and Fisheries, Rotorua, New Zealand, pers. comm.); however, by late summer the relative numbers of juvenile rainbows are considerably less and koaro and the common bully are much more numerous than the trout. No critical evaluation of redd superimposition has been made for rainbow trout in the Hinemaiaia River.

Only the occasional adult brown trout has ever been observed in the upper reaches of any of these three streams and small schools of common smelt have been observed in the lower reaches in all three streams (my observations).

Table 3.1.--Characteristics of the study streams. Discharge data and water chemistry from Schouten et al. (1981). Water chemistry is tabulated as the flow-weighted mean and samples were taken at state highway bridges, sample sizes are in brackets.

| Feature | Waimarino River | Tokaanu River | Hinemaiaia River |
|---|---|---|---|
| Mean annual discharge ($m^3s^{-1}$) | 3.1 | 1.8 | 5.9 |
| Maximum discharge ($m^3s^{-1}$) | 44.0 | 3.7 | 50.7 |
| Minium discharge ($m^3s^{-1}$) | 0.5 | 1.3 | 0.7 |
| Catchment area ($km^2$) | 79 | 35 | 165 |
| Mean gradient (%) | 1.3 | 0.4 | 0.9 |
| Water source | surface run-off | groundwater | surface run-off and groundwater |
| Flow regime (Fig. 3.1) | variable; unregulated | stable; unregulated | daily, seasonal variability; regulated |
| Conductivity @ 25°C (mS $m^{-1}$) | 4.7 (11) | 24.8 (14) | 5.3 (10) |
| Reactive phosphorus (mg $m^{-3}$) | 11 (13) | 44 (16) | 29 (11) |
| Inorganic nitrogen (mg $m^{-3}$) | 74 (13) | 180 (16) | 68 (11) |

Figure 3.1.--Minimum, mean, and maximum monthly flows (1976 to 1981) in the study streams. Data courtesy of the Department of Scientific and Industrial Research, Water Quality Centre, Hamilton, New Zealand. Mean monthly flow = (o).



50000
40000
30000
20000
10000
0
Waimarino R.
Tokaanu R.
Hinemaiaia R.
FLOW l/s
1976
1977
1978
1979
1980
1981

Figure 3.2.--Water temperatures in the study streams. Measurements are shown as either the minimum and maximum recorded temperatures, as measured by maximum/minimum thermometers (1988-89), or spot temperatures (1976-89), as recorded by the New Zealand Department of Scientific and Industrial Research (Water Quality Centre, Hamilton, New Zealand) and this study. Hinemaiaia River temperatures recorded at State Highway 1 bridge, Tokaanu River temperatures recorded at the New Zealand Department of Conservation adult fish trap, and Waimarino River temperatures recorded at the Kepa Road bridge.

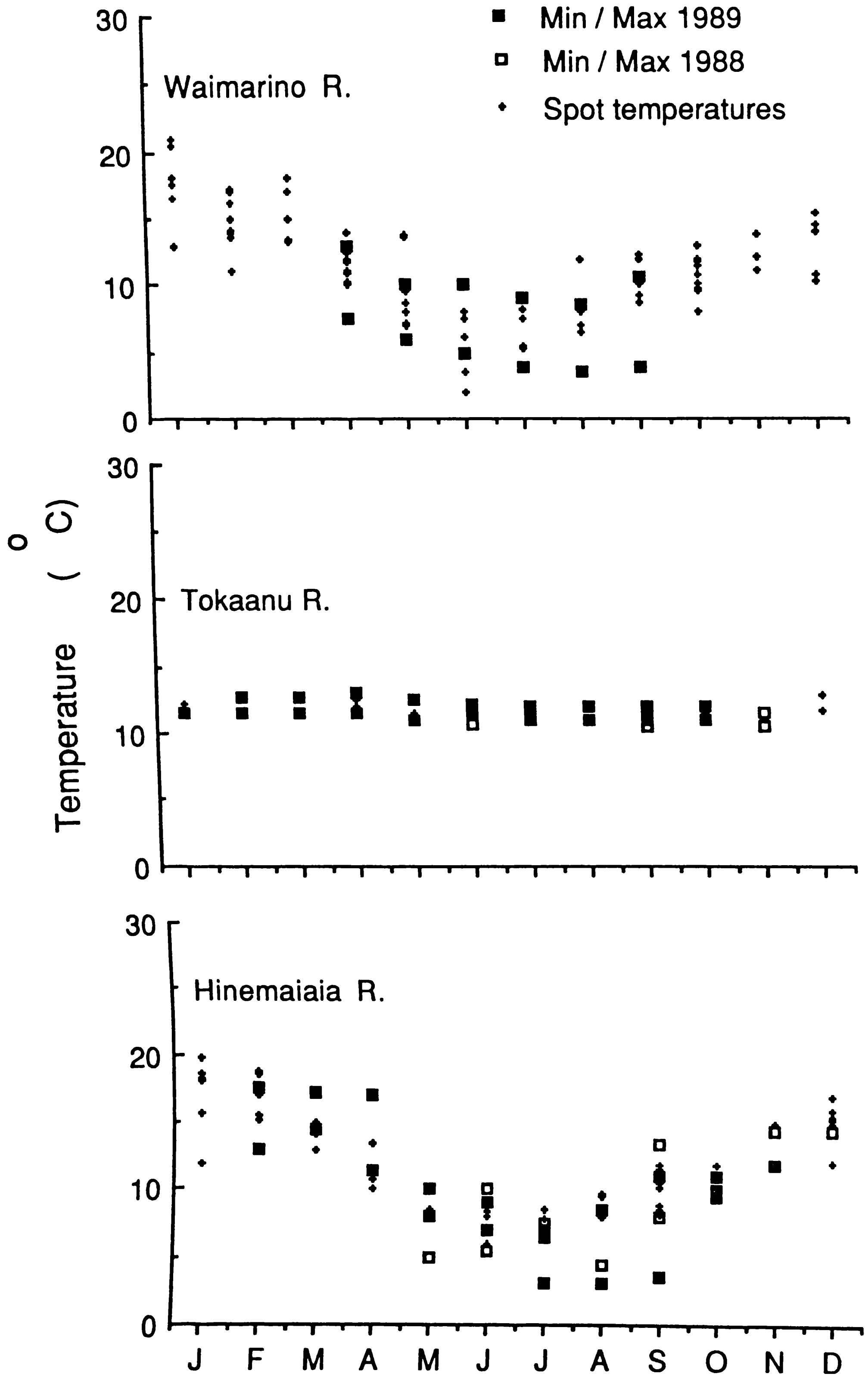

■ Min / Max 1989
□ Min / Max 1988
◆ Spot temperatures
Waimarino R.
Tokaanu R.
Hinemaiaia R.
Temperature (°C)
0
10
20
30
J
F
M
A
M
J
J
A
S
O
N
D

Figure 3.3.--Hydrograph of daily flow in the Hinemaiaia River showing fluctuations resulting from hydro-electric scheme, 11-14 April 1977. Data collected near State Highway Bridge 1 and are courtesy of the Department of Scientific and Industrial Research, Water Quality Centre, Hamilton, New Zealand.

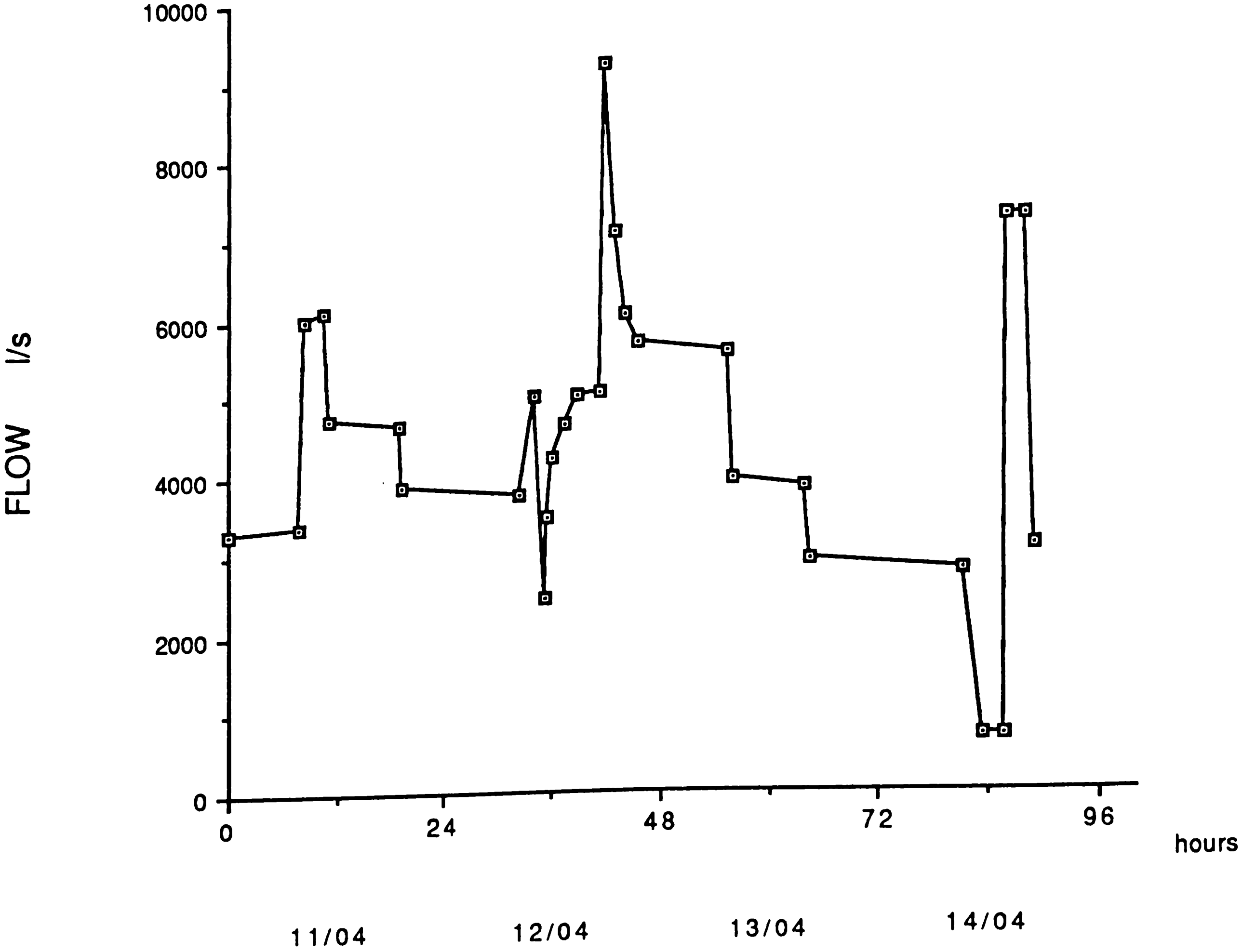

FLOW l/s
10000
8000
6000
4000
2000
0
0
24
48
72
96
hours
11/04
12/04
13/04
14/04

Plate 3.1.--Waimarino River downstream of Kepa Road bridge.

Plate 3.2.--Tokaanu River at the Department of Conservation fish fence.

Plate 3.3.--Hinemaiaia River approximately two kilometres downstream of the lower hydro-electric dam.

Plate 3.4.--Juvenile rainbow trout from the Tokaanu River.

Plate 3.5.--Adult rainbow trout from the Hinemaiaia River.

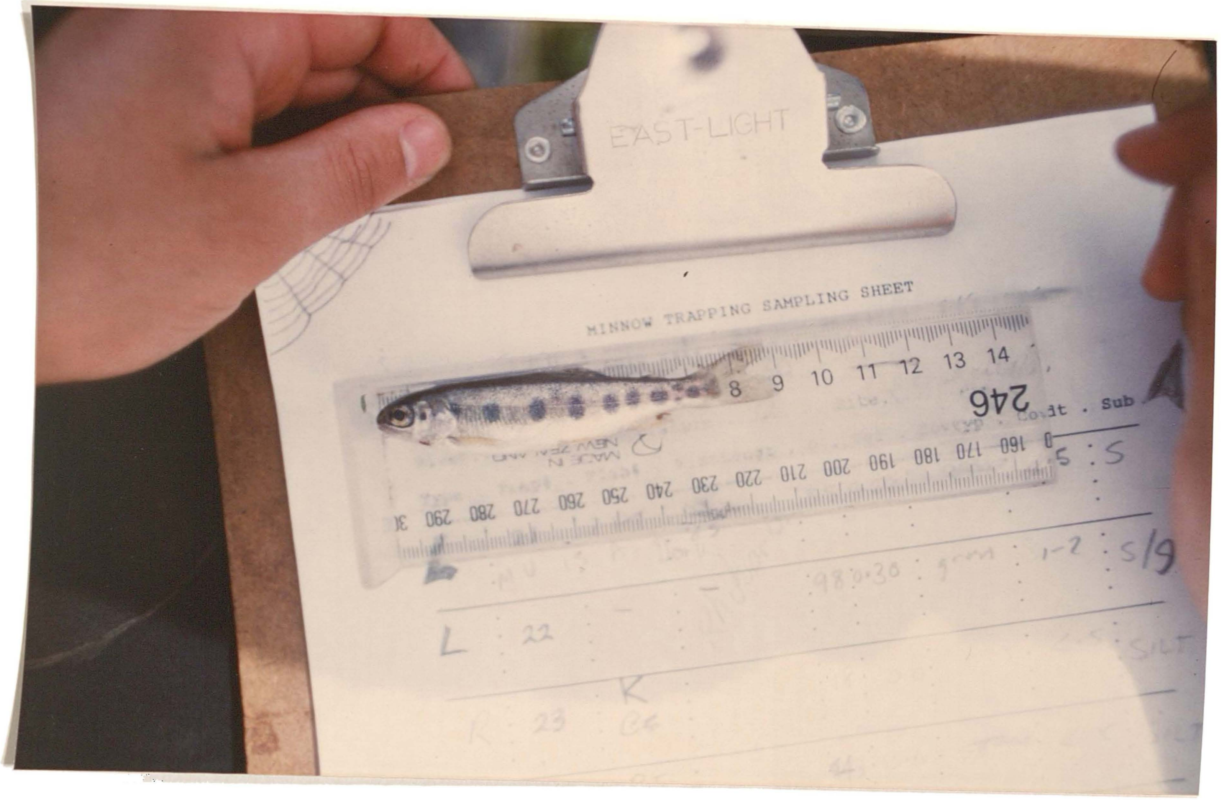

EAST-LIGHT
MINNOW TRAPPING SAMPLING SHEET
246
MADE IN NEW ZEALAND

Plate 3.6.--Common bully from the Tokaanu River.

Plate 3.7.--Koaro from the Tokaanu River.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# SECTION II--FLUVIAL REARING BY JUVENILES

## Chapter 4.--NATAL-STREAM REARING

### 4.0 INTRODUCTION

A prolonged period of stream residence is a feature of many populations of migratory rainbow trout and steelhead. Various studies (e.g., Biette et al. 1981; Ward and Slaney 1988) have shown that survival to maturity for lake- or ocean-rearing populations of this species may first involve several years of stream rearing. These studies indicated a pre-migratory minimum size of rainbow trout before they could survive in the lake or ocean. Indeed, over geographically large rearing areas (e.g., the Great Lakes (USA), the eastern Pacific Ocean) there are remarkable similarities among populations throughout the range in the sizes of the juveniles at emigration to the lacustrine or marine environment (Biette et al. 1981; Ward and Slaney 1988). However, because of varying inter-year or inter-stream productivity levels, and corresponding differences in growth rates, the age at emigration by the young trout from the stream may vary considerably among populations or years (Ward and Slaney 1988).

In a recent study (Stephens 1989), features of the scales of adult rainbow trout taken from Lake Taupo indicated two major zones of circulus distribution: an inner, closely-spaced group of circuli, and a separate, widely-spaced set of outer circuli. Since circulus spacing of the inner zone in lake-caught rainbow trout scales looked similar to the pattern found on the scales of the juvenile trout residing in Lake Taupo spawning streams, Stephens (1989) suggested that the inner pattern on the scales of the larger, lake-caught trout represented stream growth and proposed that stream rearing may be an important component of the life history of Lake Taupo rainbow trout. Thus, the purpose of this part of the study was to investigate the importance of natal-stream rearing to rainbow trout in Lake Taupo and its implications for management of these fisheries.

As part of the investigation, I examined the scale features of mature adult rainbow trout known to have migrated from Lake Taupo into the three study tributaries: the Waimarino, Tokaanu, and Hinemaiaia Rivers. I also looked at the change in size (growth) and numbers of juvenile rainbow trout in these same rivers over the period of a year. It was my intention to compare the interpretation of adult scale patterns to the sizes and ages of juvenile rainbow trout residing in their respective streams.

My study hypotheses were: 1) that Lake Taupo rainbow trout which survive to maturity normally undergo a protracted period of juvenile-stream rearing before emigrating to the lake and this is reflected in two different scale-circulus features in the adults: an inner zone of narrowly-spaced, and an outer zone of widely spaced, circuli and 2) that environmental differences among natal-rearing streams result in growth differences among these populations during the fluvial-growth period; this results in inter-population variability in the stream-zone scale patterns as well as differences in size-at-age as juveniles in the stream, and age-at-migration to the lake.

## 4.1 METHODS

### Scale analysis

In September 1987, 100 sexually mature rainbow trout were tangle-netted with gill-nets (stretched-mesh 90 mm) from each of the study streams. September is around the peak spawning period for Lake Taupo rainbows and, based on body sizes, these fish were identified as having recently come from Lake Taupo (Table 4.1 cf., Tully 1989). Six scales were taken from a "key scale" region; this was located along a diagonal line from the posterior insertion of the dorsal fin down to the lateral line in a posterior direction, and two rows up. All scales were taken from the left side of the fish's body. The scales were examined at 50X magnification using a microfiche-type scale reader. One scale from each slide was chosen for all measurements and scales showing abnormalities were not included in the analyses.

To minimise observer bias and ensure accuracy and precision, the following procedures were used. Firstly, the presence of any circulus discontinuities or "checks" were noted; then the number of circuli and distances between checks were counted and measured along the radius (longest axis) of the scale from the centre of the focus to the edge of the scale. A check was defined as the last narrowly spaced circulus, of a group of narrow circuli, preceding a group of more widely spaced circuli (Bilton and Robins 1971a). Average circulus spacing was determined by dividing the distance along the radius, for the zone of interest, by the number of circuli located within that zone. Four readings were made to ensure consistency in measurements and counts for each scale; discrepancies were less than 5% of the total sample for each population.

The back-calculated lengths of the fish at the various scale checks were estimated using Stephens' (1989) scale-radius:fork-length relationship for maiden Lake Taupo rainbow trout. His regression equation was:

$$\underline{L} = 153\ \underline{S} + 30 \qquad \underline{R}^2 = 0.97 \quad N = 111,$$

where $\underline{L}$ is the estimated fish fork length (in mm), for a particular point on the radius of the scale, and $\underline{S}$ is the distance (in mm) along the radius from the focus to that particular point on the scale (Fig. 4.1). Only immature trout were included in his analysis because of possible problems associated with resorption of scales at spawning.

### Juvenile sampling

To examine population changes in juvenile-fish size and abundance in the study streams, I trapped each of the rivers once each season from the winter of 1988 to the autumn of 1989. Small portable, wire (mesh size 3 and 6 mm) "minnow-traps" (Swales 1987), baited with thumbnail-sized pieces of trout ova, were used to catch the fish. The traps were set overnight and retrieved the next morning.

Three sites were sampled on each river and each averaged about 0.5 km in length. The sites were chosen to reflect the variation in the reach characteristics of each stream. Individual traps were set according to the variation in site characteristics (velocity, depth, substrate, presence or absence of cover) occurring within a study section. The number of traps varied slightly among seasons but was similar among study sites within rivers and among rivers for any particular season (Table 4.2). Trapped fish were identified to species and measured (fork length). Catch-per-unit effort (CPUE) of trout was calculated by averaging the number of fish caught per trap over all of the sites within a stream in a season; this value was assumed to reflect relative changes in abundance within and among streams and seasons.

The juvenile trout caught by trapping were grouped into year classes based on length-frequency distributions. Scales from a sample of these fish, over the range of lengths in the distribution, were inspected to confirm the age classifications. Winter checks were seen in some juveniles of all three populations. A year-class was defined as those fish that emerged from the spawning gravel between 1 June and 30 May. This time period was based on known spawning times (Tully 1989) and the size-frequency of the catches in this study.

For all statistical tests in this study a probability level of $P<0.05$ was considered to be biologically significant.

Figure 4.1.--Scale-radius:fork-length relationship for maiden Lake Taupo rainbow trout. L is the estimated fork length in mm, S is the distance along the radius to that particular point along the scale; data from R. Stephens (Department of Conservation, Hamilton, New Zealand, pers. comm.) and used with permission.

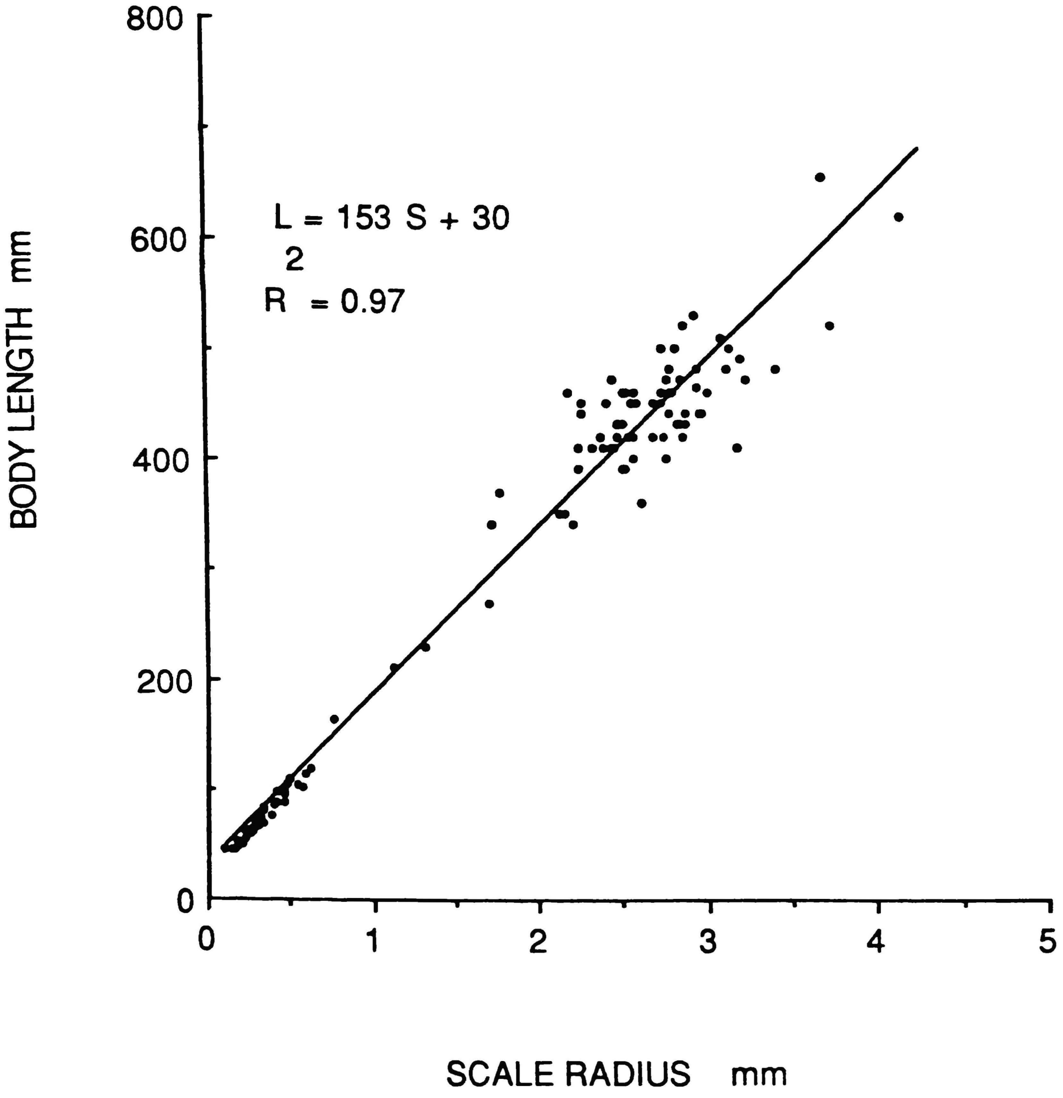

L = 153 S + 30
2
R = 0.97
BODY LENGTH mm
SCALE RADIUS mm
0
200
400
600
800
0
1
2
3
4
5

Table 4.1.--Average post-orbital to hypural lengths of adult trout used for scale analysis. Measurements in mm and with standard deviations and ranges. The fish were measured from the posterior of the eye socket to the hypural crease (post-orbital to hypural length) in order to avoid problems associated with changes in snout length and caudal-fin damage in spawning fish.

| | Males | | | | Females | | | |
|---|---|---|---|---|---|---|---|---|
| | n | length | SD | range | n | length | SD | range |
| Waimarino | 36 | 401 | 26 | 364-475 | 48 | 417 | 27 | 364-475 |
| Tokaanu | 27 | 384 | 37 | 338-480 | 52 | 407 | 24 | 370-512 |
| Hinemaiaia | 61 | 412 | 24 | 332-481 | 33 | 409 | 22 | 362-497 |

## 4.2 RESULTS

### Adult scale patterns

#### Lake-growth zone

The Waimarino, Tokaanu, and Hinemaiaia Rivers samples had 84, 79, and 94 trout with readable scales, respectively. All scales had two primary circulus features: including an inner zone of closely spaced circuli surrounding the focus (S1, S2), and an outer, more distal, zone having wider and homogeneous spacings between circuli (L) (Plate 4.1). The check between these two zones was abrupt and easily recognised. Because the scales examined in this study were taken from recent migrants known to have emigrated from the lake where they had spent many months to years, the whole of this homogeneously spaced outer part of the scale (Plate 4.1 L) represented lake growth and is hereafter referred to as the lake-growth zone. There were no significant differences among populations in the average widths between circuli for this zone of the scale (Table 4.3A; ANOVA F=0.319, P=0.727). The average back-calculated fork lengths of the juvenile rainbow trout at the start of the lake-growth zone was 145, 136, and 139 mm for the Waimarino, Tokaanu, and Hinemaiaia Rivers, respectively, and these lengths are not significantly different (Table 4.4A; ANOVA F=1.699, P=0.185). The minimum back-calculated fork length at emigration to the lake was about 94 mm and was consistent among all three populations (Table 4.4; Fig. 4.2.).

#### Stream-growth zone

The inner zone of closely spaced circuli surrounding the focus and on outward to the start of the lake-growth zone (Plate 4.1; S1, S2) was present on all scales examined and hereafter is referred to as the stream-growth zone. Two predominant stream-growth patterns were found: including 1) those scales having a distinct check located some distance between the centre of the focus and the start of the lake-growth zone (Plate 4.1A; S1+S2), or 2) those scales which showed no check in this area of the scale (Plate 4.1; S1 only). Scales which showed a check in the stream-growth zone of circuli will be referred to as having an overwintering pattern and those scales not having the check, a non-overwintering pattern. The overwintering pattern varied in frequency among the study populations: Waimarino 70% (59/84 fish); Tokaanu 49% (39/79 fish); Hinemaiaia 36% (34/94 fish) ($\chi^2$= 20.79, P<0.001).

As an approximate estimate of the trout length at the end of their first growing season, a back-calculation was made to the first scale check, regardless of the overwintering pattern; the average fish length to this check was different among populations (Table 4.4) with the mean lengths of the trout from the Hinemaiaia and Tokaanu Rivers significantly greater than from the Waimarino River (ANOVA F=10.69, P<0.001; Tukey's HSD W T H). The length of the trout at emigration to the lake (lake/stream check) was also significantly greater in the overwintering trout than in the non-overwintering fish (Table 4.5A vs C; Waimarino t=5.929, P<0.001; Tokaanu t=2.859, P=0.007; Hinemaiaia t=6.174, P<0.001) but the non-overwintering fish were longer at emigration to the lake than the overwintering trout were at the formation of the winter check (Table 4.5B vs C; Waimarino t=5.320, P<0.001; Tokaanu t=9.120, P<0.001; Hinemaiaia t=4.132, P<0.001), and this was consistent for all populations.

There were highly significant within-population differences in the circulus spacing between the stream-growth and the lake growth zones of the scale (Table 4.3A vs B -- Waimarino R. t=21.059 P<0.001, Tokaanu R. t=19.094 P<0.001, Hinemaiaia R. t=18.282, P<0.001). There were also significant among-population differences in the average spaces between circuli in the stream-growth zone of the scale from the focus to the stream/lake-growth zone check (Table 4.3B; ANOVA F=4.617, P=0.011; Tukey's HSD T W H) as well as from the focus to the first check regardless of winter pattern (Table 4.3C; ANOVA F=3.587, P=0.027; Tukey's HSD T W H); the Hinemaiaia fish had the widest average spacings, and the Tokaanu the narrowest.

## Juvenile trout sampling

### 1988 year class, young-of-the-year trout: 0+

By spring, catches of young-of-the-year rainbow trout, most of whom had just recently emerged (c. 25 mm, Fig. 4.3), increased substantially over winter catches in all three streams with the Hinemaiaia River CPUE's being especially high (7X Waimarino River; 40X Tokaanu River) (Fig. 4.4); peak emergence may have been earliest in the Hinemaiaia River. However, while the catches of these fish remained relatively high through to autumn in the Waimarino and Tokaanu Rivers, they fell to very low levels in the Hinemaiaia River by autumn (Fig. 4.4). The 0+ trout from all of the populations showed significant inter-seasonal increases in length from emergence through until the end of the study (Fig. 4.3). However, growth appeared to be greatest in the Hinemaiaia River over the whole sampling period; by summer, the mean length of its young-of-the-year trout was about 20 mm longer than that of the other two populations (Fig. 4.3). Indeed, during the autumn the few Hinemaiaia River trout that were caught continued to average considerably longer than fish of the other two populations; over 50% of Hinemaiaia rainbow trout were equal to or longer than 94 mm while only 27% of the Waimarino and 9% of the Tokaanu trout surpassed this length.

### 1987 year class: 1+

In contrast to the other streams, few rainbow trout of the 1+ year class could be found in the Hinemaiaia River during any sampling period (Fig. 4.4). However, there were substantial reductions in catches of the 1+ fish from winter to spring in the other two streams; at this time the Waimarino River had the highest catches (Fig. 4.4). The few Hinemaiaia rainbow trout that were trapped in spring continued to average considerably larger than the trout of the other two populations (Fig. 4.3).

### 1986 year class: 2+

Few of the 1986 year class of rainbow trout were captured in any of the rivers during this study at any time of the year (<10 fish for each stream). Drift diving observations confirmed the low number of this size/age class of rainbow trout in these streams.

Table 4.2.--Number of traps set per (austral) season in the sampling streams, from winter 1988 to autumn 1989. Each unit represents one standard overnight trapping session.

| | Winter Jun-Aug 1988 | Spring Sept-Nov 1988 | Summer Dec-Feb 1988-89 | Autumn Mar-May 1989 |
|---|---|---|---|---|
| Waimarino | 151 | 134 | 174 | 176 |
| Tokaanu | 137 | 135 | 178 | 179 |
| Hinemaiaia | 134 | 135 | 162 | 168 |

Table 4.3.--Among-population comparisons of average widths between circuli for the adult trout scales. Values are in mm x 50 (scale-reader magnification), with standard deviations, and *n* values in brackets.

A. Lake-growth zone--from stream-growth zone to scale edge.
B. From centre of focus to end of stream-growth zone--all rearing patterns combined.
C. From centre of focus to first circulus check regardless of winter rearing pattern.

| | Waimarino River | Tokaanu River | Hinemaiaia River |
|---|---|---|---|
| A. | 1.712 ±0.117 (84) | 1.698 ±0.139 (79) | 1.711 ±0.133 (94) |
| B. | 1.296 ±0.138 (84) | 1.260 ±0.150 (79) | 1.328 ±0.154 (94) |
| C. | 1.277 ±0.153 (84) | 1.269 ±0.183 (79) | 1.330 ±0.160 (94) |

Table 4.4.--Among-population comparisons of juvenile trout fork lengths back-calulated from the adult trout scales. Lengths (mm) were estimated using the Stephens (1989) regression formula $L = 153\ S + 30$, with standard deviations, $n$ values in brackets, and with ranges.

A. At emigration to the lake.
B. To first circulus check regardless of overwintering pattern.

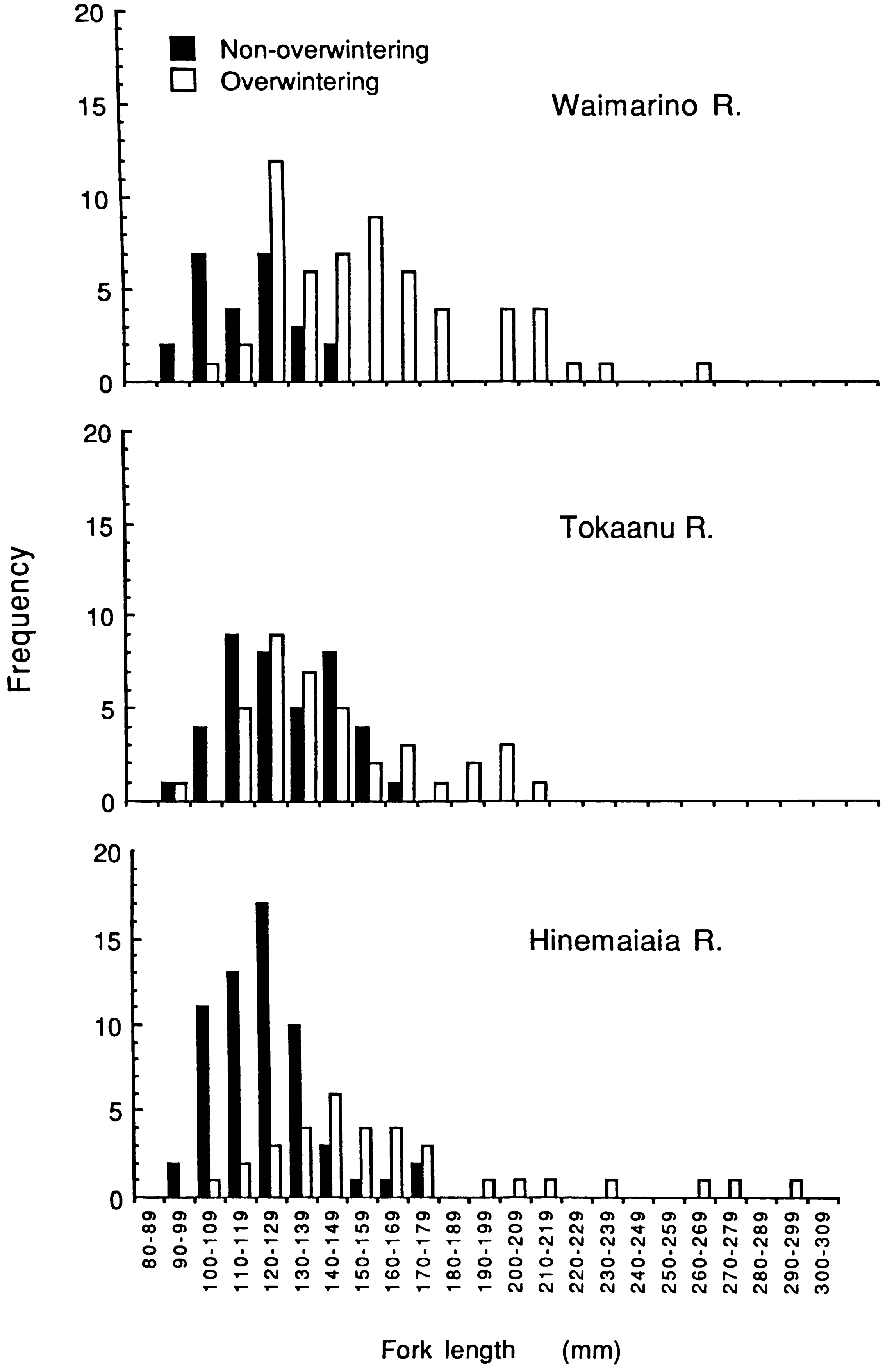
| | Waimarino River | Tokaanu River | Hinemaiaia River |
|---|---|---|---|
| A. | 144.5 ±32.2 (84) 94-256 | 135.7 ±23.8 (79) 94-201 | 138.5 ±36.3 (94) 97-299 |
| B. | 103.6 ±18.1 (84) 70-149 | 111.5 ±24.1 (79) 67-168 | 117.9 ±19.7 (94) 76-171 |

Table 4.5.--Fork lengths of juvenile rainbow trout back-calculated from the adult scales. Lengths (mm) were estimated using the Stephens (1989) regression formula, $L = 153 S + 30$, with standard deviations, $n$ values in brackets, and with ranges.

A: *Overwintering scale pattern*: fish length at emigration to the lake.
B: *Overwintering scale pattern*: fish length at winter discontinuity.
C: *Non-overwintering scale pattern*: fish length at emigration to lake.

| | Waimarino River | Tokaanu River | Hinemaiaia River |
|---|---|---|---|
| A. | 160.0 ±30.9 (59) 103-256 | 143.1 ±27.3 (39) 94-201 | 164.5 ±46.3 (34) 103-299 |
| B. | 97.6 ±16.3 (59) 70-140 | 93.9 ±16.5 (39) 67-140 | 107.7 ±20.8 (34) 76-149 |
| C. | 117.6 ±14.1 (25) 94-149 | 128.5 ±17.1 (40) 97-167 | 123.8 ±16.5 (60) 97-171 |

Figure 4.2.--Frequency distribution of estimated juvenile rainbow trout lengths at emigration to the lake as back-calculated from the adult scale patterns.



Non-overwintering
Overwintering
Waimarino R.
Tokaanu R.
Hinemaiaia R.
Frequency
0
5
10
15
20
80-89
90-99
100-109
110-119
120-129
130-139
140-149
150-159
160-169
170-179
180-189
190-199
200-209
210-219
220-229
230-239
240-249
250-259
260-269
270-279
280-289
290-299
300-309
Fork length (mm)

Figure 4.3.--Average lengths and standard deviations of minnow-trapped juvenile rainbow trout. Austral seasons are: June to August (winter), September to November (spring), December to February (summer), and March to May (autumn).

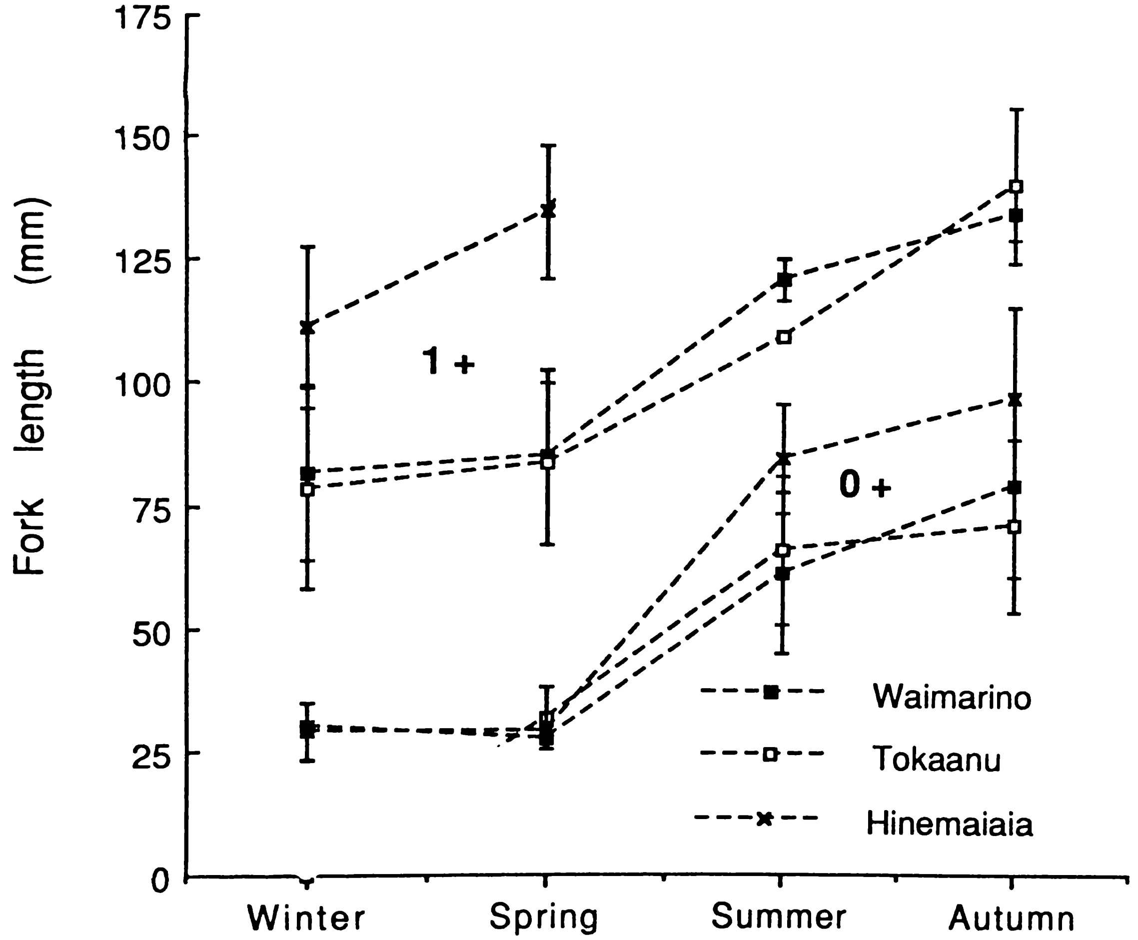

Fork length (mm)
175
150
125
100
75
50
25
0
Winter
Spring
Summer
Autumn
1 +
0 +
Waimarino
Tokaanu
Hinemaiaia

Figure 4.4.--Catch-per-unit effort of minnow-trapped juvenile rainbow trout. An overnight set by one trap was considered to be one trapping unit of effort. Austral seasons are: June to August (winter), September to November (spring), December to February (summer), and March to May (autumn), ± standard errors.

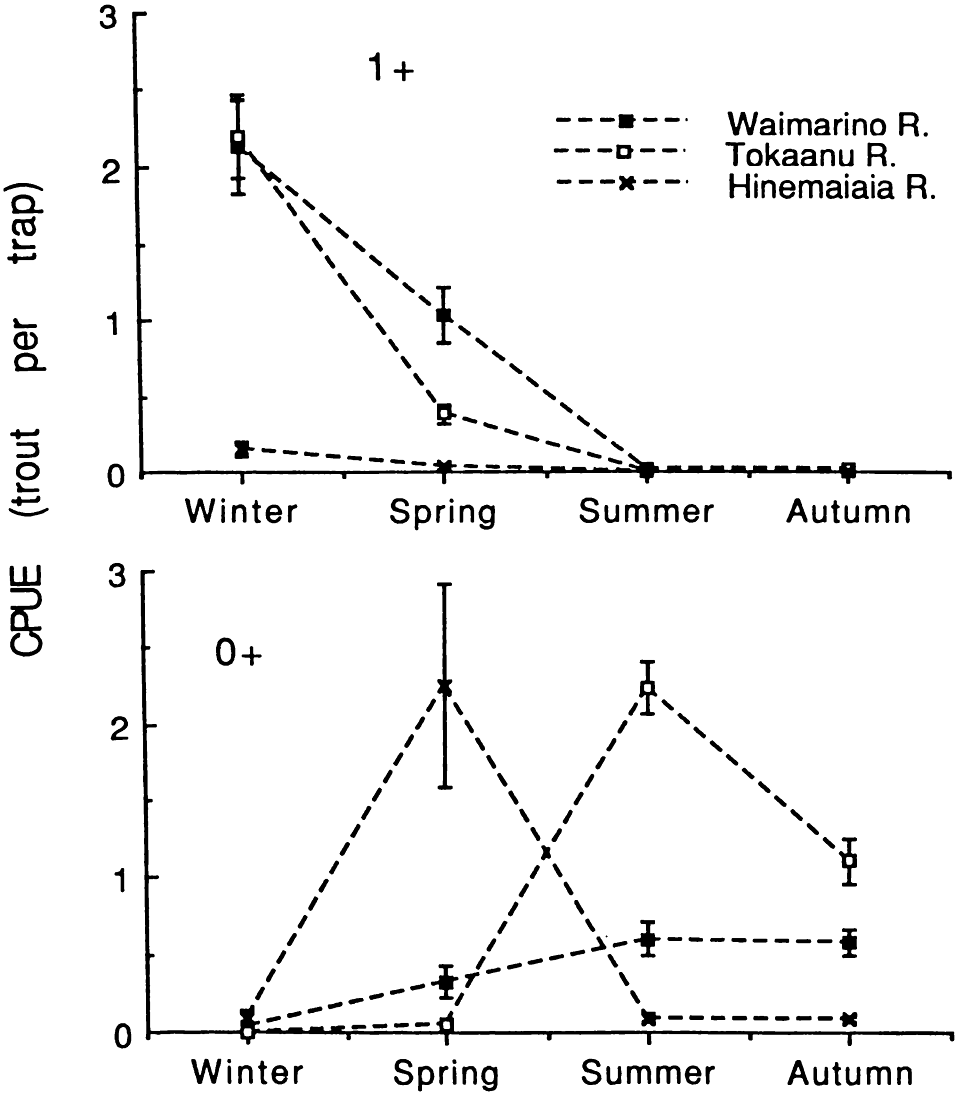
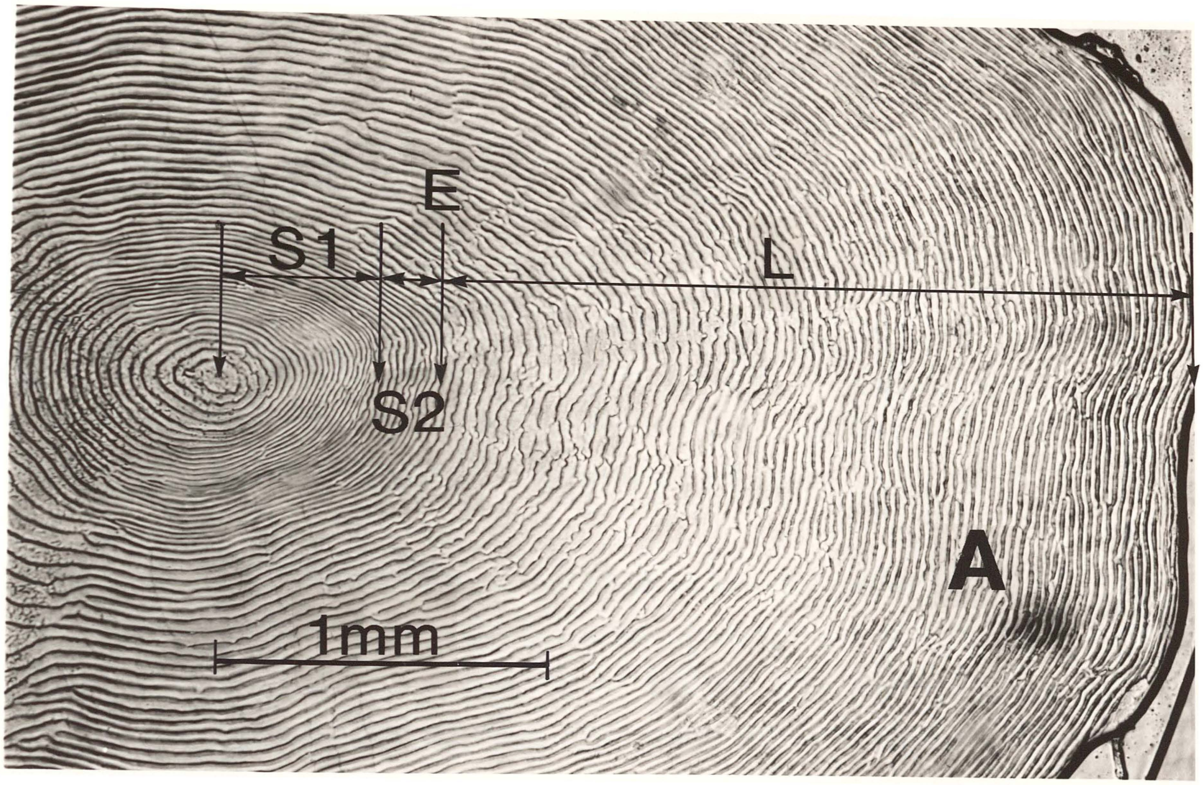
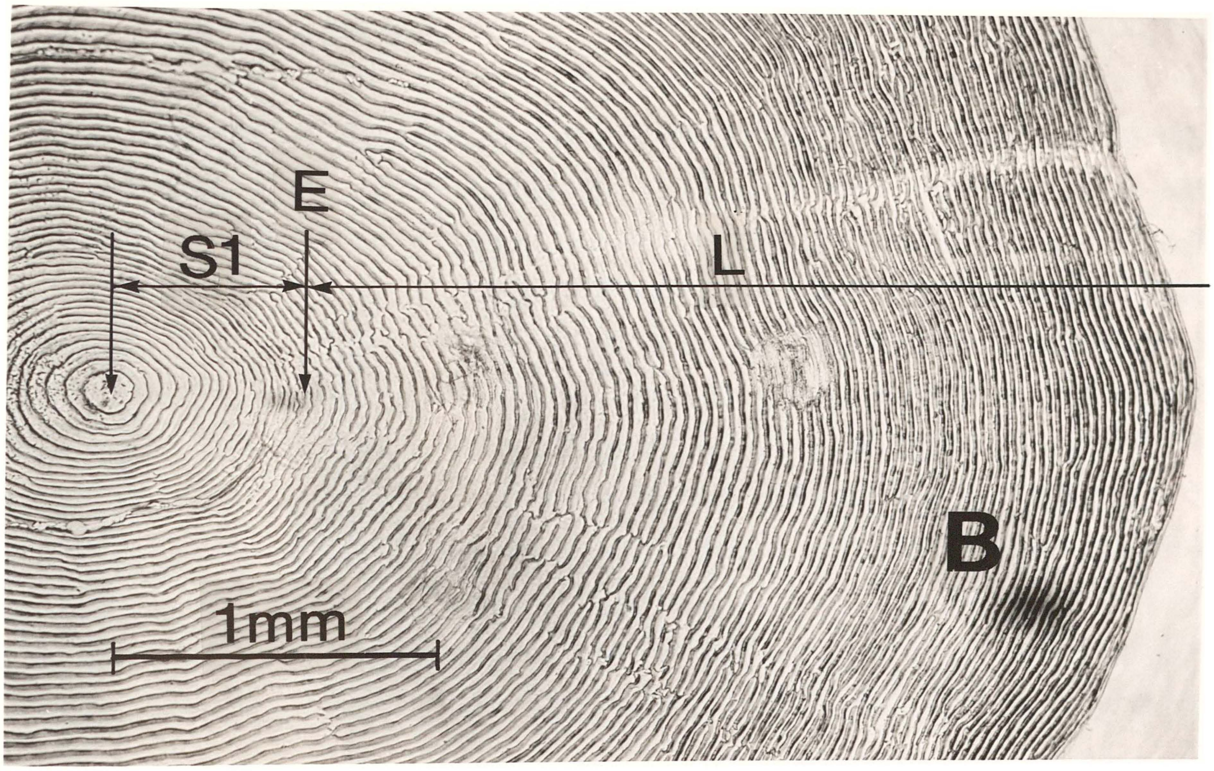

1+
0+
Waimarino R.
Tokaanu R.
Hinemaiaia R.
CPUE (trout per trap)
0
1
2
3
Winter
Spring
Summer
Autumn

Plate 4.1.--Scales of spawning-run Lake Taupo rainbow trout. A. Stream overwintering pattern. B. Stream non-overwintering pattern. L=lake-growth zone, S1=pre-winter stream growth, S2=post-winter stream growth. E=emigration to lake.


E
S1
L
S2
A
1mm


E
S1
L
B
1mm

## 4.3 DISCUSSION

All of the adult rainbow trout scales in this part of the study showed two basic features including an inner zone of closely spaced circuli surrounding the focus, and a more distally located outer zone having much wider average spaces between circuli. Sequential natal-stream and lake rearing periods of slower and faster growth, respectively, appear to account for these two patterns.

Variation in surface features of scales develops through changes in the frequency of circulus deposition and the spacings between circuli can be changed by alterations in the growth rate of the fish (Doyle et al. 1987). This rate varies as a function of physiological responses to exogenous and endogenous conditions (Casselman 1987) and includes changes in food, temperature, light, sexual maturity, etc. The variation seen in Lake Taupo rainbow trout scales appears to be primarily a functional response to different growth conditions.

### Lake-growth zone

The scales examined in this study were taken from fish that had recently migrated from Lake Taupo; thus, it is reasonable to suggest that the wide outer zone of homogeneously spaced circuli, seen reaching to the outer margin on all scales (Plate 4.1; L), represents rearing in the lake. Furthermore, there were no among-population differences in the average circulus spacing of the outer-growth zone of the scale suggesting that all of these fish were rearing under similar conditions, or in a common environment, during its formation. Although most Lake Taupo rainbow trout are thought to mature only after at least one winter of rearing in the lake (Stephens 1989) there were no marked yearly checks, or annuli (Tesch 1971), in the outer-growth zone. The absence of annuli in this scale-area may be due to the narrow range of temperatures (Forsyth and Howard-Williams 1983) and the even spread of primary production (Viner and White 1987) occurring in Lake Taupo over an annual period.

Thus, all evidence suggests that this outer zone of the scale represented lake growth.

### Stream-growth zone

A distinct inner-circulus pattern, present on all Lake Taupo rainbow trout scales examined (Plate 4.1; S1, S2), appears to represent a stream-growth zone; its position on the scale (starting from the focus outward) indicates that this zone was laid down soon after emergence of the young fry from the redd. Because the spacings between circuli in this scale zone were narrow compared to the lake-growth zone it is reasonable to suggest that they were formed under considerably different rearing conditions, and probably in physically different locations.

Rearing in the lake during the formation of this zone is a possibility but appears unlikely. Intensive sampling of both the limnetic and littoral zones of Lake Taupo over the last ten years, using a variety of techniques including seining, gill-netting, echo-sounding, drop-netting and SCUBA-diving, demonstrated that rainbow trout less than about 94 mm in length were rare in these habitats (Stephens 1989). Newly emergent trout fry enter Lake Taupo in large numbers but apparently suffer from high mortality rates soon after reaching the lake (Stephens 1989).

The among-population variability in various characteristics seen in this scale-zone suggests that the three stocks had reared under environmentally different conditions during its formation; the natal-stream could provide the possible habitat for these differences. For example, I observed the variable presence of a pronounced circulus check in the inner-growth zone of the scale ranging in frequency from 70% (Waimarino) to 36% (Hinemaiaia). It seemed likely that this inner-growth zone check was an overwintering mark as it resembles the published descriptions of a winter annulus (e.g., Tesch 1971). Water temperatures in the Waimarino and Hinemaiaia Rivers can approach 0°C in the winter (Fig. 3.2) and under such conditions the growth of any stream-rearing fish would virtually cease thereby forming a check on the scale.

Since no such drop in temperature occurs in the Tokaanu River (Fig. 3.2) the explanation for the presence of a winter mark in the stream-growth zone of these trout is more equivocal. However, factors other than temperature (e.g., seasonal changes in light and food) are known to produce a scale check (Bilton and Robins 1971a,b).

Average spacings between circuli also differed among populations for the stream-growth zone of the scale. The widest spacings were found in the Hinemaiaia trout suggesting that they had the greatest average growth rates (cf., Doyle et al. 1987) during the formation of this part of the scale (Table 4.3B,C); by contrast, the Tokaanu rainbow trout had the narrowest circuli spacings suggesting they grew the most slowly. I suggest that substantial environmental differences occurring among the respective natal-stream environments, and specifically in temperature (Fig. 3.2) and nutrients (Table 3.1), could account for differences in growth rates as inferred by the circulus spacing.

Finally, I observed among-population variation in the back-calculated average lengths of juvenile trout estimated to the end of their first growing season. For this comparison, I assumed that for non-overwintering fish, the lake/stream check represented the greatest possible pre-winter length of the trout; similarly, for overwintering trout, the winter check was assumed to also represent a maximum pre-winter length. Thus, Hinemaiaia and Tokaanu rainbow trout were the longest at the end of their first growing season whereas the Waimarino juveniles were the shortest. Considering that most Hinemaiaia trout showed a non-overwintering pattern and would have emigrated well before winter this comparison becomes even more striking.

Those Hinemaiaia trout surviving to adulthood seemed to have substantially greater growth rates than the same year class in the Waimarino river and a greater pre-winter length in the Hinemaiaia trout may be aided by a somewhat earlier emergence allowing for a longer growing period before winter. Tokaanu trout, living in an environment of moderate and somewhat lower summer temperatures, but higher winter temperatures, may grow for most of the year and "catch up" to the Hinemaiaia trout by the formation of the winter check.

### Field sampling

Results from the minnow-trapping surveys strongly corroborated the adult scale observations. Despite seemingly good recruitment and growth, there were substantially lower catches of 0+ rainbow trout in the Hinemaiaia river by autumn of 1989; similarly, 1+ trout were virtually non-existent in this stream at any time yet were found in relatively high abundances in the Tokaanu and Waimarino Rivers during the winter and spring of the study. The implications of these observations are that emigration and/or mortality of young-of-the-year rainbow trout occurred earlier and at higher rates in the Hinemaiaia River so that few fish were left in this stream by winter. Thus, if a much higher proportion of Hinemaiaia trout emigrate to the lake before winter, and since a winter check does not appear in fish rearing in the lake, most of these fish would not should show an overwintering scale pattern.

The growth patterns of the minnow-trapped trout also corresponded closely with the scale observations. The minnow-trapped Hinemaiaia trout consistently reached a larger size, earlier, than the same age-class of the other two populations (Fig. 4.3); thus, the Hinemaiaia fish seemed to be growing at a faster rate. In addition, Hinemaiaia rainbow trout may have been emerging earlier than the fry of the other populations (Fig. 4.4) and additional growing time would contribute to their reaching a larger size before winter.

### Role of natal-stream rearing

Natal-stream rearing is a common life-history strategy for many populations of migratory rainbow trout. The anadromous form, the steelhead trout, undergoes a protracted period of stream rearing before migrating to the Pacific Ocean (Shapovalov and Taft 1954; Ward and Slaney 1988). Furthermore, these fish reached a clearly defined minimum size that was similar among populations or years (c. 130 mm for Keogh River; Ward and Slaney 1988). Similar observations have also been made for Great Lakes populations of migratory rainbow trout; the age at emigration to the lakes varies and generally increases from south to north with the average length at any given age for the southern populations larger than for the northern populations (Biette et al. 1981). Great Lakes rainbows generally smolt from 1 to 3 years and vary in length from 64 to 244 mm (Biette et al. 1981).

However, not all lake-rearing populations of rainbow trout spend a protracted period of stream rearing prior to migrating to lacustrine waters (Hayes 1988b). The optimal length at emigration may differ for each population but appears to usually be set by conditions in the lake or ocean.

My study suggests that surviving Lake Taupo rainbow trout rear in their natal streams for a protracted period of time before emigrating to the lake. Although the age at emigration varied among the study populations, the mean and minimum sizes at emigration for trout surviving to adulthood, as determined by back-calculation, were similar among streams, or about 140 mm and 94 mm, respectively (Table 4.5). Although large numbers of recently emerged fry are known to move downstream in Lake Taupo spawning streams (Stephens 1989), there appears to be strong selection against fish that leave the stream below a threshold size. The length-frequency distributions of the emigrants, as estimated by back-calculation procedures, show a sharp left-hand truncation terminating at about 94 mm for all populations (Fig. 4.2). This implies that for any rainbow trout smaller than this size, mortality rates are extreme. Among-population differences in age at migration for the Lake Taupo trout surviving to adulthood was therefore a function of varying growth rates among the different natal streams.

Cryer (1991) suggests that juvenile rainbow trout recruit into Lake Taupo at all times of the year but that most of the emigrants arrive in the lake by mid-summer.

These fish grow to about 50 cm by the following summer or autumn. There is considerable mortality amongst small trout before they become of legal size, or 350 mm.

The minimum size for survival may be dictated by common habitat features encountered by all rainbow trout while rearing in Lake Taupo since there seems to be little advantage in remaining in the apparently less productive stream environment. Thorpe's (1982) explanation for this seemingly paradoxical phenomenon was that although the stream may be a less productive environment than the ocean or a lake, it is often incapable of supporting many large predators and a prior period of stream rearing can be viewed as a balanced risk trading off a greater growth opportunity for a lessened exposure to predators.

For Lake Taupo, Stephens (1989) suggests that recently emerged rainbow trout may be excluded from the littoral zone through competition or predation by other fish (eg., common smelt (**Retropinna retropinna**), brown trout (**Salmo trutta**), common bully (**Gobiomorphus cotidianus**), catfish (**Ictalurus nebulosus**), koaro (**Galaxias brevipinnis**), and adult rainbow trout). Alternatively, these small trout may not be able to make a living in the pelagic areas of the lake as they would: 1) be out-competed for food by the planktivorous smelt and 2) be too small to forage on the smelt, a relatively large and active prey item. Rainbow trout in Lake Taupo feed almost exclusively (97%) on the common smelt (mean size of smelt c. 40 mm; Stephens 1989) and Cryer (1991) found that 78% of all items found in the stomachs of juvenile rainbow trout (<250 mm) were smelt and this comprised 94 to 99% of the consumed biomass. Presumably, there is a minimum size that a Lake Taupo rainbow trout must reach before it is able to catch and ingest a prey item of this size and this may be about 94 mm, or the length at the survival threshold.

With regards to the length of the juvenile fish at emigration, there were some striking comparisons in the growth patterns of overwintering and non-overwintering fish. Those fish that did not overwinter were larger at outmigration than overwintering trout were at the formation of their winter check (Table 4.5, C vs B). However, those fish which stayed and put on additional growth after winter averaged a greater length at emigration to the lake than those fish which migrated before winter (Table 4.5, A vs C). This suggests that the largest young-of-the-year juveniles, regardless of stream origin, tended to emigrate if they had reached the threshold size by winter. Those fish that did not grow larger than this size before winter either stayed in the stream and put on additional growth the next year and then emigrated, or else succumbed to mortality--either in the lake if they emigrated at a sub-threshold size, or in the stream if they stayed. Those populations with slow growing fish would, therefore, have more juveniles staying in the stream for a longer period of time before reaching the appropriate minimum length.

Lake Taupo rainbow trout are thought to be derived from introductions of California steelhead (Scott et al. 1978) and they are known to require a period of stream growth before migration to the ocean (Shapovalov and Taft 1954). Presuming that extended stream-rearing has a genetic component in steelhead, Lake Taupo rainbow trout may have been "pre-adapted" with an exceptionally successful life-history pattern for survival in this watershed. Nevertheless, production of rainbow trout in Lake Taupo appears to be limited by the numbers and sizes of the juveniles produced by the tributary streams.

# Chapter 5.--JUVENILE SCALE PATTERNS

## 5.0 INTRODUCTION

Stephens (1989) and Pitkethley (1990) provided strong empirical evidence that a period of extended stream growth was necessary for the survival of rainbow trout in Lake Taupo. Their conclusions were primarily based on a comparison of adult and juvenile trout rainbow trout scales from fish captured in the lake and its tributary-spawning streams. They suggested that the inner-growth zone of the adult trout scales remarkably resembled the scale patterns of juveniles rearing in the natal streams and concluded that this zone was a result of natal-stream growth.

Further to these studies, in an examination of the inner-growth zone of the adult rainbow trout scales from the Waimarino, Tokaanu and Hinemaiaia Rivers, I showed that there were significant among-population differences in the: 1) frequency of overwintering patterns, and 2) average widths between circuli (Chapter 4; Rosenau 1991). These observations suggested that among-population differences in the inner-growth zone scale patterns was a function of variability in the juvenile-rearing environments, and the probable location of which was the natal stream. However, there is a school of thought which maintains that lake rearing by recently emerged juveniles is possible even though significant numbers of these very small fish have not been found in Lake Taupo despite extensive seining, gill-netting and echo-sounding surveys (Stephens 1984, 1989; Cryer 1991).

To provide further evidence that the inner-growth zone of the adult scale was, indeed, the result of stream growth, I examined the scales of stream-rearing juvenile trout from the Waimarino and Tokaanu Rivers. Assuming that the central portion of narrowly-spaced circuli on the adult rainbow trout scales truly represents stream growth, then scales of juveniles from the respective streams should show corresponding within- and between-population similarities and differences with regards to these patterns. Hence, I hypothesised that:

1) given that there are substantial differences in the physical and biotic conditions of the study streams (Chapter 3), between-population growth rates are likely to be different and there should be stock variability in the circuli patterns on the juvenile trout scales, and

2) these patterns should have similar characteristics to those seen on adult trout scales.

## 5.1 METHODS

On 15 June 1988, and 8 February 1991, juvenile rainbow trout were captured both from the Waimarino River using a fine-meshed pole seine, and from the Tokaanu River using roe-baited minnow traps. A "smear" of scales was taken from the "key scale" region of each fish (Chapter 4.1) and mounted between two glass slides held together with adhesive tape. Fork length (mm) was also recorded for each fish sampled. Only a single year class of fish was included in each year's analysis. Based on length-frequency distributions, these fish were young-of-the-year juveniles. Unfortunately, Hinemaiaia River rainbow trout of a similar size range were not captured during this sampling period.

All scales were then examined as per the adult scales (Chapter 4.2) to determine average spacings between circuli. To calculate these averages, the length of the scale, from the centre of the scale focus to the posterior edge along the longest radius, was divided by the number of circuli intersecting that radius line. These between-population data were compared using t-tests. The length distributions of fish were kept similar for both populations to minimize circulus-spacing differences due to fish size. Photo-micrographs of both pre-winter young-of-the-year and yearling rainbow trout, captured on the same day (February 1991), were taken for comparison.

## 5.2 RESULTS

### Circulus spacing

The February 1991 sample of fish lengths ranged from 55 to 70 mm with a mean of 64.0 and 62.3 for the Waimarino and Tokaanu Rivers, respectively; these lengths were not significantly different (t=2.073 df=1,51 p=0.152). The average circulus spacing for each of these groups of trout was 1.56 and 1.72 (mm x 50), respectively, and these mean values were significantly different (t=6.006 df=1,51 p=0.017; Fig. 5.1).

The June 1988 sample of fish lengths ranged from 70 to 112 mm, with means of 86.5 and 85.0 for the Waimarino and Tokaanu Rivers, respectively; these mean lengths were not significantly different (t=0.066 df=1,18 p=0.788). The average circulus spacing for each of the streams was 1.29 and 1.35 (mm x 50) (Fig. 5.1), respectively, and these mean values were not significantly different (t=0.634 df=1,18 p=0.442; Fig. 5.1).

### Winter check

Unlike the scales of young-of-the-year rainbow trout caught during the summer (February 1991), the scales of the early-winter (June 1991) fish showed a band of compressed circuli near the posterior edge of the scale. An example of the narrowing of spaces between circuli, resulting from overwintering in the stream, can be seen by comparing the patterns on the scales of fish of differing size and age captured on the same date (February 1991; Plate 5.1). Photo A is a scale from a 0+ (fork length 84 mm) or young-of-the-year fish whereas photo B is of a 1+ (fork length 149 mm) or yearling rainbow trout.

The interpretation of the patterns on these two scales is as follows. The evenly spaced circuli of the scale in Photo A represents approximately continuous growth from emergence to time of capture. In contrast, the portion of scale B with narrowly spaced circuli, situated along the posterior edge of S1 and at the start of S2, reflects a slowing of growth, probably due to the winter conditions that the rainbow trout encounters during this period in the natal stream. The subsequent wider-spaced circuli to the edge of the scale (S2) in photo B reflects "plus", or post-winter growth that would have been accumulated during the next spring and/or summer.

Figure 5.1.--Comparison of lake- and stream-growth zone widths between circuli (± SE's) for adult and juvenile rainbow trout scales from the study populations. Adult-scale circuli widths are reported in Table 4.3 A & B. Pre-winter = February 1991; Winter = June 1988.

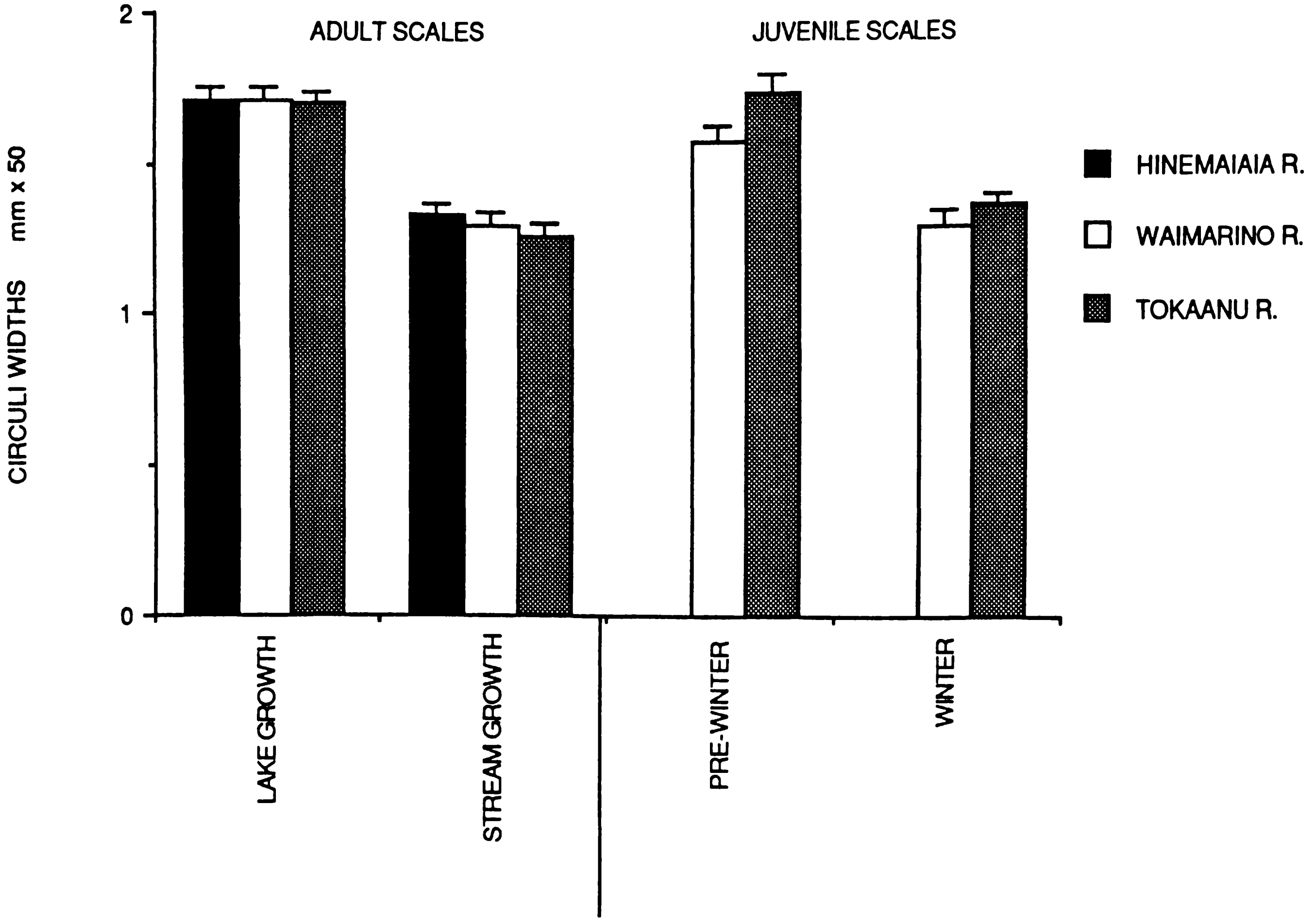
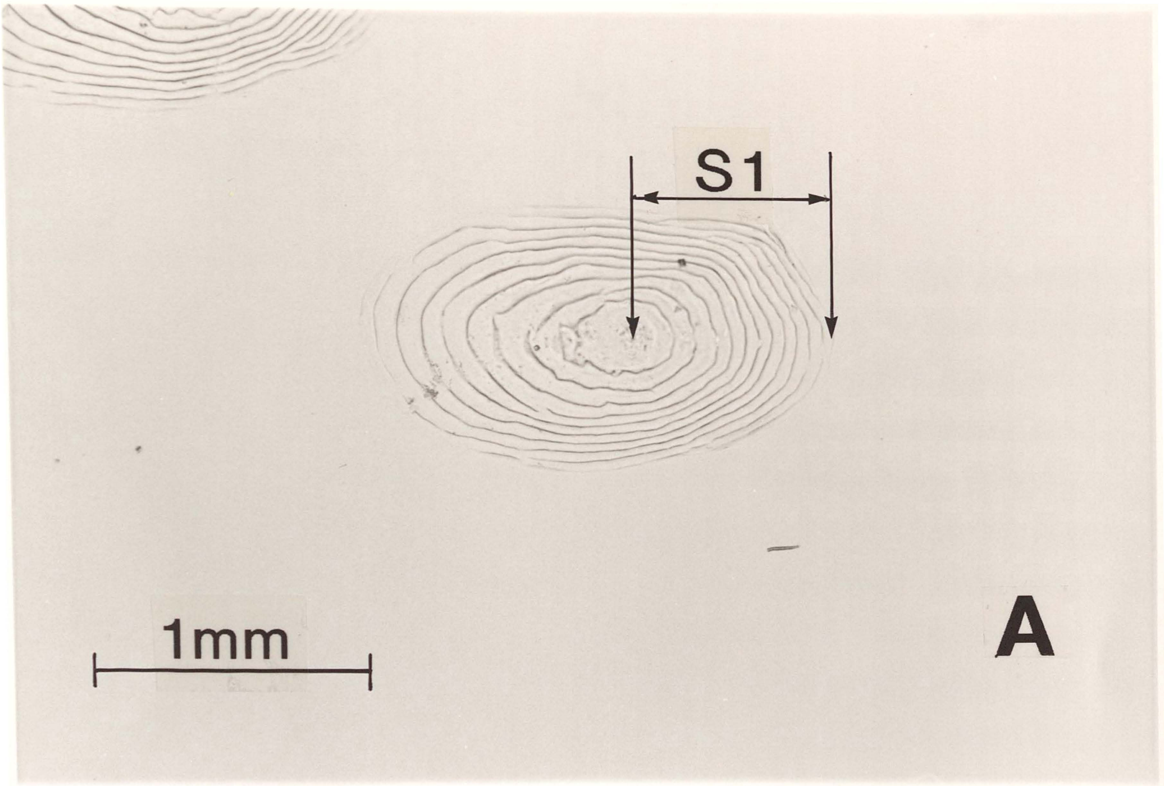
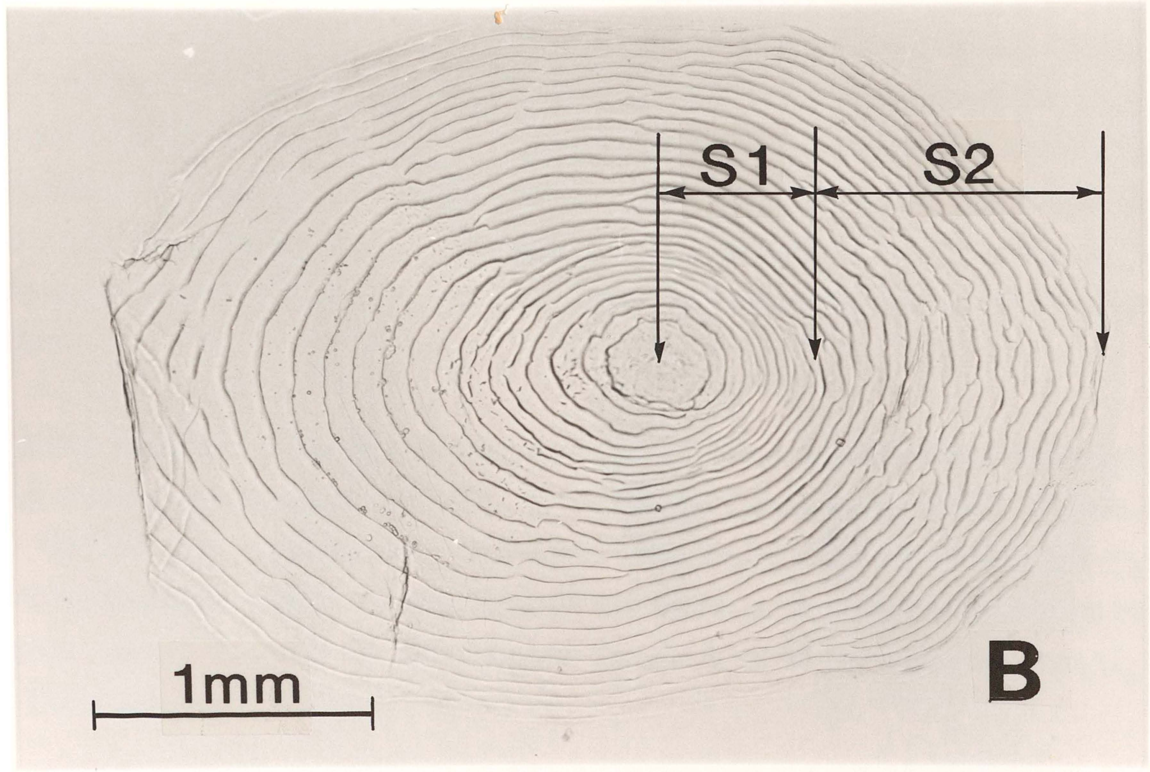

ADULT SCALES
JUVENILE SCALES
CIRCULI WIDTHS mm x 50
2
1
0
LAKE GROWTH
STREAM GROWTH
PRE-WINTER
WINTER
HINEMAIAIA R.
WAIMARINO R.
TOKAANU R.

Plate 5.1.--Scales of juvenile rainbow trout captured from the Waimarino River, February 1991. A--scale of a 0+ 84 mm non-overwintering fish; B--scale of a 1+ 149 mm overwintered fish; S1, pre-winter stream growth; S2, post-winter stream growth; note the compression of circuli, or winter check, preceding the start of S2 which is located midway through scale B. Both fish were taken approximately 2 km downstream of the Kepa Road bridge. Compare with adult trout scales (Plate 4.1).


S1
1mm
A


S1
S2
1mm
B

## 5.3 DISCUSSION

The results in this chapter further support the assertion that the inner-growth zone seen on the scales of adult Lake Taupo rainbow trout is due to natal-stream growth. The between-stream differences in average circuli widths seen on the scales of the mid-summer fish (February 1991) support the suggestions made in Chapter 4 that rainbow trout in the various Lake Taupo natal streams have dissimilar growth patterns and that these are a function of different environmental/rearing conditions in the respective streams. That there are: 1) no significant between-population differences in widths between circuli on these juvenile trout scales in mid-winter fish (corresponding to the lack of significant differences between Waimarino and Tokaanu River adult average inner-growth zone circuli widths (Chapter 4), and 2) the mean value of these widths are similar to the corresponding stream-rearing circuli widths on the adult scales (Fig. 5.1), lends further credence to the hypothesis that a period of natal-stream growth is a normal part of the life history of a Lake Taupo rainbow trout.

In the previous chapter I demonstrated that a number of among-population character differences for the inner-growth zone of the adult trout scales (Rosenau 1991; Chapter 4) but I found no among-stock variability in average widths between circuli for the outer lake-growth zone. I contended that the inner-growth zone, with its corresponding among-population variability in scale features, could have only been formed under differing environmental conditions whereas the outer-growth zone, with its among-population similarity, would have been formed under similar environmental conditions.

Others have found strong correlations between varying scale-circuli spacing and differing rearing conditions (e.g., food, temperature, Doyle et al. 1987; Casselman 1987). Indeed, among-population variation in the scale patterns of fish rearing in different natal-stream or lake rearing is often the basis for population discrimination in multi-stock salmon fisheries (S. Cox-Rogers, Pacific Salmon Commission, Vancouver, British Columbia, pers. comm.).

The only two possible areas for juvenile rearing in the Lake Taupo watershed are the tributary streams and the lake proper. Furthermore, the physical, biological, chemical and temperature conditions among streams are very dissimilar (Table 3.1; Figs. 3.1, 3.2; Schouten et al. 1981) whereas there is considerable within-year uniformity in the average conditions in the lake; Lake Taupo water temperatures are known to have a relatively narrow yearly range (Forsyth and Howard-Williams 1983) and there is an even spread of primary production throughout the period of a year (Viner and White 1987).

Circulus formation in the outer, lake-growth zone of the adult rainbow trout scales was seen to be very similar among-populations and constant (Chapter 4; Plate 4.1). Indeed, a winter check (compression of circuli) for this zone is not present on any of the adult scales that I examined even though mature trout are known to reside in the lake for at least one, and often two, winters (Cryer 1991). Thus, it seems unlikely that a winter annulus would be formed in the inner-growth zone of a scale of a juvenile rainbow trout rearing in the lake since a winter check does not form on the outer zone of the scale which is unequivocally known to be a lake-growth zone.

If a check did form on the scales of a recently emerged rainbow trout rearing which was rearing in the lake the incidence of checks should be similar among populations, assuming that emergence timing and emigration to the lake is approximately similar; this was not shown to be the case (Chapter 4). While 70% of the Waimarino River trout showed a juvenile winter check, and 49% of the Tokaanu fish, only 36% of the Hinemaiaia River rainbow trout had this mark and these differences are statistically significant. Likewise, if the juveniles of the various populations were rearing under similar conditions in the lake during the formation of the inner-growth zone, there would not have been any among-population differences in the average circulus spacings (Chapter 4).

The within-population:between-season differences in circulus spacing seen on the juvenile scales (pre-winter vs winter; Fig. 5.1) are a function of: 1) differential growth rates (during winter rainbow trout growth in the natal streams slows or ceases and the circuli become more compressed resulting in smaller average spacings), and 2) allometric changes in growth (the average circuli widths in the smaller, summer fish are inflated by the "wideness" of the focus radius and the first few circuli). Thus, after a summer's growth the circulus spacings of young-of-the-year rainbow trout were wide and, especially in the Tokaanu, similar to the lake-growth zone circulus widths (c.f., lake-growth adult scales vs pre-winter juvenile scales; Fig. 5.1). By winter the widths between circuli had declined to about the same values observed on the stream-growth zone of the adult rainbow trout scales.

The compression of circuli occurring during the winter growth period can clearly be seen on the juvenile scales by comparing the patterns of different sized rainbow trout (Plate 5.1). Although both the fish in Plate 5.1 were caught on the same day, they varied considerably in size (84 vs 149 mm fork length). Thus, the larger fish had already spent over one year in the stream while the smaller trout would yet to have experienced a winter period with its subsequent slowing or cessation of growth during this season. The slowing of growth is reflected in the narrowing of spaces between circuli and was seen both on the outer perimeter of the winter-caught (June 1988) juvenile rainbow trout scales and mid-way through the scale of the 149 mm trout.

Thus, in summary, the conclusions drawn from the observations presented in this chapter provide evidence further strengthening the argument for a natal-stream rearing period in Lake Taupo rainbow trout.

# Chapter 6.--HABITAT UTILIZATION BY JUVENILE RAINBOW TROUT

## 6.0 INTRODUCTION

Many salmonids, including rainbow trout, live in streams for an extended period of time before emigrating to a lake or the ocean as smolts for further rearing (Scott and Crossman 1973). The subsequent survival of these fishes in the lentic or marine environments is often a function of the body size first attained in the fluvial environment (Ward and Slaney 1988; Holtby et al. 1990) and this relationship is particularly evident for Lake Taupo rainbow trout (Chapter 4; Rosenau 1991).

Considerable among-stream variation in the unit production of salmon and trout juveniles is commonly observed, even under conditions of sufficient juvenile recruitment. The differences in the rate of juvenile growth and/or survival among streams is often a result of variability in the quality and quantity of the rearing environment. In recent years much research has focused on understanding the relationship between habitat quality and abundance and the production of salmonids in streams. The reasons for these studies include:

1) the need to mitigate or compensate for habitat losses resulting from anthropogenic impacts (**dams**--Slaney et al. 1984; Hamre 1985; Sheppard and Johnson 1985; Mundie and Bell-Irving 1986; Henriques 1987; **roads**--Rosenau 1990b; Rosenau et al. 1987; **forestry and agriculture**--Graynoth 1979; Chapman and Knudsen 1980; Binns and Eiserman 1979; Platts et al. 1983; Gibbons 1990),

2) re-creating salmonid-riverine habitat lost through natural flood events (e.g., Rosenau 1990a,b), and

3) attempting to increase numbers of trout in streams for anglers (e.g., citations in Duff and Wydoski 1982).

Four of the physical variables that have been identified as being of paramount importance for the production of juvenile salmonids in streams include water depth, water velocity, substrate, and instream cover (Sale 1985). The temporal-spatial diversity of these variables within the stream channel, along with nutrients and temperature, appear to be the most important factors controlling the numbers and biomass of these fishes (Binns and Eiserman 1979; Bovee 1982; Fausch 1984).

Nevertheless, determining what controls trout production in streams is still not completely understood (Heede and Rinne 1990). Furthermore, some researchers have suggested that New Zealand streams have different bio-physical characteristics than fluvial environments in the North Hemisphere, where most of the research has been conducted (Winterbourn et al. 1981).

Thus, a better understanding of what constitutes habitat for fish in Lake Taupo streams would be of considerable benefit to New Zealand's fisheries managers and scientists. Because of the unequivocal importance of extended juvenile stream rearing for the production of rainbow trout in this lake (Chapters 4, 5; Stephens 1989; Pitkethley 1990; Rosenau 1991), I decided to investigate how the physical factors comprising the fluvial environment influences the usage of habitat by fish in these Lake Taupo tributary streams.

The purpose of this part of my study was to describe how stream-resident native fishes and juvenile rainbow trout of various size groups associate with each other and with the above four physical characteristics of the stream. The Waimarino River was chosen for as a study stream because it is considered to be an important rainbow trout-producing stream and is physically and chemically like many other such streams in the Lake Taupo watershed (R.T.T. Stephens, Department of Conservation, Hamilton, New Zealand, pers. comm.).

## 6.1 METHODS

### Background

A variety of techniques have been used to examine how juvenile salmonids in streams utilize the available habitat; all these methodologies are subject to problems and biases (Orth et al. 1981; Bain et al. 1982; Gatz et al. 1987). For example, Heggenes et al. (1991) indicated that most studies investigating the microhabitat use by salmonids in streams visually observe the physical positions held by individual fish and then measure the characteristics at those locations; however, during a 24 hour period trout move about and, even if an observer is able to record exactly where fish are located during the light of day, the early-morning, late-evening and night-time observations are not possible due to low-light conditions. Furthermore, the utilization of particular habitat types may be more critical during those times when we cannot see the fish than when we can (Campbell and Neuner 1985).

To circumvent some of these problems, small portable minnow traps can be an excellent tool with which to investigate microhabitat use by lotic fishes (Culp and Glozier 1989). These traps can be set in precise locations, fish can enter them at any time of the day or night, physical measurements can be easily taken from the surrounding area, and they appear to give a good "average photograph" of the daily comings and goings of the fish. Thus, for this study, minnow traps were chosen to describe the association of habitat and fish. The physical conditions at trap locations where fish of a particular species or size class were captured, compared to the characteristics where other fish were caught, were assumed to reflect their relative differences in distribution and/or choice with respect to the availability of the various habitat types.

## Procedure

A series of small, portable, wire-mesh (mesh size 3 and 6 mm) "Gee's minnow-traps" (Plate 6.1; Swales 1987), baited with thumbnail-sized pieces of trout ova, were used to sample the fish in three sites on the Waimarino River (A, B, C; Fig. 7.1) once each season, from the winter of 1988 to the autumn of 1989. Each site was about 0.5 km in length. In this part of my study, the term "site" refers to the macro-sampling area within the stream; this is in contrast to a trap "location" which refers to the spot that an individual trap was set onto within a site; thus, each trap was set on an unique trapping location within a site. The three Waimarino sites were approximately similar to one another in their physical characteristics and the within-season data from each site were pooled. Chapter 4 and Chapter 7 outlines the methods and site locations in more detail.

At a site, about 50 traps were set overnight and then retrieved the next morning. Any trapped fish were identified to species and fork lengths were measured. Rainbow trout juveniles were separated into three size classes: "fry" (<45 mm), "fingerlings" (≥ 45mm, <94 mm), or "smolts" (≥ 94 mm). The separation between fingerlings and smolts was based on the threshold size that rainbow trout must attain before survival can occur in Lake Taupo (Chapter 4). In this study, the term "smolt" refers to juvenile rainbow trout that is capable of migrating to Lake Taupo and surviving. Although the term "smolt" was originally applied to salmonids undergoing the physiological transition from freshwater to marine environments, others have also used it to refer to juvenile salmonids migrating from fluvial to lacustrine waters (e.g., Sheppard and Johnson 1985).

The number of traps used in this habitat-utilization study varied slightly among seasons (Table 6.1). Traps of one of two mesh-sizes were used for this part of my study and they were comprised of either: 1) fine-meshed and 2) a coarse-meshed types (Plate 6.1). (The data obtained from a third trap type (large), included in a previous part of my thesis (Chapter 4), were excluded from the habitat analysis because of the small sample sizes involved (6 traps or less per site).)

The traps were set in a pattern designed to sample all the macro-habitat types were represented within a site (i.e., pools, riffles, runs), although not necessarily at the same frequency of occurrence. At the mid-point of each trap location I made a measurement or assessment of:

1) mean water-column velocity (cm/s)--as measured 0.6 x depth from the surface of the water with an electric water velocitymeter (Platts et al. 1983),

2) depth of the water column (cm)--from the surface of the water to the substrate,

3) substrate type (fine or coarse)--substrate containing at least some (40% or greater) clay, silt, sand, or very fine gravel (<4 mm diameter--very fine gravel; Platts et al. 1983) was classified as "fine substrate"; substrate with a mixture of material having mostly (i.e., greater than 60%) particles of a diameter of ≥4 mm or greater (fine gravel; Platts et al. 1983) was classified as "coarse substrate".

4) presence or absence of instream cover:

i) **woody** (including willow (**Salix** sp.), manuka (**Leptospermum scoparium**), and pine (**Pinus radiata**) (The woody material had to be branching, and a minimum length of 1 m and minimum diameter of 15 cm, to be considered cover),

ii) **undercut banks** (Platts et al. 1983),

iii) **herbaceous**, including a) blackberry (**Rubus fruticosus**), b) toetoe (**Cortaderia** sp.) and c) grassy (any submerged aquatic plants (e.g., **Egeria densa**, **Coronopus** sp., **Ranunculus trichophyllus**) or terrestrial grasses (Gramineae),

iv) **cobble** (Platts et al. 1983), and

v) **boulder cover** (small and large boulder of Platts et al. (1983) i.e., >305 mm diameter).

vi) **nil**, or no cover.

A trap was deemed to be associated with cover if it was set within 1 m of the material or structure. The cover had to be at least partially submerged to be considered.

The physical data were considered to reflect the characteristics of habitat choice for any fish caught in a trap that the measurements were taken for. If more than one fish was caught in a trap, all were considered to have made the same habitat choice. For the analysis, fish catches were adjusted by weighting the frequencies or averages for the physical observations to the numbers of fish caught in the trap. Not all traps caught fish, while some traps caught many fish, but it was assumed that a trapped fish did not interfere with others also entering the same trap; however, this was not tested.

Frequency differences amongst groups of fish, for substrate and cover variables were determined using the G-test (Sokal and Rohlf 1981); where more than two groups of fish were concerned, the order was determined using an **a posteriori** test by STP, of the homogeneity of sets of replicates tested for goodness of fit, as outlined by Sokal and Rohlf (1981). Also, groups with expected frequencies of less than 5 were combined with adjacent classes and this is signified with a "+" in the Results. Depth and velocity differences were compared with ANOVA and Tukey's HSD test (Sokal and Rohlf 1981).

Among- and within-season habitat-associations were compared for all groups of fish using the pooled data for both the coarse and fine traps since the proportions of these types remained roughly similar among seasons. However, the data for species or size classes with less than 20 fish were not considered to be statistically large enough to be included in this analysis. Because the coarse-meshed traps retained only rainbow trout larger than 44 mm, a separate analysis was conducted for fry (<45 mm) using the data of the fine-mesh traps only. Because fry were trapped in statistically sizeable numbers only in spring and summer the data for these two seasons were pooled for the fine-mesh trap analysis. Again, where less than 20 fish were caught (koaro, rainbow trout smolts) the data were not included in the fine-mesh trap analysis.

Plate 6.1.--Fine- and coarse-meshed "Gee's" minnow traps used in the habitat-utilization study.

## 6.2 RESULTS

### 6.2.1 Fry Habitat Characteristics

A total of 100 fine-meshed traps were set in the Waimarino River at the three sample sites during the spring/summer sampling periods: however, only bullies and rainbow trout fry and fingerlings were caught in sufficient numbers for analysis (Table 6.1). The numbers and average lengths of these three groups of fish caught during this sampling session are listed in Table 6.2. Each of these three groups of fish were caught in habitats that were distinctly different by one or more of the following variables and the following generalizations can be made.

#### Depth

Rainbow trout fry were caught in the shallowest traps while bullies were found in the deepest; fingerlings were captured in intermediate water depths (Fig. 6.1; Table 6.3).

#### Velocity

Bullies were caught in traps set in the slowest water velocities whereas fingerlings were found in traps positioned in significantly faster moving water; fry were caught in traps located in water velocities that were intermediate between those for bullies and fingerlings (Fig. 6.1; Table 6.3).

#### Substrate

Fry, fingerlings and bullies were caught at similar frequencies over coarse and fine substrates (Table 6.3).

### Cover

Significantly more fry and fingerlings were captured near herbaceous cover than were bullies (Fig. 6.2; Table 6.4). Nevertheless, the majority of the fry were trapped near toetoe whereas the fingerlings were found near grassy cover. Bullies were often trapped near woody cover, unlike the other two groups of fish (Fig. 6.2; Table 6.4).

More rainbow trout fry were captured near herbaceous and cobble cover than they were caught near undercut+boulder cover; traps set near the woody and nil categories registered intermediate catches of fry (Fig. 6.2; Table 6.4). During this sampling period, rainbow trout fingerlings did not associate with any one of the sampled cover types more than another (Fig. 6.2; Table 6.4). In contrast, many more bullies were caught near woody and undercut-bank cover than any of the other cover types (Fig. 6.2; Table 6.4).

## 6.2.2 Both Trap-Mesh Sizes

A total of 131, 123, 160 and 166 traps were set in the Waimarino River during the winter, spring, summer and autumn sampling periods of 1988-89, respectively. The average water-column depths and mean-water column velocities, substrate-type frequencies, and the occurrence of the various cover types at the locations where the minnow traps were set, were generally similar among seasons although the summer water velocities were statistically slightly greater than in spring (Fig. 6.3; Table 6.5); cobble cover was also somewhat under-represented in autumn (Fig. 6.4; Table 6.5). Nevertheless, because the habitat sampling was so similar among the various seasonal periods, among-season comparisons were considered to be valid.

#### 6.2.2.1 Within-species:among-season comparisons

**Rainbow trout fingerlings** (Figs 6.5, 6.6; Table 6.6)

The average fork lengths of minnow-trapped fingerlings were similar for all seasons, except summer when the mean length was slightly less. Compared to all other seasons, fingerlings were captured in the deepest water during spring. There was also a trend for fingerlings to be captured in increasingly faster water, from winter throughout the year to autumn. However, there were no among-season frequency differences in the type of substrate that fingerlings were found utilizing; regardless of sampling period, about 70% of the fish were caught over fine substrate and 30% were trapped over coarse material.

There were considerable within- and among-season differences in the types of cover that the fingerlings were utilizing. For example, during winter and spring, traps set undercut bank, herbaceous and woody cover had the highest catches, whereas traps set next to cobble, nil and boulder cover registered the lowest captures. In contrast, during the summer period, the catch rate of fingerlings was proportionally similar at all cover types. Finally, in autumn, and compared to all other cover types, fingerlings were rarely found near the nil and undercut-bank categories.

**Rainbow trout smolts** (Figs 6.7, 6.8; Table 6.7)

The average fork lengths of the minnow-trapped smolts were the same for all seasons where there was a sufficient sample of fish but an analysis of the summer data was not included due to a low sample size. The average water depths and velocities that the smolts were captured in did not change for the three seasons. Regarding substrate choices for smolts, about 65% of the fish were captured over fine material regardless of season. There were, however, significant among-season differences in the type of cover that smolts were trapped near. During winter and spring, traps set near woody, undercut banks, and herbaceous cover had proportionally the highest catches. In contrast, during autumn, the there were no differences in the relative catch rates among the various cover types.

**Koaro** (Fig. 6.9)

Only during summer were enough koaro captured in the Waimarino River for habitat analysis. During this season they were only captured in traps set near nil, undercut bank, herbaceous and woody cover although most of the fish were caught in traps set near the latter two categories.

**Common bully** (Figs 6.10, 6.11; Table 6.8)

The average lengths of minnow-trapped bullies were similar among-seasons except for a 10 mm difference between spring and winter. Throughout the seasons, bullies did not change their utilization of habitat with respect to the four variables studied; that is, regardless of sampling period, the average water depths and velocities of the traps with fish, and the proportion of fish caught over a particular substrate type, or near a type of cover, was the same. Woody and herbaceous cover were dominant in all seasons for bullies.

#### 6.2.1.2 Among-species habitat comparisons

**Depth and velocity** (Figs. 6.12, 6.13; Table 6.9)

There was a positive relationship between size of rainbow trout and the water column depths and water velocities that these fish were caught in; the larger trout were captured in the deeper and faster water than the smaller rainbows except in winter when fingerlings and smolts overlapped in their distributions with regards to these variables. All groups of fish could be separated from each other during any season by either water depth and/or velocity; the only anomaly to this trend was during winter when the average water depths and velocities of fingerlings and smolts were caught were both similar. Therefore, there was a clear among-group and among-species segregation of these species by space in the Waimarino River.

Bullies were consistently trapped in the slowest of waters compared to the rest of the groups. Nevertheless, occasionally there was an overlap with bullies and another group for the water velocity variable; however, a spatial segregation was always maintained between bullies and the other overlapping group of fish by a second variable. For example, in spring the average water column velocities where bullies and fry were caught in were similar but these two groups were found in very different water depths, with bullies occupying deeper water. Similarly, in summer koaro and bullies were caught in waters with the same average velocities and the average water-column depths that koaro and fry were captured in were also similar. However, among-species spatial segregation was maintained with koaro being trapped in faster water than fry, but in shallower water than those utilized by bullies.

### **Substrate** (Fig. 6.14; Table 6.10)

There were clear among-group differences in the type of substrate that the various species or size classes of trout were utilizing. Bullies were almost always caught over fine substrate whereas a higher proportion of fingerlings and smolts were associated with coarser stream-bottom material. Similarly, a greater proportion of fry were caught over finer substrate than was used by fingerlings and/or smolts.

Although there were no statistically-significant differences between fingerlings and smolts with regards to their substrate preferences, in all seasons where comparisons were made the latter had a greater % occurrence over larger material. Again, there appeared to be a positive relationship between size of fish and the diameter of substrate that rainbow trout juvenile were trapped over: the larger the fish, the coarser the substrate.

### **Cover–woody material** (Figs. 6.15; Table 6.11)

Except for autumn, bullies had a significantly higher catch rates near woody cover than did rainbow trout of any size class. Bully and koaro catches near woody cover did, however, overlap in summer. Proportionally, more rainbow trout smolts were caught near woody cover than were fingerlings over all seasons, although in no instance was this difference statistically significant. Furthermore, in spring, fingerlings and smolts were caught near woody cover at a greater rate than were the smaller-sized fry. Thus, there appeared to be an positive relationship between the size of juvenile trout and their tendency to be utilizing woody cover.

### **Cover–herbaceous material** (Fig. 6.16; Table 6.11)

Fingerlings utilized herbaceous cover more so than bullies, particularly in the spring and summer periods. Only during spring did I catch large enough numbers of rainbow trout fry, fingerlings and smolts to make comparisons of their relative use of herbaceous cover. Although there were no significant among-group differences, there was a size related trend for rainbow trout juveniles and herbaceous cover; the smallest fish showed the greatest propensity for being caught near herbaceous cover while the largest fish showed the weakest association.

Figure 6.1.--The averages, and SE's, of the water depth, flow velocity, and the percent occurrence of coarse or fine substrates, at the fine-meshed minnow-traps only (spring and summer combined), and for the catch-adjusted traps with fry, fingerlings, or bullies caught in them.

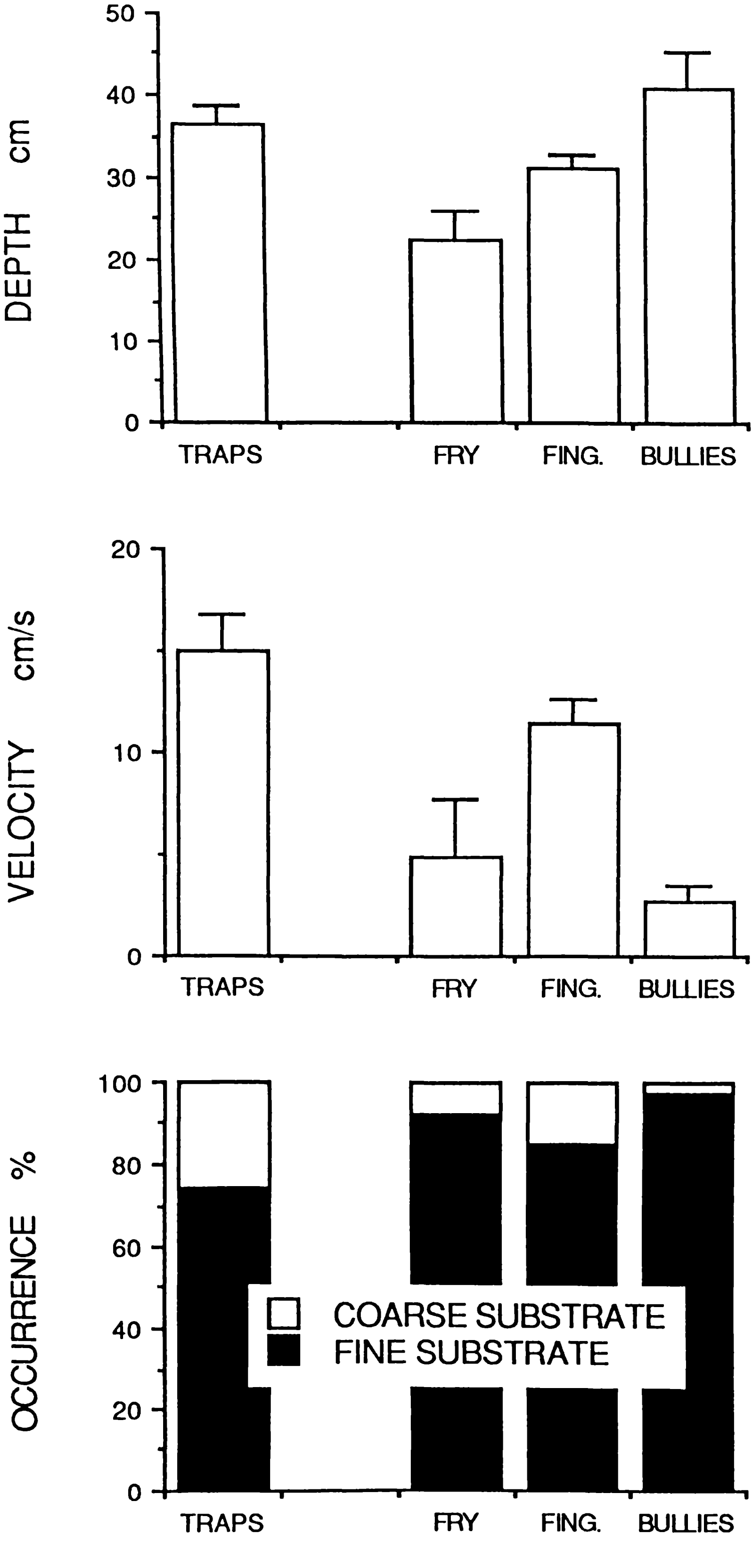
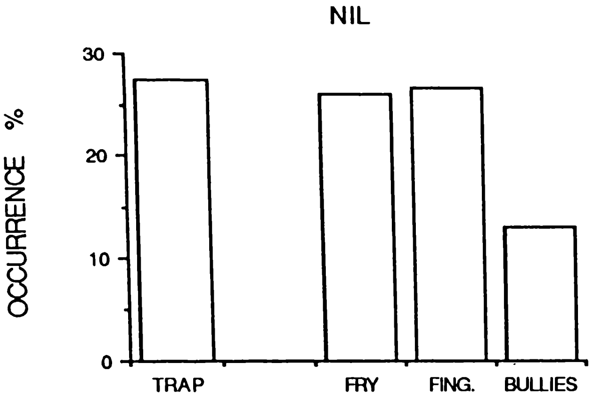
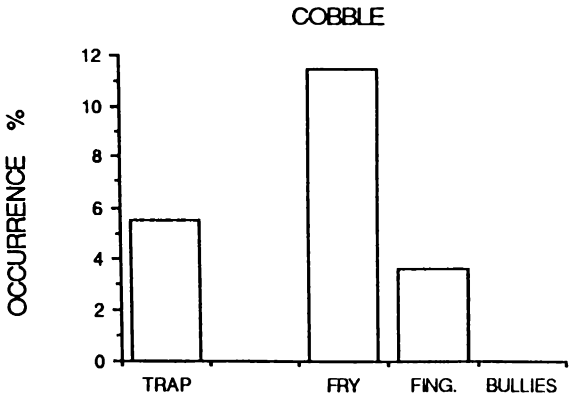
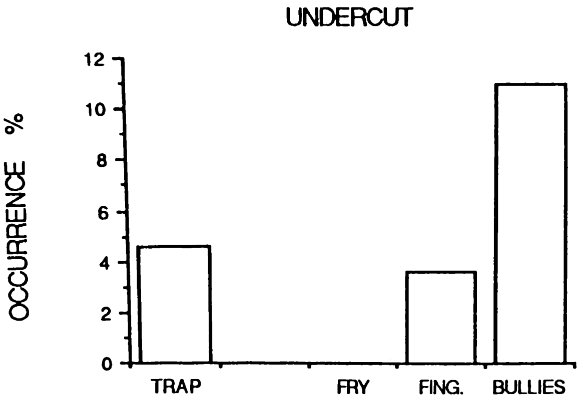
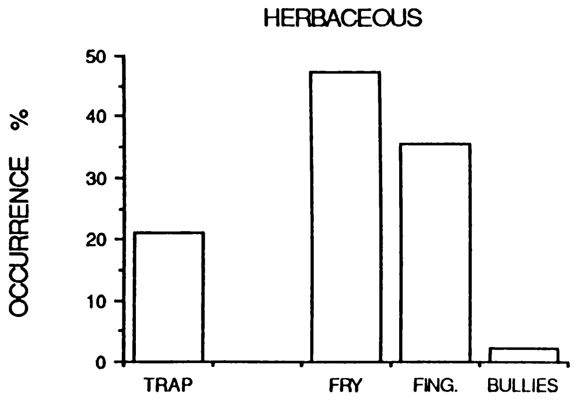

DEPTH cm
50
40
30
20
10
0
TRAPS
FRY
FING.
BULLIES
VELOCITY cm/s
20
10
0
TRAPS
FRY
FING.
BULLIES
OCCURRENCE %
100
80
60
40
20
0
COARSE SUBSTRATE
FINE SUBSTRATE
TRAPS
FRY
FING.
BULLIES

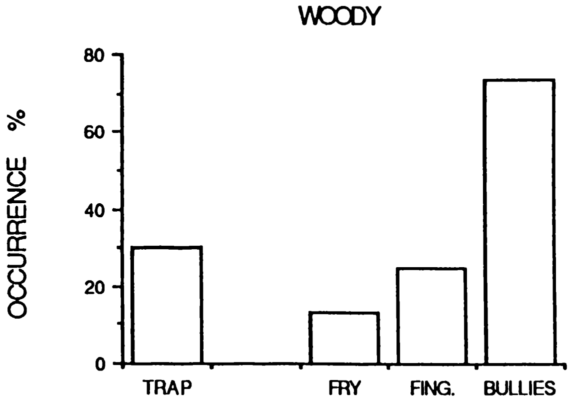
Figure 6.2.--Percent occurrence of each cover type at the fine-meshed minnow-traps only, and for the catch-adjusted traps with fry, fingerlings, or bullies, spring-summer 1988/89.


NIL
OCCURRENCE %
0
10
20
30
TRAP
FRY
FING.
BULLIES


COBBLE
OCCURRENCE %
0
2
4
6
8
10
12
TRAP
FRY
FING.
BULLIES


UNDERCUT
OCCURRENCE %
0
2
4
6
8
10
12
TRAP
FRY
FING.
BULLIES


HERBACEOUS
OCCURRENCE %
0
10
20
30
40
50
TRAP
FRY
FING.
BULLIES


WOODY
OCCURRENCE %
0
20
40
60
80
TRAP
FRY
FING.
BULLIES

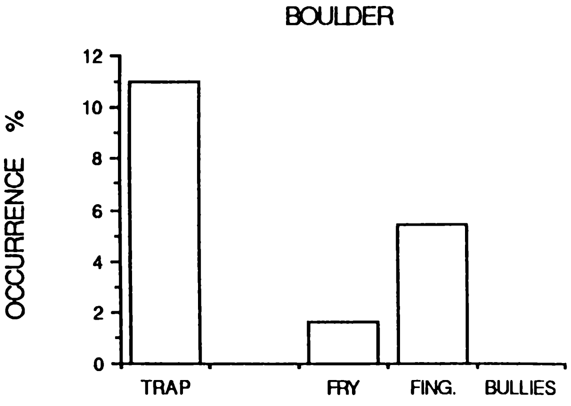
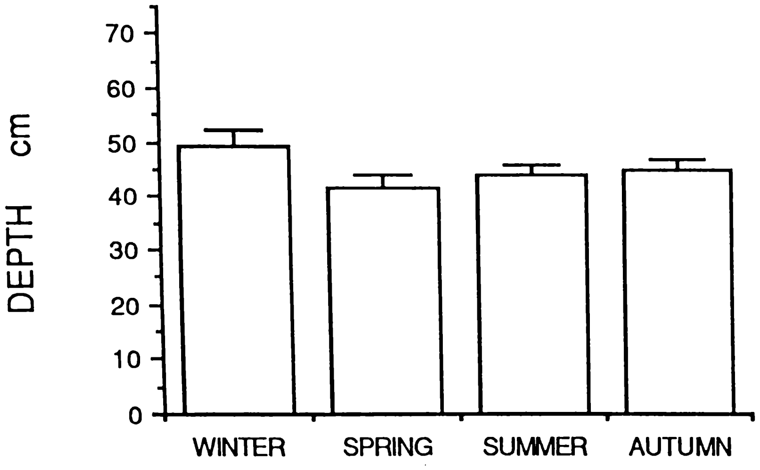
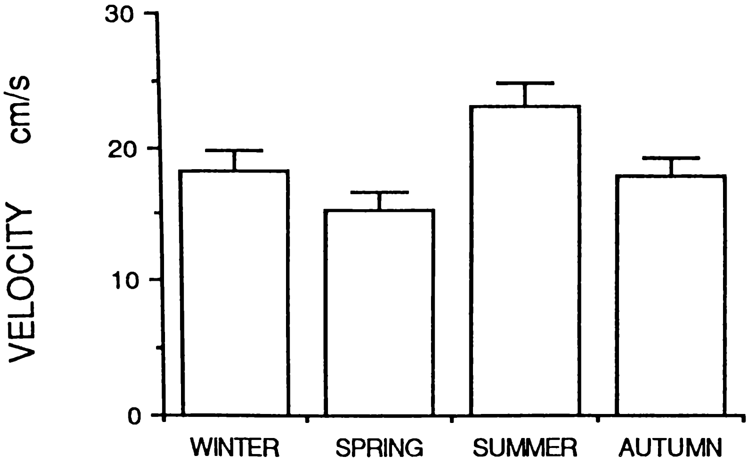

BOULDER
OCCURRENCE %
0
2
4
6
8
10
12
TRAP
FRY
FING.
BULLIES

Figure 6.3.--The average water depths and velocities, with S.E.'s, and substrate-type percent occurrence for the combined fine-and coarse-meshed minnow traps, winter 1988 to autumn 1989. **VELOCITY**, average mean-water-column velocity; **DEPTH**, water column depth at trap mid-point; **COARSE or FINE SUBSTRATE**, particle size of substrate at trap mid-point.


DEPTH cm
70
60
50
40
30
20
10
0
WINTER
SPRING
SUMMER
AUTUMN


VELOCITY cm/s
30
20
10
0
WINTER
SPRING
SUMMER
AUTUMN

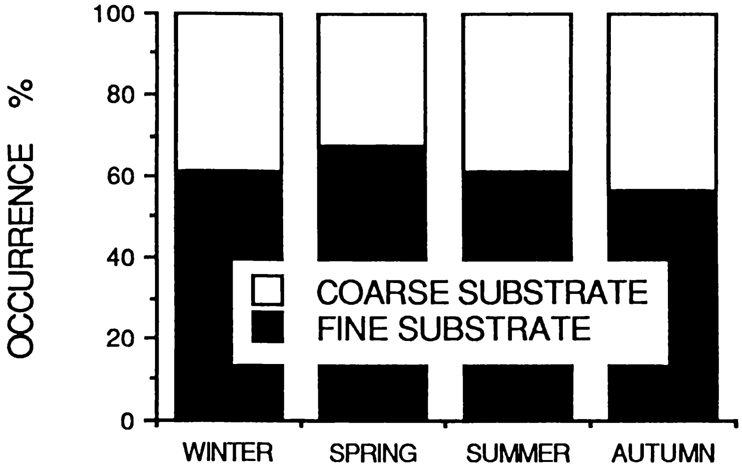

OCCURRENCE %
100
80
60
40
20
0
☐ COARSE SUBSTRATE
■ FINE SUBSTRATE
WINTER
SPRING
SUMMER
AUTUMN

Figure 6.4.--Minnow-trap cover-type percent occurrence for the combined fine- and coarse-mesh minnow traps, winter 1988 to autumn 1989. **NIL**, no cover; **WOODY**--woody cover; **U/CUT**--undercut bank; **HERB.**--herbaceous cover; **COBBLE**--cobble cover; **BOULDER**--boulder cover.

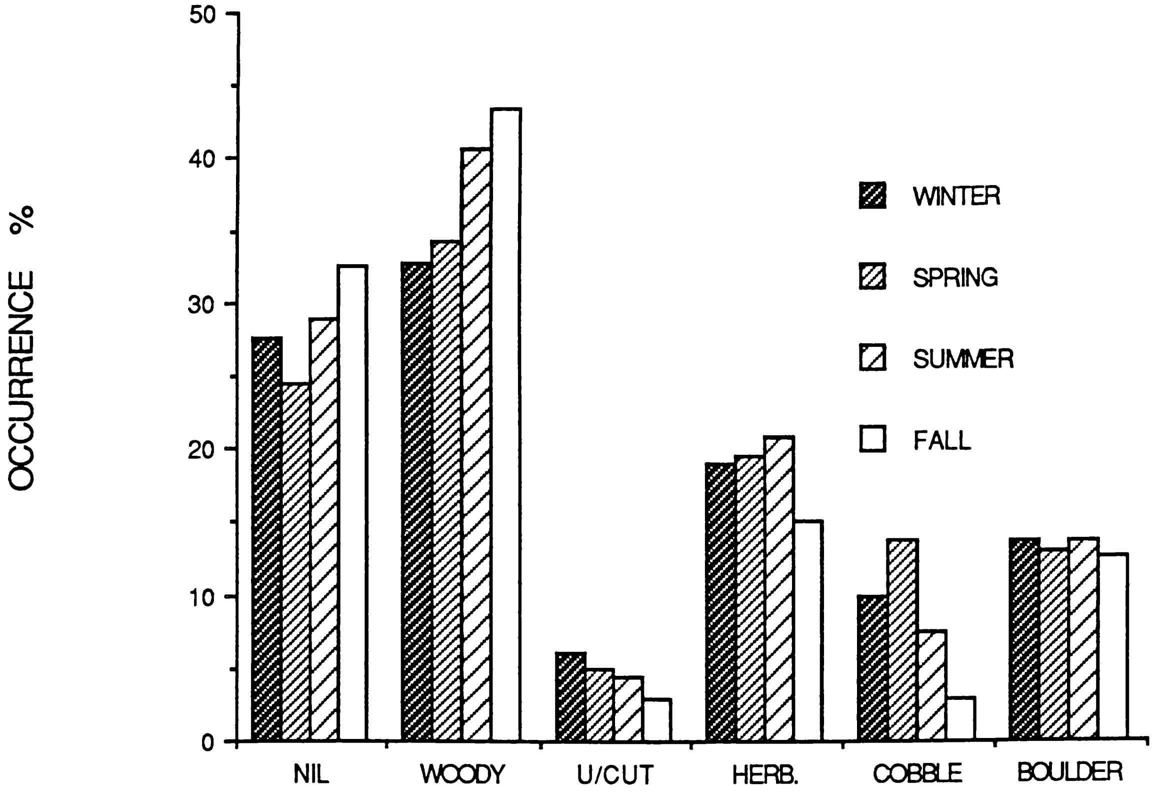
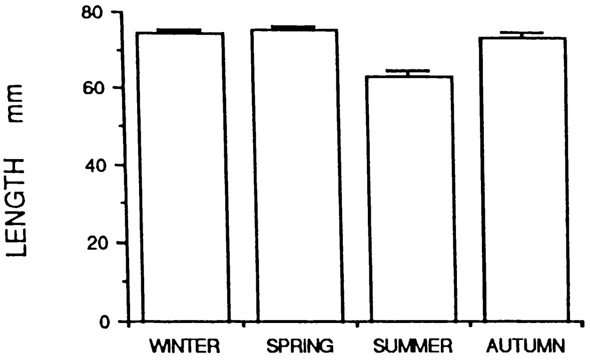
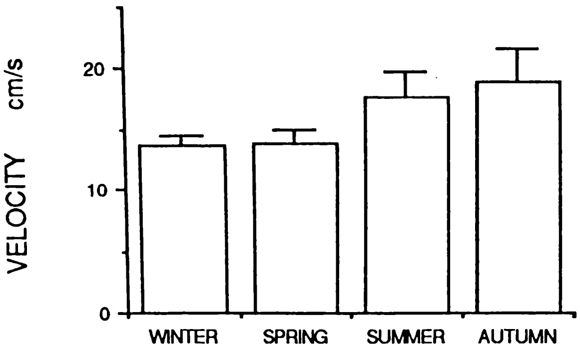
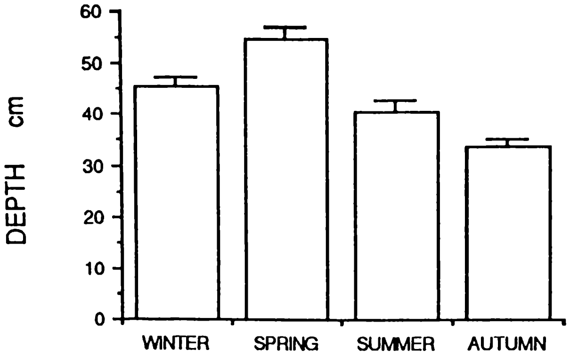

OCCURRENCE %
50
40
30
20
10
0
NIL
WOODY
U/CUT
HERB.
COBBLE
BOULDER
WINTER
SPRING
SUMMER
FALL

Figure 6.5.--The fork lengths and catch-adjusted average water depths and velocities, with S.E.'s, and substrate-type percent occurrences for fingerlings caught in the combined fine- and coarse-meshed minnow traps, winter 1988 to autumn 1989. **VELOCITY**, average mean-water-column velocity; **DEPTH**, water column depth at trap mid-point; **COARSE or FINE SUBSTRATE**, particle size of substrate.


LENGTH mm
80
60
40
20
0
WINTER
SPRING
SUMMER
AUTUMN


VELOCITY cm/s
20
10
0
WINTER
SPRING
SUMMER
AUTUMN


DEPTH cm
60
50
40
30
20
10
0
WINTER
SPRING
SUMMER
AUTUMN

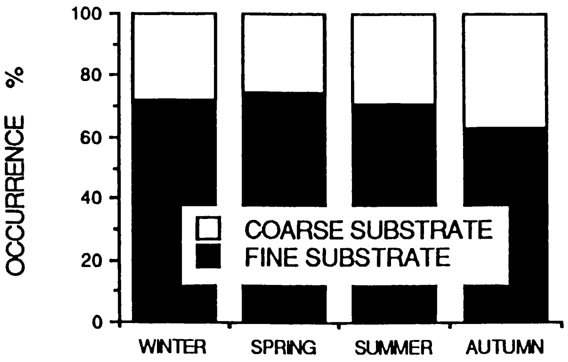
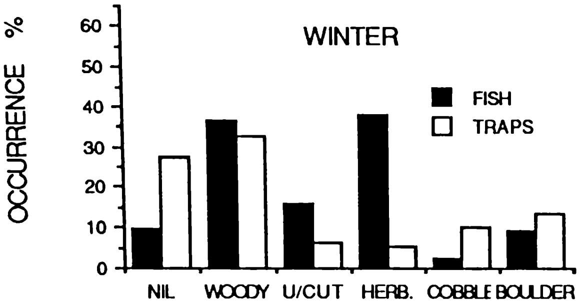
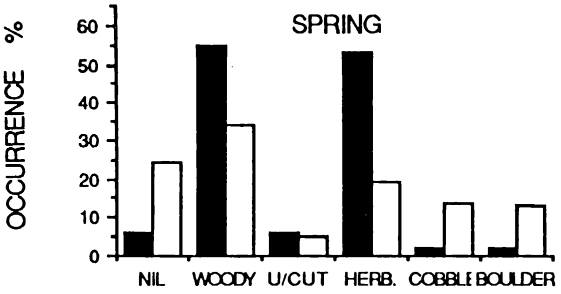
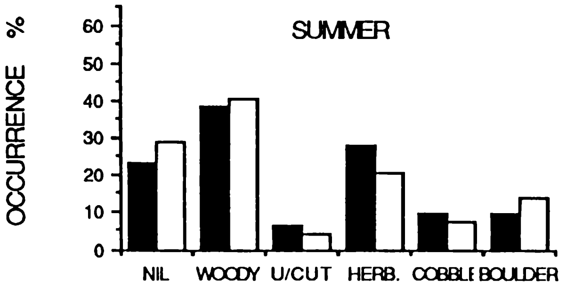

OCCURRENCE %
100
80
60
40
20
0
☐ COARSE SUBSTRATE
■ FINE SUBSTRATE
WINTER
SPRING
SUMMER
AUTUMN

Figure 6.6--The cover-type percent occurrence for fingerlings caught in the combined fine- and coarse-meshed minnow traps, winter 1988 to autumn 1989. **NIL**, no cover; **WOODY**--woody cover; **U/CUT**--undercut bank; **HERB.**--herbaceous cover; **COBBLE**--cobble cover; **BOULDER**--boulder cover; **FISH**--catch-adjusted frequency of fish at type of cover; **TRAPS**--frequency of type of cover at traps.


WINTER
FISH
TRAPS
OCCURRENCE %
0
10
20
30
40
50
60
NIL
WOODY
U/CUT
HERB.
COBBLE
BOULDER


SPRING
OCCURRENCE %
0
10
20
30
40
50
60
NIL
WOODY
U/CUT
HERB.
COBBLE
BOULDER


SUMMER
OCCURRENCE %
0
10
20
30
40
50
60
NIL
WOODY
U/CUT
HERB.
COBBLE
BOULDER

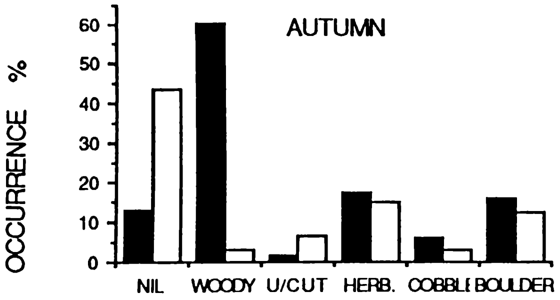
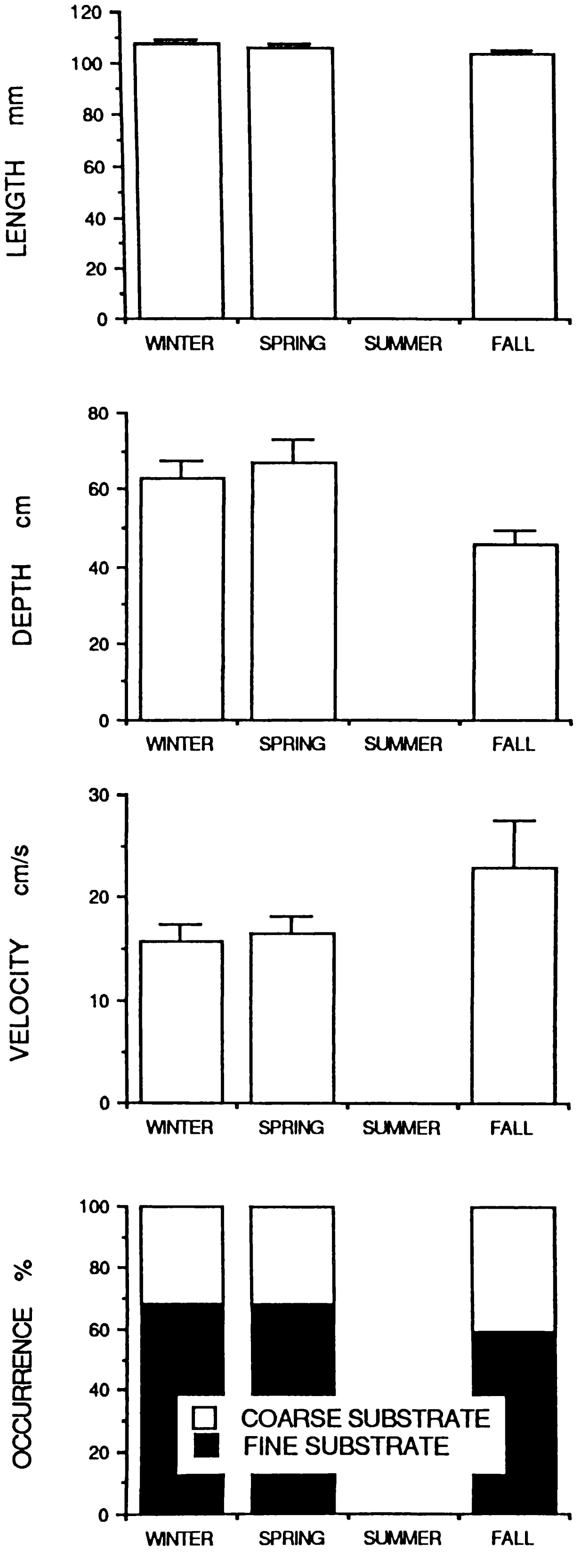
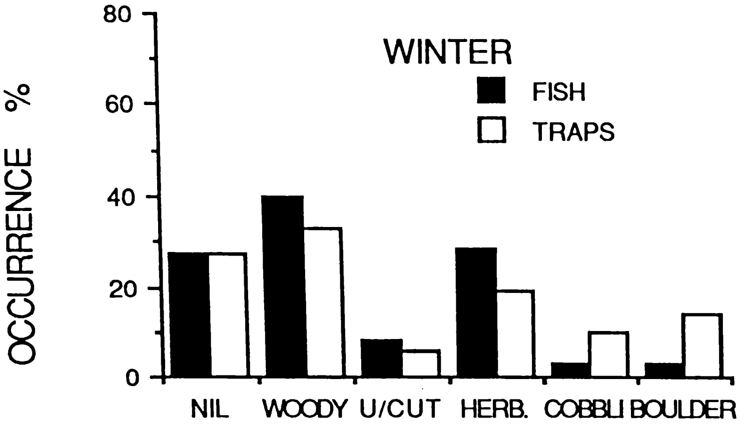

AUTUMN
OCCURRENCE %
0
10
20
30
40
50
60
NIL
WOODY
U/CUT
HERB.
COBBLE
BOULDER

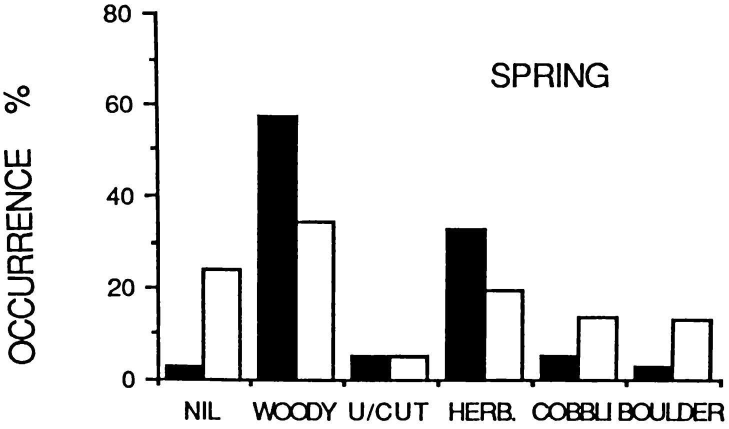
Figure 6.7.--The fork lengths and catch-adjusted average water depths and velocities, with S.E.'s, and the percent occurrence of substrate types for smolts caught in the combined fine- and coarse-meshed minnow traps, winter 1988 to autumn 1989. **VELOCITY**, average mean-water-column velocity; **DEPTH**, water column depth at trap mid-point; **COARSE or FINE SUBSTRATE**, particle size of substrate.



LENGTH mm
0
20
40
60
80
100
120
WINTER
SPRING
SUMMER
FALL
DEPTH cm
0
20
40
60
80
WINTER
SPRING
SUMMER
FALL
VELOCITY cm/s
0
10
20
30
WINTER
SPRING
SUMMER
FALL
OCCURRENCE %
0
20
40
60
80
100
☐ COARSE SUBSTRATE
■ FINE SUBSTRATE
WINTER
SPRING
SUMMER
FALL

Figure 6.8--The catch-adjusted cover-type percent occurrences for smolts caught in the combined fine- and coarse-meshed minnow traps, winter 1988 to autumn 1989. **NIL**, no cover; **WOODY**--woody cover; **U/CUT**--undercut bank; **HERB.**--herbaceous cover; **COBBLE**--cobble cover; **BOULDER**--boulder cover; **FISH**--catch-adjusted frequency of fish at type of cover; **TRAPS**--frequency of type of cover at traps.


WINTER
FISH
TRAPS
OCCURRENCE %
80
60
40
20
0
NIL
WOODY
U/CUT
HERB.
COBBLI
BOULDER


SPRING
OCCURRENCE %
80
60
40
20
0
NIL
WOODY
U/CUT
HERB.
COBBLI
BOULDER

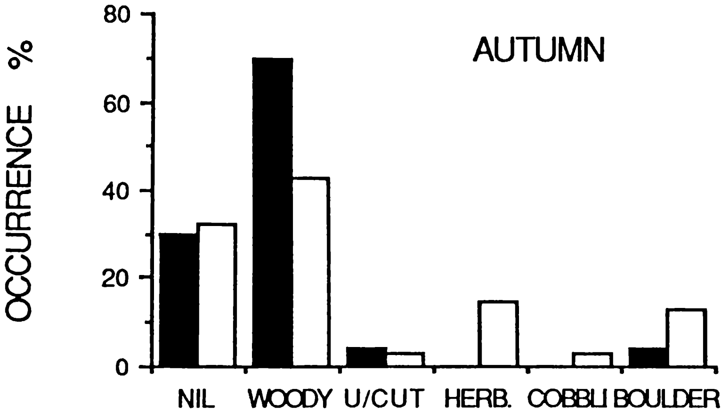

AUTUMN
OCCURRENCE %
80
60
40
20
0
NIL
WOODY
U/CUT
HERB.
COBBLI
BOULDER

Figure 6.9--The total fish lengths and the catch-adjusted minnow-trapping average water depths and velocities, with S.E.'s, and the frequency of substrate and cover types for koaro caught in the combined fine- and coarse-mesh minnow traps, summer 1988. **VELOCITY**, average mean-water-column velocity; **DEPTH**, water column depth at trap mid-point; **COARSE or FINE SUBSTRATE**, particle size of substrate. **NIL**, no cover; **WOODY**--woody cover; **U/CUT**--undercut bank; **HERB.**--herbaceous cover; **COBBLE**--cobble cover; **BOULDER**--boulder cover; **FISH**--catch-adjusted frequency of fish at type of cover; **TRAPS**--frequency of type of cover at trap.

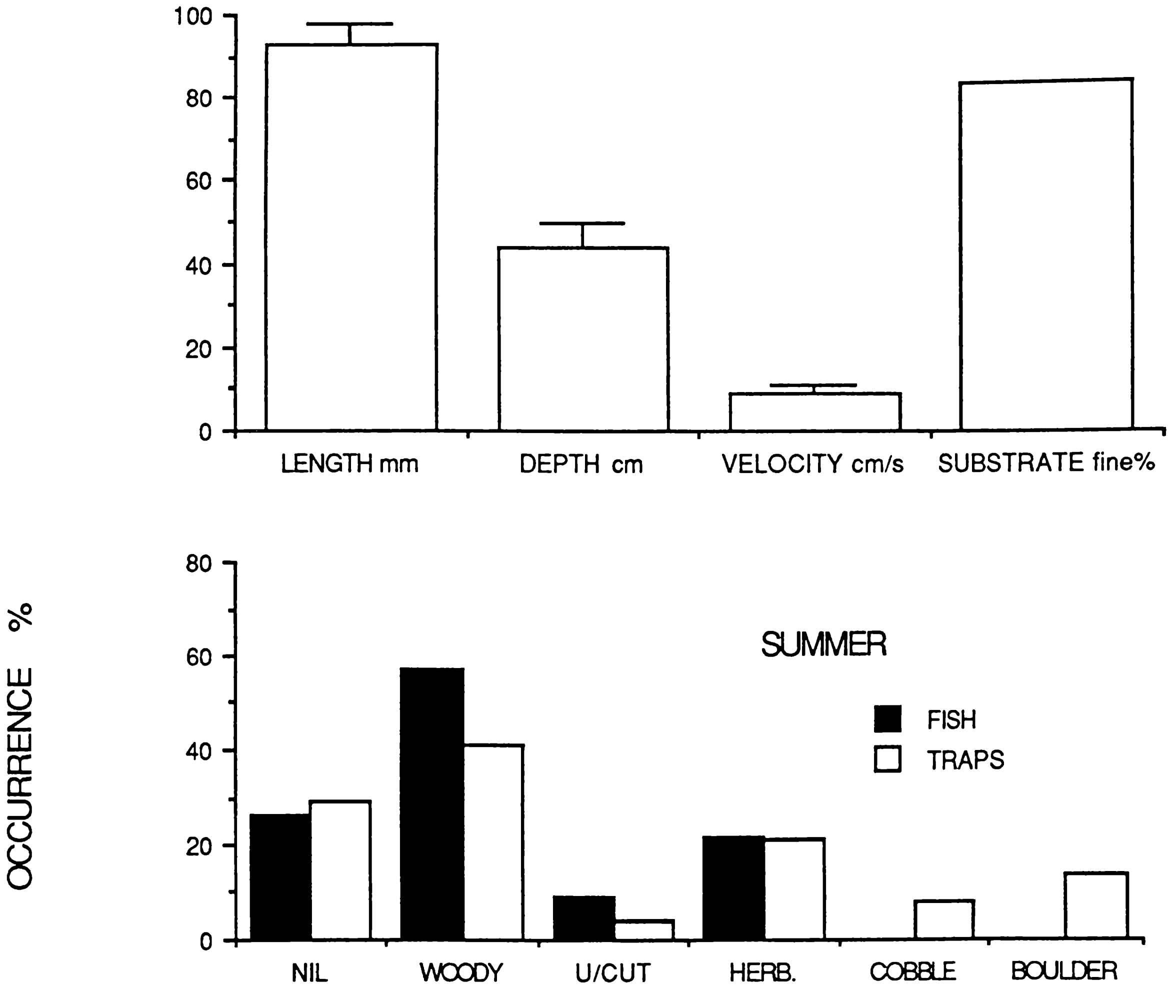
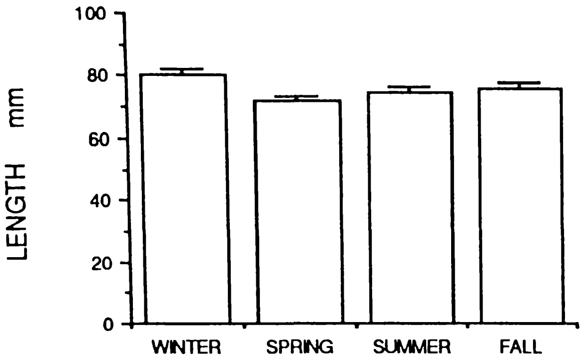
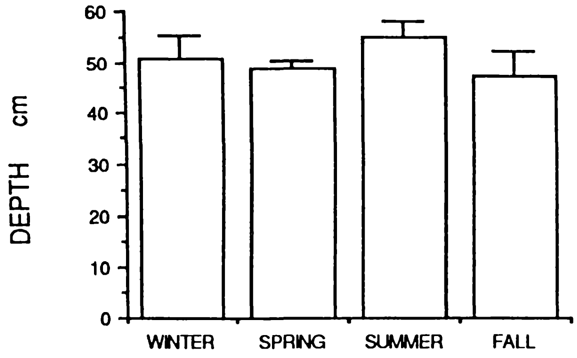
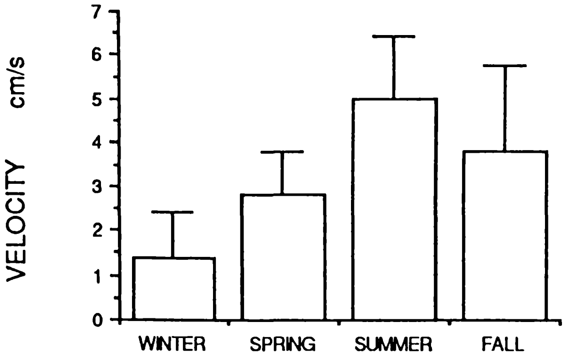

100
80
60
40
20
0
LENGTH mm
DEPTH cm
VELOCITY cm/s
SUBSTRATE fine%
OCCURRENCE %
80
60
40
20
0
SUMMER
FISH
TRAPS
NIL
WOODY
U/CUT
HERB.
COBBLE
BOULDER

Figure 6.10.--The total fish lengths and catch-adjusted average water depths and velocities, with S.E.'s, and frequency of substrate types for bullies caught in the combined fine- and coarse-mesh minnow traps, winter 1988 to autumn 1989. **VELOCITY**, average mean-water-column velocity; **DEPTH**, water column depth at trap mid-point; **COARSE/FINE**, particle size of substrate.


LENGTH mm
100
80
60
40
20
0
WINTER
SPRING
SUMMER
FALL


DEPTH cm
60
50
40
30
20
10
0
WINTER
SPRING
SUMMER
FALL


VELOCITY cm/s
7
6
5
4
3
2
1
0
WINTER
SPRING
SUMMER
FALL

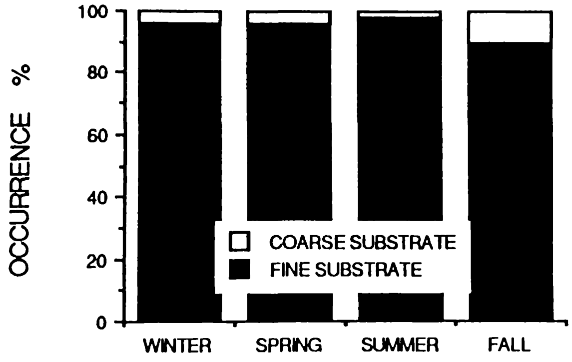
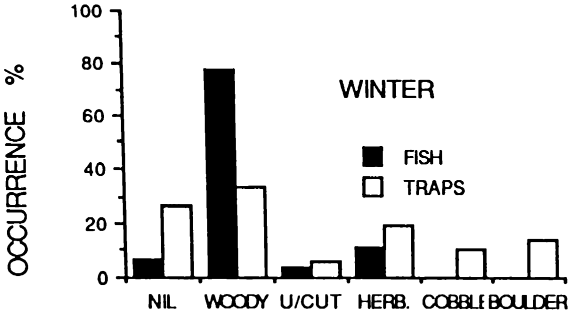
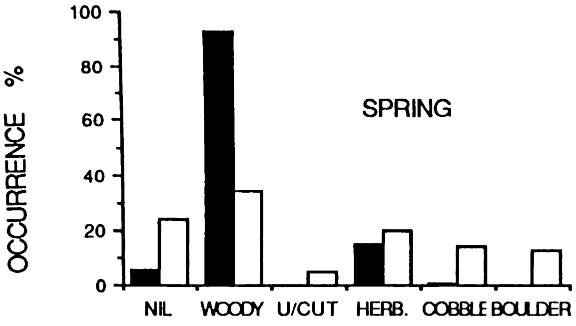
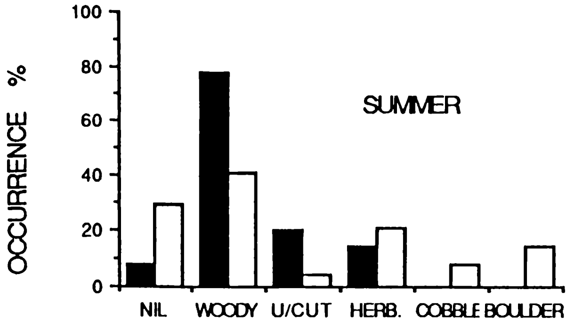

OCCURRENCE %
100
80
60
40
20
0
☐ COARSE SUBSTRATE
■ FINE SUBSTRATE
WINTER
SPRING
SUMMER
FALL

Figure 6.11--The catch-adjusted frequency of cover types for bullies caught in the combined fine- and coarse-meshed minnow traps, winter 1988 to autumn 1989. **NIL**, no cover; **WOODY**--woody cover; **U/CUT**--undercut bank; **HERB.**--herbaceous cover; **COBBLE**--cobble cover; **BOULDER**--boulder cover; **FISH**--catch-adjusted frequency of fish at type of cover; **TRAPS**--frequency of type of cover at traps.


OCCURRENCE %
100
80
60
40
20
0
WINTER
■ FISH
□ TRAPS
NIL
WOODY
U/CUT
HERB.
COBBLE
BOULDER


OCCURRENCE %
100
80
60
40
20
0
SPRING
NIL
WOODY
U/CUT
HERB.
COBBLE
BOULDER


OCCURRENCE %
100
80
60
40
20
0
SUMMER
NIL
WOODY
U/CUT
HERB.
COBBLE
BOULDER

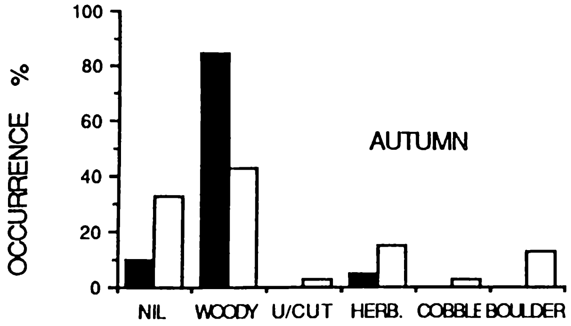

OCCURRENCE %
100
80
60
40
20
0
AUTUMN
NIL
WOODY
U/CUT
HERB.
COBBLE
BOULDER

Figure 6.12.--Catch-adjusted average water depths, with S.E.'s, for all species of fish caught in the combined fine- and coarse-meshed minnow traps, winter 1988 to autumn 1989. **TRAPS**--non-adjusted average water depths at the traps.

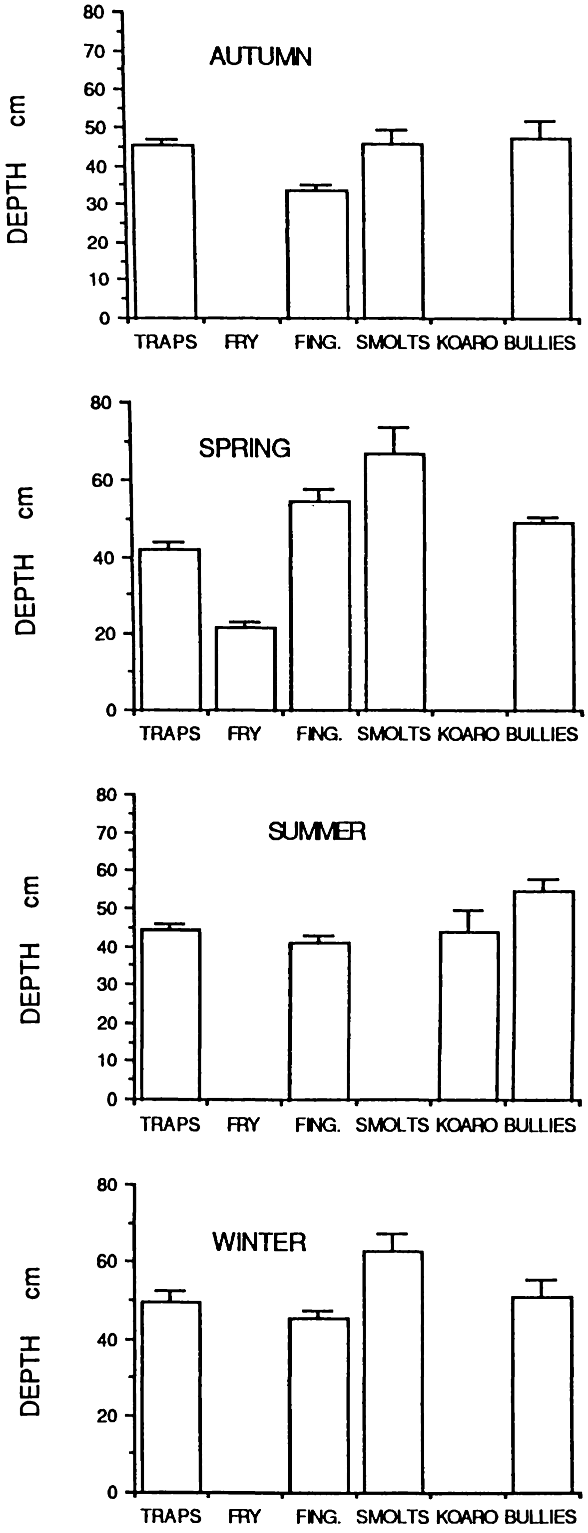

AUTUMN
DEPTH cm
80
70
60
50
40
30
20
10
0
TRAPS
FRY
FING.
SMOLTS
KOARO
BULLIES
SPRING
DEPTH cm
80
60
40
20
0
TRAPS
FRY
FING.
SMOLTS
KOARO
BULLIES
SUMMER
DEPTH cm
80
70
60
50
40
30
20
10
0
TRAPS
FRY
FING.
SMOLTS
KOARO
BULLIES
WINTER
DEPTH cm
80
60
40
20
0
TRAPS
FRY
FING.
SMOLTS
KOARO
BULLIES

Figure 6.13--Catch-adjusted average water velocities, with S.E.'s, for all species of fish caught in the combined fine- and coarse-meshed minnow traps, winter 1988 to autumn 1989. **TRAPS**--non-adjusted average water velocities at the traps.

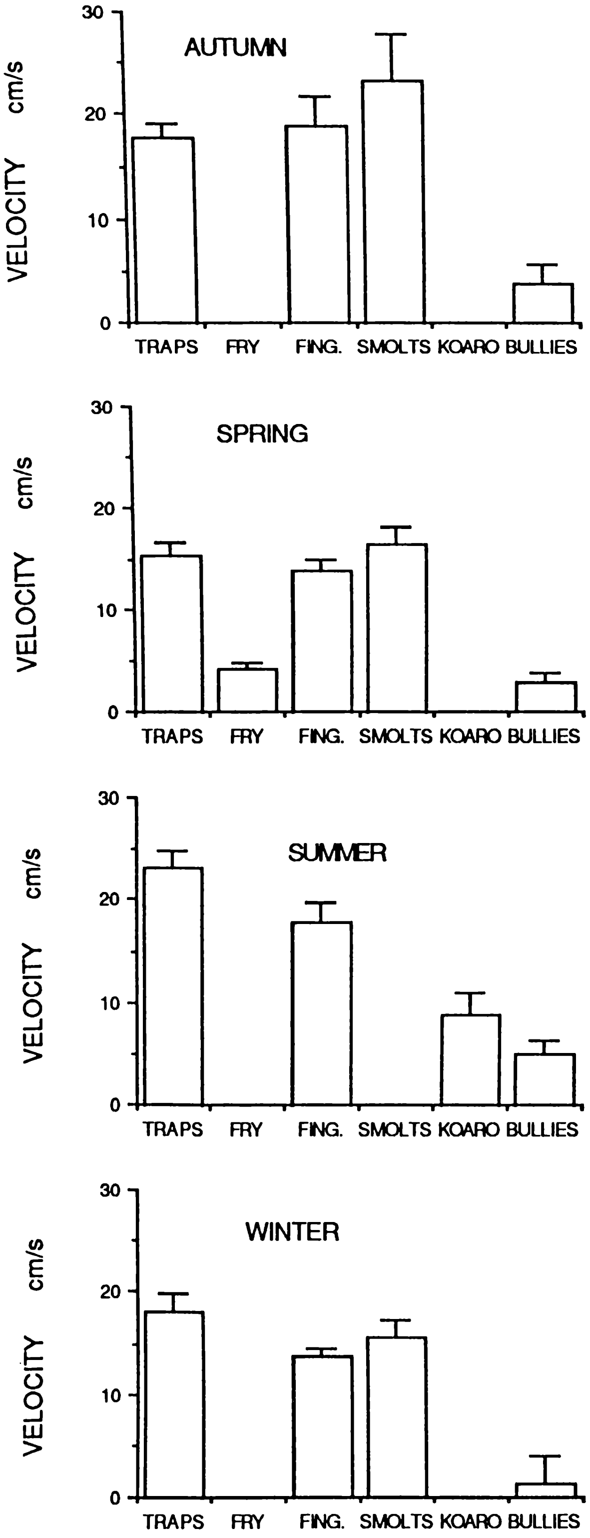

AUTUMN
SPRING
SUMMER
WINTER
VELOCITY cm/s
0
10
20
30
TRAPS
FRY
FING.
SMOLTS
KOARO
BULLIES

Figure 6.14--Catch-adjusted substrate-type percent occurrence for all species of fish caught in the combined fine- and coarse-meshed minnow traps, winter 1988 to autumn 1989. **TRAPS**--the non-adjusted percent occurrence of substrate type at the traps.

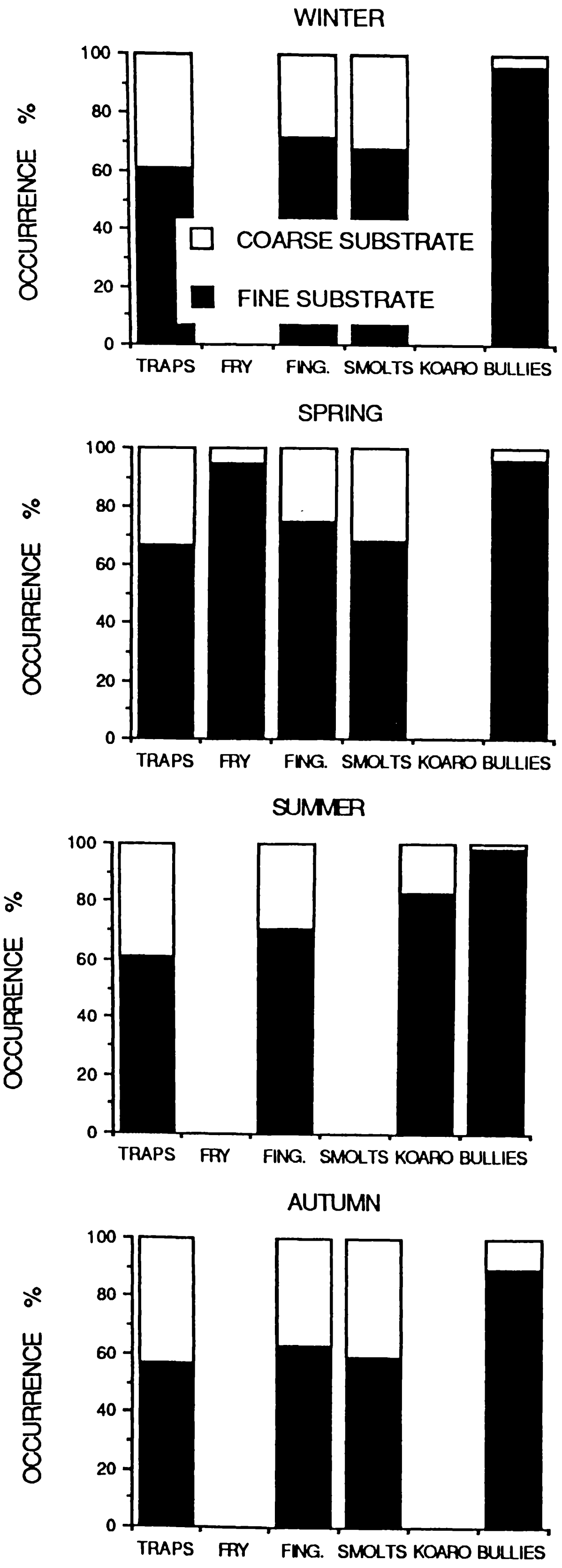
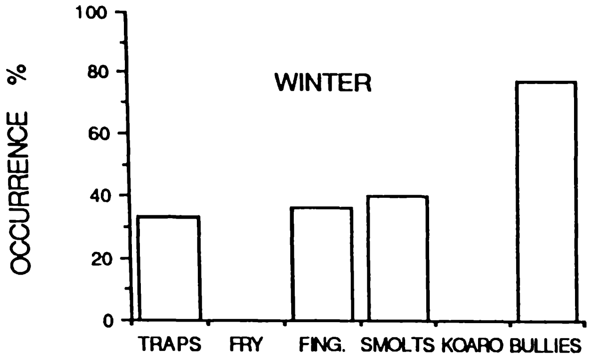
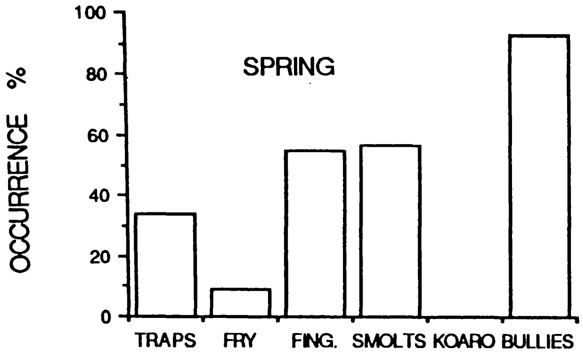
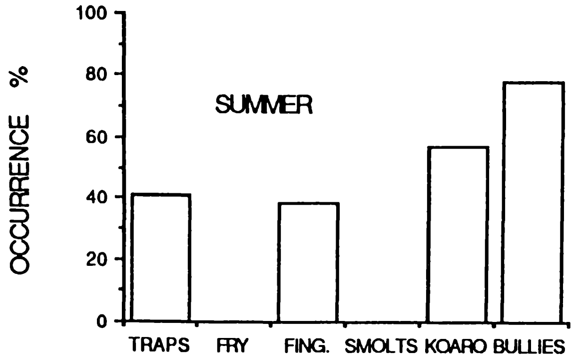

WINTER
SPRING
SUMMER
AUTUMN
OCCURRENCE %
0
20
40
60
80
100
TRAPS
FRY
FING.
SMOLTS
KOARO
BULLIES
☐ COARSE SUBSTRATE
■ FINE SUBSTRATE

Figure 6.15--Catch-adjusted woody cover percent occurrence for all species of fish caught in the combined fine- and coarse-meshed minnow traps, winter 1988 to autumn 1989. **TRAPS**--the non-adjusted percent occurrence of woody cover at the traps.


WINTER
OCCURRENCE %
100
80
60
40
20
0
TRAPS
FRY
FING.
SMOLTS
KOARO
BULLIES


SPRING
OCCURRENCE %
100
80
60
40
20
0
TRAPS
FRY
FING.
SMOLTS
KOARO
BULLIES


SUMMER
OCCURRENCE %
100
80
60
40
20
0
TRAPS
FRY
FING.
SMOLTS
KOARO
BULLIES

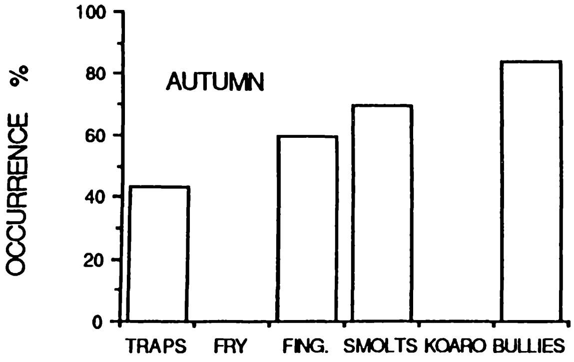
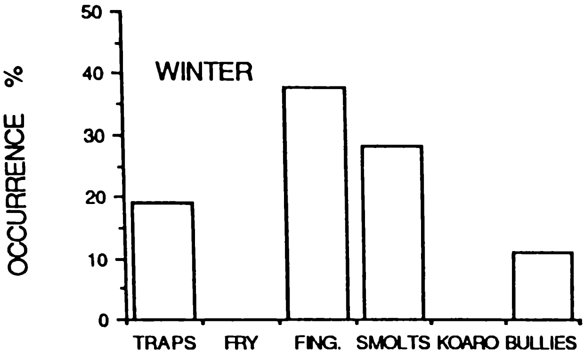
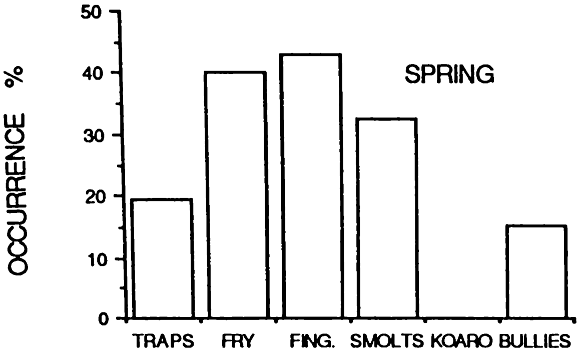
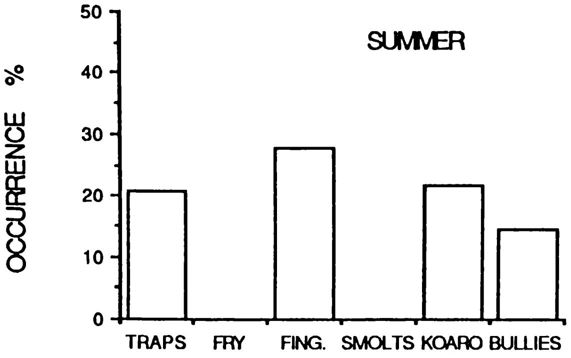

AUTUMN
OCCURRENCE %
100
80
60
40
20
0
TRAPS
FRY
FING.
SMOLTS
KOARO
BULLIES

Figure 6.16--Catch-adjusted herbaceous-cover percent occurrence for species of fish caught in the combined fine- and coarse-meshed minnow traps, winter 1988 to autumn 1989. **TRAPS**--the non-adjusted percent occurrence of herbaceous cover at the traps.


WINTER
OCCURRENCE %
0
10
20
30
40
50
TRAPS
FRY
FING.
SMOLTS
KOARO
BULLIES


SPRING
OCCURRENCE %
0
10
20
30
40
50
TRAPS
FRY
FING.
SMOLTS
KOARO
BULLIES


SUMMER
OCCURRENCE %
0
10
20
30
40
50
TRAPS
FRY
FING.
SMOLTS
KOARO
BULLIES

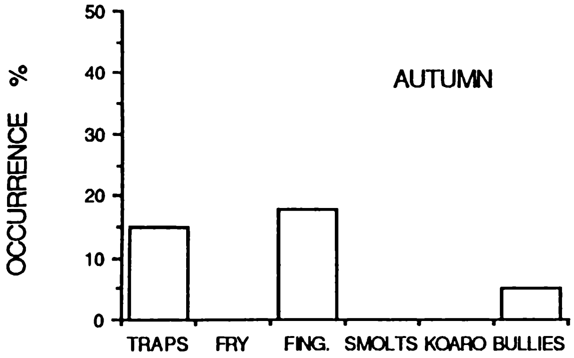

AUTUMN
OCCURRENCE %
0
10
20
30
40
50
TRAPS
FRY
FING.
SMOLTS
KOARO
BULLIES

Table 6.1.--Stream temperatures, number of traps used, and sizes of catches for the various groups and species of fish captured in the combined fine- and coarse-meshed minnow-trapping habitat analysis. "*" indicates a group not included in the habitat analysis due to a low sample size.

| | Winter | Spring | Summer | Autumn |
|---|---|---|---|---|
| TEMPERATURE °C | 6.0 | 9.5 | 15.7 | 10.7 |
| SAMPLE SIZES | | | | |
| traps | 131 | 123 | 160 | 166 |
| fine | 35 | 38 | 62 | 67 |
| coarse | 96 | 85 | 98 | 99 |
| rainbow trout | | | | |
| fry | 5* | 45 | 15 | 5* |
| fingerlings | 247 | 95 | 65 | 68 |
| smolts | 63 | 37 | 6* | 27 |
| koaro | 4* | 9* | 23 | 13* |
| bullies | 27 | 72 | 49 | 20 |

Table 6.2.--Numbers and lengths of fish caught in the fine-meshed minnow traps, spring/summer 1988-89.

| Species or size group | Mean Length mm | SD | N |
|---|---|---|---|
| rainbow trout fry (<45 mm) | 29.7 | 4.98 | 53 |
| rainbow trout fingerlings (≥45 mm, <94 mm) | 66.0 | 14.03 | 58 |
| common bully | 73.5 | 11.49 | 41 |

Table 6.3.--Among-species comparisons of catch-adjusted fine-meshed minnow trap water depths and velocities, and percent occurrence of substrate-type, for spring summer 1988-89. Level of significance for Tukey's and G-test, $p<0.05$; compare with Fig. 6.1. "traps" refers to the non-adjusted trap values.

**AVERAGE DEPTH**

ANOVA--df=3,234 F=10.192 $p<0.001$
Tukey's HSD
fry fingerlings traps bullies

**AVERAGE VELOCITY**

ANOVA--df=3,234 F=12.839 $p<0.001$
Tukey's HSD
bullies fry fingerlings traps

**SUBSTRATE**

Coarse vs Fine--trap ratio 26:74
Homogeneity of groups
$G_H = 5.20$ df= 2 $\chi^2 = 5.99$ ns
Goodness-of-fit to trap ratio (pooled)
$G_P = 25.75$ df= 1 $\chi^2 = 3.84$ *

Table 6.4.--Among-species comparisons of the catch-adjusted frequency of occurrence of cover types for the fine-mesh minnow traps, spring/summer 1988. Level of significance, $p<0.05$; df in brackets; combined samples indicated with a "+"; compare with Fig. 6.2.

**AMONG SPECIES**

| Cover Type | Trap Ratio present:absent | Homogeneity of Groups | Goodness of Fit to Trap Ratio |
|---|---|---|---|
| **nil** | 30:70 | 5.16 (2) ns | 5.62 (1) * |
| **woody** | 33:67 | 46.54 (2) * | 0.13 (1) ns |
| | fry fingerling bully | | |
| **undercut** | (insufficient sample size) | | |
| **herbaceous** | 21:79 | 34.60 (2) * | 4.858 (1) * |
| | bully fingerling fry | | |
| **cobble** | (insufficient sample size) | | |
| **boulder** | (insufficient sample size) | | |

**WITHIN SPECIES**

**fry** $G_H=19.41$ df=4 $\chi^2=9.488$ *
undercut+boulder woody nil cobble+herbaceous

**fingerling** $G_H=3.882$ df=3 $X^2=7.815$ ns

**bullies** $G_H=30.45$ df=2 $\chi^2=5.991$ *
boulder+cobble+herbaceous nil undercut+woody

Table 6.5.--Comparisons of water depths and velocities, and frequency of substrate and cover types, for the combined fine- and coarse-meshed minnow traps, winter 1988 to autumn 1989. Level of significance for Tukey's and G-test, $p<0.05$; compare with Figs. 6.3, 6.4.

---

**DEPTH** ANOVA--df=3, 576 F=1.895 p=0.127 ns
**VELOCITY** ANOVA--df=3, 576 F=4.242 p=0.01 *
Tukey's HSD Spring Summer Autumn Winter

**SUBSTRATE** G=3.535 df=3 ns
**COVER**
**NIL** G=2.529 df=3 ns
**WOODY** G=4.753 df=3 ns
**UNDERCUT BANK** G=1.720 df=3 ns
**HERBACEOUS** G=1.948 df=3 ns
**COBBLE** G=12.62 df=3 * Spring Winter Summer Autumn

**BOULDER** G=0.120 df=3 ns

---

Table 6.6.--Among-season comparisons of average water depths and velocities, and frequency of substrate and cover types for minnow-trapped fingerlings, winter 1988 to autumn 1989. Level of significance for Tukey's and G-test, $p<0.05$; combined samples identified with a "+"; compare with Figs. 6.5, 6.6.

---

**FORK LENGTH** ANOVA--df=3, F=18.366 p<0.01 *
Tukey's HSD Summer Autumn Winter Spring
**DEPTH** ANOVA--df=3, F=9.171 p<0.01 *
Tukey's HSD Autumn Summer Winter Spring

**VELOCITY** ANOVA--df=3, F=2.922 p=0.034 *
Tukey's HSD Winter Spring Summer Autumn

**SUBSTRATE** seasons $G_H=2.894$ df=3 $X^2=7.815$ ns
traps **vs** fish $G_P=247.8$ df=1 $\chi^2=3.841$ *
**COVER**
**winter** $G_H=67.43$ df=5 $\chi^2=11.07$ *
cobble nil boulder woody herbaceous undercut

**spring** $G_H=44.07$ df=5 $\chi^2=11.07$ *
cobble boulder nil undercut woody herbaceous

**summer** $G_H=1.655$ df=4 $\chi^2=9.488$ ns (nil + undercut combined)
**autumn** $G_H=8.438$ df=2 $\chi^2=5.991$ *
nil+undercut woody+herbaceous cobble+boulder

Table 6.7.--Among-season comparisons of average water depths and velocities, and frequency of substrate and cover types for minnow-trapped smolts, winter 1988 to autumn 1989. Level of significance for Tukey's and G-test, $p<0.05$; combined samples identified with a "+"; summer data not included due to low numbers; compare with Figs. 6.7, 6.8.

---

**FORK LENGTH** ANOVA--df=2, 124 $F=2.064$ $p=0.131$ ns
**DEPTH** ANOVA--df=2, 124 $F=3.041$ $p=0.051$ ns
**VELOCITY** ANOVA--df=2, 124 $F=2.333$ $p=0.101$ ns
**SUBSTRATE** seasons $G_H=0.715$ df=2 $X^2=5.991$ ns
traps **vs** fish $G_P=1.334$ df=1 $\chi^2=3.841$ ns
**COVER**
**winter** $G_H=13.95$ df=3 $\chi^2=7.815$ *
boulder+cobble nil woody+undercut herbaceous

**spring** $G_H=10.81$ df=3 $\chi^2=7.815$ *
nil cobble+boulder woody+undercut herbaceous

**autumn** $G_H=2.884$ df=1 $\chi^2=3.841$ ns

---

Table 6.8.--Among-season comparison of average water depths and velocities, and frequency of substrate and cover types for minnow-trapped bullies, winter 1988 to autumn 1989. Combined samples identified with a "+"; level of significance for Tukey's and G-test, $p<0.05$; compare with Figs. 6.10, 6.11.

---

**FORK LENGTH** ANOVA--df=3, 163 $F=4.250$ $p<0.01$ *
Tukey's HSD spring summer autumn winter

**DEPTH** ANOVA--df=3, 163 $F=1.635$ $p=0.183$ ns
**VELOCITY** ANOVA--df=3, 163 $F=1.222$ $p=0.304$ ns
**SUBSTRATE** seasons $G_H=1.934$ df=3 $\chi^2=7.815$ ns
traps **vs** fish $G_P=113.1$ df=1 $\chi^2=3.841$ *

**COVER--within seasons:among types**
**winter** $G_H=12.49$ df=1 $\chi^2=3.841$ *
nil+undercut+boulder+cobble **vs** woody+herbaceous
**spring** $G_H=46.41$ df=1 $\chi^2=3.841$ *
nil+undercut+boulder+cobble **vs** woody+herbaceous
**summer** $G_H=7.617$ df=1 $\chi^2=3.841$ *
nil+undercut+boulder+cobble **vs** woody+herbaceous
**autumn** $G_H=5.211$ df=1 $\chi^2=3.841$ *
nil+undercut+boulder+cobble **vs** woody+herbaceous

Table 6.9.--Among-species catch-adjusted comparisons of average depths and velocities for the combined fine- and coarse-meshed minnow traps. Level of significance for Tukey's test is $p<0.05$; compare with Figs. 6.12, 6.13.

---

**DEPTH**

**WINTER** ANOVA--df=3,464 F=4.981 p=0.002 *
Tukey's HSD fingerlings traps smolts bullies
**SPRING** ANOVA--df=4,365 F=20.964 p<0.001 *
Tukey's HSD fry traps bullies fingerlings smolts

**SUMMER** ANOVA--df=3,293 F=4.165 p=0.007 *
Tukey's HSD fingerlings koaro traps bullies
**AUTUMN** ANOVA--df=3,277 F=5.451 p=0.001 *
Tukey's HSD fingerlings traps smolts bullies

**VELOCITY**

**WINTER** ANOVA--df=3,464 F=9.943 p<0.001
Tukey's HSD bullies fingerlings smolts traps
**SPRING** ANOVA--df=4,365 F=17.340 p<0.001
Tukey's HSD bullies fry fingerlings traps smolts
**SUMMER** ANOVA--df=3,293 F=14.255 p<0.001
Tukey's HSD bullies koaro fingerlings traps
**AUTUMN** ANOVA--df=3,293 F=4.124 p=0.007
Tukey's HSD bullies traps fingerlings smolts

---

Table 6.10.--Among-species catch-adjusted comparisons for substrate types for the combined fine- and coarse-meshed minnow traps. Level of significance, $p<0.05$; df in brackets; compare with Fig. 6.14.

| Season | Trap Ratio coarse:fine | Homogeneity of Groups | Goodness of Fit to Trap Ratio |
|---|---|---|---|
| **WINTER** | 51:80 | 11.34 (2) * | 21.19 (1) * |
| bullies fingerlings smolts | | | |
| **SPRING** | 40:83 | 26.88 (2) * | 32.12 (1) * |
| bullies+fry fingerlings smolts | | | |
| **SUMMER** | 62:98 | 17.57 (2) * | 29.15 (1) * |
| bullies koaro fingerlings | | | |
| **AUTUMN** | 72:94 | 1.70 (1) ns | 79.61 (1) * |
| fingerlings smolts | | | |

Not included in the autumn analysis: bullies (2/18 fish)

Table 6.11.--Among-species catch-adjusted comparisons for cover for the fine- and coarse-meshed minnow traps. Level of significance, $p<0.05$; df in brackets; compare with Fig. 6.15.

| Season | Trap Ratio present:absent | Homogeneity of Groups | Goodness of Fit to Trap Ratio |
|---|---|---|---|
| | | **NIL** | |
| **WINTER** | 25:75 | 12.10 (2) * | 42.69 (1) * |
| | bullies fingerlings smolts | | |
| **SPRING** | 22:78 | 24.96 (3) * | 30.71 (1) * |
| | smolts+bullies+fingerlings fry | | |
| **SUMMER** | 25:75 | 6.43 (1) * | 36.76 (1) * |
| | fingerlings+bullies koaro | | |
| **AUTUMN** | 30:70 | 4.12 (2) * | 15.13 (1) * |
| | bullies, fingerlings, smolts | | |
| | | **WOODY** | |
| **WINTER** | 30:70 | 17.31 (2) * | 8.38 (1) * |
| | fingerlings smolts bullies | | |
| **SPRING** | 31:69 | 91.18 (3) * | 59.93 (1) * |
| | fry fingerlings smolts bullies | | |
| **SUMMER** | 35:65 | 17.98 (2) * | 12.24 (1) * |
| | fingerlings koaro bullies | | |
| **AUTUMN** | 40:60 | 4.84 (2) ns | 25.92 (1) * |
| | fingerling, smolts, bullies | | |
| | | **HERBACEOUS** | |
| **WINTER** | 17:83 | 2.60 (2) ns | 5.87 (1) * |
| | bullies, fingerlings, smolts | | |
| **SPRING** | 18:82 | 15.17 (3) * | 20.77 (1) * |
| | bullies smolts fingerlings fry | | |
| **SUMMER** | 18:82 | 14.12 (2) * | 7.43 (1) * |
| | bullies koaro fingerlings | | |
| **AUTUMN** | 18:82 | 3.951 (1) ns | 0.13 (1) ns |
| | bullies, fingerlings | | |

Not included in analysis: smolts (0/27 fish), bullies (1/20 fish)

## 6.3 DISCUSSION

### Rainbow trout

Fluvial-rearing habitat for fishes is characterized by the area of the stream as well as: 1) water depth, 2) current velocity, 3) substrate features, and 4) cover from high flows, predators and competitors. These variables figure largely in salmonid stream-habitat models (see citations in Fausch et al. 1988) and their aggregation, in part, defines the limits to production of fish in lotic environments. Thus, it was these features that were investigated in this part of my study.

With regards to these above four variables, there was a clearly defined segregation of habitat by the various size groups of rainbow trout and the native fishes in the Waimarino River. Furthermore, the habitat utilization changed depending on the size of the trout and the time of year. Firstly, in the Waimarino River there was a positive relationship between the size of trout and the water depths and velocities that the fish were captured in; fry were found in water that was shallower and of slower velocity than that utilized by the larger fingerlings and, in turn, smolts were usually found in faster and deeper water than fingerlings.

Similar results have been observed by other researchers investigating the habitat preferences of juvenile salmonids. For example, Bovee (1982) showed that, for salmonids in streams, depth and velocity requirements are positively related with the size of the fish for salmonids in streams. Likewise, Baltz et al. (1991) also observed that in a small river in northern California, as rainbow trout juveniles grew larger, they moved into deeper, faster water. Lewis (1969), Bisson et al. (1982) and Campbell and Neuner (1985) also reported similar positive relationships between fish size and depths and velocities in rainbow trout.

The choice of a particular stream depth or velocity for a given body-size of juvenile rainbow trout is thought to be the result of a complex functional relationship amongst various requirements for survival including: 1) the need to prevent downstream displacement, 2) acquiring enough food for growth and survival, and 3) obtaining protection from predators. Giger (1973) suggested that smaller trout stay inshore because they cannot maintain position in the face of the mid-stream higher velocity water, while the larger trout find little shelter from predators in these inshore, shallow depths. However, Gosse and Helm (1981) found that brown trout fry only stay in shallow water to avoid predation from larger conspecifics; when the larger trout were absent they moved offshore into deeper water. Alternatively, Smith and Li (1983) invoked an energetics model to explain the depth and velocity choices of juvenile rainbow trout in a California, USA, stream; as the juvenile trout increased in size, they also chose faster water velocities in order to be near a greater amount of food; the drifting invertebrates upon which rainbow trout were feeding on were more abundant in faster flowing water.

In the Waimarino River, there were also seasonal trends in the distribution of rainbow trout juveniles with regards to depth and velocity; in the colder temperatures of winter and spring the fish were found in slower and deeper water than in the warmer autumn and summer waters, although the differences were not statistically significant in all cases. Similarly, Hartman (1965), Bustard and Narver (1975a) and Baltz et al. (1991) found that rainbow trout move into deeper, slower water during periods of colder water temperatures. In California, Smith and Li (1983) also found that at higher temperatures rainbow trout moved into higher velocity, shallower waters. Smith and Li's explanation for this behaviour was based on an energetics model; during summer more food is available in the shallower, faster water and it was to the advantage of the trout to be feeding in these areas.

The threshold temperature that signals the shift of salmonids from shallower, faster water to slower, deeper water appears to be 10°C; during my sampling periods, the spring and winter temperatures were less than 10°C while in summer and autumn the water was warmer. For Atlantic salmon (**Salmo salar**), Rimmer et al. (1984) also found distinct distributional and behavioural differences above and below this temperature; hiding in deep, slow water was the norm in colder water. Rainbow trout in California as well as British Columbia also seem to go into an overwinter-behaviour pattern, seeking out deeper, slower water, below 10°C (Baltz et al. 1991; Rosenau and Slaney 1991; respectively).

Changes in water temperature also affected the distribution patterns of the various size groups of rainbow trout with respect to each other. Unlike at all other times of the year, during winter Waimarino River rainbow fingerlings and smolts did not segregate one from the other in their depth and velocity preferences; substrate and cover choices were also similar during this period. Baltz et al. (1991) found a similar convergence in the habitat preferences for different size classes of California rainbow trout during the cold-water periods although in their study the groups were still somewhat segregated.

Because the energetic demands of salmonids are not as great in colder water, and they become torpid and exhibit hiding behaviour, competition within and among species for food and space tends to be minimized during this time period (Smith and Li 1983). Low water temperatures reduce the swimming performance of the fish (Brett et al. 1958; Hartman 1963; Bell 1973) and, consequently, salmonids seek greater shelter from stream velocities at colder temperatures and are increasingly found in pools which have deeper, slower water (Campbell and Neuner 1985). This behaviour affords protection against predation and downstream displacement (Boussu 1954; Hartman 1963) and reduces energy expenditures (Giger 1973). Of course, this assumes that the appropriate overwintering habitats are in sufficient abundance to accommodate all size groups of fish (Mason 1976).

Besides depth and velocity, the size of the substrate particles is thought to be important in determining juvenile-salmonid distributions in streams (Bovee 1982; Heggenes 1988). In the Waimarino River, there was a trend for larger rainbow trout to be more closely associated with coarser substrate than were the smaller fish. Although fingerlings and smolts were not statistically separable with regards to their choice of substrate, the proportion of smolts over coarse substrate was consistently numerically greater than for fingerlings for all seasons that comparisons could be made. Furthermore, in spring when fry were abundant enough to be compared to the other groups of fish, they were trapped over finer substrate than were fingerlings and smolts.

Heggenes (1988) also found that brown trout fry moved over coarser substrates as they grew larger. He suggested that the larger the substrate particle diameters, the greater the number of low velocity micro-niches that there are for fish to gain shelter from flows and competitors. Smith and Li (1983) and Baltz et al. (1991) also showed that as rainbow trout in California grew larger they were found more often over coarser substrate. However, the interpretation of the functional utility between size of fish and substrate must be treated with some caution. Because there is also a close inter-relationship between water velocity and substrate-particle size in streams, the association of larger fish with larger substrate may not be functionally related, but simply a correlation between these two variables.

Cover is the fourth habitat feature investigated in this study and it is also known to have important effects on the distribution, abundance and production of stream rearing salmonids. Instream cover can take a variety of forms (Platts et al. 1983) and can provide protection from: 1) being eaten by conspecifics and other fish, as well as avian and mammalian predators, 2) displacement due to floods, and 3) loss of territory due to agonistic activity from conspecifics or other, closely related, species of fish.

There were clear differences in the utilization of cover by the various size-classes of trout in the Waimarino River. For example, a substantially greater proportion of fry were found near the "NIL" category than were any other size class of rainbow trout suggesting that cover is not utilized by these smaller fish to the same degree as it is by the larger rainbows. Similarly, Saunders and Smith (1962), Hunt (1978) and Bisson et al. (1982) also found that older trout were more inclined to associate with cover than the smaller young-of-the-year fish.

In the Waimarino River, the fry that associated with cover had a strong tendency to be caught near either cobble or herbaceous (grassy) material. Campbell and Neuner (1985) also found that in Washington, USA, streams rainbow trout were strongly associated with these two types of cover. In contrast, the larger fingerlings and smolts in the Waimarino River tended to be more strongly associated with woody, herbaceous (blackberry bushes) and undercut bank cover. Bisson et al. (1982) found that wood debris was the preferred cover type for age 1+ (fingerling) steelhead but, again and like this study, they also found that fry were less inclined to use woody debris. The results of Bisson et al. (1982) indicate that wood debris, especially large stems and rootwads, was the most favoured cover type for most juveniles and, as they suggest, may hold the greatest promise for enhancement projects.

In the Waimarino River there were significant among-season differences in the utilization of cover by juvenile rainbow trout. For example, fingerlings and smolts were caught near woody and herbaceous cover much more frequently during colder water conditions. This is not surprising as strong shifts into microhabitats with cover during winter appear to be characteristic of many stream-dwelling salmonids (Chapman and Bjornn 1969; Bustard and Narver 1975ab; Rimmer et al. 1984; Cunjak and Power 1986; Murphy et al. 1986). Furthermore, the functional significance of this behaviour has been investigated by Tschaplinski and Hartman (1983) who found that in winter, sections of streams containing an abundance of deep pools, log jams, and undercut banks having tree roots and debris, lost fewer fish during freshets and maintained higher numbers of juvenile salmonids than sections without these habitats. Bustard and Narver (1975b) found that locations under or downstream of upturned tree roots or logs were most frequently occupied by young salmon and trout in winter and Murphy et al. (1986) found that instream woody debris was important in maintaining winter densities of juvenile salmonids. Furthermore, like the juvenile trout in this study, Wilzback's (1985) work with cutthroat trout (**O. clarki**) demonstrated that at warmer temperatures the level of food abundance is overriding in determining the microhabitat distribution of these fish in streams and the fish become less closely associated with cover.

In recent years a considerable amount of research has been conducted investigating the role of instream-woody debris as cover for salmonids and other fishes (Heede 1972; Swanson and Lienkaemper 1978; Keller and Tally 1979; Bilby and Likens 1980; Bryant 1983; Lisle 1986). Although wood in streams can occasionally have negative consequences for fish production (fine debris can clog fish-spawning and insect-rearing substrates; large debris can block the migration of fishes), the beneficial aspects of woody debris far outweigh these bad effects. The positive benefits of instream woody debris have been surveyed by Gibbons et al. (1990) and include:

1) cover for juvenile and adult fish,
2) protection for spawning adults from predators,
3) habitat diversity for fish and aquatic insects,
4) aid to fish migrating during periods of low water by creating "channel-stepping" pools,
5) a trap for gravel that can be used for spawning habitat,
6) a trap for sediment, and
7) a stabilizing factor for stream banks.

The number of juvenile salmonids in a stream is often directly related to the amount of instream woody debris (Murphy et al. 1986; Bisson et al. 1987) and removal of this material usually considerably reduces the numbers of these fish (Dolloff 1986; Elliott 1986). Furthermore, the removal of woody material from the stream-edge riparian zone can have long-lasting negative effects for the recruitment of instream woody cover. Murphy and Koski (1989), working on Alaska streams, found that 90 years after clear-cut logging without a stream-side buffer strip, large woody debris was reduced by 70% and recovery to prelogging levels was predicted to take more than 250 years. They found that, because most large woody debris was derived from within 30 m of the stream edge, a buffer strip of this width should be maintained to ensure adequate recruitment of this material. Research on streams in coastal Oregon indicated that trees must be left to grow longer than 50 yr to ensure that there is an adequate, long-term supply of woody debris available to the streams. Indeed, in some instances government agencies have gone so far as to anchor cut-coniferous trees within the wetted perimeter of the stream to provide both fish habitat and bank stabilization (Sheeter and Claire 1981; Rosenau et al. 1987; Rosenau 1990a,b). Another type of woody material, anchored root wads, has also been shown to have potential for providing fish habitat in streams. Shirvell (1990) found that rainbow trout juveniles occupied previously infrequently-used mid-channel areas of the stream once rootwads were placed in these locations.

Another effect on aquatic biota by removing riparian vegetation is increased sediment input into streams. Sediment which settles on, or penetrates into, the stream bed is of more concern than suspended settlement, and can lead to long term deleterious changes to fish and invertebrate populations by smothering spawning beds and insect-rearing substrates (Campbell and Doeg 1986).

Although woody cover is important for stream rearing juvenile salmonids, other types of cover, such as boulder cover can have a high utility for these fishes (Ward and Slaney 1979). However, in the Waimarino River boulder cover was the preferred choice of cover only for fingerlings, and then just in autumn. Bisson et al. (1982) found a similar lack of response by juvenile steelhead to increased boulder cover and this is contrary to the experience of Hartman (1965), Facchin and Slaney (1977) and Ward and Slaney (1979); the latter found strong relationships between boulders and juvenile steelhead utilization in British Columbia streams. However, perhaps the lack of boulder use by juvenile rainbow trout in the Waimarino River only reflects the greater preference of these fish for other types of cover that are readily available in this stream.

### Koaro

The CPUE of koaro in the Waimarino River was low compared to any of the other groups of fish in this study. Thus, based on catch rates, and compared to other streams in the Lake Taupo drainage (Kusabs 1989; Hicks and Rosenau, in prep.), koaro are a comparatively depauperate species in the Waimarino River. Nevertheless, during the summer enough koaro were trapped to provide some habitat-utilization comparisons with the other groups of fish.

The koaro that were caught during summer were physically segregated from rainbow trout fingerlings by water velocity criteria, and from bullies by water depth; fry and smolts were not caught in large enough numbers during this time of the year to make any meaningful comparisons with koaro. Furthermore, more koaro were caught over coarse substrates than were bullies, but not than fingerlings. This suggests that koaro were more disposed to utilize habitats having coarser substrates than those used by the bullies. Compared to all other cover types, koaro had the greatest catch-frequency with the "NIL" cover rating during summer than any other group of fish; this suggests that compared to the other groups they were not nearly so inclined to associate with the physical features that I designated as "cover". Thus, the generalized profile of koaro in the Waimarino River is that, with regard to their physical distribution and utilization, they are intermediate between rainbow trout and bullies. This may, however, be the result of interactive segregation through competition for space by rainbow trout and bullies rather than by innate choice of the habitat types that they were found to occupy (interactive versus selective segregation, Brian 1956; Nilsson 1967). Indeed, the greatest competition for space that koaro are likely to encounter is from the non-native rainbow trout; these two species did not evolve together in sympatry and because they have similar habitat requirements (Kusabs 1989), the potential for competition between these two species is considerable.

To utilize Lake Taupo tributaries, larval koaro (whitebait) first make upstream migrations and the fish then rear to adulthood in these lotic habitats (Kusabs 1989).

Prior to the introduction of rainbow and brown trout, the Lake Taupo watershed abounded in koaro but the numbers of the latter were dramatically reduced after the trouts became established (McDowall 1990). Predation by the trout in the lake is thought to be the primary reason for the subsequent koaro population crash. However, recent evidence suggests that other factors may have also been involved in reducing the numbers of koaro in Lake Taupo including: 1) habitat exclusion by trout through competition in the fluvial environments (Kusabs 1989), or 2) predation of young koaro by trout in their rearing streams (Kusabs 1989). Nevertheless, further investigation needs to be undertaken to truly understand the relationships between koaro and their fluvial-habitat requirements.

### Bullies

In this study, bullies were segregated from all other groups of fish by one or more of the four physical variables of water depth, velocity, substrate and cover. Most strikingly, and with the exception of fry during spring and koaro in summer, bullies clearly chose the slowest water velocities compared to all other groups. However, where fry and koaro had similar water velocity characteristics in common with bullies, the latter were found in considerably deeper water than these two species. Bullies also had a much stronger tendency to associate with fine substrates than any of the other groups of fish, with the exception of fry in spring; again, although the substrate choices overlapped during this time, fry chose much shallower water than bullies thus ensuring a physical segregation between these two species. Nevertheless, the reason that bullies had a strong tendency to be found over fine substrates may have simply been a correlation with slow moving waters; fine material would be more prone to drop out of the water column and on to the substrate.

That bullies in the Waimarino River chose deeper and slower water than all the other groups of fish present in this stream is not surprising. Clearly, the body morphology of the bully is not designed for swimming in fast waters (Plate 3.7) and it certainly does not have the streamlined, fusiform shape that stream-living salmonids have; from its body form alone, the common bully would not be expected to live in high velocity waters. Indeed, McDowall (1990) describes the common bully as a fish that is generally found in lakes and gently flowing streams.

Compared to all the other groups in this study, the bullies in the Waimarino River had a much higher propensity to be found near woody cover, especially in winter and spring. McDowall (1990) suggests that in rivers common bullies are often found hiding in margin cover (overhanging banks, logs, large rocks, and debris and rocks) and that this may be the result of an anti-predator behaviour. Adult brown trout, a bully predator, are common in the lower reaches of the Waimarino River during certain times of the year (Tully 1989); this is also where most of the bullies in the Waimarino River are found (see Chapter 7). Furthermore, Dickinson (1951) also described the common bully as being the most important food item of some of the New Zealand fish-eating species of birds including the shags (**Phalacrocorax** sp.), which are common to the Lake Taupo watershed. Certainly, the bullies living in the slow-moving waters and relatively shallow habitats of the lower Waimarino River may be especially vulnerable to fish or bird predators and woody cover may provide the necessary habitat component for their survival.

Bullies in the Waimarino River did not significantly vary in their relative among-season habitat preferences; that is, the water depth, velocity, substrate and cover preferences remained the same regardless of the time of year. Interestingly, there was a slight, but statistically non-significant tendency for bullies to be found in faster water during warmer months. As with the observations for juvenile trout, this change in behaviour may be a function of higher temperatures and greater energy demands during these periods of the year (see Smith and Li 1983).

# Chapter 7.--DISTRIBUTION PATTERNS OF STUDY-STREAM FISHES

## 7.0 INTRODUCTION

The distribution of fishes in a stream is related to historical events as well as the physical, chemical, and biological features within the watershed. Jowett (1990) provides an excellent example of this when describing the biogeographic distribution of rainbow and brown trout in New Zealand.

Lake Taupo streams are well known for their rainbow trout, yet, little information is available regarding the composition and distribution of other fluvial fishes throughout this watershed. The few studies that have been conducted, however, indicated that there is a considerable among-stream variability in the densities and sizes of a variety of species of fish. For example, Pitkethley (1990) found that juvenile brown trout were common in some areas of the Mangamawhitiwhiti Stream yet rare in the similar-flow and geographically-nearby Waihukahuka (Hatchery) Stream. Kusabs (1989) provided an in-depth description of the species composition of three small Lake Taupo tributary streams, the Omori, the Waiotaka, and the Waipehi, and he found that koaro were generally absent in streams with high juvenile rainbow trout densities.

The three streams in my study, the Waimarino, Tokaanu and Hinemaiaia Rivers, are recognized for their substantial spawning runs of rainbow trout and their for rearing of the juveniles prior to emigration to Lake Taupo (Rosenau 1991). Because the distribution of fluvial fishes is related to physical, biological and historical characteristics, and since these features differ considerably in these streams (Chapter 3), I speculated that the species composition may also differ accordingly. Therefore, the purpose of this chapter is to describe and compare the species compositions, numbers, sizes and ages of fish caught in the minnow traps at each of my study sample sites for each season throughout the period of one year. My comparisons included: 1) within-season:among-rivers, 2) within-season & river:among-sites, and 3) among-seasons:within-site. The format of this chapter is predominately descriptive and it is not my intent to be rigorously quantitative; nevertheless, I hope that this information will aid fisheries managers and scientists working on these watersheds in the future.

## 7.1 METHODS

Three study sites were chosen from each of my study streams. Each of the sites were characteristic of the most common reach types accessible to migratory rainbow trout. To assess the size composition of juvenile trout as well as common bullies and koaro, a series of baited minnow-traps were set in each of the sampling sites once a season from winter 1988 to autumn 1989. Chapter 4 gives a more complete description of the methods employed in the capture of fish and the numbers of traps set per season. Flow, temperature, and physical and chemical features are recorded in Chapter 3.

At each trap location, water-column depth and average water-column velocity was measured (at 0.6x the depth using an electric watervelocity meter; Platts et al. 1983). The fork length and species of each fish caught in each trap was recorded. Rainbow trout were aged by length-frequency-distribution analysis (Tesch 1971); scales from fish of lengths near the edges of the frequency-distribution modes were examined to confirm the a age classes. It was assumed that between-site catch-per-unit effort (CPUE) differences reflected fish density differences for the various size-classes of the different species of caught therein.

Each site was also characterized by its average physical features as determined at each trap location. These values were assumed to give an approximate site measure of relative water depths and velocities when compared to other sites (i.e., is Site A deeper and faster than Site B?); however, no formal sampling was undertaken to determine if this assumption was valid. Distances of the study sites upstream from Lake Taupo, and gradients, were taken from a topographical map (NZMS 260 T19 TONGARIRO Edition 1, NZMS 260 U18 TAUPO Edition 1).

## 7.2 SITE DESCRIPTIONS

### 7.2.1 Waimarino River

#### Physical characteristics

Site A (Fig. 7.1) on the Waimarino River is located the farthest upstream of the three sites on this stream, or about 8 km from Lake Taupo. This site has an abundance of boulder cover, little instream-organic cover, and numerous riffles and short runs. The river channel at Site A is constrained by steep valley walls; bedrock outcroppings form many of the scour pools on this part of the river. There is little stream-channel meander at Site A and this reach has a steeper gradient than the other two sites on the Waimarino River. The river channel depths are shallower at this location when compared to the other Waimarino River sites (Fig. 7.4) and this is probably related to the higher gradient and stream-bed composition of larger material. The water velocities measured at this site were approximately similar to the other Waimarino River sites (Fig. 7.4).

Site B (Fig. 7.1) is located midway between the other two sites on this stream about 5 km upstream from Lake Taupo. This site has comparatively little boulder cover and a moderate amount of instream organic cover. Here the river channel follows an unrestricted meander pattern with approximately equal areas of pools or glides and riffles. The average minnow-trap depths at Site B were intermediate compared to the other Waimarino River sites (Fig. 7.4); the average water velocities were similar to the other sites on this stream (Fig. 7.4).

Waimarino River Site C (Fig. 7.1) is nearest to Lake Taupo of the three sites, or about 3 km upstream from the confluence. This site is similar to Site B in its physical characteristics except that the average minnow-trap water depths in the former tended to be greater (Fig. 7.4).

The velocities and depths in the Waimarino River had the least amount of among-site and among-season variability of the three study streams (Fig. 7.4).

### Fish population characteristics

There was surprisingly little among-season or among-site variation in the CPUE of rainbow trout juveniles in the Waimarino River, except for winter and Site B in autumn (Fig. 7.5). Generally, a greater proportion of the larger and older rainbow trout were caught in the more downstream sites (Fig. 7.8).

The CPUE's of koaro from the Waimarino River sites were greater than for any sites on the Tokaanu River but were usually less than the catch rates from the Hinemaiaia River (Fig. 7.6). Except for winter, there was also a tenancy for more koaro to be found in the downstream sites of the Waimarino River.

Compared to the other two streams, the common bully was not commonly trapped in the Waimarino River; while none were caught from the high gradient, upstream site (A), the majority were caught nearest to Lake Taupo, Site C (Fig. 7.7).

## 7.2.2 Tokaanu River

### Physical characteristics

Site A on the Tokaanu River (Fig. 7.2) is located the farthest upstream of all the sites on this stream, or about 5 km from the confluence with Lake Taupo. The site has an abundance of instream-herbaceous cover and has a much finer substrate than any of the sites in the Waimarino River (e.g., Fig. 10.2). There is a large input of groundwater at the Tokaanu River Site A and most of the rainbow trout spawn within one kilometre of this site; the Department of Conservation (DoC) fish fence, which is used to collect brook stock for the Tongariro Hatchery, is located at Site A. The reach at Site A has a distinctly "slow-flow" appearance (see Plate 3.2; this photo is looking downstream from the DoC fish fence). The water velocities tended to be similar to those of Site B on this stream (Fig. 7.4).

Site B (Fig. 7.2) on the Tokaanu River is located immediately downstream of the Chateau Road culvert, about 3 km upstream from Lake Taupo. This site has a lack of boulder cover but a large amount of instream herbaceous and woody cover. The cross-sectional stream morphology at this site is "U"-shaped and it is primarily a single channel. Immediately downstream of Site B, the Tokaanu River is carried across a narrow, man-made inlet of Lake Taupo via an aqueduct; this structure is part of the Tongariro/Tokaanu hydro-electric power project. The average trap depths at this Site B were the greatest of any sites in all of my study streams (Fig. 7.4).

Site C (Fig. 7.2) on the Tokaanu River is comprised of two sub-locations, C1 and C2, and these are located 0.5 and 1.75 km upstream from Lake Taupo, respectively; C1 is situated immediately upstream of the Tokaanu Baths while C2 is centred around the State Highway 1 bridge. Both of these sites are generally similar in their physical characteristics to Site B; however, at Site C2 some trapping was conducted in a shallow, off-channel flood plain and most of this sampling was in water depths that were considerably less than any other site on the other Tokaanu River. Water velocities at the Site C sites were the slowest in this stream (Fig. 7.4) and this is probably due, in part, to the lack of steep gradient and possible back-flooding from Lake Taupo.

The Tokaanu River average depths were the greatest of all the three study streams (Fig. 7.4).

### Fish population characteristics

There was a substantial amount of among-site and among-season variation in the rainbow trout size and CPUE characteristics for the Tokaanu River (Fig. 7.5 CPUE; Fig. 7.9). Although the greatest catches of rainbow trout were at the upstream site in winter and autumn, among-site CPUE's were much more alike in the other seasons (Fig. 7.5). Rainbow trout juveniles were typically larger from the more downstream sites of B and C during all seasons (Fig. 7.9).

The catches of koaro from the Tokaanu River were negligible compared to the other two streams (Fig. 7.6). In contrast, bullies were very common in the Tokaanu River in the two downstream sites; Site C showed very high densities of bullies whereas none were caught in the upstream Site A (Fig. 7.7).

### 7.2.3 Hinemaiaia River

#### Physical characteristics

Site A (Fig. 7.3) on the Hinemaiaia River is located in an overflow channel of the most downstream hydro-electric dam complex, about 4 km upstream from the confluence with Lake Taupo. Prior to the construction of this dam, the channel of this reach comprised the main stream of the Hinemaiaia River; however, the water was diverted from the main river through the hydro-electric generating station and now rejoins the river about one kilometre downstream of the dam. Thus, at low flows this channel now receives a small but constant input of hypo-limnion water through the base of the dam although there can be substantial inputs of water into the overflow channel during high flows when the hydro lake overtops the dam.

The Site A reach has an abundance of boulder and cobble cover and is a complex of pools, riffles, short runs and long, slow glides. The river channel at this location is constrained by its steep-valley and bedrock-canyon walls and there is little stream-channel meander. Site A tends to have slower water velocities and shallower depths than the other Hinemaiaia River sites (Fig. 7.4) and this is primarily related to the smaller flows in this reach.

Site B on the Hinemaiaia River is located about 2.5 km upstream from Lake Taupo (Fig. 7.3). This site has little boulder cover and a moderate amount of instream organic cover. The river channel at Site B follows an unrestricted meander pattern and has pools separated by glides and riffles. Site B has intermediate water velocities when compared to the other Hinemaiaia River sites (Fig. 7.4).

Site C on the Hinemaiaia River is located about 1.5 km upstream of Lake Taupo (Fig. 7.3). This site is similar in its physical characteristics to Site B except that water velocities tended to be faster (Fig. 7.4).

The Hinemaiaia River water velocities had the greatest amount of among-site variability of the three study streams (Fig. 7.4).

### Fish population characteristics

Few rainbow trout were caught in the Hinemaiaia River at any of the sites during the sampling over the year except in spring (Fig. 7.5). Nevertheless, although large catches of young-of-the-year rainbow trout juveniles were made during spring at Sites B and C, few fish were caught at Site A (Fig. 7.10).

The koaro catches in the Hinemaiaia River were greater than from any other stream, while the CPUE's of koaro from the upstream Site A by far surpassed any other location in all the three watersheds (Fig. 7.6). The catches of koaro at the downstream Hinemaiaia River Sites B and C were also generally greater than most other sites on the other streams with Site C on the Waimarino River being the only site with similar koaro capture rates. As a rule there was a negative relationship between trout and koaro catches in these three streams (c.f., Figs. 7.5, 7.6).

Bullies were relatively common from all the Hinemaiaia River sampling sites but the greatest catches occurred from the downstream sites (B & C; Fig. 7.7).

Figure 7.1.--Map of the Waimarino River sampling sites. See Fig. 1.1 for the location of this stream in the Lake Taupo watershed.

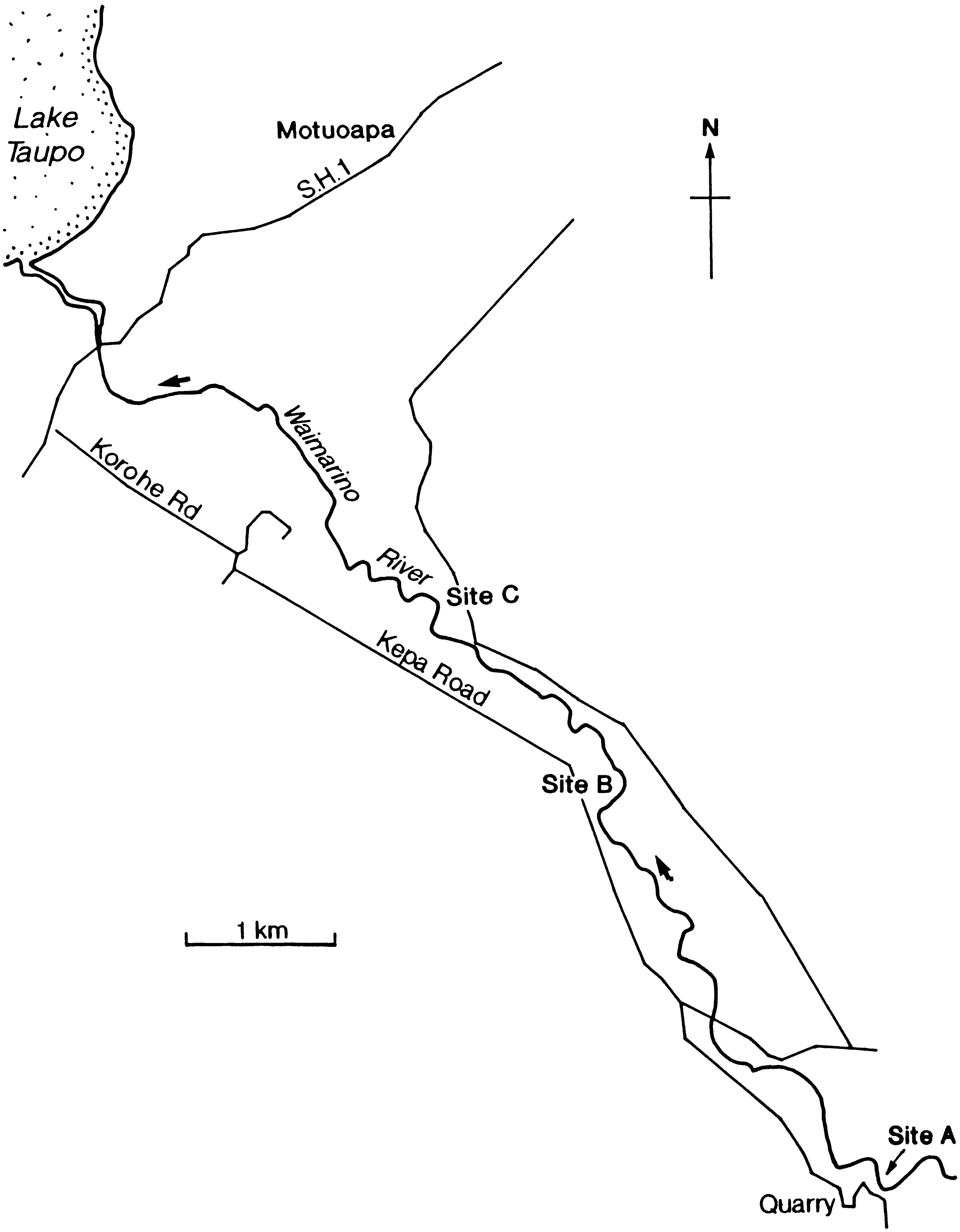

Lake Taupo
Motuoapa
S.H.1
N
Waimarino
River
Korohe Rd
Kepa Road
Site C
Site B
Site A
Quarry
1 km

Figure 7.2.--Map of the Tokaanu River sampling sites. See Fig. 1.1 for the location of this stream in the Lake Taupo watershed.

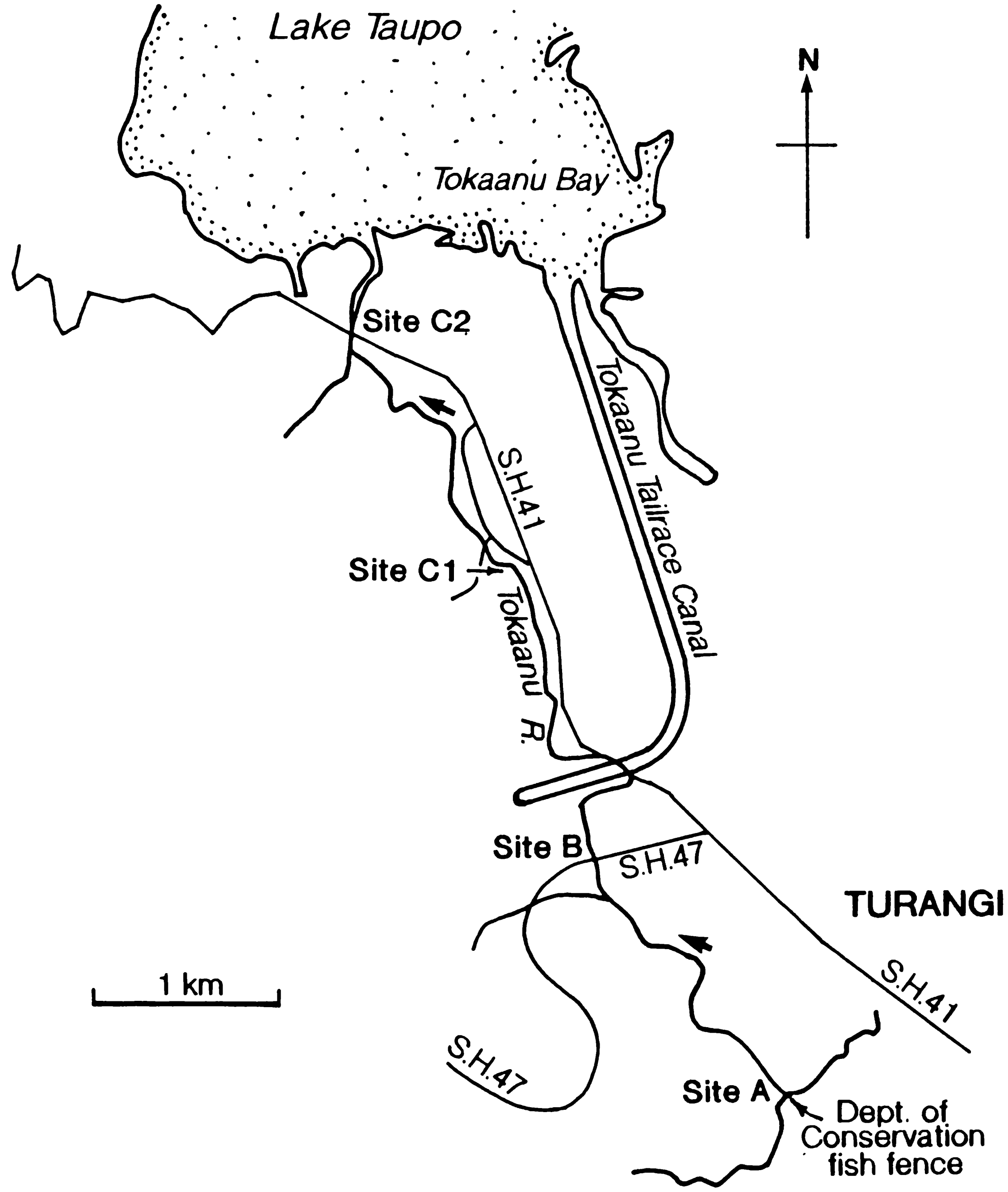

Lake Taupo
N
Tokaanu Bay
Site C2
S.H.41
Tokaanu Tailrace Canal
Site C1
Tokaanu R.
Site B
S.H.47
TURANGI
1 km
S.H.41
S.H.47
Site A
Dept. of Conservation fish fence

Figure 7.3.--Map of the Hinemaiaia River sampling sites. See Fig. 1.1 for the location of this stream in the Lake Taupo watershed.

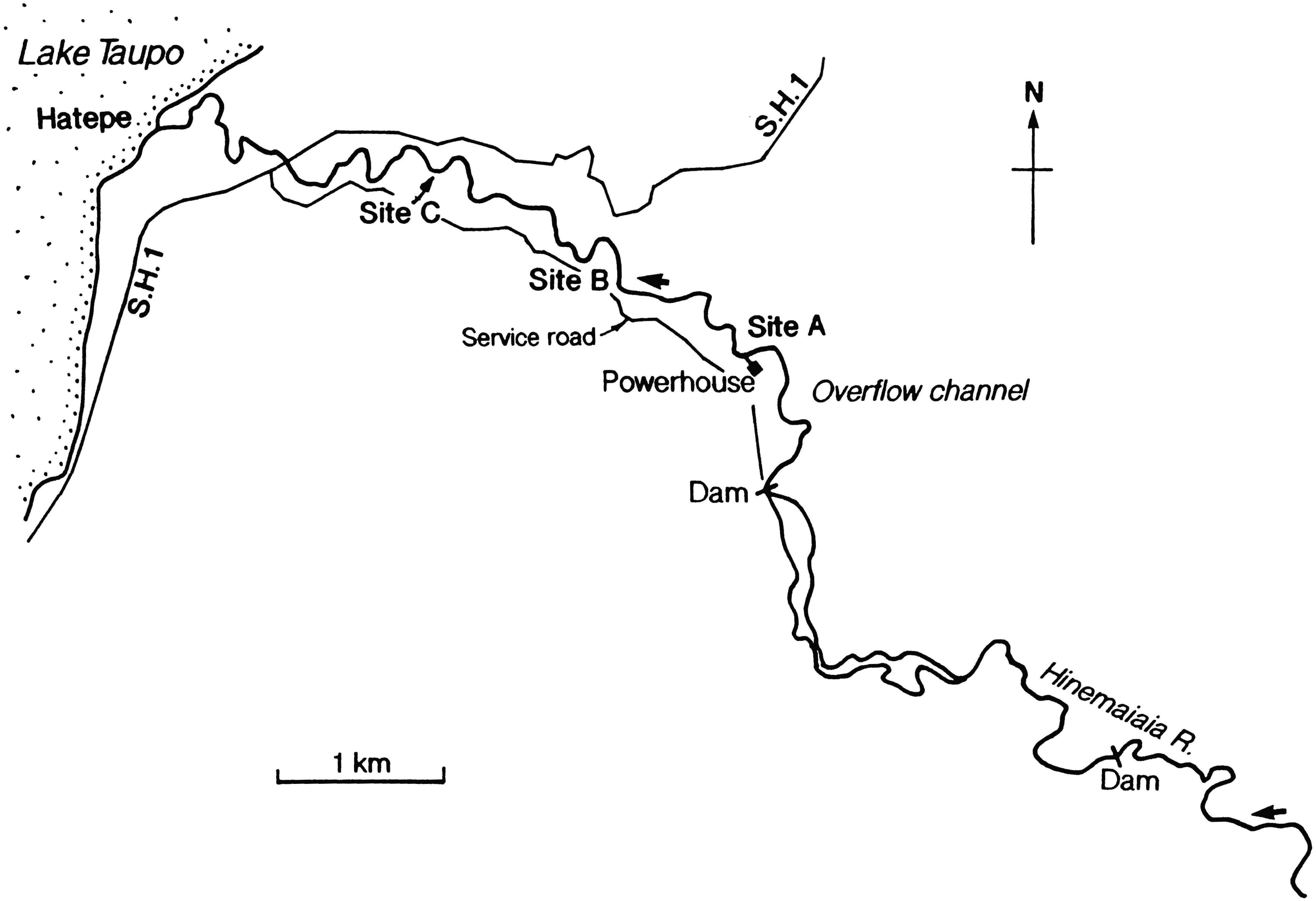

Lake Taupo
Hatepe
S.H.1
S.H.1
N
Site C
Site B
Site A
Service road
Powerhouse
Overflow channel
Dam
Hinemaiaia R.
Dam
1 km

Figure 7.4.--Average minnow-trap depths and velocities for all seasons and sampling sites, winter 1988 to autumn 1989. With SE's.

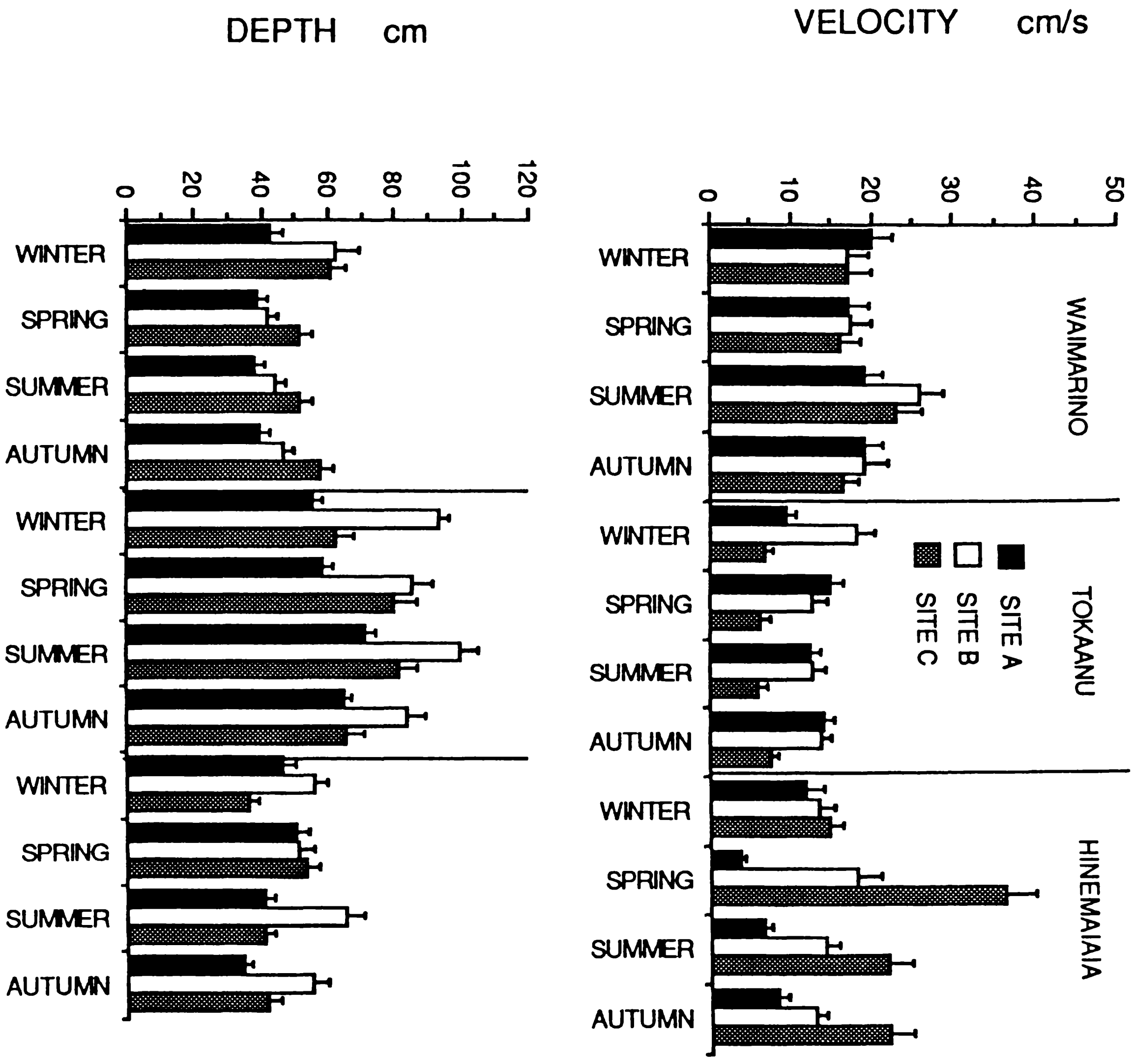
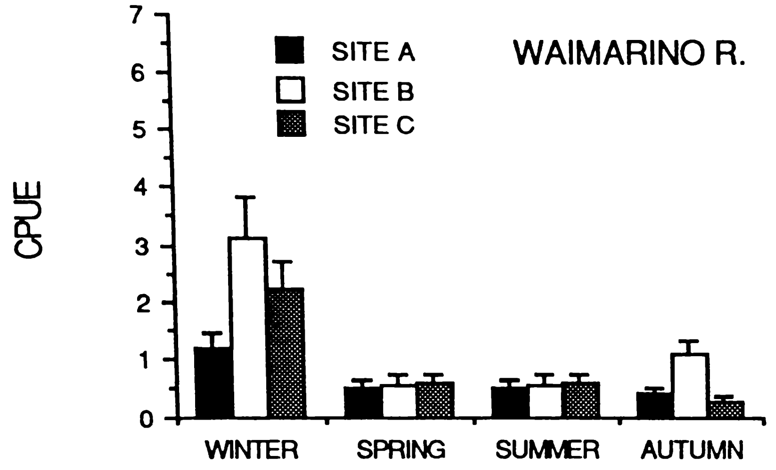
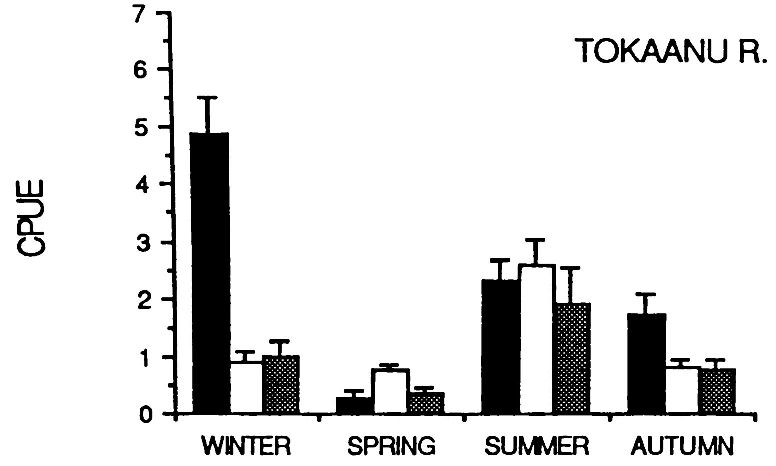

VELOCITY cm/s
0
10
20
30
40
50
WAIMARINO
TOKAANU
HINEMAIAIA
SITE A
SITE B
SITE C
WINTER
SPRING
SUMMER
AUTUMN
DEPTH cm
0
20
40
60
80
100
120

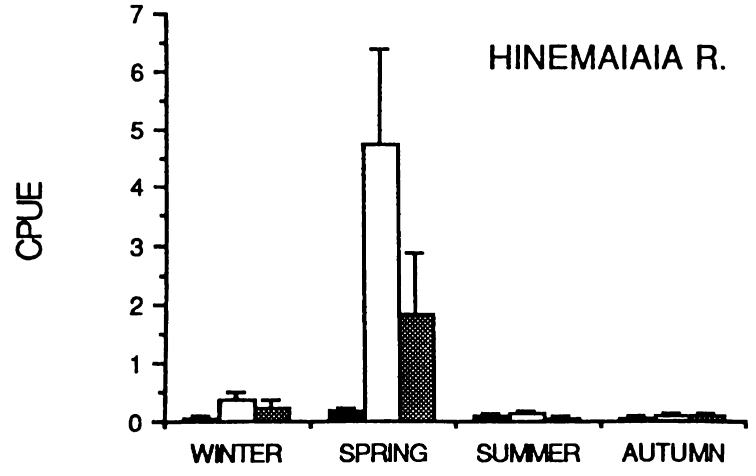
Figure 7.5.--Minnow-trapping CPUE's of rainbow trout for Waimarino, Tokaanu and Hinemaiaia Rivers, winter 1988 to autumn 1989. With SE's.



WAIMARINO R.
SITE A
SITE B
SITE C
CPUE
0
1
2
3
4
5
6
7
WINTER
SPRING
SUMMER
AUTUMN



TOKAANU R.
CPUE
0
1
2
3
4
5
6
7
WINTER
SPRING
SUMMER
AUTUMN



HINEMAIAIA R.
CPUE
0
1
2
3
4
5
6
7
WINTER
SPRING
SUMMER
AUTUMN

Figure 7.6.--Minnow-trapping CPUE's of koaro for Waimarino, Tokaanu and Hinemaiaia Rivers, winter 1988 to autumn 1989. With SE's.

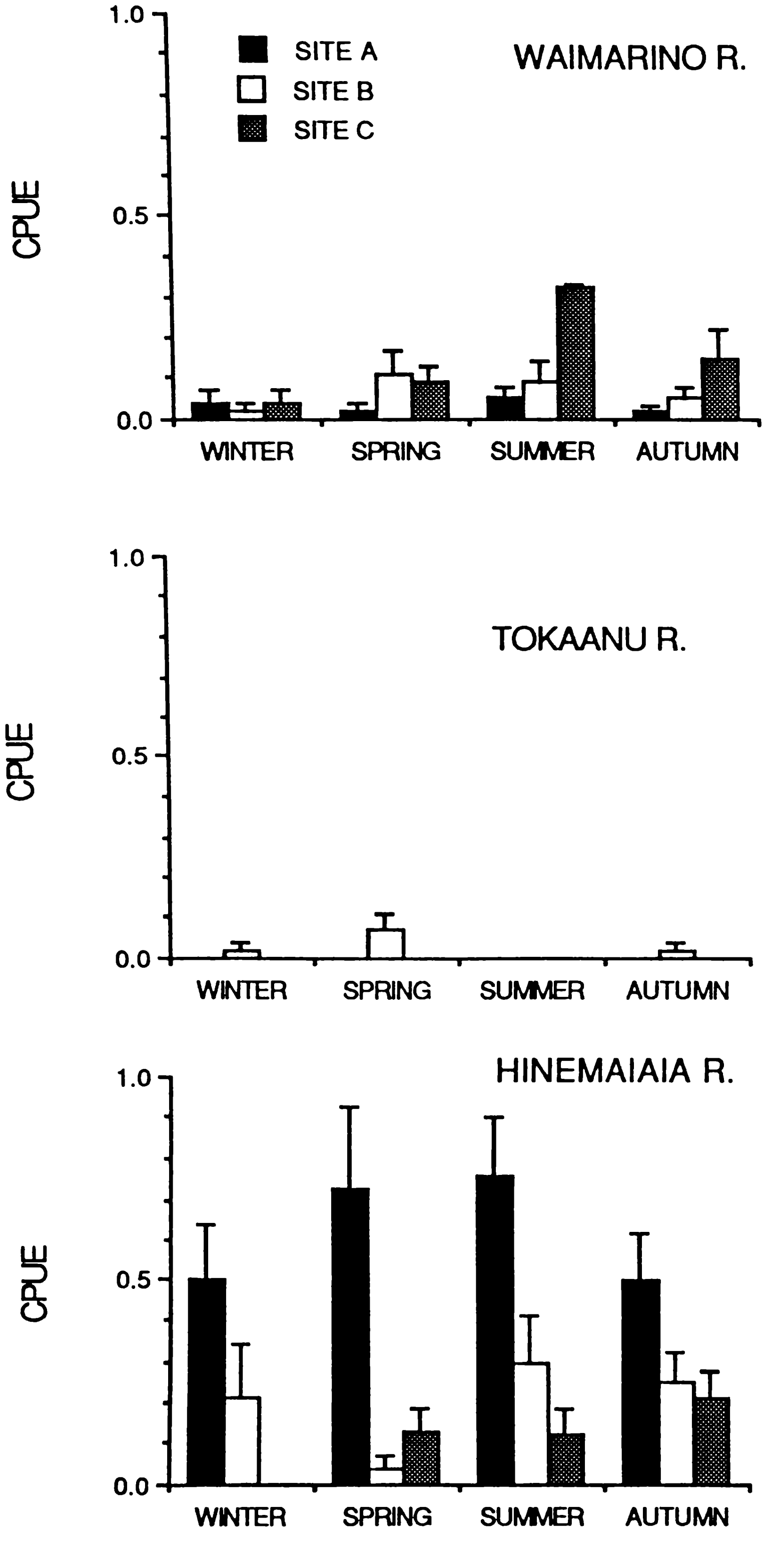

WAIMARINO R.
SITE A
SITE B
SITE C
CPUE
1.0
0.5
0.0
WINTER
SPRING
SUMMER
AUTUMN
TOKAANU R.
CPUE
1.0
0.5
0.0
WINTER
SPRING
SUMMER
AUTUMN
HINEMAIAIA R.
CPUE
1.0
0.5
0.0
WINTER
SPRING
SUMMER
AUTUMN

Figure 7.7.--Minnow-trapping CPUE's of common bully for Waimarino, Tokaanu and Hinemaiaia Rivers, winter 1988 to autumn 1989. With SE's.

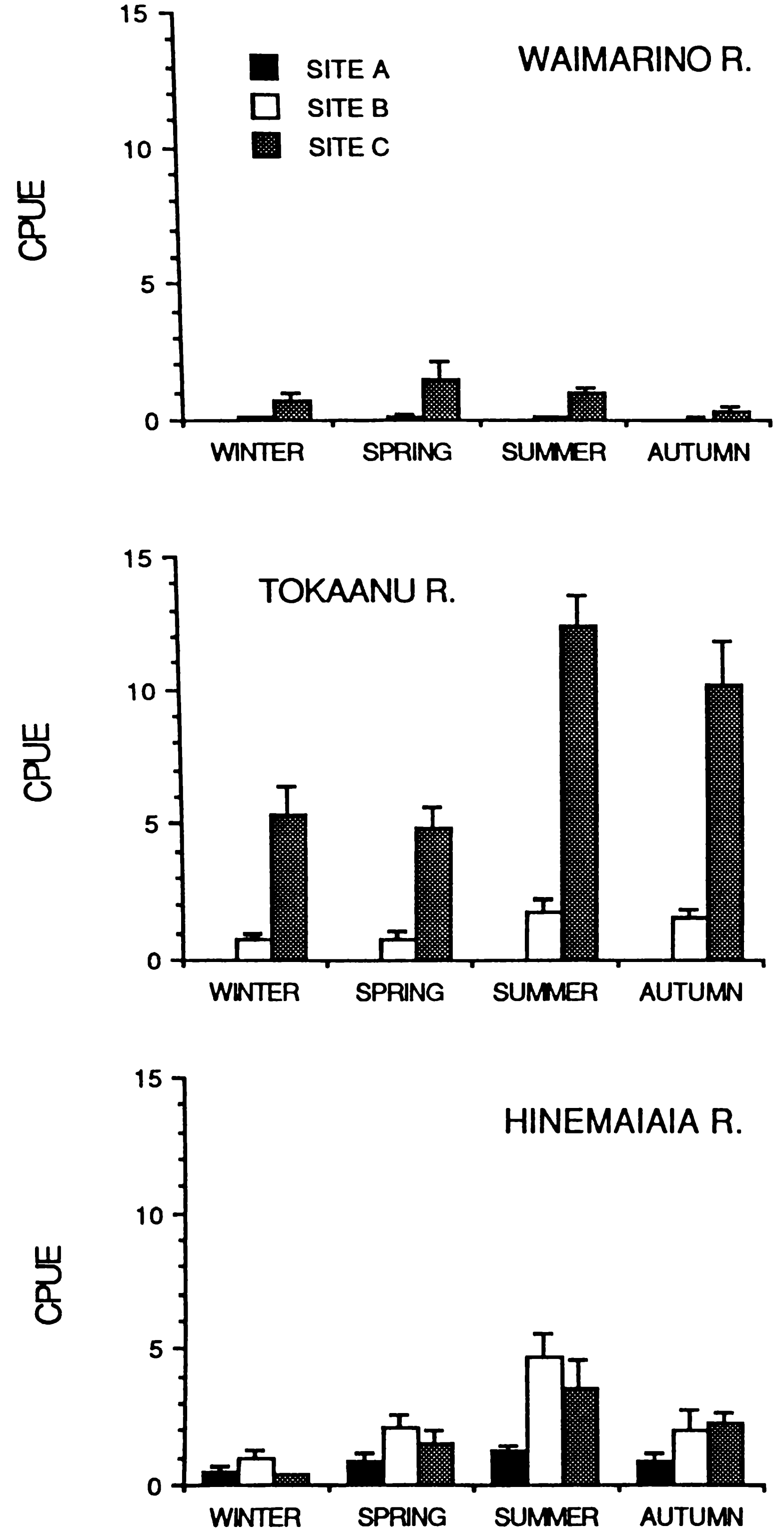

15
10
5
0
CPUE
■ SITE A
□ SITE B
▨ SITE C
WAIMARINO R.
WINTER
SPRING
SUMMER
AUTUMN
15
10
5
0
CPUE
TOKAANU R.
WINTER
SPRING
SUMMER
AUTUMN
15
10
5
0
CPUE
HINEMAIAIA R.
WINTER
SPRING
SUMMER
AUTUMN

Figure 7.8.--Total catches and length-frequency distribution of minnow-trapped rainbow trout from the Waimarino River, by site, winter 1988 to autumn 1989.

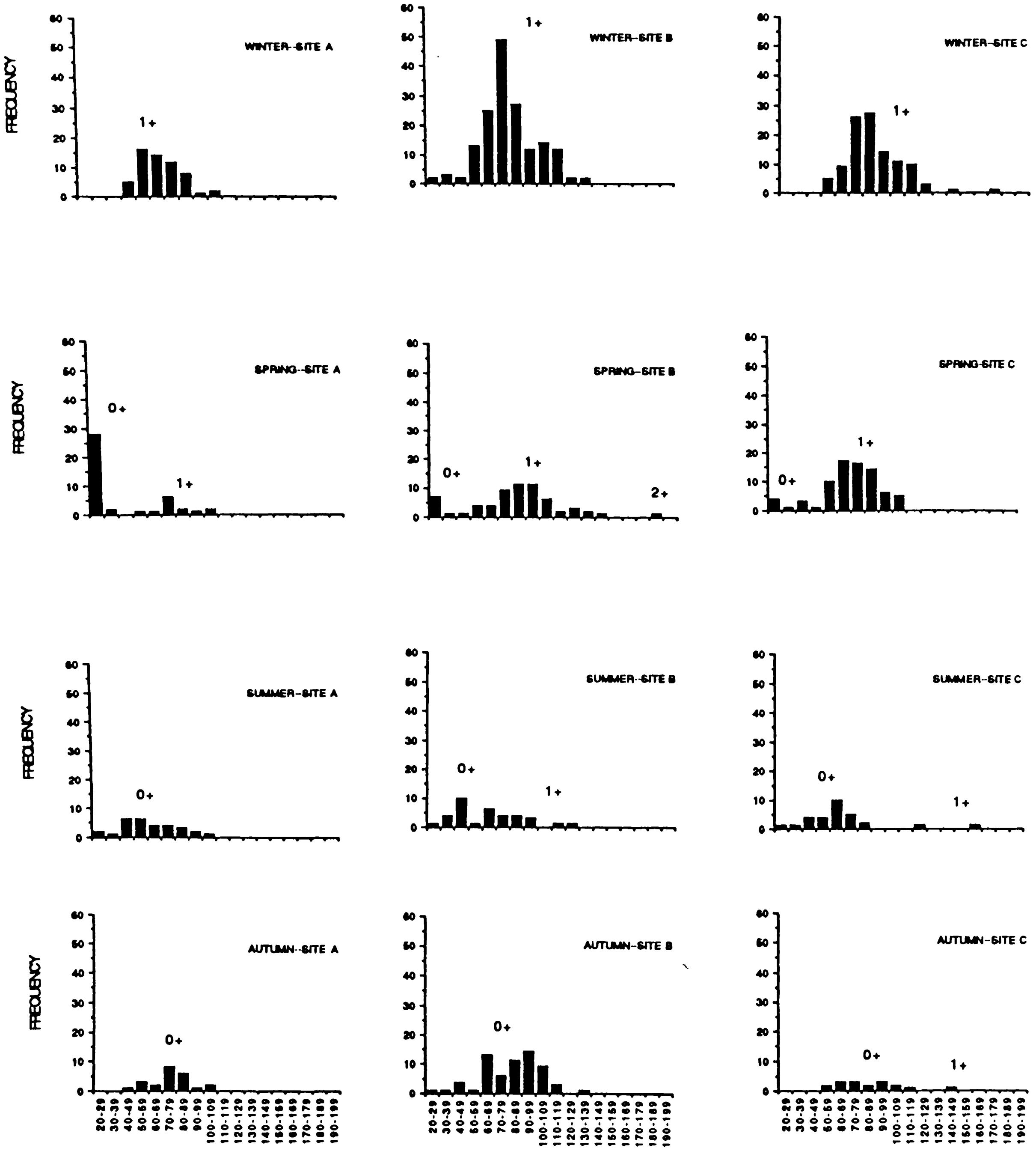

FREQUENCY
0
10
20
30
40
50
60
WINTER--SITE A
WINTER--SITE B
WINTER--SITE C
SPRING--SITE A
SPRING--SITE B
SPRING-SITE C
SUMMER--SITE A
SUMMER--SITE B
SUMMER--SITE C
AUTUMN--SITE A
AUTUMN--SITE B
AUTUMN--SITE C
0+
1+
2+
20-29
30-39
40-49
50-59
60-69
70-79
80-89
90-99
100-109
110-119
120-129
130-139
140-149
150-159
160-169
170-179
180-189
190-199

Figure 7.9.--Total catches and length-frequency distribution of minnow-trapped rainbow trout from the Tokaanu River, by site, winter 1988 to autumn 1989.

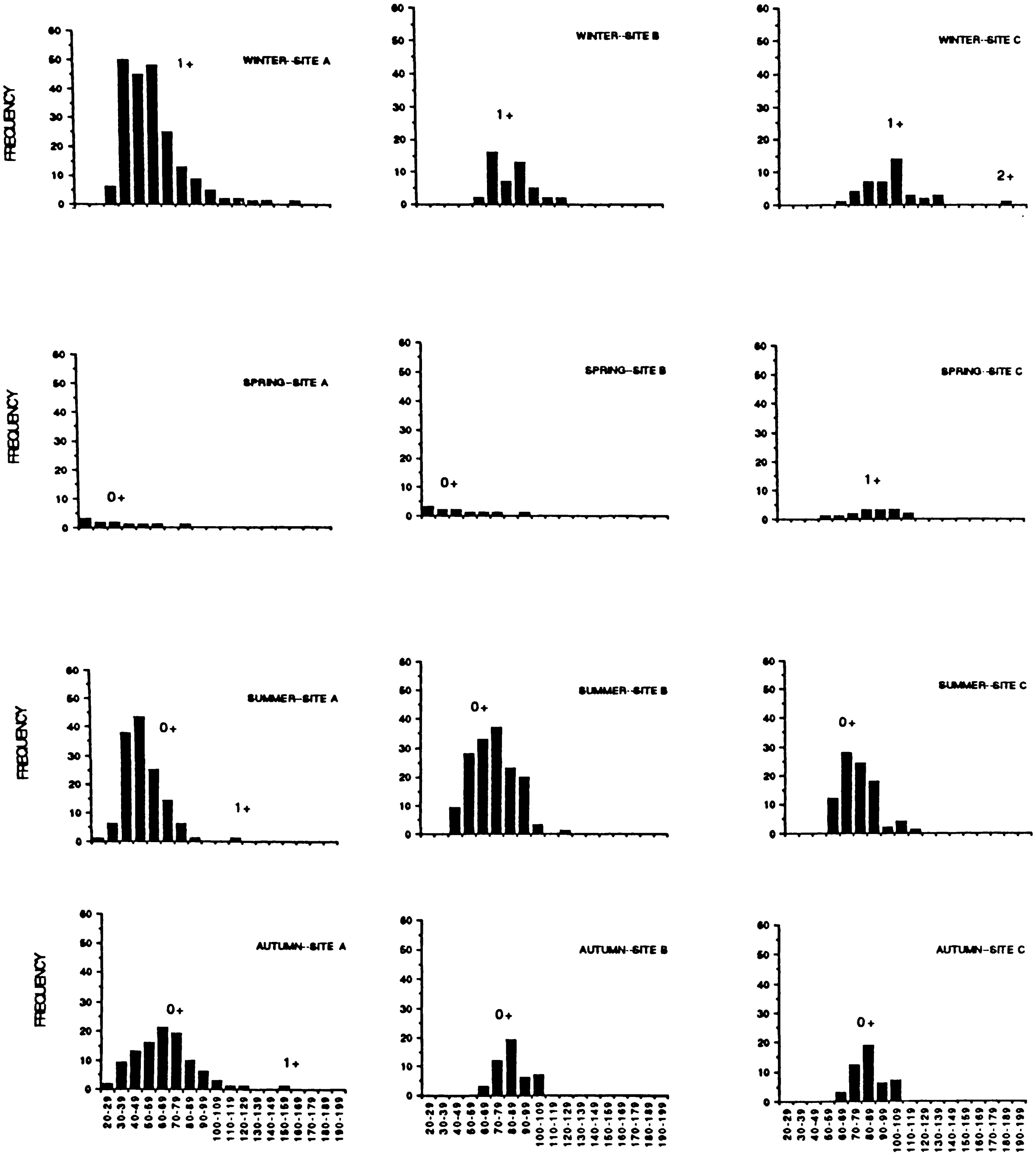

FREQUENCY
0
10
20
30
40
50
60
WINTER--SITE A
WINTER--SITE B
WINTER--SITE C
SPRING--SITE A
SPRING--SITE B
SPRING--SITE C
SUMMER--SITE A
SUMMER--SITE B
SUMMER--SITE C
AUTUMN--SITE A
AUTUMN--SITE B
AUTUMN--SITE C
0+
1+
2+
20-29
30-39
40-49
50-59
60-69
70-79
80-89
90-99
100-109
110-119
120-129
130-139
140-149
150-159
160-169
170-179
180-189
190-199

Figure 7.10.--Total catches and length-frequency distribution of minnow-trapped rainbow trout from the Hinemaiaia River, by site, winter 1988 to autumn 1989.

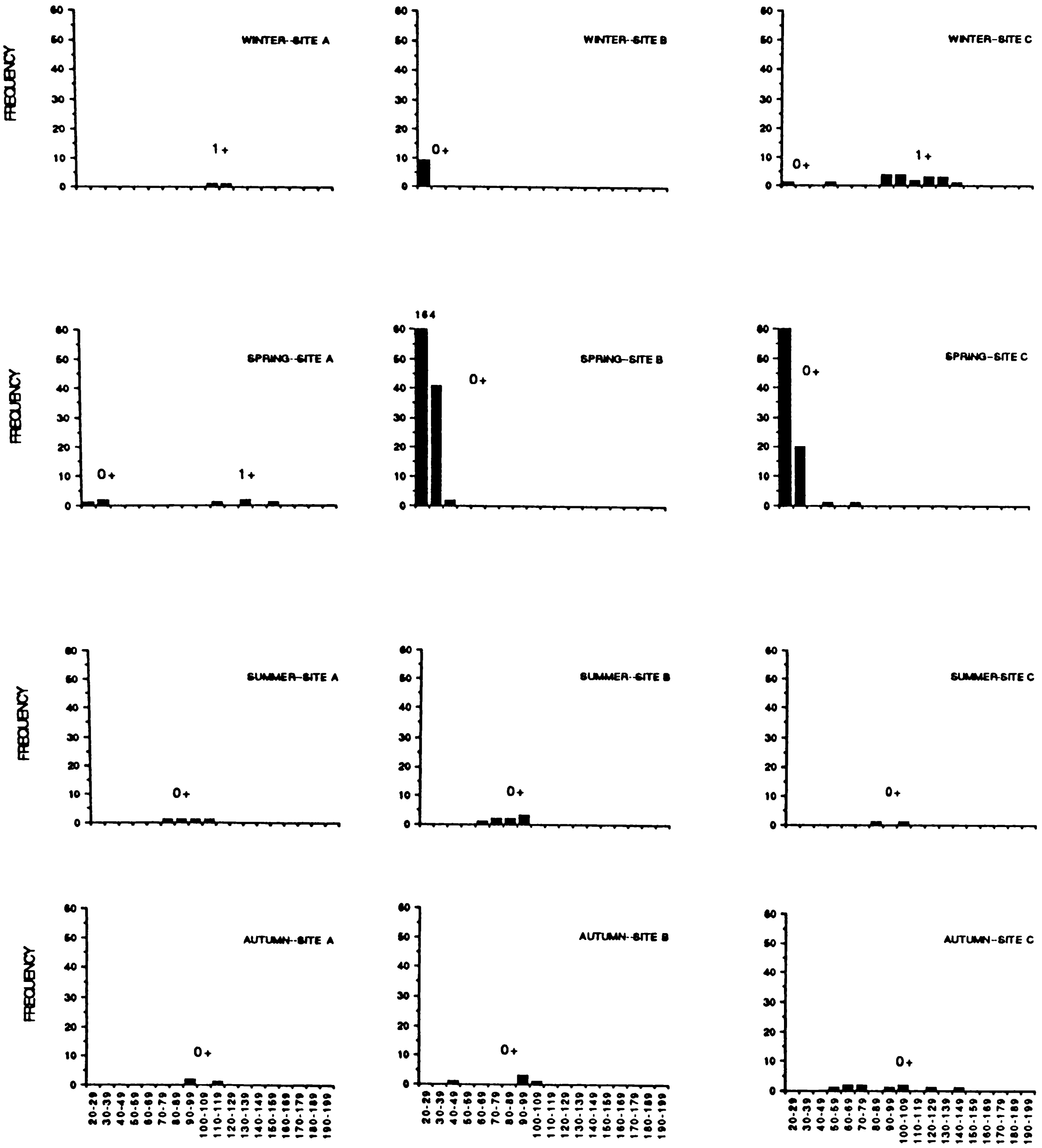

FREQUENCY
0
10
20
30
40
50
60
WINTER--SITE A
1+
WINTER--SITE B
0+
WINTER--SITE C
0+
1+
SPRING--SITE A
0+
1+
164
SPRING--SITE B
0+
SPRING--SITE C
0+
SUMMER--SITE A
0+
SUMMER--SITE B
0+
SUMMER-SITE C
0+
AUTUMN--SITE A
0+
AUTUMN--SITE B
0+
AUTUMN--SITE C
0+
20-29
30-39
40-49
50-59
60-69
70-79
80-89
90-99
100-109
110-119
120-129
130-139
140-149
150-159
160-169
170-179
180-189
190-199

Table 7.1.--Minnow-trapping catch statistics for koaro and bullies, winter 1988 to autumn 1989, for all of the study streams. All lengths in mm.

| | KOARO | | | | | BULLIES | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | n | av length | SE | min len | max len | n | av length | SE | min len | max len |
| WAIMARINO R. | | | | | | | | | | |
| Winter | 5 | 110.2 | 16.38 | 72 | 178 | 34 | 80.9 | 1.72 | 48 | 96 |
| Spring | 10 | 103.5 | 7.31 | 74 | 138 | 72 | 72.1 | 1.10 | 52 | 91 |
| Summer | 26 | 95.2 | 5.00 | 45 | 140 | 53 | 74.7 | 1.58 | 46 | 95 |
| Autumn | 13 | 97.8 | 5.55 | 60 | 127 | 21 | 75.8 | 2.13 | 46 | 86 |
| TOKAANU R. | | | | | | | | | | |
| Winter | 1 | 104.0 | 0.00 | 104 | 104 | 187 | 76.0 | 1.00 | 37 | 107 |
| Spring | 3 | 104.3 | 12.52 | 79 | 102 | 147 | 71.6 | 1.19 | 21 | 115 |
| Summer | 0 | -- | -- | -- | -- | 256 | 60.7 | 1.10 | 30 | 113 |
| Autumn | 1 | 98.0 | 0.00 | 98 | 98 | 65 | 52.3 | 1.83 | 34 | 94 |
| HINEMAIAIA R. | | | | | | | | | | |
| Winter | 31 | 106.1 | 3.67 | 66 | 144 | 78 | 71.5 | 1.75 | 40 | 112 |
| Spring | 41 | 88.9 | 2.73 | 55 | 132 | 203 | 64.8 | 1.10 | 35 | 203 |
| Summer | 62 | 101.3 | 2.88 | 51 | 142 | 118 | 63.7 | 1.20 | 36 | 92 |
| Autumn | 54 | 98.8 | 2.92 | 54 | 142 | 129 | 67.3 | 1.24 | 39 | 91 |

## 7.3 DISCUSSION

I found considerable within- and among-stream differences in the species composition and distribution of fishes in the three study streams; this variability is undoubtedly, in part, due to the physical, chemical and biological differences encountered by these fishes in their respective environments (Table 3.1). The two salient features that define these differences are: 1) the source of water and 2) gradient. For example, the Waimarino River arises out of a cultured-forest, mountainous area and its flows are comprised primarily of surface water and therefore it has considerable flow and temperature variability. In contrast, the low-gradient Tokaanu River receives most of its water from groundwater vents; consequently the flows and temperatures tend to be very constant. Finally, the Hinemaiaia River, apparently a mixture of both surface run-off and groundwater (J. Gibbs, Department of Conservation, Turangi, New Zealand, pers. comm.), has a flow regime that has a high degree of daily variability as it's flows are modified by a hydro-electric scheme; however, the temperature variability in this stream may be somewhat dampened due to the modifying effect of the hydro lakes and the groundwater influence.

### Rainbow trout

The among-stream variation in the numbers, sizes and ages of juvenile rainbow trout in the study streams has already been extensively commented on in Chapters 4, 5, and Rosenau (1991). Nevertheless, it is worth mentioning some of the within-stream:among-sites observations with regards to these fishes. For example, in the Waimarino River I caught more recently-emerged young-of-the-year trout from the most upstream site (A) than any of the other sites during spring; this may have been a function of either: 1) a greater adult rainbow trout spawning density occurring in this part of the stream, or 2) more abundant habitat for this size range of trout (e.g., shallower water). In Chapter 6 I showed that, compared to the larger juvenile trout, small young-of-the-year fry were primarily found in shallow and slow-velocity water.

In contrast, the greater catches of larger, older juveniles from the two downstream sites in the Waimarino River were probably a function of greater water depths and the higher levels of instream-woody cover in these areas.

The distribution of rainbow trout juveniles in the Tokaanu River also varied considerably among sites and between seasons. During winter the highest CPUE's of rainbow trout were from the most upstream site (Site A); this may be related to the influence of the constant-temperature groundwater input at this location. Other studies have shown that fluvial salmonids will often aggregate in areas of temperature-modified groundwater during the winter (Cunjak and Power 1986). These authors suggest that the relatively higher water temperatures found in groundwater springs during this time of the year permit trout to maintain metabolic rates closer to the physiological optimum for this species.

As in the Waimarino River, smaller-sized Tokaanu River young-of-the-year rainbow trout were generally captured in the most upstream site while the larger (and older) juveniles tended to be found in more downstream habitats. These differences in fish distribution may be related to variation in habitat type and quality (e.g., depths, cover) or, alternatively, may simply be the result of the higher spawning densities in the upstream areas.

Finally, there was a considerable amount of among-site and within- and among-season variability in the catches of juvenile rainbow trout in the Hinemaiaia River. The surprising lack of juvenile rainbow trout in the Hinemaiaia River during all seasons of the year, except for spring, is related to the high growth rates and the early emigration to the lake by these fish (Rosenau 1991; Chapter 4). Current studies by the New Zealand Ministry of Agriculture and Fisheries (MAF) have also found fast growth and early emigration of Hinemaiaia River rainbow trout juveniles (B. Hicks, MAF, Rotorua, New Zealand, pers. comm.). Consequently, the Hinemaiaia River is "empty" of juvenile rainbow trout for a substantial portion of the year. An enhancement technique having some promise involves "seeding" this stream with juvenile rainbow trout (fry) during the periods of the year when these fish are present in low numbers.

The low catches of young-of-the-year rainbow trout seen during spring in the overflow channel (Site A) of the Hinemaiaia River was particularly surprising considering the high density of spawners observed in this area (Tully 1989; my observations). I have no explanation for this; the habitat is of sufficient quality for koaro and bullies considering that they were found in comparatively high numbers at all times of the year in this site.

### Koaro

Koaro are thought to have declined considerably in numbers in the Lake Taupo area since the introduction of trout (McDowall 1990). Nevertheless, koaro were caught by my minnow traps from all three of the study streams, although in very low numbers in the Tokaanu River; the fluvial habitat in the Tokaanu River is considerably different from that of the other two study streams and may not be conducive to koaro production. Indeed, McDowall (1990) suggests that koaro are commonly found in mountain streams with tumbling, rocky, boulder torrents; this description is unlike any habitat found in the Tokaanu River.

Koaro catches in the Waimarino River were intermediate compared to the other two streams and most of the fish were concentrated in the downstream site (Site C) and primarily during summer and autumn. The higher summer and autumn catches of koaro at this site may have been a function of spawning migrations of which koaro are known to undertake during this time of the year in the Lake Taupo watershed (Kusabs 1989).

Finally, high catches of koaro were made from the Hinemaiaia River imply that these fish were relatively more abundant in this stream. Kusabs (1989) compared the minnow-trap catch rates from the Hinemaiaia River other small Lake Taupo tributary streams, and concluded that the former has high densities of this species. Moffat (1984; loc. cit. Kusabs 1989) suggested that the preference of adult koaro is for swiftly flowing water and cobble substrate. Cobble habitats are abundant in the Hinemaiaia River at Site A and this habitat may also account for the high CPUE's of koaro at this location.

Kusabs (1989) found that the densities of rainbow trout and koaro were negatively correlated in three Lake Taupo tributaries. He concluded that trout were probably interfering with the production of koaro in these streams through predation and/or competition for food. Similarly, I consistently registered the lowest catches of rainbow trout, of any sample site on any of the rivers, in the Hinemaiaia overflow channel (Site A) yet found, by far, the highest numbers of koaro. Likewise, at Site B on the Hinemaiaia, during spring when the numbers of trout were the highest, koaro were at their lowest levels, although during the other seasons, when trout were absent, the catches of koaro at this site were considerably higher.

These observations suggest that once juvenile rainbow trout leave the Hinemaiaia River, koaro may be occupying the habitat that the trout formerly used. The high concentrations of juvenile rainbow trout in the Waimarino River, throughout the year, may be excluding koaro from this watershed even though it appears to have excellent koaro habitat. My observations in Chapter 6 suggest that when trout and koaro cohabit the same stream, there is little micro-habitat overlap between them. Kusabs (1989) indicated that these two species were partitioning food and feeding times with koaro being much more nocturnal than trout.

### The common bully

The common bully is widespread throughout Lake Taupo and its slower velocity tributaries (Stephens 1983) yet, like koaro and rainbow trout, there was considerable among-site variation in the CPUE's of this fish. For example, no bullies were found in the upstream Site A of the Waimarino River while considerably higher densities were in Site C; this difference may be a function of the habitat, specifically steeper gradients and faster water velocities in addition to a paucity of organic (woody and herbaceous) cover at the upstream location.

The extremely high numbers of bullies found in the most downstream Tokaanu River site (Site C) appears to be related to the slow water velocities, greater water column depths and high abundance of instream cover at this location; these criteria apparently describe good habitat for this species (McDowall 1990). It is surprising that bullies were not found at the upstream Site A in the Tokaanu River; this site is a comparatively short distance from Lake Taupo and, while there is a very low gradient over this distance, bullies should not be restricted from reaching this site. In contrast, bullies were very common throughout the much longer and higher gradient Hinemaiaia River. However, there is a cross-stream fish fence with a concrete drop-sill of about 0.5 m at this location on the Tokaanu River. Any fish migrating upstream of the fence would have to navigate this height to ascend the barrier. The small-sized common bully is unlikely to overcome this obstacle. Furthermore, predation by adult rainbow trout may also restrict bully distribution at Site A on the Tokaanu River; high densities of spawning adult trout are found at this location throughout the year and McDowall (1990) suggests that rainbow trout will utilize the common bully for food.

# SECTION III--ADAPTATION TO THE FLUVIAL ENVIRONMENT

## Chapter 8.--JUVENILE RAINBOW TROUT MERISTICS--PARR MARKS

### 8.0 INTRODUCTION

Parr marks are discrete aggregations of chromatophores located on the lateral sides of stream-living juvenile salmonids (Donnelly and Dill 1984; Fig. 8.1). Similar markings are also present on many other fluvial fishes including the common minnow (**Phoxinus phoxinus**), sticklebacks (**Gasterosteus** spp.), the North American minnows (**Rhynichthys** spp.) and the cottids (**Cottus** spp.) (Nikolsky 1961; Scott and Crossman 1973).

The functional significance of these markings is unknown but has been investigated by Hoar (1958), Donnelly and Dill (1984), as well as Maeda and Hidaka (1979). Hoar (1958) and Donnelly and Dill (1984) suggest that the parr marks are used primarily in anti-predator protection through crypsis in the stream environments. These authors speculate that the blotchy, approximately oval marks are used for background matching over pebble or stony stream substrates. Indeed, juvenile salmonids show considerable interspecific variation in the size and shape of their parr marks (Scott and Crossman 1973) and the differences seem to be highly correlated to the substrate-type composition that each species normally encounters in nature (Donnelly and Dill 1984). Alternatively, Maeda and Hidaka (1979) and P. Mylechreest (Fish and Game Council, Rotorua, New Zealand, pers. comm.) have found that cherry salmon (**Oncorhynchus masou**) and rainbow trout, respectively, use parr marks as a signalling mechanism for territorial defence.

In addition to among-species variation in size and shape of parr marks, between-population variation in the number has been shown for salmonids in a number of studies (Smith 1969; Taylor and Larkin 1986; Taylor 1988); this can have a genetic component (Beacham 1990) although incubation temperature is also known to affect the formation of the number of marks formed (Taylor 1988; Beacham 1990).

Lake Taupo has a number of discrete runs of rainbow trout that spawn and rear in its inflowing tributary streams (Tully 1989; Pitkethley 1990; Rosenau 1991). The recapture of marked, migratory spawners through Department of Conservation fish fences (J. Gibbs, Department of Conservation, Turangi, New Zealand, pers. comm.) suggest that these reproductively semi-isolated groups of fish can be considered to be "populations" or "stocks" (see Ricker 1972). While no among-population allozyme differences have been found in Lake Taupo rainbow trout (Snowdon 1991), there appear to be other inherited between-stock differences in this watershed including: 1) agonistic behaviours (Chapter 9), 2) developmental characters (Chapter 10) and 3) adult morphometrics (Tully 1989). These inherited between-population differences are thought to be adaptive as they correspond to various biological or physical differences in the respective natal streams.

The juvenile rainbow trout that rear in these two streams do so for an extended period of time before migrating to Lake Taupo for further growth (Chapter 4; Rosenau 1991). At the size ranges of these fluvial juveniles, parr marks are a salient feature of the trout anatomy. Therefore, if the Waimarino and Tokaanu Rivers have considerably different substrate compositions, and if matching the parr marks to the appropriate substrate is important to the survival of these fish, parr-marks may vary in these two populations of rainbow trout. Since substrate composition in streams is a function of gradient, flow regime, and the surrounding geology and length of the stream, the substrate-particle size composition is likely to be very different in these two streams; while the Tokaanu River is a short, low-gradient stream (0.4 %) with highly stable flows and temperatures, the Waimarino River is a considerably longer, higher gradient stream (1.3 %) with variable flows and temperatures (Fig. 3.2, 3.2).

Thus, based on the hypothesis of Hoar (1958) and Donnelly and Dill (1984) that parr marks are used for crypsis through the matching of background patterns, I predicted that there would be selection for differences in parr mark characteristics in these two stream rearing populations of Lake Taupo rainbow trout. The main objectives of this part of my study were:

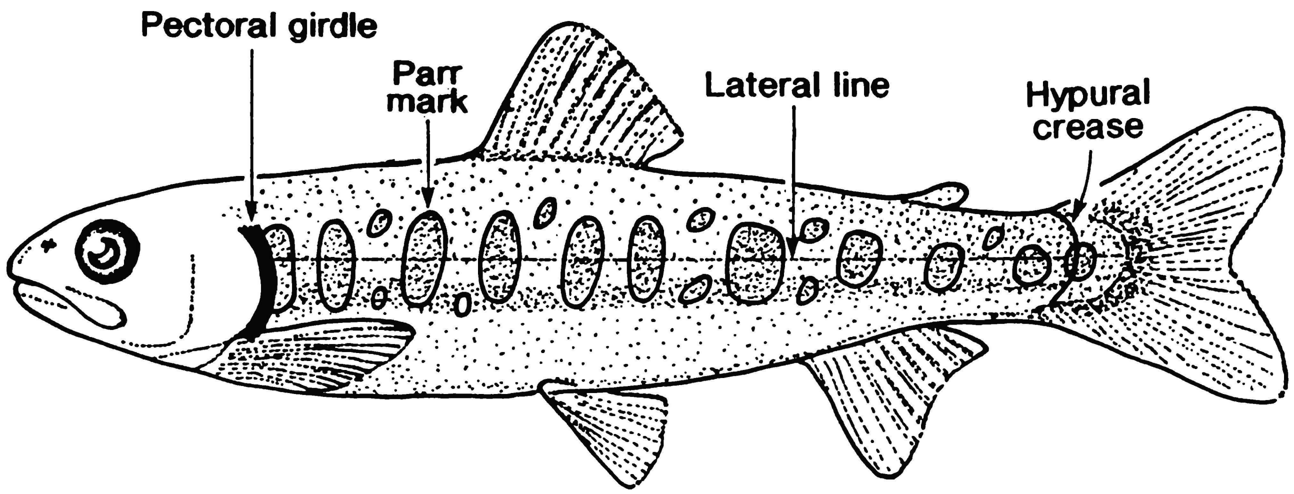
1) to examine and compare the stream-substrate particle-size composition in the Waimarino and Tokaanu Rivers, and if there are significant between-stream differences,

2) examine the number of parr marks in juvenile rainbow trout from the two populations, incubated and reared under identical and tightly controlled laboratory conditions, and ascribe any between-cross differences to genetic differences in the samples of the parents taken from these stocks, and

3) determine if there are any parr-mark number differences between wild-reared rainbow trout from these two streams, as well as among the wild and laboratory groups of fish.

Reciprocal hybrids can tell us much about the genetic underpinning of inherited traits in salmonids (Rosenau and McPhail 1987; Chapter 10). Reciprocal crosses were thus made in this study to further our understanding of any inherited differences in parr-mark number in these two populations.

Figure 8.1.--Parr marks along the lateral line of a rainbow trout juvenile. Note position of the hypural crease and the pectoral girdle; these features were used as external body landmarks when counting parr marks.


Pectoral girdle
Parr mark
Lateral line
Hypural crease

## 8.1 METHODS

### Substrate particle composition

I collected gravel samples from 10 rainbow trout redds from each of the Tokaanu and Waimarino Rivers; these samples were from another part of my study of the fluvial biology of rainbow trout in Lake Taupo waters (Chapter 10). Because salmonid redds are generally located at the downstream outlet or "tail-out" of pools, this was considered to be a good standardized location for comparing substrate composition in these two streams. Rainbow trout juveniles were known to rear in the general areas from which the gravel samples were taken. The method of collection, sorting and measuring the samples are outlined in Chapter 10. From the gravel sample data I calculated a fredle index which describes the measure of the central tenancy of the distribution of the sediment particles in a sample, and the statistical dispersion of particles in relation to this value (Lotspeich and Everest 1981). Thus, this fredle value appeared to be a good method of comparing the sizes of particles taken from substrates of the two streams.

### Incubation and rearing

I caught and spawned three ripe male and three ovulated female rainbow trout of similar sizes from each of the study streams on 19 October 1987. Two "pure" and two "reciprocal-hybrid" crosses were made in the field and comprised: 1) Tokaanu males X Waimarino females, 2) Waimarino males X Waimarino females, 3) Tokaanu males X Tokaanu females, and 4) Waimarino males X Tokaanu females. The gametes from each trio of fish were pooled before the various crosses were made. Fertilization took place at a water temperatures of 12°C and the embryos were then brought back to the laboratory in a cooler filled with a slurry of ice and water. The embryos were incubated under controlled conditions at a target temperature of 12°C (fertilization to 50% hatch--average 11.98°C SD=0.071; hatch to 50% emergence--average 11.79°C

SD=0.291). These crosses were also part of a survival- and incubation-rate experiment (Chapter 10).

At emergence, on 15 December 1987, 200 fry of each cross were placed into one of four 400 l rearing tanks; all crosses were kept separate. Total flow-through of water for all tanks was maintained at about 26 l $min^{-1}$ and the fish were fed with commercial trout food **ad libitum** 3 to 5 times per day. Water temperatures were kept the same amongst rearing tanks (Table 8.1). On 11 March 1989 all surviving juveniles were killed in 40% formalin and preserved in 40% isopropanol for at least 3 months prior to fork-length measurement and counts of parr marks. Survival rates and average fork lengths at the end of the experiment were also determined for each of the crosses.

All parr marks intersected by, or touching, the lateral line, and located anterior to the hypural crease, were counted on the left side of each fish; any parr mark touching the pectoral girdle, or any having greater than 50% of its area located posterior to the hypural crease, was not counted. Two people were employed in the counting process. Each person counted the marks independently and then the numbers were compared. When a discrepancy occurred, the counts were each made again and the differences resolved by discussion between the counters.

Parr-mark counts were also made of wild-caught rainbow trout from these two streams. As part the natal-stream rearing study (Chapter 4; Rosenau 1991), wild juvenile rainbow trout were captured from the Waimarino and Tokaanu Rivers using baited minnow traps. The fish were fixed in 10% formalin, then washed, and preserved in 40% isopropanol. All measurements and parr-mark counts were made in the same fashion as for the laboratory reared fish.

## 8.2 RESULTS

### Substrate-particle sizes

There were considerable differences in the particle size-frequency distribution for the redd-gravel samples taken from the two study streams; the Waimarino River samples had much higher fredle values (Fig. 8.2; t= -5.011 df=18, p<0.001) indicating a greater average particle size for substrate in this stream; hence, Tokaanu River redd gravel samples were comprised primarily of fine material whereas the substrate in the Waimarino River was much coarser (see also Fig. 10.2).

### Parr marks

There were no relationships between fish-fork lengths and parr-mark number in either the laboratory or wild-caught rainbow trout (ANOVA p>0.05; Fig. 8.3). That is, parr-mark number did not increase or decrease as a function of fish length within the size range of fish examined. The average fork lengths of the various laboratory crosses of rainbow trout were significantly different but there was no significant difference in length between the fish from the wild-caught populations (Tables 8.2; 8.3).

There were significant among-group differences in parr-mark number for the laboratory-reared crosses; the Waimarino pure rainbow trout had the greatest numbers of parr marks while, except for an overlap with the Waimarino males X Tokaanu females cross, the Tokaanu pure crosses had the lowest mean values (Table 8.4; Fig. 8.4). The reciprocal hybrids were generally intermediate between these pure crosses and not significantly different from each other (Table 8.4; Fig. 8.4). The number of parr marks on the wild-caught rainbow trout fell intermediate between the two pure laboratory incubated and reared crosses (Fig. 8.4) but there were no significant differences in parr-mark number between the wild Waimarino and Tokaanu River rainbow trout (Table 8.4).

Figure 8.2.--Average fredle-index values, ± S.E.'s, for gravel sampled in the Waimarino and Tokaanu Rivers. See also Fig. 10.2 for a more detailed description of the particle-size distribution for these values.

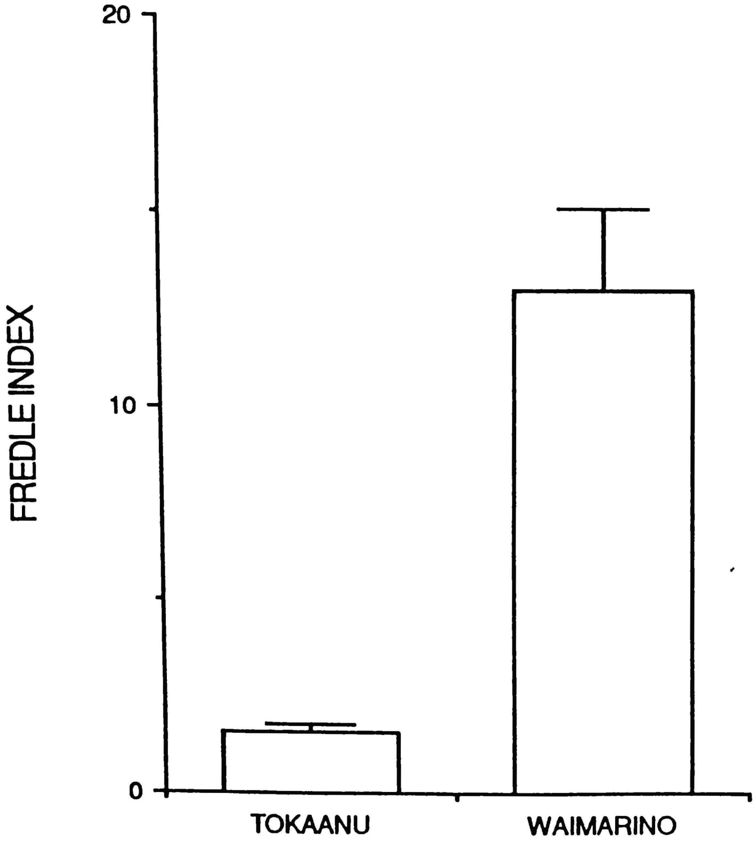
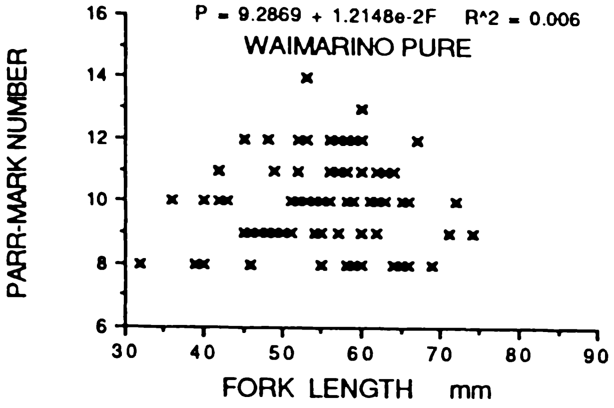
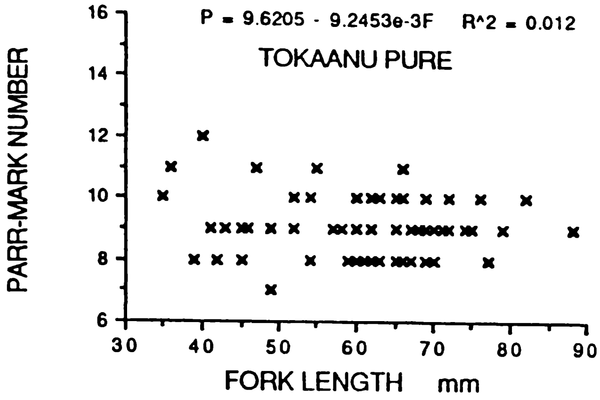
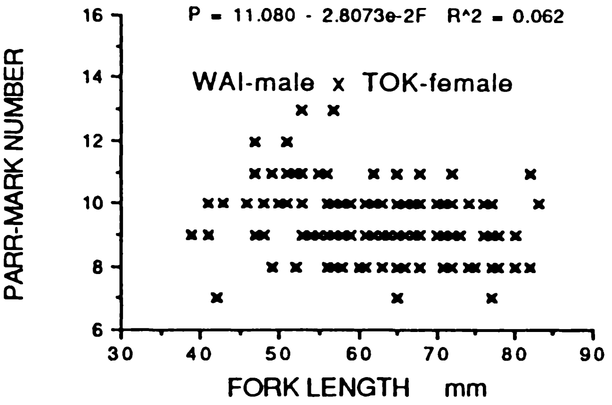
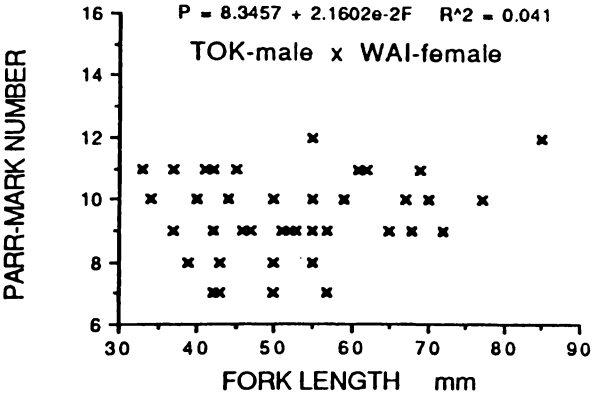

20
10
0
FREDLE INDEX
TOKAANU
WAIMARINO

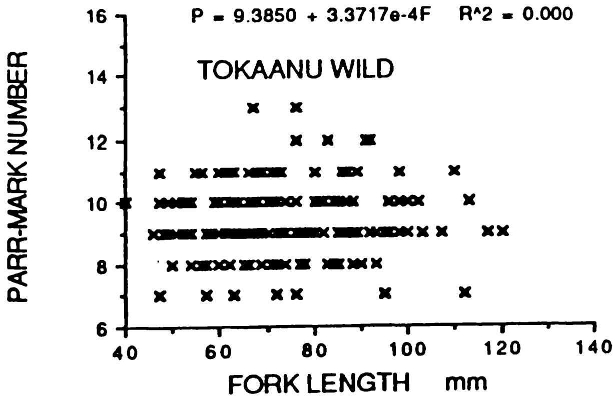
Figure 8.3.--Relationship between parr-mark number and fish length in the laboratory and wild groups of Tokaanu and Waimarino River rainbow trout. **P**, parr-mark number; **F**, fish fork length in mm.


P = 9.2869 + 1.2148e-2F R^2 = 0.006
WAIMARINO PURE
PARR-MARK NUMBER
16
14
12
10
8
6
30
40
50
60
70
80
90
FORK LENGTH mm


P = 9.6205 - 9.2453e-3F R^2 = 0.012
TOKAANU PURE
PARR-MARK NUMBER
16
14
12
10
8
6
30
40
50
60
70
80
90
FORK LENGTH mm


P = 11.080 - 2.8073e-2F R^2 = 0.062
WAI-male x TOK-female
PARR-MARK NUMBER
16
14
12
10
8
6
30
40
50
60
70
80
90
FORK LENGTH mm


P = 8.3457 + 2.1602e-2F R^2 = 0.041
TOK-male x WAI-female
PARR-MARK NUMBER
16
14
12
10
8
6
30
40
50
60
70
80
90
FORK LENGTH mm


P = 9.3850 + 3.3717e-4F R^2 = 0.000
TOKAANU WILD
PARR-MARK NUMBER
16
14
12
10
8
6
40
60
80
100
120
140
FORK LENGTH mm

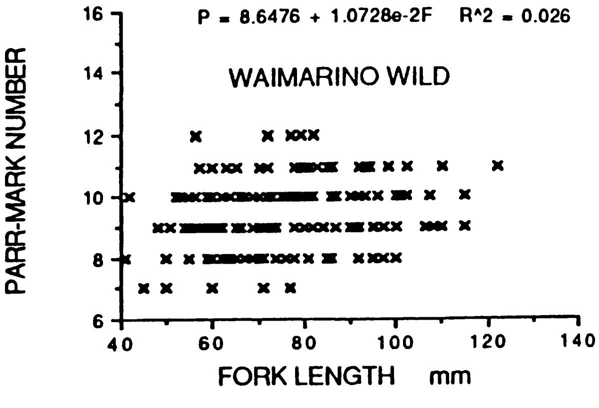

P = 8.6476 + 1.0728e-2F R^2 = 0.026
WAIMARINO WILD
PARR-MARK NUMBER
16
14
12
10
8
6
40
60
80
100
120
140
FORK LENGTH mm

Figure 8.4.--Average number of parr marks, ± S.E.'s, for each of the laboratory and the wild groups of Tokaanu and Waimarino River rainbow trout.

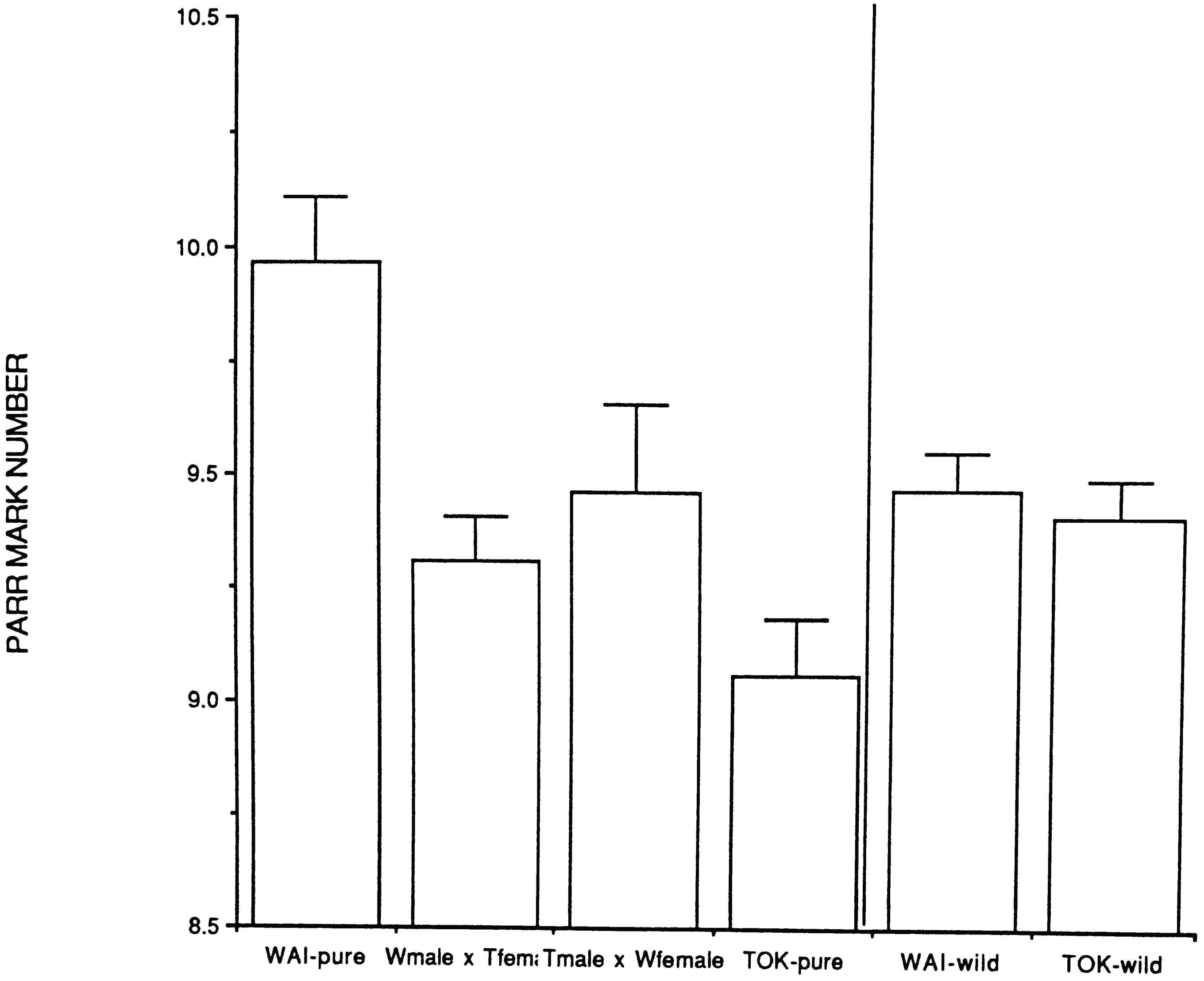

PARR MARK NUMBER
10.5
10.0
9.5
9.0
8.5
WAI-pure
Wmale x Tfem
Tmale x Wfemale
TOK-pure
WAI-wild
TOK-wild

Table 8.1.--Average rearing-tank water temperatures and survival rates of the rainbow trout crosses for the parr-mark study. Temperatures were taken once a day in mid-morning.

| CROSS | WAI-pure | WmTf | TmWf | TOK-pure |
|---|---|---|---|---|
| TEMPERATURE °C | 20.8 | 20.7 | 20.7 | 20.7 |
| SD | 0.759 | 0.783 | 0.801 | 0.763 |
| NO. OF DAYS | 79 | 79 | 79 | 79 |
| SURVIVAL % | 43.0 | 64.5 | 22.5 | 32.0 |

Table 8.2.--Average body lengths of the juvenile trout used in the parr-mark study.

| CROSS | AVERAGE FORK LENGTH mm | SD | n |
|---|---|---|---|
| WAI-pure | 55.8 | 8.39 | 86 |
| WAI-males x TOK-females | 63.0 | 9.93 | 129 |
| TOK-males x WAI-females | 51.9 | 11.76 | 45 |
| TOK-pure | 60.4 | 11.80 | 64 |
| WAI-wild | 76.7 | 16.14 | 183 |
| TOK-wild | 73.8 | 16.09 | 183 |

Table 8.3.--Among-group fork length comparisons for rainbow trout used in the parr-mark study.

LABORATORY CROSSES

| Source | df | MS | F | P |
|---|---|---|---|---|
| Between groups | 3 | 1790.6 | 16.905 | <0.001* Within |
| groups | 320 | 105.9 | | |

TOKAANU WILD VERSUS WAIMARINO WILD

t=1.704 df=364 p=0.09

Table 8.4.--Among-group ANOVA statistics for parr mark comparisons.

LABORATORY CROSSES

| Source | df | MS | F | P |
|---|---|---|---|---|
| Between groups | 3 | 34.953 | 8.37 | <0.001* |
| Within groups | 320 | 1.392 | | |

Duncan's Multiple Range Test p<0.05

TOK-pure Wmale x Tfemale Tmale x Wfemale WAI-pure

TOKAANU WILD VERSUS WAIMARINO WILD

t=0.523 df=364 p=0.601 ns

## 8.3 DISCUSSION

There was a clear difference in the number of parr marks on the laboratory reared rainbow trout juveniles; pure Waimarino River trout averaged almost a full parr mark more than the pure Tokaanu River fish. Because these fish were incubated and reared under highly controlled environmental conditions, this among-group character variation must be the result of genetic differences. Furthermore, because the reciprocal hybrids showed approximately intermediate numbers of parr marks, as compared to the pure crosses, this provides additional evidence for a genetic mechanism controlling parr-mark number in the laboratory rainbow trout. Intermediacy in an inherited trait suggests a polygenic system in which the controlling loci confer approximately equal and additive effects (Avers 1980; Kirpichnikov 1981; Barnard 1983).

That the TOK-pure and WAI-male x TOK-female groups are not statistically separable with regards to parr-mark number may be due to maternal effects. For example, Beacham (1990) looked at various developmental effects on the formation of meristic and morphometric characters in juvenile chum salmon (**Oncohynchus keta**) and found that, of all the modifiers that he examined, maternal effects were the most influential. Similarly, the direction of the number of parr marks on the hybrid groups were more similar to the pure groups of their mothers than of their fathers, further implying both a maternal and genetic effect for the inheritance of this character variation in Lake Taupo rainbow trout.

The wild-caught rainbow trout juveniles did not show a similar between-population difference in parr-mark number, unlike the laboratory incubated and reared rainbow trout. Thus, it must be asked, "Do the parr-mark numbers in the laboratory trout represent the wild population values for this character?" Three males and three females, comprising the number of parents used from each population in these experiments, do not constitute a "large" sample size with respect to the genetic composition of the wild populations which comprises these fish (D. Adam, University of Waikato, Hamilton, New Zealand, pers. comm.). Thus, while the laboratory results demonstrate that parr-mark number does have a heritable component, the data may not truly reflect the natural situation. Sample error may, in part, account for the observed among-cross genetic differences in parr-mark number in the fish that I incubated in these experiments.

Nevertheless, the phenotypic expression of a biological character is the result of genetic as well as environmental influences. For example, variation in incubation temperature is known to affect the number of parr marks in salmonids (Beacham 1990; Taylor 1988). Furthermore, the temperature regimes in these two study streams were considerably different with the Waimarino River ranging from about 0°C in winter to over 20°C in summer, while the Tokaanu River has very stable temperatures of about 11°C throughout the year (Fig. 3.2).

If temperature were the only external factor controlling parr-mark number on juvenile rainbow trout in these streams, and if the average genotype controlling this character were the same in these two populations, then we should expect that the number of parr marks on the wild rainbow trout in the Waimarino and Tokaanu Rivers would be very different. Because they are not different, and there is a convergence to the same average number of parr marks as the wild fish, this suggests that both the different temperatures seen in these rivers and genetic differences are controlling parr-mark number in these two populations in their natural habitats.

Taylor (1988) found that in the wild, and under considerably different natural temperature regimes, two populations of juvenile chinook salmon (**O. tshawytscha**) had significantly different numbers of parr marks; yet, under controlled laboratory conditions and when incubated under the same temperatures, fish of both of these stocks had similar numbers of parr marks. He did not speculate on the function reason for the variation of this character on these fish in the wild but suggested that an increase in incubation temperature results in a decrease in numbers of parr marks in British Columbia chinook salmon. In contrast, Beacham (1990) reported that an increase in temperature causes an increase in parr marks in chum salmon; these differences may be species specific.

The functional significance of the between-population similarity in numbers of parr marks these Lake Taupo wild rainbow trout is unknown. Because the substrates are so different, I expected that there should be a significant difference in parr marks on rainbow trout from the two populations in order to provide a cryptic camouflage; this was not shown to occur. However, parr-marks may be used in the wild by these fish for reasons other than crypsis including territorial communication (Maeda and Hidaka 1979); if parr-mark number is important in the defence of territory in these stream rearing juvenile trout, the requirements for a particular parr-mark number may be the same for both populations.

Nevertheless, because the results of this parr-mark study are equivocal, further work should be undertaken to resolve whether or not there is truly a genetically mediated difference in parr-mark number in these two populations. The functional significance of any similarities or differences should then also be investigated to further our understanding of these fish.

# Chapter 9.--A PRELIMINARY INVESTIGATION OF BETWEEN-POPULATION DIFFERENCES IN AGONISTIC BEHAVIOUR IN JUVENILE LAKE TAUPO RAINBOW TROUT

## 9.0 INTRODUCTION

Agonistic behaviours are used by stream dwelling juvenile rainbow trout in the defence of territories against conspecifics or closely related species of fish (Newman 1956; Hartman 1965; Jenkins 1969). Two hypotheses have been advanced to explain the role of territoriality in young stream-dwelling salmonids and both are not necessarily mutually exclusive (Rosenau and McPhail 1987). This includes the concepts that territoriality acts to disperse individuals within a population: to 1) decrease the incidence of disease, parasitism and predation (Chapman 1962), and 2) ensure that there is an adequate food supply where it may be a limiting resource (Chapman 1962; Dill 1978; Dill et al. 1981).

Agonistic behaviour has a genetic component in rainbow trout (Ferguson et al. 1987) and studies have demonstrated inherited between-population variability in the agonistic behaviours of coho (**Oncorhynchus kisutch**) (Rosenau 1984; Taylor and Larkin 1986; Rosenau and McPhail 1987; Swain and Riddell 1990) and chinook (**O. tshawytscha**) salmon (Taylor and Larkin 1986). These inter-stock differences are assumed to be adaptive although the selective mechanisms causing the differences seen in these studies have not been determined. One hypothesis suggests that varying intensities of predation and/or amounts of food are involved as the primary selective mechanisms (Rosenau and McPhail 1987; Swain and Holtby 1989; Swain and Riddell 1990). In these studies, the between-population differences in this character were particularly pronounced when the two rearing environments had greatly dissimilar characteristics (e.g., hatchery versus wild; Swain and Riddell 1990).

As outlined in previous chapters, many Lake Taupo streams differ considerably in their physical and biological attributes including the Waimarino and Tokaanu Rivers.

Variation in productivity levels (as reflected by juvenile trout growth rates; Chapter 4) and possible differences in numbers and sizes of predators (bullies; Chapter 7) were observed in these two streams. Thus, because levels of food and predation appear to vary considerably, I speculated that inter-population genetic differences may have also evolved in the territorial repertoire of juvenile rainbow trout in these two streams.

Behaviour patterns in fishes are easily modified by non-genetic or environmental influences. Thus, in order to determine innate, genetically-mediated population differences in agonistic behaviours, it is important to eliminate biases resulting from external experiences and environmental effects. Therefore, I first incubated fish from both populations in the laboratory under highly controlled and similar environments and then tested all fish under standardized conditions. Any detectable between-group differences in agonistic behaviour could therefore be attributed to genetic differences (see Rosenau and McPhail 1987; Swain and Riddell 1990).

## 9.1 METHODS

Laboratory incubated Tokaanu and Waimarino rainbow trout fry were obtained from the 12°C incubation experiments reported in Chapter 10. On 14 December 1987 three groups of five equal-sized fish (fork length 25 mm) from each of the two pure crosses (WAI-males x WAI-females and TOK-males x TOK-females) were each placed in separate and visually isolated sections of a re-circulating stream tank (Fig. 9.1). Thus, within the six sections of tank, each had a group of five fish and all were of the same cross.

The newly emerged rainbow trout were allowed to acclimate for two days and behavioural observations were begun on the third day. The stream tank was isolated from human disturbance with a black cloth; unobtrusive observer-slits allowed viewing without disturbing the fish. The trout were fed commercial trout food after each observation.

Observations took place once each day from 16 to 18 December and I observed each tank for ten minutes. Water temperatures were 22.3°C the first two days and 23.5 on day three. Mid-tank average water velocities were less than 5 cm $s^{-1}$. This experiment was terminated on day four due to equipment failure.

The behaviours recorded in this study are outlined in Table 9.1. Between-population comparisons of behavioural activity were made with all overt agonistic activities (chases, charges and nips) grouped into one class of behaviour and the dorsal-fin displays as second class. Comparisons were made using a repeated-measures ANOVA and this analysis was considered appropriate as the experiment involved repeated measures over time (Winer 1962; Edwards 1979).

Figure 9.1--Re-circulating stream tank used in the agonistic-behaviour observations.

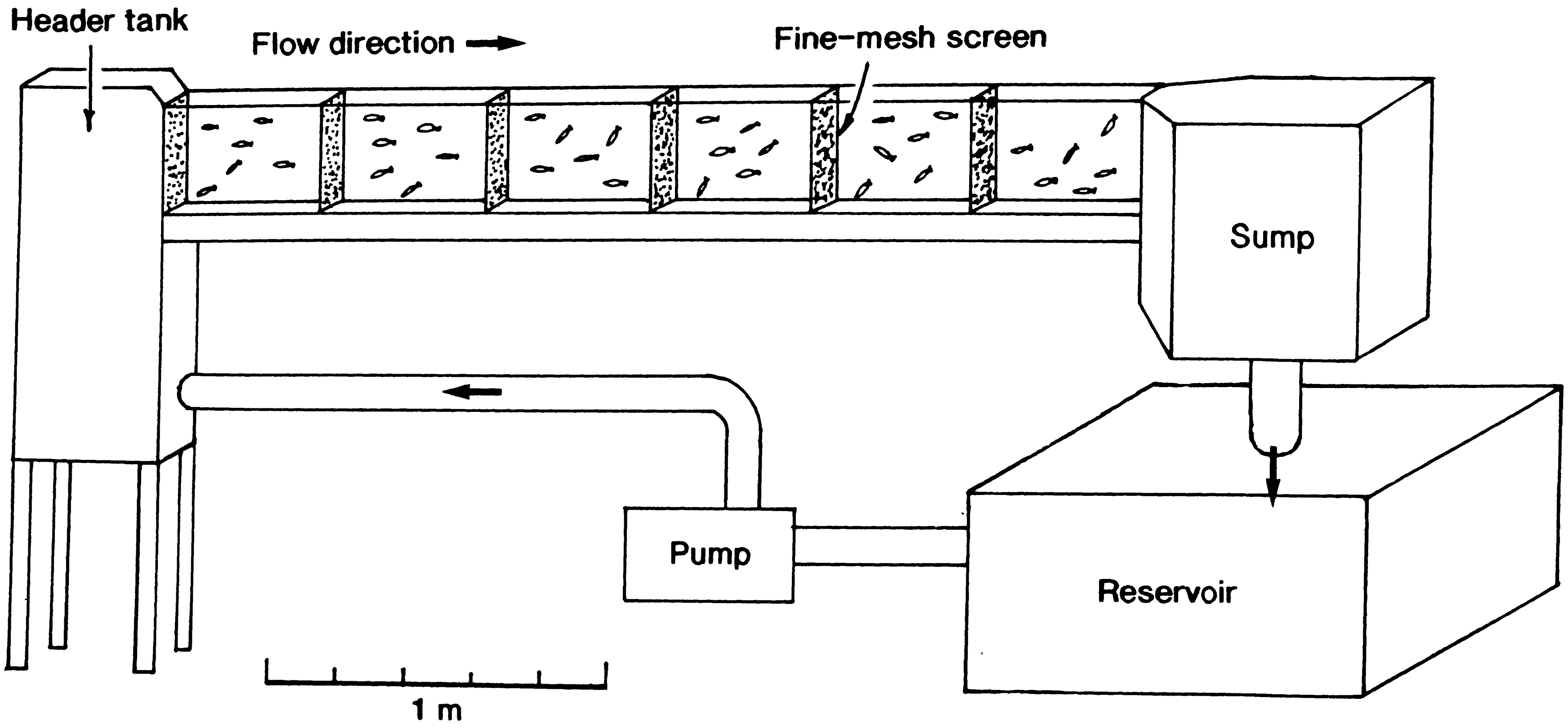

Header tank
Flow direction
Fine-mesh screen
Sump
Pump
Reservoir
1 m

Table 9.1--Agonistic behaviours recorded in the stream-tank observations. Categories defined after Rosenau and McPhail 1987.

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OVERT BEHAVIOURS

**Charge**--swimming with increased velocity directly at another fish (Keenleyside and Yamamoto 1962; Dill 1978).

**Chase**--one fish pursues another past the point from where the chased fish was originally stationed (Chapman 1962).

**Nip**--a bite directed toward or physically touching another fish (Chapman 1966).

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DORSAL-FIN-DISPLAY BEHAVIOURS

**Dorsal-fin erection**--maximally extended dorsal fin while the fish is motionless. The orientation of the fish is generally parallel to the fish being displayed to and the anal fin is usually extended simultaneously (Rosenau 1984).

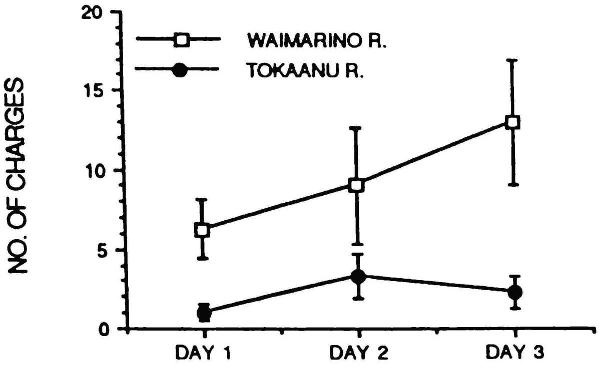
**Wig-wag**--extended dorsal and anal fins, opening of the mouth, and a stiffening of the body while swimming in an accentuated motion and performed parallel to the other fish which is being displayed at (North 1979; Rosenau and McPhail 1987).

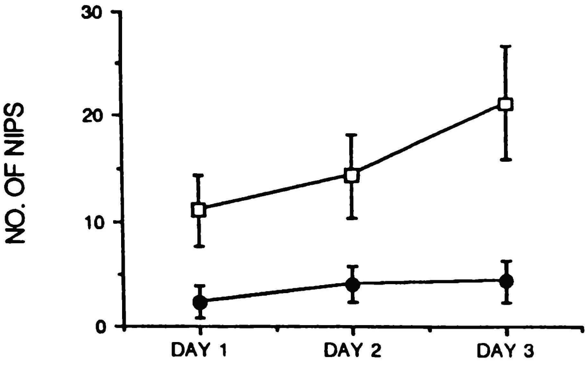
## 9.2 RESULTS

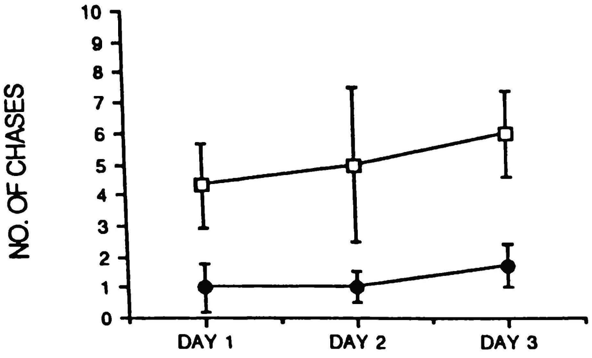
There were clear between-population differences in the levels of agonistic activity by the laboratory-incubated rainbow trout juveniles. The Waimarino River trout interacted with the other fry in their tanks significantly more than did the Tokaanu River fish (ANOVA: F=9.786, df=1,16, p=0.007; Fig. 9.2).

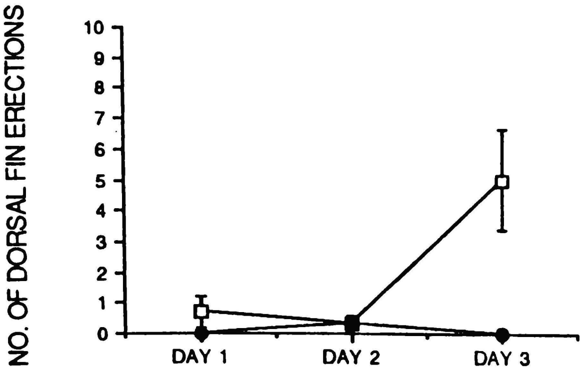
The number of overt agonistic displays (including charges, chases and nips) generally increased for each group of fish over time (Fig. 9.2). By the third day, the Waimarino River trout showed considerably more dorsal-fin erections than the Tokaanu River fish (Fig. 9.2). However, wig-wag displays were not seen at any time for either population time during the observation period.

Figure 9.2.--Average frequency of the various agonistic behaviours observed in the stream tanks. With SE's; see Table 9.1 for a description of each behaviour.


NO. OF CHARGES
20
15
10
5
0
WAIMARINO R.
TOKAANU R.
DAY 1
DAY 2
DAY 3


NO. OF NIPS
30
20
10
0
DAY 1
DAY 2
DAY 3


NO. OF CHASES
10
9
8
7
6
5
4
3
2
1
0
DAY 1
DAY 2
DAY 3


NO. OF DORSAL FIN ERECTIONS
10
9
8
7
6
5
4
3
2
1
0
DAY 1
DAY 2
DAY 3

## 9.3 DISCUSSION

Between-population variability in agonistic behaviour has been observed for a number of species of salmonids (Rosenau 1984; Taylor and Larkin 1986; Rosenau and McPhail 1987; Swain and Riddell 1990); this variation is thought to be adaptive and the result of selection occurring in the respective rearing environments. Similarly, in this study the laboratory-incubated Tokaanu and Waimarino River rainbow trout juveniles had differing intensities of agonistic activity with the latter showing higher levels. These differences may be adaptive and I speculate that they would have evolved as a result of selection in the respective rearing streams.

The functional significance of among-population variation in behavioural traits has been discussed by various researchers (Tinbergen 1967). We can assume that because a character is inherited, and at a high frequency in a population, it is likely to be important to the fitness of the organism (Hinde 1975). Furthermore, some studies have experimentally correlated between-population behaviour differences in salmonids with a corresponding environmental difference. For example, Brannon (1967) showed that newly emerged sockeye salmon fry exhibit the appropriate current taxis in the direction leading to their subsequent rearing lake, either upstream or downstream, and that these behaviours were genetically controlled.

Examples of selection causing differences in agonistic behaviour include Rosenau and McPhail (1987) who suggested that differing levels of agonistic activity in two populations of coho salmon was caused by dissimilar levels of predation and/or differing abundances of food. Likewise, Ballin (1973) and Seghers (1974), both working with guppies (**Poecilia reticulata**), showed that there was a reduction in display behaviours in those populations living in environments with large numbers of predators. In these instances agonistic activity appears to alert predators to the presence of the displaying guppies and the most active fish are differentially removed from the population leaving less agonistic individuals.

In my study, much higher densities of the common bully were found in the Tokaanu River (Chapter 7). McDowall (1990) suggested that the common bully is omnivorous and will eat small fishes. Indeed, during spring, when the young-of-the-year rainbow trout are just emerging from the redd gravel, I caught bullies in the Tokaanu River up to 115 mm which is 24 mm greater than any bully caught in the Waimarino River (Table 7.1). These Tokaanu River bullies were certainly large enough to ingest the body of a recently emerged rainbow trout (fork length ca. 22 mm). Thus, highly aggressive rainbow trout in the Tokaanu River may have been selected against through predation by bullies.

An alternate hypothesis which might explain differences in agonistic activity relates to the availability of food and productivity differences in the two streams (see also Rosenau and McPhail 1987). The rainbow trout in the Tokaanu and Waimarino Rivers must rear to a minimum length of 94 mm before survival in the lake is possible. Rainbow trout that cannot hold feeding territories in their natal streams may be displaced downstream into Lake Taupo where survival is very low (Chapter 4; Rosenau 1991). Growth rates appear to be greater in the Tokaanu River and only 49% of the juvenile trout surviving to adulthood must remain over winter in their first year, until they reach the appropriate size before survival can occur; in the Waimarino River the percentage of overwintering trout is about 70 (Chapter 4; Rosenau 1991). Thus, if the Waimarino River is an environment with lower levels of food, the more aggressive trout may have higher survival rates and there may be selection against the more "passive" fish through starvation by displacement into habitats that contain less food (and/or more predators).

Swain and Riddell (1990) found that under controlled test conditions hatchery-strain coho salmon were considerably more aggressive than their wild counterparts. They suggested that highly aggressive hatchery fish may not need to "worry" about exposing themselves to predators, but may be able to obtain more food than their more passive counterparts and thus grow larger in a shorter time period. They cited evidence showing that larger salmonid smolts have greater survival, and higher fitness levels, than their smaller, slower growing counterparts.

Finally, because the numbers of fish in this experiment were small, the results of this study should be considered only preliminary and, therefore, treated with caution. However, if my observations reflect what is occurring in the wild, the results of my study have implications for fisheries managers; if agonistic behaviours vary among populations of rainbow trout, some stocks may be more appropriate than others for aquaculture and/or introduction into new environments. Tokaanu River trout are used as a donor stock for hatchery plantings throughout North and South Islands of New Zealand. The innate levels of aggressive activity shown by this stock may not always be the most appropriate genotype for a particular hatchery release.

# Chapter 10.--DEVELOPMENTAL BIOLOGY

## 10.0 INTRODUCTION

The period when salmonids are undergoing embryonic formation in the redd gravel is one of the most sensitive and critical phases in the life history of these fishes (Bams 1969). Factors known to affect the rates of embryo and alevin development and survival in trout and salmon include both physical and biological components (**temperature**--Brannon 1987; Beacham and Murray 1986, 1987; **dissolved gasses**--Reiser and Bjornn 1979; **substrate quality**--Chapman 1988; **the timing of egg deposition**--Ricker 1972; Brannon 1987; **egg size**--Brannon 1987; Beacham and Murray 1987; Fleming and Gross 1990; **the inherent biochemical-physiology**--Allendorf et al. 1983; Ferguson et al. 1985, 1987; Danzmann et al. 1986; 1989). Under experimental conditions, various studies have demonstrated a surprising amount of inherited variability in these incubation and survival rates (Ferguson et al. 1985, 1987, Beacham and Murray 1986, 1987, 1988; Brannon 1987, Brannas 1988, Danzmann et al. 1989; Fleming and Gross 1990). At least some of this genetic variation may be the result of selection and, thus, can be said to be adaptive. Any differences in developmental traits that are adaptive will be important to the survival and fitness of these young fish in their natal streams. However, the reason for this inter-population variability (i.e., the selective mechanism), for the most part, is usually unknown and can be explained only through conjecture.

Lake Taupo rainbow trout spawn and rear in a number of its inflowing tributaries (Tully 1989; Pitkethley 1990; Rosenau 1991) and there is a considerable amount of variation in the physical and biological characteristics among these streams (Schouten et al. 1981). Two such streams are the Waimarino and Tokaanu Rivers (Table 3.1; Figs. 3.1, 3.2) and both are considered to be important to the recruitment of fish into the Lake Taupo sport fishery (J. Gibbs, Department of Conservation, Turangi, New Zealand, pers. comm.). The Waimarino River is a surface-fed stream and has high intra-redd dissolved oxygen levels whereas the Tokaanu River is a groundwater-fed stream with intra-redd oxygen concentrations that are marginal for salmonid egg incubation (Tully 1989). Temperature and flow also vary considerably between these streams (Figs. 3.1, 3.2)

Tully (1989) found that adult rainbow trout spawning in these streams were very different with respect to fecundity; Waimarino River females had lower numbers of eggs than Tokaanu females and, by implication, the former would then have larger eggs for fish of the same size. Tully speculated that these differences were inherited and have evolved in response to the dissimilar environmental conditions encountered by the embryos and alevins in these two streams. Under low oxygen conditions, small eggs are thought to have greater survival rates, than large eggs, due to a relatively greater surface-to-volume ratio and a greater amount of oxygen uptake per mass; the absorbtion of oxygen from water by fish embryos is a function of the surface area of the egg (Beacham and Murray 1985). Thus, selection through environmental differences may have produced a smaller sized egg in Tokaanu River rainbow trout. In addition, there may also have been selection for other between-population differences in characters such as the developmental and survival rates of rainbow trout embryos and alevins in these two populations.

Thus, this part of my study examined possible genetically-mediated character differences in development for Waimarino and Tokaanu River embryos and alevins; it was my intention to relate any such observed differences in these two populations to the physical or biological differences seen in the respective watersheds. My study hypotheses were:

1) because of the relatively more adverse incubation conditions (i.e., low dissolved oxygen levels; Tully 1989) in the Tokaanu River, there would have been selection for rainbow trout embryos and alevins that have faster development rates resulting in alevins that leave the gravel as quickly as possible and escape these negative circumstances, and

2) since the between-stream temperatures are so different, the embryos and alevins of these two populations will be adapted most closely to the temperatures that they are normally exposed to in their respective natural environments; this will be reflected in different among-population survival and development rates when incubated under various incubation temperatures.

To determine among-population genetic differences in these two stocks, and eliminate any environmental effects, eggs and milt were collected from ripe wild spawners taken from each of these streams on the same day; all crosses were then made simultaneously and the resulting embryos were incubated in the same water baths under standardized and highly controlled conditions.

Two incubation target temperatures, 7 and 12°C, were used in the experimental design. I felt that the former represented the temperature regime that most Waimarino River rainbow trout embryos would be exposed to under natural and average conditions (Fig. 3.2), while 12°C is close to the temperatures that Tokaanu River embryos would encounter (Fig. 3.2). Reciprocal hybrids were also made to account for any phenotypic effects in survival or development rates resulting from among-population egg-size differences. The size of the egg can affect these rates in salmonid embryos and alevins (Murray 1980; Brannon 1987) and maternally dictated effects resulting from variability in the size or quality of the egg can be eliminated by crossing the female gametes with fathers of both populations; assuming that there are no phenotypic-paternal effects, any resultant character variability can then be attributed to genetic differences between father groups. Wood and Foote (1990) used this reciprocal-cross technique very successfully to determine genetically-mediated developmental variation between the different-sized eggs of landlocked (kokanee) and anadromous sockeye salmon (**Oncorhynchus nerka**).

## 10.1 METHODS

### 10.1.1 Incubation

I collected the gametes of three ripe male and three ovulated female rainbow trout from each of the two study streams on 19 October 1987. The gametes from each trio of fish were pooled before the various crosses were made in the field; this included two "pure" and two "reciprocal-hybrid" crosses or: 1) Tokaanu males X Waimarino females (TOK-males x WAI-females, 2) Waimarino males X Waimarino females (WAI-pure), 3) Tokaanu males X Tokaanu females (TOK-pure), and 4) Waimarino males X Tokaanu females (WAI-males x TOK-females). I fertilized the eggs at 12°C and the embryos were allowed to water harden for 1 h before being brought back to the laboratory in a cooler filled with a slurry of ice and water. Upon reaching the laboratory, all crosses were divided into two batches and one batch of each cross was placed either in temperature-controlled water baths maintained at 7 or 12°C. The day that I fertilized these crosses was considered to be "Day 0".

During incubation, embryos from each cross were held separately in "incubation baskets", each of which was half-filled with small, clean gravel and submerged in the water baths (Plates 10.1, 10.2; compare with the apparatus outlined in Murray and McPhail 1988). Air-saturated water was supplied to the embryos by pumping air through standpipes which penetrated through the gravel to the bottom of the basket. The developing embryos and alevins were kept in the dark by black-plastic curtains and were exposed to light only briefly during daily-temperature or dead-egg checks, as well as during the alevin light-taxis tests. Dead eggs were removed and preserved in Stockard's solution (Rugh 1952) and these were later examined and classified as "fertilized" if some evidence of cell division was seen (Knight 1963; Velsen 1980). Non-fertilized eggs were not included in subsequent survival-rate calculations. To determine cross-egg size, weights were taken of water-hardened and fertilized eggs (n=100 eggs per cross) which were preserved for at least three months in 10% formalin (Beacham and Murray 1985). Upon hatching, the alevins were removed from their respective incubation baskets and counted, and five hundred alevins were then returned. The "50%-hatch day" was considered to be the date when the cumulative sum of alevins reached one-half of the total number that were to ultimately hatch.

The incubation of alevins then proceeded until their yolk reserves were less than about 75% and there was a substantial increase in the swimming activity of the fish when they were exposed to light. Then the fish of each incubation basket were tested once a day to determine their taxis to light by providing a choice of daylight or darkness for a period of 15 minutes.

Salmonid juveniles are ready to emerge once they become photopositive and the test apparatus used to determine the light taxis of these juveniles was similar to that described by Mason (1976). Firstly, an incubation basket containing alevins was removed from the incubation water-bath and then inserted into an opaque test container (Plate 10.3); this was then placed into a water-temperature controlled bath (Plate 10.4) and the number of fish escaping into daylight was counted. Juveniles were allowed to swim from the darkened apparatus into the light through an opening located on the upper surface of this opaque test container. Once the day's testing for each incubation basket was completed, the photo-positive fry were then removed from the test bath and counted. The rest of the photo-negative alevins in the incubation basket were returned back to the incubation chamber to await the next day's testing. This procedure was then repeated with the next incubation basket of alevins until all basket had been tested for that day.

The testing for photopositiveness of fry continued on a daily basis until over 95% of all the alevins had emerged from each of the incubation baskets. The first 100 emerging fry of each cross were preserved in 10% formalin for subsequent length and weight measurements.

A plot of cumulative-percent fry-emergence, versus time, gives a sigmoid curve with the mid-period of emergence approximating a straight line to which a regression line can be fitted by least squares (Godin 1980); a comparison of regressions can be used to determine among-cross and between-temperature differences in the rates of development to emergence. The 50% hatch day was considered to be "Day 0" for alevins and these cumulative-percent data were log(10) transformed. The cumulative-percentages, from 35 to 65%, were then transformed into a probit scale and the 50% emergence day was estimated using the inverse prediction (Sokal and Rohlf 1981).

Survival-rates of the various crosses, at either temperature regime, were calculated as the percentage of fertilized eggs or alevins that survived either development period, respectively. Heterogeneity of embryo and alevin survival rates, among crosses and temperatures, were compared using a likelihood ratio (G-test; Sokal and Rohlf 1981). A homogeneity-of-replicates comparison for goodness of fit was used to test which crosses were different from one another (Sokal and Rohlf 1981).

The standard lengths and weights of fry at emergence (preserved wet-weight; Murray 1980) were compared for the various crosses and temperatures using analysis of variance.

### 10.1.2 Between-population egg-size and fecundity comparisons

A relationship was developed between the weight of eggs taken from ovulated females versus fish-fork lengths for rainbow trout from both study populations; the resulting regressions were compared using analysis of covariance. Ovulated eggs were obtained in two ways. Firstly, on September 1987, 100 mature rainbow trout were tangle-netted with gill-nets (mesh size 90 mm knot to knot) from each of the study streams and frozen for later examination (Tully 1989; Rosenau 1991). Upon thawing, females which had ovulated were measured to fork length and a sample of eggs was placed in water to swell and harden. Despite freezing, most samples of eggs water hardened normally although only eggs which showed complete swelling were used in the analysis and any deformed eggs were excluded from the analysis. A second sample of eggs were obtained from live females netted throughout the spawning period 1988 and 1989; these fish were also measured for fork length and the eggs were water hardened prior to preservation.

All eggs were preserved in 10% formalin and these samples were held for at least 3 months prior to weighing (Beacham and Murray 1985). The use of egg weight as a measure of egg size is more consistent than linear measures of diameter (Fleming and Ng 1987). Average egg weights from the ovulated fish were determined by weighing a sample of 30 preserved eggs from each fish; the eggs were blotted dry of formalin before weighing.

Between-population comparisons of egg size were made by first standardizing the egg weights for each population to a common fish length and then testing for egg weight differences with a t-test. The method of size-standardization is outlined in Reist (1985) and Beacham and Murray (1987):

$$W_t = W_o \frac{(\bar{L})^b}{(L_o)}$$

where $W_t$ = the weight of the standardized egg, $W_o$ = the observed weight of egg, $\bar{L}$ = fish fork length that the egg weight was standardized to (531 mm, or mean fork length for the samples of females from both populations), $L_o$= observed fish fork length, and b = regression coefficient of ln(L). An allometric regression to a standardized body length is the preferred method of removing variation in physical characters among individuals along a range of body sizes (Reist 1985; Beacham and Murray 1987).

A fecundity comparison was also made for these populations by further analyzing data collected by Tully (1989). As with egg-size contrasts, the fecundity measurements were first standardized to a common body fork length before between-population comparisons were made. The method is similar the equation above where:

$$F_t = F_o \left(\frac{\overline{L}}{L_o}\right)^b$$

where $F_t$ = the fecundity of the standardized female, $F_o$ = the observed fecundity, $\overline{L}$ = fish fork length that the fecundity was standardized to (527 mm, or mean fork length for the samples of females from both populations), $L_o$= observed fish fork length, and b = regression coefficient of ln(L). One outlier was removed from this data set before analysis (Tokaanu--fork length 497 mm; fecundity 8496 eggs, Tully 1989).

### 10.1.3 Redd-gravel particle sizes

In the winter of 1989, gravel samples were taken from ten redds throughout the reaches of the Tokaanu and Waimarino Rivers which had the highest spawning densities. A scoop of gravel was taken to a depth of about 20 cm, from the crown of the "tailspill" (Chapman 1988) and, in an upstream direction, to the lowest elevation of the "pot" of the redd (Crisp and Carling 1989). The 20 cm depth was chosen because it falls within the range of depths that trout are known to bury their eggs (Hobbes 1937; Crisp and Carling 1989). The gravel samples were dried and then sifted with graded wire-mesh sieves ranging in a geometric progression of 12 size classes from 0.062 to 100 mm. For each gravel sample, the weights of material in each size class were determined and a proportion was calculated. These data were then used to calculate a "fredle index" of the gravel particle sizes. This index uses a measure of the central tendency of the distribution of sediment particle sizes in a sample and the dispersion of particles in relation to this value. The equation used to calculate the fredle index is:

$$f_i = \frac{d_g}{S_o}$$

where $f_i$ is the fredle index, $d_g$ is calculated as the geometric mean of the 12 size classes of redd material:

$$d_g = [\ d_1^{w_1} \times d_2^{w_2} \ldots\ldots \times d_{12}^{w_{12}}\ ]$$

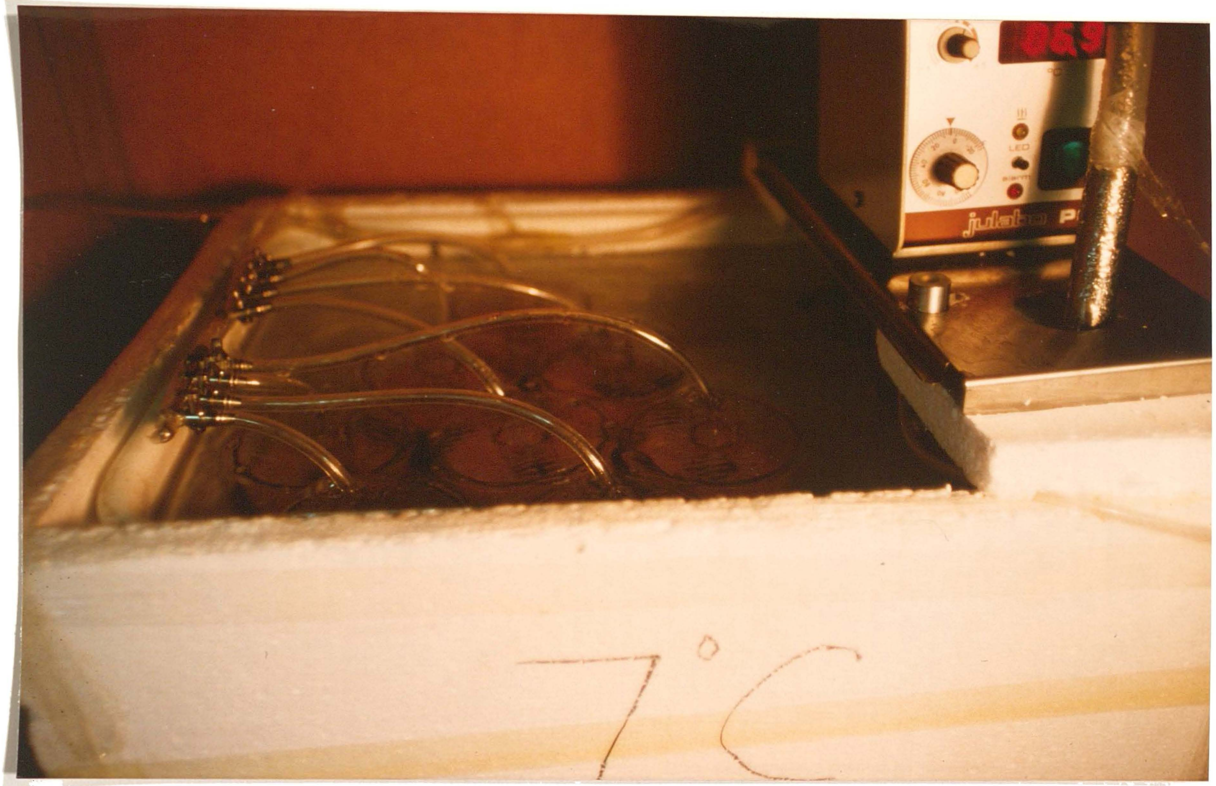
with $d_g$ being the geometric mean particle size, d is the midpoint diameter of particles retained by a given sieve, and w is the decimal fraction by weight of particles retained by a given sieve, and $S_o$ is derived by taking the square root of the quotient of the grain size at the 75th percentile divided by the same at the 25th percentile, or:

$$S_o = \sqrt{\frac{d_{75}}{d_{25}}}$$

A relationship between the fredle index and incubation-survival rate has been determined and is useful for comparing quality of spawning gravel (Lotspeich and Everest 1981).

Plate 10.1.--Temperature-controlled water bath used to incubate eggs and alevins. This was covered by a black polyethylene sheet to ensure that incubation took place in total darkness.

Plate 10.2.--Incubation basket used in egg- and alevin-incubation experiments. This apparatus was constructed from an aquarium filter and partially filled with clean pea gravel.


julabo
7°C


TOK-2-12

Plate 10.3--Apparatus used to determine the photo-positive state of emerging fry. The incubation basket is placed in a blackened container; a slit in the upper corner of this container allowed a small amount of light to come in contact with the fish. Any photo-positive fry could escape the container through the slit, towards the light, and into the emergence-test water bath (see Plate 10.4).


To♂ W♀-1-

Plate 10.4--Emergence-test water bath for determining the photo-positive state of the experimental crosses. The apparatus shown in Plate 10.3 was placed in a controlled-temperature water bath into which photopositive fish were allowed to escape.

## 10.2 RESULTS

### 10.2.1 Developmental biology

#### Size of eggs used in the incubation experiment

There were significant among-cross differences in the size of the eggs used in the incubation experiment; eggs of Tokaanu River females were heavier than the Waimarino River eggs; crosses having the same mothers but different fathers were not different from one another (Table 10.1). The fork lengths of spawning adults used in this experiment were similar for both sexes and populations (fork length (mm)--Waimarino males 514-547, females 527-555; Tokaanu males 531-556, females 530-566).

#### Development rates

The incubation temperatures were maintained close to either 12 or 7°C for both experiments (TARGET TEMPERATURE 7°C--fertilization-to-hatch average 7.0°C (SD 0.07), hatch-to-emergence average 6.9°C (SD 0.49); TARGET TEMPERATURE 12°C--fertilization-to-hatch average 12.0°C (SD 0.07), hatch-to-emergence average 11.8°C (SD 0.29) ). From fertilization to 50% hatch, the length of the incubation period was the same for all crosses within temperature, but it took about twice as long at 7°C (51 d) as compared to 12°C (27 d). Likewise, at 7°C the number of days from hatch to emergence was about twice that of 12°C (Fig. 10.1). However, within temperature regimes there were significant among-cross differences in the length of time taken from hatch until 50% emergence. For those crosses having the same fathers but different mothers (regardless of temperature), those juveniles with Tokaanu mothers took longer to emerge than those with Waimarino mothers (ANCOVA $p<0.05$) (Fig. 10.1). Similarly, for rainbow trout having the same mothers but different fathers, and regardless of temperature, juveniles with Waimarino fathers took longer to emerge than those with Tokaanu fathers (ANCOVA $p<0.05$) (Fig. 10.1). The 50% emergence of the juveniles of the TOK-males x WAI-females cross was sooner than the WAI-pure cross by about 2 d at 12°C and 4 d at 7°C; likewise, the fry of the TOK-pure cross emerged before the WAI-males x TOK-females cross by about 3 d at 12°C and 2 d at 7°C. The maximum among-cross difference, to emergence, occurred between the reciprocal hybrids (TOK-males x WAI-females and the WAI-males x TOK-females) and was about 5 days at both temperatures. Regression equations were developed for the curves in Fig. 10.1 and are tabulated in Table 10.2.

### Survival rates

Survival rates, from fertilization to hatch, and from hatch to emergence, were high (above 90%) for all crosses at 12°C (Table 10.3). Likewise, hatching-survival rates were above 90%, for all crosses at 7°C; however, the 7°C hatch to emergence survival rates were substantially lower and significantly different than the equivalent survival rates at 12°C for all groups (WAI-pure $G=154.8$, WAI-males x TOK-females $G=212.9$, TOK-males x WAI-females $G=10.4$, TOK-pure $G=256.2$).

Within temperatures, and from fertilization to hatch, there were small but significantly different survival rates among crosses with different mothers (but the same fathers); this pattern was identical for both temperatures (G-test--12°C Wm x Tf Tpure < Tm x Wf Wpure; 7°C Tpure Wm x Tf < Wpure Tm x Wf) (Table 10.3); that is, crosses of small eggs had similar survival rates one to another but had higher survival rates than crosses of large eggs, which in turn were also similar to each other.

For the 7°C regime, and from hatch to emergence, the TOK-males x WAI-females cross of alevins had the highest survival, the pure groups were next and statistically inseparable from one another, and the WAI-males X TOK-females group had the lowest survival of all the crosses (G-test $p< 0.05$--Tm x Wf Wpure Tpure Wm x Tf).

### Alevin lengths and weights

There were significant among-cross size differences in the lengths and weights of emerging fry, between and within temperatures (Tables 10.4, 10.5). Firstly, all crosses showed a temperature effect and the fry were lighter but longer at 12°C, and shorter and heavier at 7°C. The effect of females was also significant and those fish with Tokaanu mothers (i.e. larger eggs, or TOK-pure & WAI-males x TOK-females) were heavier and longer than their counterparts with Waimarino mothers, regardless of temperature (i.e. smaller eggs, or WAI-pure & TOK-males x WAI-females). Within each egg-size group (same mothers, different fathers), crosses which emerged earlier (those sired by Tokaanu males) were generally heavier than those crosses that emerged later (those sired by Waimarino males) and this was consistent within and between temperatures for all contrasts. (except for TOK-pure versus WAI-males x TOK-females at 12°C which was significant at p=0.065). Regardless of temperature, TOK-pure juveniles were longer than their TOK-female x WAI-male counterparts. However, there were no between-cross length differences for the juveniles of WAI-females regardless of temperature.

### 10.2.2 Among-population egg-size and fecundity comparisons

At a common size (fork length, 531 mm), the Waimarino female rainbow trout had heavier eggs than the Tokaanu trout (Table 10.6). In contrast, Tokaanu River rainbow trout averaged over 500 more eggs per fish at a fork length of 525 mm. Thus, Tokaanu rainbow trout have smaller eggs and a higher average fecundity than equivalent-sized Waimarino female trout.

### 10.2.3 Redd-particle size differences in the study streams

There were substantial differences in the sizes of particles from the redds of the two study streams. The fredle values, calculated for these redds, were significantly different (fredle value--Tokaanu 1.494, SD = 0.5463; Waimarino 12.874, SD = 6.4810; $t_{df=18}$= -5.011 $p<0.001$ *). Thus, the Tokaanu River rainbow trout redds were comprised of much smaller particles than the material in the Waimarino redds (Figure 10.2).

Figure 10.1.--Cumulative-percent emergence of all incubation-experiment crosses.

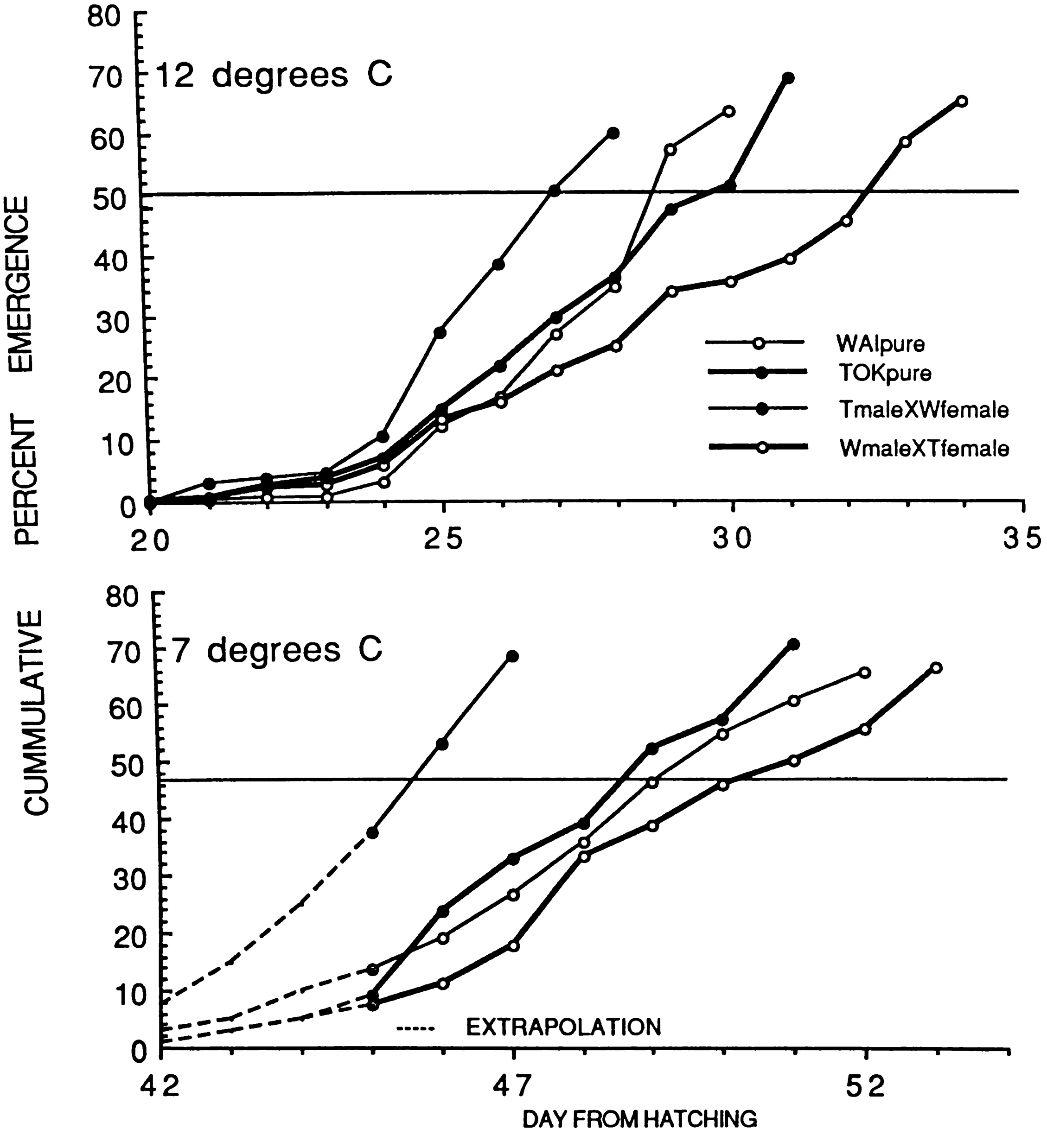

12 degrees C
7 degrees C
CUMMULATIVE PERCENT EMERGENCE
DAY FROM HATCHING
WAIpure
TOKpure
TmaleXWfemale
WmaleXTfemale
----- EXTRAPOLATION
0
10
20
30
40
50
60
70
80
20
25
30
35
42
47
52

Figure 10.2.--Particle-size distribution of the gravel in the Waimarino and Tokaanu rainbow trout spawning redds. Each bar represents the proportion of the total weight of the sample of that size interval; ±SD's.

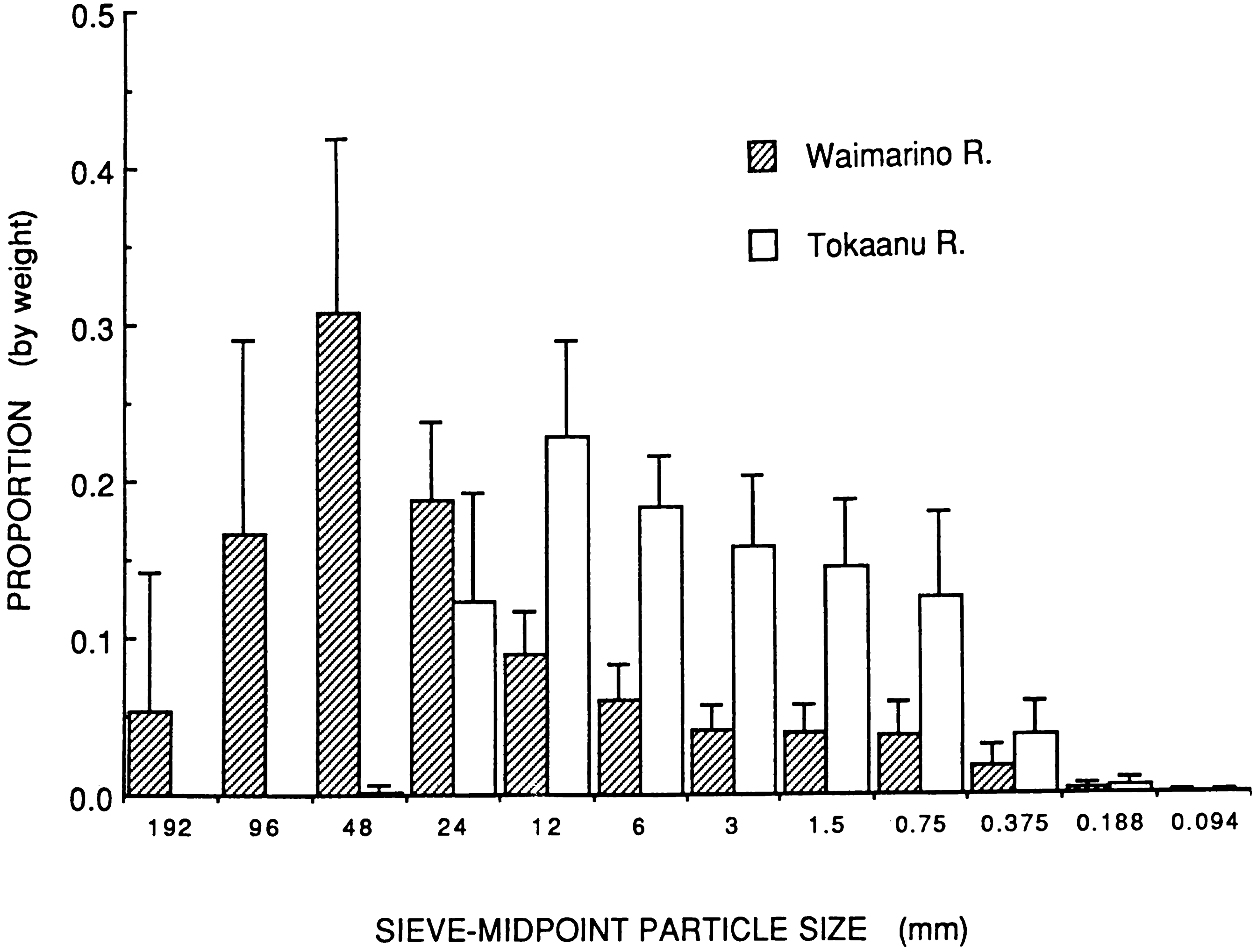

0.5
0.4
0.3
0.2
0.1
0.0
PROPORTION (by weight)
▨ Waimarino R.
☐ Tokaanu R.
192
96
48
24
12
6
3
1.5
0.75
0.375
0.188
0.094
SIEVE-MIDPOINT PARTICLE SIZE (mm)

Table 10.1.--The sizes of eggs used in the incubation experiments.

| CROSS | AVERAGE EGG WEIGHT gm | SD | N |
|---|---|---|---|
| WAI-pure | 0.078 | 0.011 | 100 |
| WAI-females X TOK-males | 0.076 | 0.011 | 100 |
| TOK-pure | 0.094 | 0.009 | 100 |
| TOK-females X WAI-males | 0.095 | 0.008 | 100 |

ANOVA F= 110.3 df=3,396 $p < 0.001$

Tukey's HSD, $p < 0.05$

Tm x Wf  Wpure Tpure  Wm x Tf

Table 10.2.--Regression equations of cumulative-percent emergence curves for all crosses in the incubation experiment (see Fig. 10.1). E, the cumulative percentage of fish emerged for a cross; D, is the emergence day, and is computed as number of days from 50% hatch day.

| CROSS | EMERGENCE ORDER within female groups | T °C | REGRESSION | $R^2$ |
|---|---|---|---|---|
| | | | **WAIMRINO FEMALES** | |
| TOK-males x WAI-females | 1 | 12 | Probit E = 17.1 log(10)D - 19.5 | 0.997 |
| WAI-pure | 2 | 12 | Probit E = 24.6 log(10)D - 31.0 | 0.914 |
| TOK-males x WAI-females | 1 | 7 | Probit E = 42.1 log(10)D - 64.9 | 0.999 |
| WAI-pure | 2 | 7 | Probit E = 21.8 log(10)D - 31.8 | 0.981 |
| | | | **TOKAANU FEMALES** | |
| TOK-pure | 1 | 12 | Probit E = 17.7 log(10)D - 21.0 | 0.937 |
| WAI-males x TOK-females | 2 | 12 | Probit E = 14.5 log(10)D - 16.8 | 0.962 |
| TOK-pure | 1 | 7 | Probit E = 27.4 log(10)D - 41.3 | 0.977 |
| WAI-males x TOK-females | 2 | 7 | Probit E = 19.5 log(10)D - 28.2 | 0.963 |

Table 10.3--Survival-rate statistics for embryos and alevins of all incubation experiment crosses.

| CROSS | TEMP °C | 50% HATCH DAYS FROM FERTILIZATION | 50% HATCH SURVIVAL RATE % | 50% EMERGENCE DAYS FROM HATCH | 50% EMERGENCE SURVIVAL RATE % |
|---|---|---|---|---|---|
| WAI-pure | | | | | |
| | 7 | 51 | 97.8 | 49.6 | 69.8 |
| | 12 | 27 | 97.7 | 28.9 | 97.0 |
| WAI-females x TOK-males | | | | | |
| | 7 | 51 | 97.9 | 45.8 | 85.6 |
| | 12 | 27 | 96.5 | 27.0 | 91.6 |
| TOK-pure | | | | | |
| | 7 | 51 | 92.5 | 48.9 | 64.6 |
| | 12 | 27 | 93.8 | 29.4 | 99.4 |
| TOK-females x WAI-males | | | | | |
| | 7 | 51 | 93.2 | 50.8 | 54.2 |
| | 12 | 27 | 92.4 | 32.1 | 93.0 |

Table 10.4.--Average weights of emerged juvenile trout and statistical-test contrasts for all incubation crosses. Sample n's = 100; SE's in brackets; $t_p$, t(pooled variance estimate); $t_s$, t(separate variance estimate); df's for $t_p$=396 and $t_s$=198.

| **CROSS** | **T °C** | **WEIGHT** gm | **T °C** | **WEIGHT** gm |
|---|---|---|---|---|
| WAI-pure | 7 | 0.093 (0.0013) | 12 | 0.085 (0.0015) |
| WAI-females x TOK-males | 7 | 0.100 (0.0017) | 12 | 0.090 (0.0014) |
| TOK-pure | 7 | 0.133 (0.0016) | 12 | 0.110 (0.0020) |
| TOK-females x WAI-males | 7 | 0.124 (0.0022) | 12 | 0.105 (0.0020) |

**SAME-SIZED EGGS**

**Waimarino females**--ANOVA df=3,396 F=20.099 $p<0.001$ *

WAI-pure versus TOK-males x WAI-females
12°C $t_p=-2.471$ $p=0.013$ *
$t_s=-2.522$ $p=0.012$ *
7°C $t_p=-3.667$ $p=0.001$ *
$t_s=-3.595$ $p=0.001$ *

WAI-pure 7°C versus 12°C
$t_p=-3.916$ $p<0.001$ *
$t_s=-4.080$ $p<0.001$ *

TOK-males x WAI-females 7°C versus 12°C
$t_p=-5.112$ $p<0.001$ *
$t_s=-4.921$ $p<0.001$ *

**Tokaanu females**--ANOVA df=3,396 F=45.275 $p<0.001$ *

TOK-pure versus WAI-males x TOK-females
12°C $t_p=-1.856$ $p=0.061$ ns
$t_s=-1.828$ $p=0.065$ ns
7°C $t_p=-3.475$ $p=0.001$ *
$t_s=-3.528$ $p=0.001$ *

TOK-pure 7°C versus 12°C
$t_p=-6.946$ $p<0.001$ *
$t_s=-6.517$ $p<0.001$ *

WAI-males x TOK-females 7°C versus 12°C
$t_p=-8.565$ $p<0.001$ *
$t_s=-9.214$ $p<0.001$ *

**DIFFERENT-SIZED EGGS**

**Waimarino males**--ANOVA df=3,396 F=47.922 $p<0.001$ *

WAI-pure versus WAI-males x TOK-females
12°C $t_p=-8.235$ $p<0.001$ *
$t_s=-8.085$ $p<0.001$ *
7°C $t_p=-8.194$ $p<0.001$ *
$t_s=-8.352$ $p<0.001$ *

**Tokaanu males**--ANOVA df=3,396 F=122.591 $p<0.001$ *

TOK-pure versus TOK-males x WAI-females
12°C $t_p=-12.712$ $p<0.001$ *
$t_s=-12.257$ $p<0.001$ *
7°C $t_p=-13.461$ $p<0.001$ *
$t_s=-14.000$ $p<0.001$ *

Table 10.5.--Standard lengths of emerged juvenile trout and statistical-test contrasts for all incubation crosses. Sample n's = 100; SE's in brackets; $t_p$, t(pooled variance estimate); $t_s$, t(separate variance estimate); df's for $t_p$=396 and $t_s$= 198.

| CROSS | **T °C** | **LENGTH** mm | **T °C** | **LENGTH** mm |
|---|---|---|---|---|
| WAI-pure | 7 | 19.39 (0.057) | 12 | 20.77 (0.067) |
| WAI-females x TOK-male | 7 | 19.48 (0.073) | 12 | 20.60 (0.068) |
| TOK-pure | 7 | 21.40 (0.097) | 12 | 21.71 (0.081) |
| TOK-females x WAI-males | 7 | 20.64 (0.092) | 12 | 21.39 (0.092) |

**SAME-SIZED EGGS**

**Waimarino females**--ANOVA df=3,396 F=118.7 p<0.001 *

WAI-pure versus TOK-males x WAI-females
12°C $t_p=1.801$ p=0.069 ns
$t_s=1.776$ p=0.074 ns
7°C $t_p=-0.996$ p=0.321 ns
$t_s=-1.011$ p=0.314 ns

WAI-pure 7°C versus 12°C
$t_p=14.665$ p<0.001 *
$t_s=15.719$ p<0.001 *

TOK-males x WAI-females 7°C versus 12°C
$t_p=11.867$ p<0.001 *
$t_s=11.167$ p<0.001 *

**Tokaanu females**--ANOVA df=3,396 F=25.042 p<0.001 *

TOK-pure versus WAI-males x TOK-females
12°C $t_p=-2.527$ p=0.011 *
$t_s=-2.650$ p=0.009 *
7°C $t_p=-5.873$ p<0.001 *
$t_s=-5.626$ p<0.001 *

TOK-pure 7°C versus 12°C
$t_p=5.811$ p<0.001 *
$t_s=5.727$ p<0.001 *

WAI-males x TOK-females 7°C versus 12°C
$t_p=2.465$ p=0.014 *
$t_s=2.502$ p=0.013 *

**DIFFERENT-SIZED EGGS**

**Waimarino males**--ANOVA df=3,396 F=45.098 p<0.001 *

WAI-pure versus WAI-males x TOK-females
12°C $t_p=-5.630$ p<0.001 *
$t_s=-5.442$ p<0.001 *
7°C $t_p=-10.130$ p<0.001 *
$t_s=-10.498$ p<0.001 *

**Tokaanu females**--ANOVA df=3,396 F=140.742 p<0.001 *

TOK-pure versus TOK-males x WAI-females
12°C $t_p=-10.905$ p<0.001 *
$t_s=-11.582$ p<0.001 *
7°C $t_p=-16.622$ p<0.001 *
$t_s=-15.756$ p<0.001 *

Table 10.6.--Between-population egg-weight and fecundity comparisons for rainbow trout from the Tokaanu and Waimarino Rivers. b, regression coefficient of ln(L); L, fork length of fish.

| | Standardized Fecundity gm/30 eggs | n | b | Common Fork Length mm | Standardized Egg Weight | n | b | Common Fork Length mm |
|---|---|---|---|---|---|---|---|---|
| Waimarino | 4195 | 92 | 0.63 | 527 | 2.64 | 32 | 1.66 | 531 |
| Tokaanu | 4729 | 22 | 1.06 | 527 | 2.40 | 60 | 1.37 | 531 |
| | t= -2.887, p=0.005 | | | | t= 4.091, p<0.001 | | | |

## 10.3 DISCUSSION

This study demonstrated between-population differences in alevin developmental and survival rates as well as in egg size and female fecundities. Many of the observed differences had a strongly heritable component and are probably adaptive. Presumably, these traits have evolved in response to the very different environmental conditions encountered by the fish in their respective natal streams. Since the incubation period is an especially critical time in the life-history of salmonids (Bams 1969), the adaptations are probably important contributors to the fitness and production of each stock of fish in their usual environments.

### 10.3.1 Development Rates

#### Embryo incubation

The rainbow trout embryos in my experiments took 27 and 51 days to hatch at temperatures of 12 and 7°C, respectively, regardless of cross. Elliott et al. (1987) reported an identical number of embryo incubation days at these temperatures in their desk study of European rainbow trout (see their Table 2). In contrast, some populations of North American rainbow trout do vary in their embryo development rates (Allendorf et al. 1983; Danzmann et al. 1986, 1989; Ferguson et al. 1985, 1987). Although my study did not show any among-cross variation in embryo development rates, Lake Taupo rainbow trout were only introduced into this watershed less than 100 years ago and, because they appear to have been a small number of fish from a single stock (Scott et al. 1978; Cooper 1989), the genetic variability to allow for between-population differentiation may not have been present in the donor population. Alternatively, selection may not be acting on this character trait in these Lake Taupo populations.

### Alevin incubation

There were significant differences in the emergence rates of alevins from crosses of the same egg sizes (mothers), but different fathers. Furthermore, the order that each of these crosses of alevins emerged, with respect to egg size, was consistent between temperature regimes; the progeny of TOK-males x WAI-females emerged earlier than the WAI-pure group; likewise, but in an opposite direction, the juveniles of the WAI-males x TOK-females cross emerged significantly later than the TOK-pure groups. In contrast, the 50% emergence of the pure crosses (different sized eggs) was very similar, each being only about 0.5 day apart from the other, regardless of temperature.

Because the rate of development in salmonid alevins is modified by egg size, larger alevins, arising from large eggs, generally take longer to develop than those from small eggs, all other things being equal (Smith 1958; Bagenal 1969; Heming et al. 1982; Rombough 1985). But, if egg size alone was the only influencing factor, all groups of alevins from the laboratory crosses of Waimarino mothers (small eggs) should have emerged first, and at the same time, while those crosses with Tokaanu mothers (large eggs) should have emerged last. Furthermore, there should have been no differences between the hybrids and the pure crosses of the same mothers. Although the average emergence time for small eggs was less than the average for large eggs, there were differences between crosses of the same mothers but different fathers.

Other, non-phenotypic (genetic), traits have also been shown to modify the rate of development in salmonid alevins (Brannon 1987; Wood and Foote 1990). These genetic differences were also modifying alevin development rates in my experimental crosses; the Tokaanu males provided a component for faster development while the Waimarino males conveyed slower rates.

In a similar study, Wood and Foote (1990) examined the alevin development rates of two reproductively isolated but genetically similar sympatric ecotypes which had different sized eggs; these included kokanee (small eggs) and sockeye (large eggs) salmon (**Oncorhynchus nerka**). They found that, despite the different sized eggs, alevins of pure crosses developed at the same rates but the reciprocal hybrids differed from both the pure-type alevins and from one another in their development. Wood and Foote (1990) suggested that the variety of alevin developmental rates observed among their crosses were a result of the combining male-genetic and maternal-phenotypic (egg size) effects.

Thus, if the samples of rainbow trout gametes used in my experiments genetically represented their respective populations, there is a stock difference in alevin development rates that is heritable. That is, Tokaanu River-fathered alevins were predisposed for faster development, from hatch to emergence, than Waimarino River-fathered fish. A similar genetic component may also be present in the female gametes (genetically faster developing Tokaanu eggs, slower developing Waimarino eggs); however, because of the experimental design in this study, this was not possible to determine.

### Between-population egg-size differences

Tokaanu River rainbow trout had smaller eggs than similar-sized Waimarino River trout and, at a size-adjusted fork length of 527 mm, the former had over 500 more eggs than did similar-size Waimarino females (Tully 1989; Rosenau et al. 1991). These observations agree with Svardson's (1949) study showing that egg size and egg number are usually negatively correlated in fishes. Consequently, since Tokaanu River rainbow trout have a greater fecundity for a given body length, they also have correspondingly smaller eggs.

Eggs size can vary considerably within and between populations of salmonids (e.g., Fleming and Gross 1990) and this may be either under environmental and/or genetic control. Environmental factors influencing the size of eggs include the age, size and physiological condition of the females as well as the length of the growing period, the nutritional maintenance of the fish, the time of spawning and the arrangement of ova in the ovaries (Kazakov 1981). Alternatively, Healey and Heard (1984), Manzer and Miki (1986), and Healey (1987) have demonstrated among-population differences in fecundity in salmonids rearing in the same environments and have suggested that this variability has a largely genetic component. Since both of my study populations rear in a common lake and spawn at about the same time, likely encountering similar environmental conditions during their growth to maturity, it is reasonable to suggest that the between-population variation in Waimarino and Tokaanu River rainbow trout egg size and fecundity are primarily a result of genetic differences between stocks.

### Possible reasons for among-population differences in egg size and development rates

A number of studies have correlated between-population character differences in salmonids with differences in their natal environments; that is, researchers have attempted to identify the selective forces responsible for the stock differences and these are often of a physical or chemical nature (see Ricker 1972). In my study there were some striking differences in the respective spawning environments and these may account for the selection for inherited differences in egg size and incubation rates of the fish.

Firstly, rainbow trout had smaller eggs in the Tokaanu River where the redds had low intra-gravel, dissolved-oxygen levels; embryos and alevins are known to have higher survival rates than those from larger eggs and the females from Tokaanu River had smaller eggs (Sargent et al. 1987; van den Berghe and Gross 1989) and this may explain why Tokaanu rainbow trout eggs are smaller. Recent work by Fleming and Gross (1990) showed substantial inter-population variation in fecundity and egg size in coho salmon (**Oncorhynchus kisutch**) populations and correlated these observations with varying redd-oxygen concentrations; the populations spawning in streams with poor dissolved oxygen conditions had small eggs.

Tully (1989) recorded intra-redd and mid-stream dissolved oxygen levels in the Tokaanu that averaged 7.0 and 8.4 $mgL^{-1}$, respectively while corresponding concentrations of oxygen in the Waimarino river were substantially higher at 10.4 and 11.2 $mgL^{-1}$. Rainbow trout survive very poorly when dissolved oxygen levels are below 7 $mgL^{-1}$ (Phillips and Campbell 1962). Indeed, Davis (1975) recommended that 8.1 $mgL^{-1}$ was the incipient dissolved-oxygen threshold level for incubating salmonid eggs while Silver et al. (1963) reported sub-lethal effects in steelhead trout when oxygen levels were below 10.4 $mgL^{-1}$.

A variety of factors affect the levels of dissolved oxygen in redd water. For example, the particle-size composition of the gravel in salmonid spawning streams is a primary feature affecting dissolved-oxygen levels in redds (see Chapman 1988 for a comprehensive review). In general, small particles tend to reduce water flow through the redd gravel and, consequently, the amount of water and oxygen irrigating the embryos and alevins is reduced.

The "fredle index" has been used by Lotspeich and Everest (1981) for describing redd-particle composition of salmonid redds. This index incorporates elements that integrate gravel permeability and pore size and provides a good standard with which to compare the quality of gravel among redds (Chapman 1988). The Tokaanu and Waimarino redds had mean fredle indices of 1.5 and 12.9, respectively (see also Fig. 10.2). Using published values, embryo survival for these fredle values would be less than 40% for the average Tokaanu redd while approaching 100% in the Waimarino river (Lotspeich and Everest 1981; Chapman 1988).

A second factor which can effect the level of oxygen in a redd environment is the source of the water and its initial concentration of dissolved gases. Groundwater is the primary source of water in the Tokaanu River (Michaelis 1981) and groundwater is usually low in dissolved oxygen (Hansen 1975; Sowden and Power (1985). Thus, poor groundwater and gravel quality may be limiting the amount of oxygen reaching eggs and alevins in the Tokaanu River.

Regardless of the cause, oxygen levels appear to be marginal and sub-optimal for incubation of embryos and alevins in the Tokaanu River; if small eggs have higher survival rates under low oxygen conditions, large eggs may have been selected against in this stream. Furthermore, good spawning sites seem to be limited in the Tokaanu River. Both Tully (1989) and I have seen a high degree of redd superimposition in this stream.

If spawning habitat is limited, it may be highly advantageous for Tokaanu River rainbow trout alevins to leave their redds as quickly as possible so as not to be dug out by succeeding spawners. A high degree of redd superimposition would select against genetically slower developing alevins as well as larger eggs (which, phenotypically, take longer to develop as alevins) in Tokaanu River rainbow trout.

Faster developing alevins may not be as susceptible to the sustained and prolonged sub-lethal effects of continuous low oxygen levels in this stream. Earlier emergence might help ameliorate physiological problems associated with long-term low-oxygen conditions during development.

### 10.3.2 Survival Rates

#### Embryo development

In my study, the survival of rainbow trout embryos, from fertilization to hatch, was greater than 90% for all crosses at both 7 and 12°C. High survival rates are common in rainbow trout embryos at these temperatures and Murray (1980) and Humpesch

(1985) recorded rates greater than 70% for British Columbia and European rainbow trout, respectively.

Within temperature regimes there were slight but statistically significant differences in survival between crosses of different female groups, but similar rates for crosses having the same mothers. The among-group order in survival rate was consistent regardless of temperature; all crosses with Waimarino mothers had similar survival to each other but higher rates than embryos of any of the Tokaanu-female crosses, which in turn were similar to one another.

Embryos from larger salmonid eggs generally have lower survival than those from smaller eggs (Beacham and Murray 1985). Thus, in this experiment, the alternative hypothesis would predict that the TOK-female crosses should have the lower survival because they were from the largest eggs; from the results in this study we can accept this hypothesis.

### Alevin development

Alevin survival, from hatch to emergence, was above 90% for all crosses at 12°C but considerably lower at 7°C. These results suggest that alevins of both populations were more closely adapted to the former temperature. Nevertheless, unlike at 12°C, there was a considerable amount of among-cross variability in alevin survival rates at 7°C; while alevins of the pure crosses had similar and intermediate survival, the TOK-males x WAI-females-cross survival rate was considerably higher than these and the WAI-males x TOK-females alevins had the lowest rates of all groups.

The among-cross variability in alevin survival at 7°C appears to have been a result of both phenotypic and genotypic effects. Firstly, at lower temperatures (c. 7°C), rainbow trout alevin survival is affected by size; larger alevins have lower survival rates than those that are smaller (Murray 1980). (Note: larger eggs give rise to larger alevins--see below.) Thus, all crosses from Tokaanu River mothers should, therefore, have had lower survival than alevins of Waimarino mothers and this was not the case in my results; thus, a more complete explanation is required.

Differential survival, as a function of adaptation to specific temperature regimes has been observed in alevins of different populations of salmonids. For example, Beacham and Murray (1989) demonstrated that sockeye salmon alevins that naturally incubate under warmer water conditions had relatively much lower survival rates at low temperatures when compared to populations which normally incubate in colder temperatures.

In my study, the Waimarino River alevins came from a portion of the spawning run which reproduces late in the spawning season (19 October); that is, the peak of this run is usually about one month earlier when the water temperatures are much colder. Prior to emergence, the study Waimarino River alevins would have encountered temperatures that often are normally greater than 15°C (Fig. 3.2). Thus, alevins of these late-run Waimarino rainbow trout may be adapted for survival at temperatures that are much higher than found in the constant 10.5-12°C temperature regime seen in the Tokaanu River; these warm-water adapted Waimarino alevins may have lowered survival rates when incubated at lower temperatures. Additionally, if the late-run Waimarino River spawning males (genetically warm-water adapted) used in this experiment were mated to a female with smaller eggs, they should show higher survival rates than those which were mated to larger eggs when incubated at the same temperature. Alternatively, if the colder-water adapted Tokaanu River males were mated to a female with larger eggs (in this case, the Tokaanu laboratory sample), the lowered survival rates of the larger alevins would be counteracted by the inherently higher survival rates (genetically mediated) conveyed by the males of this population. Any reciprocal crosses would also show both phenotypic and genotypic effects; when the larger experimental Tokaanu eggs were crossed with Waimarino males there would be very poor alevin survival at low temperatures; the smaller experimental Waimarino eggs, fathered by cold-adapted Tokaanu males, would have very good survival at the lower temperatures. This explanation is consistent with the experimental results.

Of further note, I would also expect that if Waimarino River spawners were taken from earlier in the spawning run when incubation temperatures are normally much colder, these fish would be adapted to the lower temperature regime. That is, there is probably a seasonal component (temperature related) to the results seen in this part of my study.

### Effects on size of emerging juveniles

In my study there was a considerable amount of between-temperature and among-cross variability in the size of the juvenile trout at emergence. Firstly, there were substantial phenotypic (maternal) effects on the length and weight of the emerging alevins; the juveniles from those crosses from larger eggs (Tokaanu females) were longer and heavier than those from smaller eggs (Waimarino females). Other studies have shown that initial egg size can account for much variation in the final size of emerging alevins (Bilton 1971; Fowler 1972; Pitman 1979; Robison and Luempert 1984; Wallace and Aasjord 1984; Beacham et al. 1985; Rombough 1985; Wood and Foote 1990). For example, Beacham and Murray (1985) found that in chum salmon larger eggs produced heavier and longer juveniles than those from smaller eggs.

There were also substantial within-cross differences in alevin length and weight due to temperature; at 7°C all crosses of emerging rainbow trout fry were shorter and heavier than those incubated at 12°C. Timoshima (1972), studying temperature effects on embryonic development in rainbow trout from 2 to 13°C, found that alevins incubated at the extremes weighed less than those incubated at intermediate temperatures. Since 7°C represents an intermediate temperature, my results closely follow Timoshima's work.

Finally, at both temperatures there were size effects on the emerging juveniles, apparently resulting from the duration of the incubation period. With the exception of the TOK-pure versus WAI-males x TOK-females group at 12°C, crosses which had the same mothers (i.e., similar egg sizes), but which took longer to emerge due to paternal effects, were lighter in weight. That is, the longer the alevins took to develop into emerging juveniles, the less they weighed at emergence all other things being equal. Wood and Foote (1990) found similar "size versus incubation-duration" effects in kokanee and sockeye salmon juveniles; the alevins which incubated for a longer time before emerging were lighter in weight than their half-sibs which took less time until emergence.

In addition to weight, alevin body length was also affected by the duration of the incubation period. In my study, crosses of alevins from the same-sized eggs, but incubating over a longer period of time, were usually greater in body length. For both 7 and 12°C, earlier emerging TOK-pure alevins were shorter than their corresponding WAI-male x TOK-female crosses which took longer to emerge. Similarly, Wood and Foote (1990) found body-length differences amongst alevins from pure and reciprocal crosses of sockeye and kokanee salmon; the early emerging groups of a particular egg size were shorter than their later emerging counterparts.

In my study length/incubation duration effects were, however, observed only for the alevins arising from the larger Tokaanu River eggs. Incubation duration related effects on length may not be as sensitive as weight for incubation in juvenile salmonids (C.B. Murray, Canada Department of Fisheries and Oceans, Nanaimo Research Station, Nanaimo, BC, Canada, pers. comm.).

### Adaptive significance of juvenile size

The body size at of recently emerged salmonids can be critical to their survival in the wild (Bams 1969; Fowler 1972; West and Larkin 1987; Healey 1982). For example, the ability of young trout and salmon to defend a territory in streams is related to size (Chapman 1962) although the smaller, earlier-emerging juveniles may sometimes be successful in defence against larger, later-emerging conspecifics (Mason and Chapman 1965).

In the previous chapter I showed that recently emerged Waimarino River juveniles have a much higher innate level of aggressive activity than Tokaanu River rainbow trout and this difference may be adaptive. Perhaps greater aggressiveness combined with larger body size in the young Waimarino River fish (resulting from the generally larger eggs found in this population of trout) is important for their survival in this stream.

# SECTION IV--SUMMARY

## Chapter 11.--GENERAL DISCUSSION

### 11.1 MANAGEMENT IMPLICATIONS

The Lake Taupo sport fishery for trout is socially and economically important to New Zealand (Shaw et al. 1985). Understanding how rainbow trout have acclimatized and adapted to this watershed is necessary for the good management of the fishery therein. My study provides useful information in this regard.

My observation that there is a size-threshold (ca. 94 mm fork length) that these pre-emigrant juvenile rainbow trout must first reach in the stream before survival can occur in the lake (Chapters 4,5) has important implications for any future hatchery-augmentation programs. Since hatchery-cultured rainbow trout which are less than this threshold size (c. 94 mm) would have a low probability of survival if placed directly into the lake and, because they would contribute nothing positive to the sport fishery, such a program would be a waste of agency time and resources. Furthermore, if sub-threshold sized juveniles were placed in streams already holding rearing trout, they would still have to grow to the appropriate minimum size and might compete with, or displace, the wild juveniles and this would result in an overall lowered production.

Fisheries managers may also decide that a cost-effective way of increasing the production of trout in this watershed would be to enhance stream habitat. Thus, it is of use to know which kinds of stream habitat (i.e., instream woody cover) may be limiting. My study outlines some of the types of physical characteristics which appear to be important for the various species and size classes of fish in the Waimarino River and draws some general conclusions with regards to the needs of these fish (Chapters 6,7). For example, herbaceous and woody cover are highly utilized by juvenile trout in these streams. However, previous management strategies have been to remove organic debris from the instream and riparian zones of spawning and rearing streams in this watershed in order to provide more room for angler's fly-fishing casts. By extirpating this valuable habitat, the negative effects may be compounded by increasing both the exploitation rates (improved angler access), as well as reducing juvenile output due to the losses of critical rearing areas. Escapements of adult trout into Lake Taupo spawning and rearing streams are now reaching historic lows and a smaller daily-harvest limit (from eight to three fish) has been initiated for the 1991 angling season.

Finally, understanding the genetic make-up of the fishes in this watershed is important to the continuation of a quality fishery. Although the stocks examined in this study do not show among-population variability with regards to allozymes (Rosenau et al. 1991; Snowdon, in prep.), other characters do vary; they include meristics (Chapter 8), agonistic behaviours (Chapter 9), and developmental and survival rates during incubation (Chapter 10). At present, the Lake Taupo trout fishery is the result of natural production but with recent drops in the escapement numbers a change in management policy may include augmentation of juveniles through hatchery programs.

The Tokaanu River is presently the source of most of the eggs that are used in the North Island hatchery programs that releases juvenile rainbow trout into other lakes and streams. My study demonstrated that Tokaanu River rainbows are genetically different for some traits when compared to other Lake Taupo stocks and as a consequence, Tokaanu River rainbow trout may not be the best adapted stock for hatchery out-plants in Lake Taupo or other watersheds.

## 11.2 SCIENTIFIC OBSERVATIONS

### Acclimatization of rainbow trout in Lake Taupo

The acclimatization of "desirable" and "pest" organisms, and their effects on other species, has recently been closely examined in a number of comprehensive studies (Courtenay and Stauffer 1984; Groves and Burdon 1986; Drake et al. 1989). In New Zealand, the perturbations caused by intentional fish introductions (e.g., the European carp (**Cyprinus carpio**), the rudd (**Scardinius erythrophthalmus**); McDowall 1984) have often been as disastrous and created as much grief to native fauna as accidental transplants (e.g., sailfin mollies (**Poecilia latipinna**); McDowall 1984).

Although rainbow trout were intentionally introduced into New Zealand in the latter half of the 19th century, by the mid-20th they were well entrenched in the freshwater ecology of this country (McDowall 1990). New Zealand is notorious for its introductions of non-indigenous species of plants and animals that have survived and flourished at the expense of the natives. Indeed, Charles Darwin, in his publication, **The Origin of Species,** stated:

> **From the extraordinary manner in which European productions have recently spread over New Zealand, and have seized on places which must have been previously occupied, we may believe if all the animals and plants of Great Britain were set free in New Zealand, that in the course of time a multitude of British forms would become thoroughly naturalized there, and would exterminate many of the natives (Peckam 1959).**

As McDowall (1990) indicates, rainbow trout have also been implicated in the reduction of population numbers of a variety of native fish species (e.g., koaro in Lake Taupo), if not the outright extinction of some rare species.

## Adaptation of rainbow trout to Lake Taupo

Trying to predict the effects on native species by a non-endemic organism is rarely correct. Nevertheless, although biologists often study the introduced organisms in their new environments with the intention of finding ways to eradicate them, the biological investigation an introduced species under novel conditions can still tell us much about the adaptive and evolutionary biology of the species. Rainbow trout in New Zealand and, indeed, in Lake Taupo have provided us with an excellent circumstance for such a study.

Adaptation has been defined as the process by which populations increase their fitness, in a given environment, through natural selection (Loeschcke 1987). Thus, the studies of ecology and genetics, and the intimate relationship between these two subjects (Barker and Thomas 1987), provide the focus of our understanding of the adaptation of rainbow trout in the Lake Taupo environment. Firstly, the simplest constraint to the adaptation of an organism to an environment is its genetic variability, or lack thereof (Loeschcke 1987). There may be fitness differences among populations or individuals, throughout both space and time, resulting from inter-group genetic variation (Barker and Thomas 1987). While natural selection acts on phenotypes, and our primary observations are at the level of the phenotype, the underlying phenomena are genetic. Therefore, we can unequivocally state that there are certain genetic boundaries which allow rainbow trout to exist in Lake Taupo.

Because a small number of rainbow trout were originally introduced into New Zealand, we would expect that there was a more limited number of genotypes, than would normally be found in an average population in the species' natal environments, for selection to act upon. Scott et al. (1978) suggest that the original population of New Zealand rainbow trout came from a small stream in central-coast California, USA, and, the fact that hatchery practices often use a restricted sample for breeding purposes, the number of parents used to produce the New Zealand populations of rainbow trout was undoubtedly highly limited. That is, the "effective population size" contributing to the introduction of New Zealand rainbow trout was certainly circumscribed and the resulting "founder effects" may have played a major role in defining the genetic make-up of Lake Taupo trout. The term "founder effect" is a term first coined by Ernst Mayr (Provine 1989) and it refers to the reduced genetic variability when a "large" population arises from a "small" number of reproducing adults.

Electrophoretic work, undertaken by Snowdon (in prep.) from the fish of the three study streams in this thesis, indicates that there is no statistically significant among-population genetic variability with regards to the allozymes examined. Furthermore, compared to California, USA, stocks of steelhead, the location of the donor population for most of the extant New Zealand rainbow trout, Lake Taupo rainbow trout appear to exhibit less heterozygosity and are statistically separable from these groups of fish. The lack of differentiation among Lake Taupo populations is thought to be due to the short time since acclimatization to the watersheds; the allozyme characters that were examined are thought to be selectively neutral (Snowdon in prep.). Thus, there is strong evidence that the initial effective population size was small enough to cause some founder effects. Nevertheless, it appears that enough genetic variability was brought into the country for a number of traits to become differentiated between populations including the characteristics examined in this and other studies (Tully 1989); this assumes that the genetic variability seen in this and Tully's study was not generated here in New Zealand (i.e., through mutation).

Introduced organisms are subjected to various ecological constraints and their ability to survive depends on previously attained adaptations to a specific environment and the behavioural and physiological plasticity should that environment change. The term "pre-adapted" has been used to describe how well an organism can fit into a novel environment (Stauffer 1984). By definition, an introduced organism has had no experience relative to its new habitat. Nevertheless, compared to most endemic populations of rainbow trout in their natal environments, these Lake Taupo fish are bigger in size, in better physical condition, and more numerous for the available amount of rearing habitat (Burstall 1983). This is also due, in part, to the extraordinary physical and biological conditions for survival encountered by these fish.

Perhaps, what is most extraordinary about rainbow trout populations worldwide, and including the populations in Lake Taupo, is that this species of fish has the ability to make a living in such diverse sorts of environments (MacCrimmon 1971). That is, within certain boundaries, they have enormous biological plasticity to acclimatise and adapt to a wide variety of conditions. This, most assuredly, is due in greater part to their genetic constitution. Rainbow trout are thought to be derived from an ancestor which arose through a tetraploid event (Allendorf and Thorgaard 1984) and it has been suggested by these authors that the extraordinary success of rainbow trout living in such diverse habitats may be due to this aspect; the doubling effect of the tetraploid genetic structure may buffer against the deleterious effects found in unusual environments by providing a greater amount of genetic variability with which selection can "play with" (Allendorf and Thorgaard 1984). Thus, the combination of the rainbow trout's extraordinary genetic constitution, and the optimal conditions found in Lake Taupo and its streams, have made this a very successful species in this watershed.

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# Natal-stream rearing in three populations of rainbow trout in Lake Taupo, New Zealand

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**Abstract** Scales were taken from adult rainbow trout (*Oncorhynchus mykiss*, previously *Salmo gairdneri*) from the Waimarino, Tokaanu, and Hinemaiaia Rivers; these are tributaries of Lake Taupo, New Zealand. The scales showed both widely-spaced outer, and narrowly-spaced inner, circulus zones. Although there were no among-population differences in average circulus spacing in the outer growth zone, there were significant among-population differences in the inner zone; these two zones are suggested to represent (common) lake and natal-stream rearing, respectively. The back-calculated minimum and average lengths at migration of juveniles from stream to lake was similar for all three populations (c. 94 mm and 140 mm, respectively) but there were significant among-population differences in age at emigration. The scale patterns and stream sampling suggested that most Hinemaiaia River rainbow trout left the river within the first year whereas much higher proportions of juveniles in the other two streams overwintered before emigrating in their second year.

**Keywords** *Oncorhynchus mykiss*; *Salmo gairdneri*; rainbow trout; juvenile; migration; natal-stream rearing; scale patterns; circuli

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## INTRODUCTION

A prolonged period of stream residence is a feature of many populations of migratory rainbow trout and steelhead (*Oncorhynchus mykiss*, previously *Salmo gairdneri*). Various studies (e.g., Biette et al. 1981; Ward & Slaney 1988) have shown that survival to maturity for lake- or ocean-rearing populations of this species may involve several years of stream rearing. These studies indicated a pre-migratory minimum size of rainbow trout before they could survive in the lake or ocean. Indeed, over geographically large rearing areas (e.g., the Great Lakes (USA), the eastern Pacific Ocean) there are remarkable similarities among populations in the sizes of the juveniles at emigration to the lacustrine or marine environment (Biette et al. 1981; Ward & Slaney 1988). However, because of varying inter-year or inter-stream productivity levels, and corresponding differences in growth rates, the age at emigration by the young trout from the stream may vary considerably among populations or years (Ward & Slaney 1988).

Lake Taupo, New Zealand, is a rearing area for several rainbow trout populations which support a world renowned sport fishery (Forsyth & Howard-Williams 1983). These trout were first introduced into the watershed about 1900, apparently from an anadromous steelhead population in California, USA (Scott et al. 1978).

In a recent study (Stephens 1989), features of the scales of adult rainbow trout taken from the lake indicated two major zones of circulus distribution: an inner, closely-spaced group of circuli, and a separate, widely-spaced set of outer circuli. Since circulus spacing of the inner zone in lake-caught rainbow trout scales looked similar to the pattern found on the scales of the juvenile trout residing in Lake Taupo spawning streams, Stephens (1989) suggested that the inner pattern on the scales of the larger, lake-caught trout represented stream growth; he proposed that stream rearing may be an important component of the life history of Lake Taupo rainbow trout. Thus, the purpose of the present study was to investigate

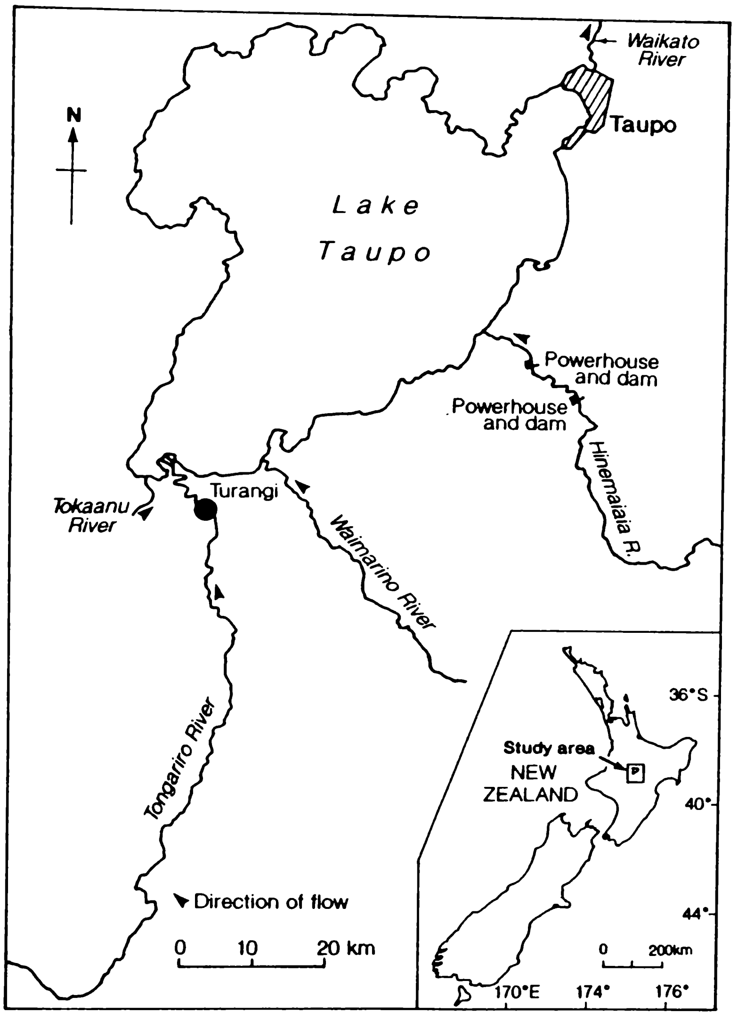

**Fig. 1** Location of the study streams flowing into Lake Taupo, central North Island, New Zealand.

**Table 1** Characteristics of the study streams. Data of discharge and water chemistry from Schouten et al. (1981). Water chemistry data are tabulated as the flow-weighted mean; samples were taken at state highway bridges; sample sizes in brackets.

| Feature | Waimarino River | Tokaanu River | Hinemaiaia River |
|---|---|---|---|
| Mean annual discharge ($m^3 s^{-1}$) | 3.1 | 1.8 | 5.9 |
| Maximum discharge ($m^3 s^{-1}$) | 44.0 | 3.7 | 50.7 |
| Minium discharge ($m^3 s^{-1}$) | 0.5 | 1.3 | 0.7 |
| Catchment area ($km^2$) | 79 | 35 | 165 |
| Mean gradient (%) | 1.3 | 0.4 | 0.9 |
| Water source | Surface run-off | Groundwater | Surface run-off and groundwater |
| Flow regime (Fig. 3) | Variable; unregulated | Stable; unregulated | Daily, seasonal variability; regulated |
| Conductivity @ 25°C ($mS\ m^{-1}$) | 4.7 (11) | 24.8 (14) | 5.3 (10) |
| Reactive phosphorus ($mg\ m^{-3}$) | 11 (13) | 44 (16) | 29 (11) |
| Inorganic nitrogen ($mg\ m^{-3}$) | 74 (13) | 180 (16) | 68 (11) |

the importance of natal-stream rearing to rainbow trout in Lake Taupo and its implications for management of these fisheries.

I examined the scale features of mature adult rainbow trout known to have migrated from Lake Taupo into three spawning tributaries of widely differing biophysical characteristics: the Waimarino, Tokaanu, and Hinemaiaia Rivers. I also looked at the change in size (growth) and numbers of juvenile rainbow trout in these same rivers over the period of a year and intended to compare the interpretation of adult scale patterns to the sizes and ages of juvenile rainbow trout residing in their respective streams.

The study hypotheses were:

(1) that Lake Taupo rainbow trout which survive to maturity normally undergo a protracted period of juvenile stream rearing before emigrating to the lake—this is reflected in two different scale-circulus features in the adults: an inner zone of narrowly spaced, and an outer zone of widely spaced circuli; and

(2) that environmental differences among natal-rearing streams result in growth differences among these populations during the fluvial-growth period; this results in inter-population variability in the stream-zone scale patterns as well as differences in size-at-age as juveniles in the stream, and age-at-migration to the lake.

## STUDY AREA

Lake Taupo is located in the central North Island of New Zealand (Fig. 1) and is the largest freshwater lake in Australasia; aspects of the lake's hydrogeology, limnology, and fisheries biology have been well described (Forsyth & Howard-Williams 1983). The three tributary streams investigated in this study were the Waimarino, Tokaanu, and Hinemaiaia Rivers. Historically, each has supported large spawning runs of migratory rainbow trout thought to contribute significantly to the Lake Taupo sport fishery. The streams vary in several biophysical characters (Table 1). However, they are similar in mean annual discharge (less than one-half an order of magnitude difference) but Tokaanu River is stable as a result of its groundwater source whereas the Waimarino and Hinemaiaia Rivers have seasonally variable flows (Fig. 2). Temperature and nutrients also differ considerably with the Tokaanu River having relatively more stable temperatures (Fig. 3) and higher levels of phosphorus and nitrogen (Table 1) than the other streams.

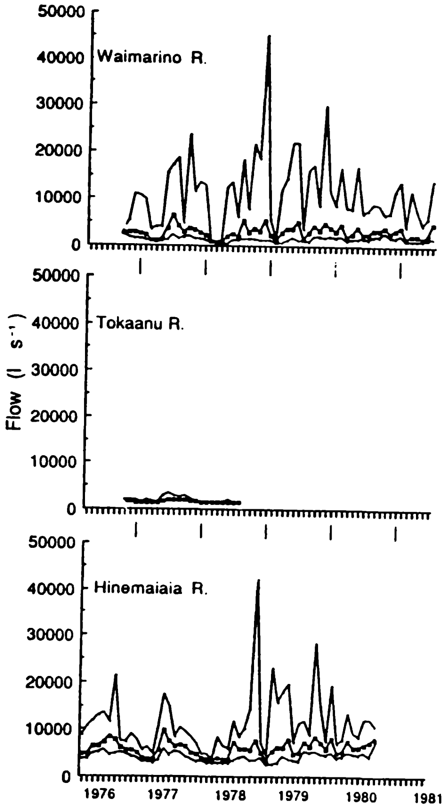

Fig. 2 Minimum, mean, and maximum monthly flows (1976 to 1981) in the study streams. Data courtesy of the Department of Scientific and Industrial Research, Water Quality Centre, Hamilton, New Zealand.

## METHODS

### Scale analysis

In September 1987, 100 sexually mature rainbow trout were tangle-netted with gill nets (stretched mesh 90 mm) from each of the study rivers. September is around the peak spawning period for Lake Taupo rainbow trout and these fish were identified as having recently come from Lake Taupo based on body sizes (Table 2; cf. Tully 1989). Six scales were taken from a "key scale" region located along a diagonal line from the posterior insertion of the dorsal fin down to the lateral line in a posterior direction, and two rows up. All scales were taken from the left side of the body. The scales were examined at 50X magnification using a microfiche-type scale reader. One scale from each slide was chosen for all measurements and scales

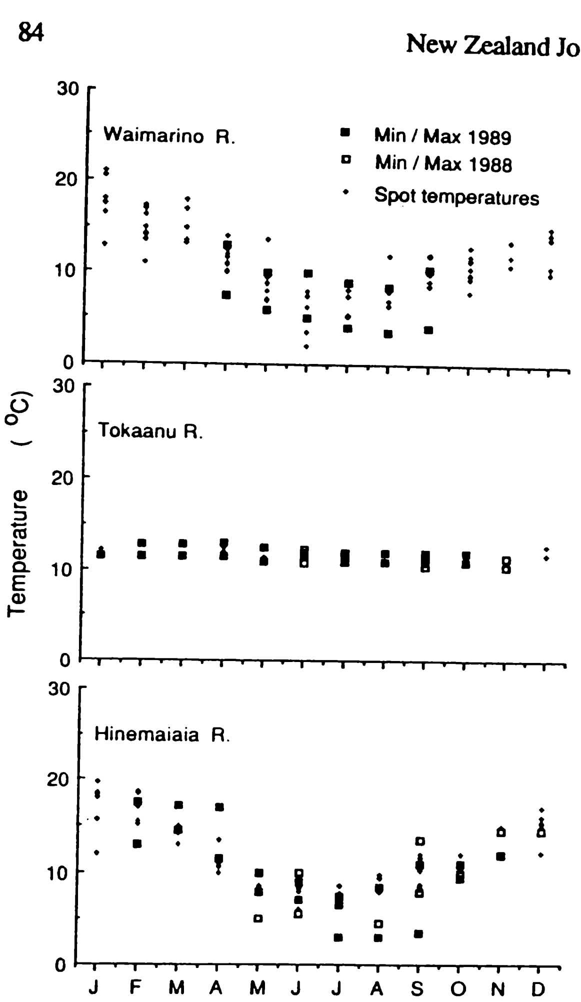

**Fig. 3** Water temperatures in the study streams. Measurements are shown as either the minimum and maximum recorded temperatures, as measured by maximum/minimum thermometers (1988–89), or spot temperatures (1976–89) as recorded by the New Zealand Department of Scientific and Industrial Research (Water Quality Centre, Hamilton, New Zealand) and this study. Waimarino River temperatures recorded at Kepa Road bridge, Tokaanu River temperatures recorded at the New Zealand Department of Conservation adult fish trap, and Hinemaiaia River temperatures recorded at State Highway 1 bridge.

showing abnormalities were not included in the analyses.

To minimise observer bias and ensure accuracy and precision, the following procedures were used. First, the presence of any circulus discontinuities or "checks" were noted; then the number of circuli and distances between checks were counted and measured along the radius (longest axis) of the scale from the centre of the focus to the edge of the scale. A check was defined as the last narrowly spaced circulus, of a group of narrow circuli, preceding a group of more widely spaced circuli (Bilton & Robins 1971a). Average circulus spacing was determined by dividing the distance along the radius, for the zone of interest, by the number of circuli located within that zone. Four readings were made to ensure consistency in measurements and counts for each scale; discrepancies were less than 5% of the total sample for each population.

The back-calculated lengths of the fish at the various scale checks were estimated using Stephens' (1989) scale-radius to fork-length relationship for maiden Lake Taupo rainbow trout. His regression equation was:

$$L = 153\,S + 30 \qquad R^2 = 0.97,$$

where $L$ is the estimated fish fork length (in mm) for a particular point on the radius of the scale, and $S$ is the distance (in mm) along the radius from the focus to that particular point on the scale. Only immature trout were included in his analysis because of possible problems associated with resorption of scales at spawning.

## Juvenile sampling

To examine population changes in juvenile-fish size and abundance in the study streams, I trapped each of the rivers once each season from the winter of 1988 to the autumn of 1989. Small portable, wire (mesh size 3 and 6 mm) "minnow-traps" (Swales 1987), baited with thumbnail-sized pieces of trout ova, were used to catch the fish. The traps were set overnight and retrieved the next morning.

**Table 2** Average post-orbital to hypural lengths of adult trout used for scale analysis. Measurements in mm and with standard deviations and ranges. The fish were measured from the posterior of the eye socket to the hypural crease (post-orbital to hypural length) to avoid problems associated with changes in snout length and caudal-fin damage in spawning fish.

| | Waimarino River | Tokaanu River | Hinemaiaia River |
|---|---|---|---|
| Males | 401 ± 26 (36) 364–475 | 384 ± 37 (27) 338–480 | 412 ± 24 (61) 332–481 |
| Females | 417 ± 27 (48) 364–475 | 407 ± 24 (52) 370–512 | 409 ± 22 (33) 362–497 |

Three sites were sampled on each river and each averaged about 0.5 km in length. The sites were chosen to reflect the variation in characteristics of each stream. Individual traps were set according to the variation in site characteristics (velocity, depth, substrate, presence or absence of cover) occurring within a study section. The number of traps varied slightly among seasons but was similar among study sites within rivers and among rivers for any particular season (Table 3). Trapped fish were identified to species and measured (fork length). Catch-per-unit effort (CPUE) of trout was calculated by averaging the number of fish caught per trap over all of the sites within a stream in a season; this value was assumed to reflect relative changes in abundance within and among streams and seasons.

The juvenile trout caught by trapping were grouped into year classes based on length-frequency distributions. Scales from a sample of these fish, over the range of lengths in the distribution, were inspected to confirm the age classifications. Winter checks were seen in some juveniles of all three populations. A year class was defined as those fish that emerged from the spawning gravel between 1 June and 30 May. This period was based on known spawning times (Tully 1989) and the size-frequency of the catches in this study.

For all statistical tests in this study, a probability level of $P < 0.05$ was considered to be biologically significant.

## RESULTS

### Adult scale patterns

***Lake-growth zone*** The Waimarino, Tokaanu, and Hinemaiaia Rivers samples had 84, 79, and 94 trout with readable scales, respectively. All scales had two primary circulus features (Fig. 4): an inner zone of closely spaced circuli surrounding the focus (S1, S2), and an outer, more distal, zone having wider and homogeneous spacings between circuli (L). The check between these two zones was abrupt and easily recognised. Because the scales examined in this study were taken from recent migrants known to have emigrated from the lake where they had spent many months to years, the whole of this homogeneously spaced outer part of the scale (Fig. 4: L) represented lake growth and is hereafter referred to as the *lake-growth zone*. There were no significant differences among populations in the average widths between circuli for this zone of the scale (Table 4A; ANOVA $F = 0.319, P = 0.727$). The average back-calculated

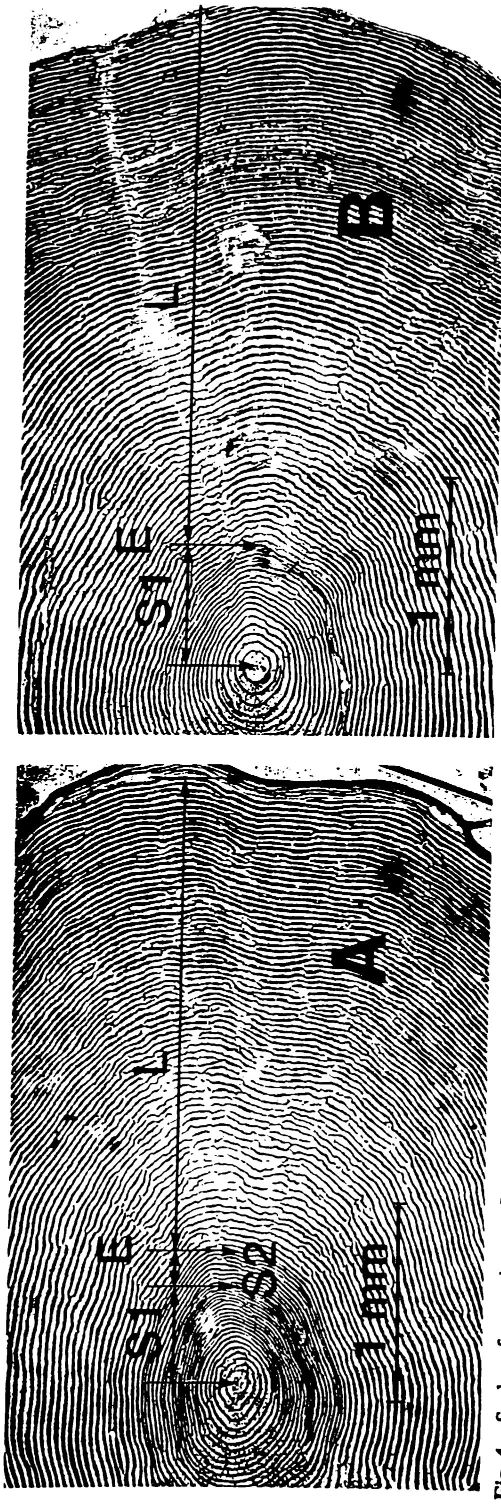

**Fig. 4** Scales of spawning-run Lake Taupo rainbow trout. A, Stream overwintering pattern. B, Stream non-overwintering pattern. L, lake-growth zone; S1, pre-winter stream growth; S2, post-winter stream growth; E, emigration to lake.

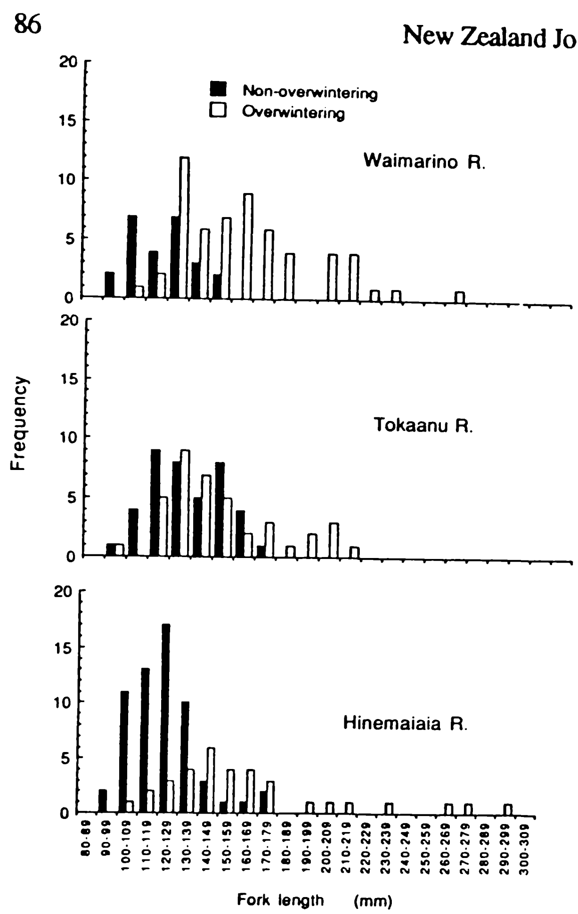

**Fig. 5** Frequency distribution of estimated juvenile rainbow trout lengths at emigration to the lake as back-calculated from the adult scale patterns.

**Table 3** Number of traps set per (austral) season in the sampling streams, winter 1988–autumn 1989. Each unit represents one standard overnight trapping session.

| | Waimarino R. | Tokaanu R. | Hinemaiaia R. |
|---|---|---|---|
| Winter | 151 | 137 | 134 |
| Spring | 134 | 135 | 135 |
| Summer | 174 | 178 | 162 |
| Autumn | 176 | 179 | 168 |

fork lengths of the juvenile rainbow trout at the start of the lake-growth zone were 145, 136, and 139 mm for the Waimarino, Tokaanu, and Hinemaiaia Rivers, respectively, and these lengths are not significantly different (Table 5A; ANOVA $F = 1.699$, $P = 0.185$). The minimum back-calculated fork length at emigration to the lake was about 94 mm and was consistent among all three populations (Table 5; Fig. 5).

***Stream-growth zone*** The inner zone of closely spaced circuli surrounding the focus and on outward to the start of the lake-growth zone (Fig. 4: S1, S2) was present on all scales examined and hereafter is referred to as the *stream-growth zone*. Two predominant stream-growth patterns were found:

1) those scales having a distinct check located some distance between the centre of the focus and the start of the lake-growth zone (Fig. 4A: S1+S2); or
2) those scales which showed no check in this area of the scale (Fig. 4B; S1 only). Scales which showed a check in the stream-growth zone of circuli will be referred to as having an *overwintering pattern* and those scales not having the check, a *non-overwintering pattern*. The overwintering pattern varied in frequency among the study populations: Waimarino R. 70% (59/84 fish); Tokaanu R. 49% (39/79 fish); Hinemaiaia R. 36% (34/94 fish) ($\chi^2 = 20.79$, $P < 0.001$).

As an approximate estimate of the trout length at the end of their first growing season, a back-calculation was made to the first scale check, regardless of the overwintering pattern; the average fish length to this check was different among populations (Table 5B) with the mean lengths of the trout from the Hinemaiaia and Tokaanu Rivers significantly greater than from the Waimarino River (ANOVA $F = 10.69$, $P < 0.001$; Tukey's HSD $\underline{\text{W}}$ $\underline{\text{T H}}$). The length of the trout at emigration to the lake (lake/stream check) was also significantly greater in the overwintering trout than in the non-overwintering fish (Table 6A vs 6C: Waimarino $t = 5.929$, $P < 0.001$; Tokaanu $t = 2.859$,

**Table 4** Among-population comparisons of average widths between circuli for the adult trout scales. Values are in mm X 50 (scale-reader magnification), with standard deviations, and *n* values in brackets. A, Lake-growth zone—from stream-growth zone to scale edge; B, from centre of focus to end of stream-growth zone—all rearing patterns combined; C, from centre of focus to first circulus check regardless of winter rearing pattern.

| | Waimarino River | Tokaanu River | Hinemaiaia River |
|---|---|---|---|
| A | 1.712 ± 0.117 (84) | 1.698 ± 0.139 (79) | 1.711 ± 0.133 (94) |
| B | 1.296 ± 0.138 (84) | 1.260 ± 0.150 (79) | 1.328 ± 0.154 (94) |
| C | 1.277 ± 0.153 (84) | 1.269 ± 0.183 (79) | 1.330 ± 0.160 (94) |

$P = 0.007$; Hinemaiaia $t = 6.174$, $P < 0.001$) but the non-overwintering fish were longer at emigration to the lake than the overwintering trout were at the formation of the winter check (Table 6B vs 6C; Waimarino $t = 5.320$, $P < 0.001$; Tokaanu $t = 9.120$, $P < 0.001$; Hinemaiaia $t = 4.132$, $P < 0.001$), and this was consistent for all populations.

There were highly significant within-population differences in the circulus spacing between the stream-growth and the lake-growth zones of the scale (Table 4A vs 4B: Waimarino $t = 21.059$ $P < 0.001$, Tokaanu $t = 19.094$ $P < 0.001$, Hinemaiaia $t = 18.282$, $P < 0.001$). There were also significant among-population differences in the average spaces between circuli in the stream-growth zone of the scale from the focus to the stream/lake-growth zone check (Table 4B: ANOVA $F = 4.617$, $P = 0.011$; Tukey's HSD T W H) as well as from the focus to the first check regardless of winter pattern (Table 4C: ANOVA $F = 3.587$, $P = 0.027$; Tukey's HSD T W H); the Hinemaiaia River fish had the widest average spacings, those from the Tokaanu River the narrowest.

## Juvenile trout sampling

***1988 year class, young-of-the-year trout: $0^+$*** By spring, catches of young-of-the-year rainbow trout, most of whom had just recently emerged (c. 25 mm, Fig. 6), increased substantially over winter catches in all three streams with the Hinemaiaia River CPUE's being especially high (7× Waimarino River; 40× Tokaanu River) (Fig. 7); peak emergence may have been earliest in the Hinemaiaia River. However, although the catches of these fish remained relatively high through to autumn in the Waimarino and Tokaanu Rivers, they fell to very low levels in the Hinemaiaia River by autumn (Fig. 7). The $0^+$ trout from all of the populations showed significant inter-seasonal increases in length from emergence through until the end of the study (Fig. 6). However, growth appeared to be greatest in the Hinemaiaia River over the whole sampling period; by summer, the mean length of its young-of-the-year trout was c. 20 mm longer than that of the other two populations (Fig. 6). Indeed, during the autumn sampling the few Hinemaiaia River trout that were caught, continued to average larger than fish of the other two populations: over 50% of Hinemaiaia rainbow trout were equal to or longer than 94 mm whereas only 27% of the Waimarino and 9% of the Tokaanu trout surpassed this length.

***1987 year class: $1^+$*** In contrast to the other streams, few rainbow trout of the $1^+$ year class could be found in the Hinemaiaia River during any sampling period (Fig. 7). However, there were substantial reductions in catches of the $1^+$ fish from winter to spring in the other two streams; at this time the Waimarino River had the highest catches (Fig. 7). The few Hinemaiaia rainbow trout that were caught in spring continued to average considerably larger than the trout of the other two populations (Fig. 6).

**Table 5** Among-population comparisons of juvenile trout fork lengths back-calulated from the adult trout scales. Lengths (mm) were estimated using Stephens' (1989) regression formula $L = 153 S + 30$, with standard deviations, *n* values in brackets, and with ranges. A, At emigration to the lake; B, to first circulus check regardless of overwintering pattern.

| | Waimarino River | Tokaanu River | Hinemaiaia River |
|---|---|---|---|
| A | 144.5 ± 32.2 (84) 94–256 | 135.7 ± 23.8 (79) 94–201 | 138.5 ± 36.3 (94) 97–299 |
| B | 103.6 ± 18.1 (84) 70–149 | 111.5 ± 24.1 (79) 67–168 | 117.9 ± 19.7 (94) 76–171 |

**Table 6** Fork lengths of juvenile rainbow trout back-calculated from the adult scales. Lengths (mm) were estimated using Stephens' (1989) regression formula $L = 153 S + 30$, with standard deviations, *n* values in brackets, and with ranges. A, Overwintering scale pattern: fish length at emigration to the lake; B, Overwintering scale pattern: fish length at winter discontinuity; C, Non-overwintering scale pattern: fish length at emigration to lake.

| | Waimarino River | Tokaanu River | Hinemaiaia River |
|---|---|---|---|
| A | 160.0 ± 30.9 (59) 103–256 | 143.1 ± 27.3 (39) 94–201 | 164.5 ± 46.3 (34) 103–299 |
| B | 97.6 ± 16.3 (59) 70–140 | 93.9 ± 16.5 (39) 67–140 | 107.7 ± 20.8 (34) 76–149 |
| C | 117.6 ± 14.1 (25) 94–149 | 128.5 ± 17.1 (40) 97–167 | 123.8 ± 16.5 (60) 97–171 |

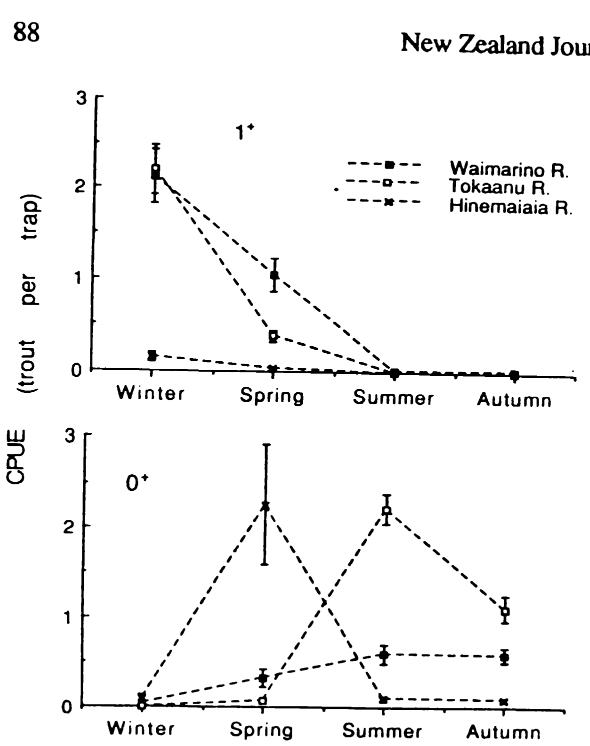

Fig. 6 Average lengths of minnow-trapped juvenile rainbow trout. With standard deviations, austral seasons are: June to August (winter), September to November (spring), December to February (summer), and March to May (autumn).

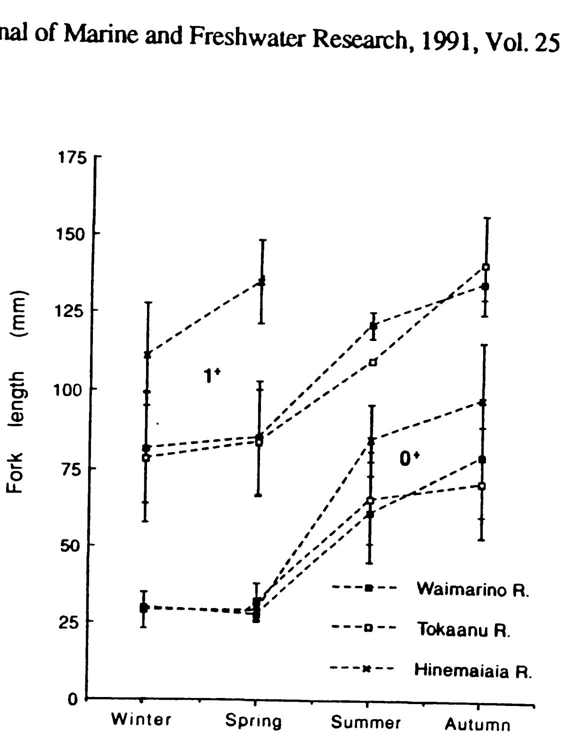

Fig. 7 Catch-per-unit effort of minnow-trapped juvenile rainbow trout. An overnight set by one trap was considered to be one trapping unit of effort. With standard errors.

*1986 year class: 2+* Few of the 1986 year class of rainbow trout were caught in any of the rivers during this study at any time of the year (< 10 fish for each stream). Drift diving observations confirmed the low number of this size/age class in these rivers.

## DISCUSSION

All the adult rainbow trout scales in this study showed the two basic features of an inner zone of closely spaced circuli surrounding the focus, and a more distally located outer zone having much wider average spaces between circuli. Sequential natal-stream and lake rearing periods of slower and faster growth, respectively, appear to account for these two patterns.

Variation in surface features of scales develops through changes in the frequency of circulus deposition and the spacings between circuli can be changed by alterations in the growth rate of the fish (Doyle et al. 1987). This rate varies as a function of physiological responses to exogenous and endogenous conditions (Casselman 1987) such as changes in food, temperature, light, sexual maturity, etc. The variation seen in Lake Taupo rainbow trout scales appears to be primarily a functional response to different growth conditions.

### Lake-growth zone

The scales examined in this study were taken from fish that had recently migrated from Lake Taupo; thus, it is reasonable to suggest that the wide outer zone of homogeneously spaced circuli, seen reaching to the outer margin on all scales (Fig. 5: L), represents rearing in the lake. Furthermore, there were no among-population differences in the average circulus spacing of the outer-growth zone of the scale, suggesting that all of these fish were rearing under similar conditions, or in a common environment, during its formation. Although most Lake Taupo rainbow trout are thought to mature only after at least one winter of rearing in the lake (Stephens 1989) there were no marked yearly checks, or annuli (Tesch 1971), in the outer-growth zone. The absence of annuli in this scale-area may be explained by the narrow range of temperatures (Forsyth & Howard-Williams 1983) and the even spread of primary production (Viner & White 1989) occurring in Lake Taupo over an annual period. Thus, all evidence suggests that this outer zone of the scale represented lake growth.

### Stream-growth zone

A distinct inner-circulus pattern, present on all Lake Taupo rainbow trout scales examined (Fig. 5: S1, S2), appears to represent a stream-growth zone; its position on the scale (starting from the focus outward) indicates that this zone was laid down soon after emergence of the young fry from the redd. Because the spacings between circuli in this scale zone were narrow compared to the lake-growth zone it is reasonable to suggest that they were formed under considerably different rearing conditions, and probably in physically different locations.

Rearing in the lake during the formation of this zone is a possibility but appears unlikely. Intensive sampling of both the limnetic and littoral zones of Lake Taupo over the last 10 years, using a variety of techniques including seining, gill-netting, echo-sounding, drop-netting, and SCUBA-diving, demonstrated that rainbow trout less than about 94 mm in length were rare in these habitats (Stephens 1989). Newly emergent trout fry enter Lake Taupo in large numbers but apparently experience high mortality soon after reaching the lake (Stephens 1989).

The among-population variability in various characteristics seen in this scale-zone suggests that the three stocks had reared under environmentally different conditions during its formation; the natal stream could provide the possible habitat for these differences. For example, I observed the variable presence of a pronounced circulus check in the inner growth zone of the scale ranging in frequency from 70% (Waimarino River) to 36% (Hinemaiaia River). It seemed likely that this inner growth zone check was an overwintering mark as it resembles the published descriptions of a winter annulus (e.g., Tesch 1971). Water temperatures in the Waimarino and Hinemaiaia Rivers can approach 0°C in the winter (Fig. 3) and under such conditions the growth of any stream-rearing fish would virtually cease, thereby forming a check on the scale. Since no such drop in temperature occurs in the Tokaanu River (Fig. 3) the explanation for the presence of a winter mark in the stream-growth zone of these trout is more equivocal. However, factors other than temperature (e.g., seasonal changes in light and food) are known to produce a scale check (Bilton & Robins 1971a, 1971b).

Average spacings between circuli also differed among populations for the stream-growth zone of the scale. The widest spacings were found in the Hinemaiaia River trout suggesting that they had the greatest average growth rates (cf., Doyle et al. 1987) during the formation of this part of the scale (Table 4B, 4C); by contrast, the Tokaanu River rainbow trout had the narrowest circuli spacings suggesting they grew the most slowly. I suggest that substantial environmental differences occurring among the respective natal-stream environments, and specifically temperature (Fig. 3) and nutrients (Table 1), could account for differences in growth rates as inferred by the circulus spacing.

Finally, I observed among-population variation in the back-calculated average lengths of juvenile trout to the end of their first growing season. For this comparison I assumed that for non-overwintering fish the lake/stream check represented the greatest possible pre-winter length of the trout; similarly, for overwintering trout, the winter check was assumed to also represent a maximum pre-winter length. Thus, Hinemaiaia and Tokaanu Rivers rainbow trout were the longest at the end of their first growing season whereas the Waimarino River juveniles were the shortest. Considering that most Hinemaiaia River trout showed a non-overwintering pattern and would have emigrated well before winter, this comparison becomes even more striking.

Those Hinemaiaia River trout surviving to adulthood seem to have substantially greater growth rates than the same year class in the Waimarino River; a greater pre-winter length in the Hinemaiaia River trout may be aided by a somewhat earlier emergence allowing for a longer growing period before winter. Tokaanu River trout, living in an environment of moderate and somewhat lower summer temperatures but higher winter temperatures, may grow for most of the year and "catch up" to the Hinemaiaia River trout by the formation of the winter check.

### Field sampling

Results from the minnow-trapping surveys strongly corroborated the adult-scale observations. Despite seemingly good recruitment and growth, substantially lower catches of $0^+$ rainbow trout were seen in the Hinemaiaia River by autumn of 1989; similarly, $1^+$ trout were virtually non-existent in this stream at any time yet were found in relatively high abundances in the Tokaanu and Waimarino Rivers during the winter and spring covered by the study. The implications of these observations are that emigration and/or mortality of young-of-the-year rainbow trout occurred earlier and at higher rates in the Hinemaiaia River; therefore, few fish were left in this stream by winter. Thus, if a much higher proportion of Hinemaiaia River trout emigrate to the lake before winter, and since a winter check does not appear in fish rearing in the lake, most of these fish would not show an overwintering scale pattern.

The growth patterns of the minnow-trapped trout also corresponded closely with the scale observations. The minnow-trapped Hinemaiaia River trout consistently reached a larger size, earlier, than the same age-class of the other two populations (Fig. 6); thus, the Hinemaiaia River fish seemed to be growing at a faster rate. In addition, Hinemaiaia River rainbow trout may have been emerging earlier than the fry of the other populations (Fig. 7) and additional growing time would contribute to their reaching a larger size before winter.

### Role of natal-stream rearing

Natal-stream rearing is a common life-history strategy for many populations of migratory rainbow trout. The anadromous form, the steelhead trout, undergoes a protracted period of stream rearing before migrating to the Pacific Ocean (Shapovalov & Taft 1954; Ward & Slaney 1988). Furthermore, these fish reach a clearly defined minimum size that was similar among populations or years (c. 130 mm for Keogh River: Ward & Slaney 1988). Similar observations have also been made for Great Lakes populations of migratory rainbow trout; the age at emigration to the lakes varies and generally increases from south to north with the average length at any given age for the southern populations larger than for the northern populations (Biette et al. 1981). Great Lakes rainbow trout generally smolt from 1 to 3 years and vary in length from 64 to 244 mm (Biette et al. 1981).

However, not all lake-rearing populations of rainbow trout spend a protracted period of stream rearing before migrating to lacustrine waters (Hayes 1988). The optimal length at emigration may differ for each population but appears usually to be set by conditions in the lake or ocean.

The present study also suggests that surviving Lake Taupo rainbow trout rear in their natal streams for a protracted period of time before emigrating to the lake. Although the age at emigration varied among my study populations, the mean and minimum sizes at emigration for trout surviving to adulthood (as determined by back-calculation) were similar among streams, or about 140 mm and 94 mm, respectively (Table 6). Although large numbers of recently emerged fry are known to move down stream in Lake Taupo spawning streams (Stephens 1989), there appears to be strong selection against fish that leave the stream below a threshold size. The length-frequency distributions of the emigrants, as estimated by back-calculation procedures, show a sharp left-hand truncation terminating at about 94 mm for all populations (Fig. 5). This implies that for any rainbow trout smaller than this size, mortality rates are extreme. Among-population difference in age at migration for the Lake Taupo trout surviving to adulthood was therefore a function of varying growth rates among the different natal streams.

This minimum size-to-survival may be dictated by common habitat features encountered by all rainbow trout while rearing in Lake Taupo, since there seems to be little advantage in remaining in the apparently less productive stream environment. Thorpe's (1982) explanation for this seemingly paradoxical phenomenon was that although the stream may be a less productive environment than the ocean or a lake, it is often incapable of supporting many large predators and a prior period of stream rearing can be viewed as a balanced risk, trading off a greater growth opportunity for a lessened exposure to predators.

For Lake Taupo, Stephens (1989) suggests that recently emerged rainbow trout may be excluded from the littoral zone through competition or predation by other fish (e.g., common smelt *Retropinna retropinna*, brown trout *Salmo trutta*, common bully *Gobiomorphus cotidianus*, catfish *Ictalurus nebulosus*, koaro *Galaxias brevipinnis*, and adult rainbow trout). Alternatively, these small trout may not be able to make a living in the pelagic areas of the lake as they would, first, be out-competed for food by the planktivorous smelt and, second, be too small to forage on the smelt, a relatively large and active prey item. Rainbow trout in Lake Taupo feed almost exclusively (97%) on the common smelt (mean size of smelt c. 40 mm: Stephens 1989) and, presumably, there is a minimum size that a rainbow trout must reach before it is able to catch and ingest a prey item of this size; this may be about 94 mm.

With regards to the length of fish at emigration, there were some striking comparisons in the growth patterns of overwintering and non-overwintering fish. Those fish that did not overwinter were larger at outmigration than overwintering trout were at the formation of their winter check (Table 6C vs 6B). However, those fish which stayed and put on additional growth after winter averaged a greater length at emigration to the lake than those fish which migrated before winter (Table 6A vs 6C). This suggests that the largest juveniles, regardless of stream origin, tended to emigrate if they had reached the threshold size by winter. Those fish that did not grow larger than this size before winter either stayed in the stream and put on additional growth the next year and then emigrated, or else succumbed to mortality—either in the lake if they emigrated at a sub-threshold size, or in the stream if they stayed. Those populations showing slow fish growth would, therefore, have more fish staying a longer period of time before reaching the appropriate minimum length.

Lake Taupo rainbow trout are thought to be derived from introductions of California steelhead (Scott et al. 1978) which are known to require a period of stream growth before migration to the ocean (Shapovalov & Taft 1954). Presuming that stream-rearing has a genetic component in steelhead, Lake Taupo rainbow trout may have been "pre-adapted" with an exceptionally successful life-history pattern for this watershed. Nevertheless, production of rainbow trout in Lake Taupo may be limited at the stream-rearing phase and this may ultimately be dictated by the lake conditions controlling the threshold size for surviving emigrants.

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Appendix 2--Rosenau, M.L., R. Snowdon, and K.D. Adam. 1991. Adaptive variation in two populations of rainbow trout from Lake Taupo, New Zealand. Poster paper presented at the Genetic Conservation of Salmonid Fishes, Moscow, Idaho and Pullman, Washington, USA, June 24-July 5, 1991. Sponsored by NATO.

# ADAPTIVE VARIATION IN TWO POPULATIONS OF RAINBOW TROUT FROM LAKE TAUPO, NEW ZEALAND

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## INTRODUCTION

Rainbow trout (Oncorhynchus mykiss) were first introduced into New Zealand in the latter half of the 19th century from a California, USA, stock of steelhead. Historical records suggest that most of the extant populations of rainbow trout in New Zealand, including the Lake Taupo fish, are derived from this one introduction.

Lake Taupo, situated in the central North Island of New Zealand (Fig. 1), lies in an extinct volcano caldera; it is the basis for one of the most important freshwater sport fisheries in the country having an annual harvest of about 100,000 trout, each averaging over 1.4 kg, and this provides the local economy with about $NZ30,000,000.

Recent research at the University of Waikato investigated the fluvial population ecology of juvenile and adult trout in Lake Taupo streams. Although a protracted period of stream rearing by these adfluvial-lacustrine juveniles is important to their subsequent survival in the lake, there are considerable environmental differences among streams which modify the length of this growth period (Rosenau 1991). The streams flowing into the Lake Taupo watershed range considerably in such features as average flow (from 0.04 to 3.1 $m \cdot s^{-1}$), in source of water (groundwater vs surface flow), gradient, as well as in temperature regimes and water chemistry. The rainbow trout that spawn and rear in these tributaries show considerable fidelity in returning to their natal streams; that is, they conform to the definition of reproductively "true populations".

Because these fish are reproductively semi-isolated and spawn and rear in streams of such varying physical and biological characteristics, it was our intention to investigate the population biology of a number of stocks with regards to genetic differentiation and adaptation.

## STUDY SITES

Two Lake Taupo spawning and rearing streams of very different physical and biological characteristics are the Waimarino and Tokaanu Rivers; their temperature (Fig. 2) and flow (Fig. 3) regimes are very unlike as well as mean gradients and water sources (1.3 vs 0.4 %, and surface water vs groundwater, respectively).

Compared to the Waimarino, the Tokaanu River has a paucity of good spawning substrate and redd superimposition is common in the latter. However, both streams are considered to be important for recruitment of juveniles to the Lake Taupo sport fishery and historically have had escapements numbering in the thousands of spawners.

## ALLOZYME DIFFERENTIATION

Tissue samples were taken from rainbow trout of the Waimarino and Tokaanu Rivers, as well as two other Lake Taupo groups of fish; an electrophoretic analysis was then undertaken to determine if there were any allozyme differences among these stocks.

No significant among-population differences in allozyme frequencies were seen (Fig. 4) but, when compared to frequencies from California, USA, populations of rainbow trout (Berg 1987), the Lake Taupo fish were electrophoretically different from the former.

Fewer alleles were found to occur in the Lake Taupo trout than in the putative extant donor populations in the USA; this can be explained by founder effects. Thus, although other studies suggest that the rainbow trout in the Waimarino and Tokaanu Rivers constitute true populations, not enough time may have

elapsed since their introduction to Lake Taupo for allozyme differentiation to have occurred.

## FECUNDITY AND EGG-SIZE DIFFERENCES

Fecundity was compared between female rainbow trout of the Waimarino and Tokaanu Rivers (data re-analyzed from Tully 1989). Differences were compared by first adjusting all females of both streams to a common length using the methods outlined by Reist (1985).

We found that, for a common fork length of 527 mm, non-ovulated Waimarino female rainbow trout had about 500 fewer eggs than the Tokaanu females (Fig. 5). Conversely, the size of ovulated eggs in Tokaanu River females were significantly smaller than similar-sized Waimarino River females (Fig. 5). This follows Svardson's (1949) study showing that in fishes egg size and fecundity are negatively correlated.

## DEVELOPMENT-RATE DIFFERENCES

Pure and reciprocal crosses of Waimarino and Tokaanu River rainbow trout were made and we incubated the eggs and alevins at controlled temperatures of 7 and 12°C; thus, four crosses were created--WAI-pure, TOK-males x WAI-females, WAI-males x TOK-females and TOK-pure. Although within-population eggs and sperm were pooled before the crosses were made, we kept egg size similar among females within each population. Egg-size is known to affect rate of alevin development in salmonids with alevins from larger eggs taking longer than those from smaller eggs. Hence, for this experiment, the egg sizes of the Tokaanu River females were larger than the Waimarino River eggs (Fig. 6).

The alevins of crosses from small eggs (Waimarino) emerged sooner, on average, than alevins of large eggs (Tokaanu). However, those alevins of similar sized eggs having Waimarino fathers emerged later than the equivalent crosses with Tokaanu fathers. This was the same regardless of temperature (Fig. 6).

Thus, these incubation experiments indicated that there was a difference in rate of developement of alevins; this was firstly due to differences in egg size and, secondly, whether the father was from the Tokaanu (fast development) or Waimarino (slow) population of rainbow trout; that is, there was a paternally mediated difference in development rate in these two populations of trout. (There may also be a genetic-maternally inherited component as well but the experimental design did not allow us to determine if this was so.)

## REASONS FOR EGG-SIZE AND DEVELOPMENT RATE DIFFERENCES IN THESE POPULATIONS

There are considerable differences in the incubation conditions in the two study streams. In contast to the Waimarino River, the Tokaanu is a short, low-gradient, groundwater-fed, stream and its spawning substrate is considerably finer (Fig. 7). Fine substrate is often associated with lowered intra-redd oxygen levels and reduced salmonid embryo and alevin survival. Indeed, when a fredle index, a measure of gravel porosity (Lotspeich and Everest 1981), was calculated for redds of the two streams, the average for the Tokaanu River was 1.5 compared to 12.9 for the Waimarino River; these values represent embryo survival rates of only 40 versus 100%, respectively, in steelhead trout (Chapman 1988). Furthermore, the mean intra-redd dissolved oxygen levels in the redds of these streams were 7.0 and 10.4 $mg \cdot l^{-1}$, respectively. Sub-lethal effects in steelhead incubation have been reported in the literature below 10.4 $mg \cdot l^{-1}$ and suvival is suggested to be very poor below 7.0.

In addition, the observation that redd-superimpostion is high in the Tokaanu River suggests that the availability of good-quality spawning gravel is at a premium in this stream and there is a high probability of embryos and alevins being dug up by succeeding spawners.

Thus, we suggest that:

a) in the Tokaanu River rainbow trout there has been selection against larger eggs as: 1) smaller eggs provide higher survival rates under low-oxygen conditions due to a greater surface-to-volume ratio allowing maximum diffusion of gases per body mass in an environment of low dissolved oxygen, and 2) smaller eggs provide faster emergence in a stressful environment (low oxygen conditions, high probability of "dig-up" by succeeding spawners) thus increasing the fishes chances of survival, and

b) there has been selection against slower inherited development of Tokaanu alevins and this allows the fish to leave the redd as quickly as possible from an environment that is less than ideal; this fast development component is known to be paternally inherited in these two stocks, but may also be present in the mothers.

## CONCLUSIONS

Lake Taupo rainbow trout populations have not differentiated with respect to allozyme frequencies. For characters which may be subject to intense selection, such as in development rates and egg size, among-population genetic differences have arisen in some Lake Taupo stocks.

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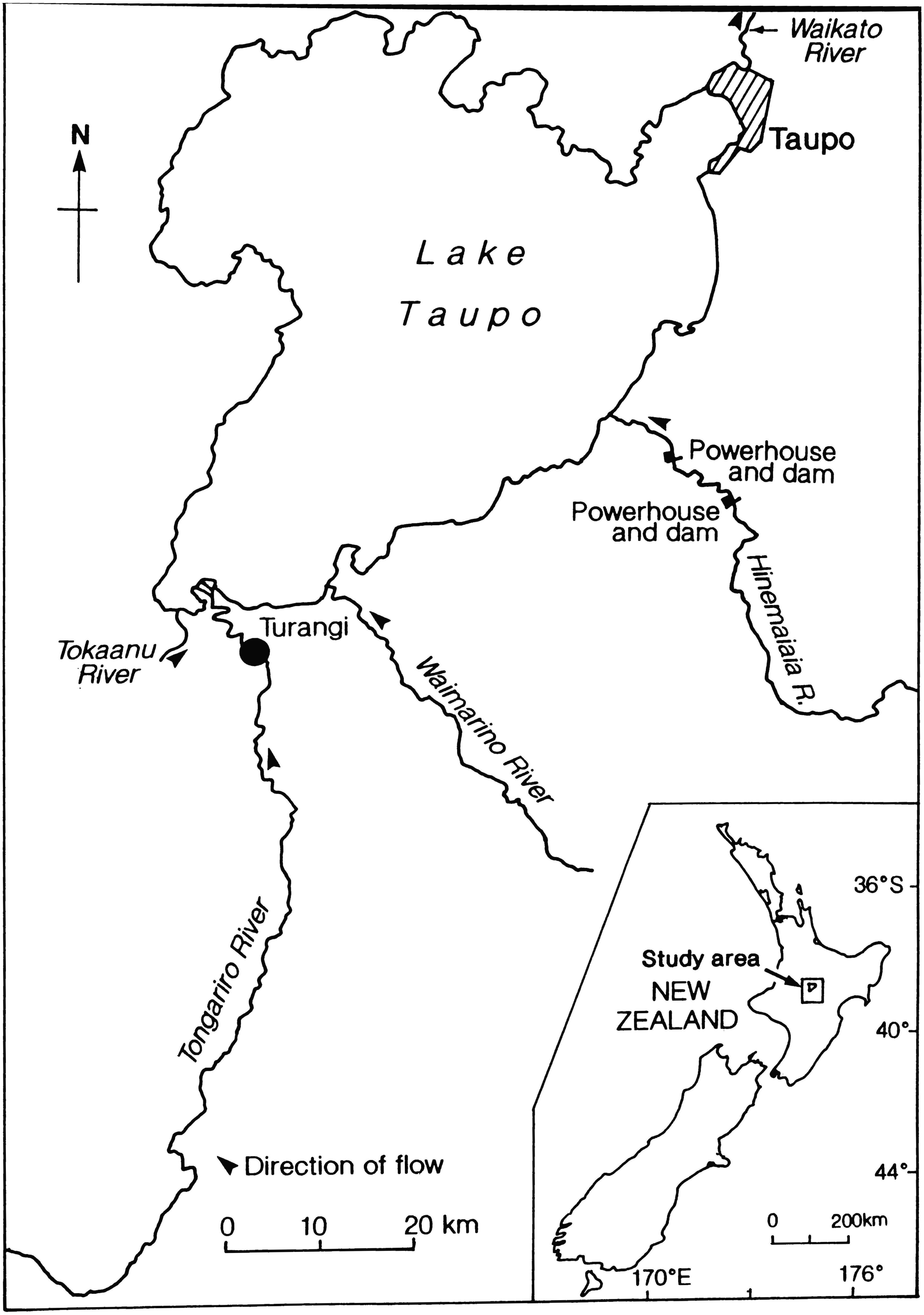


Fig. 1.—Map of the study area.

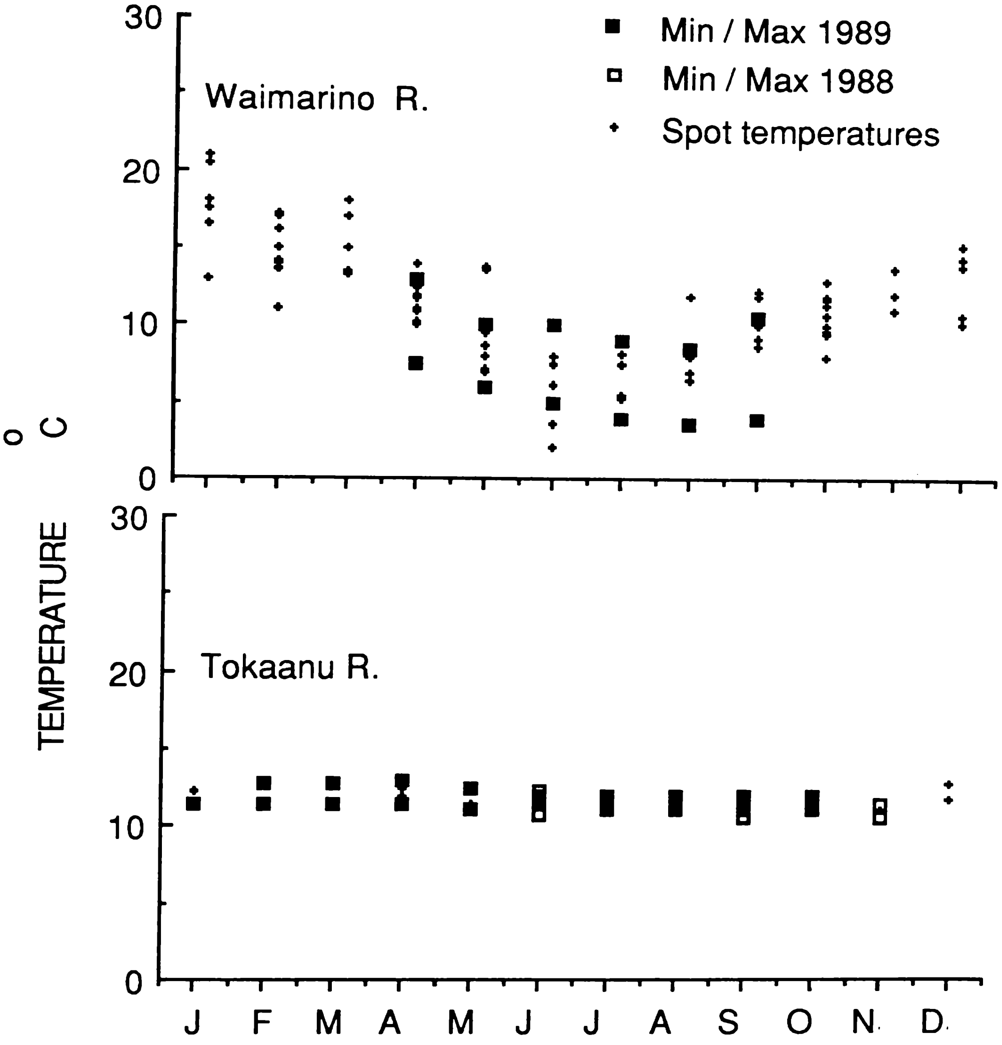


Fig. 2.--Temperatures in the study streams.

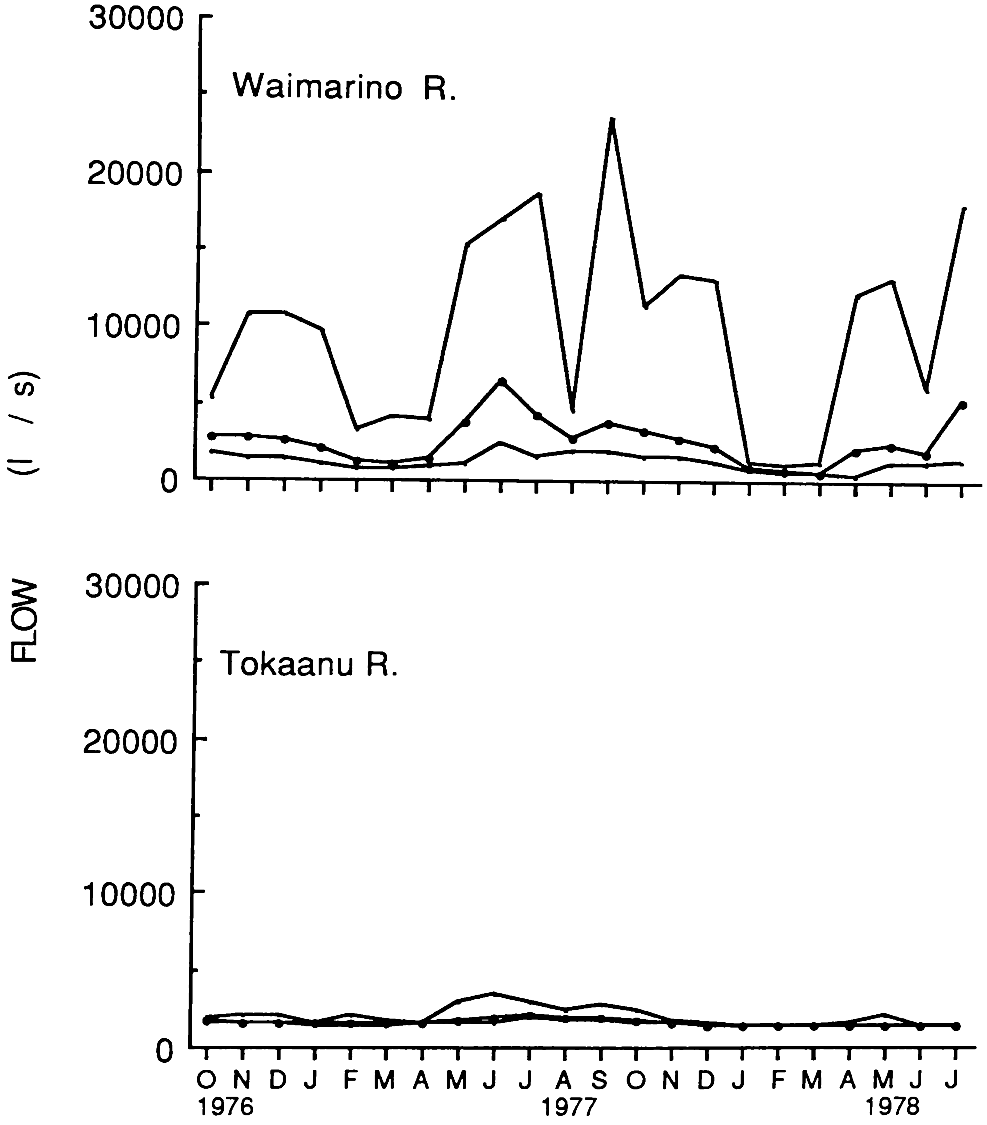
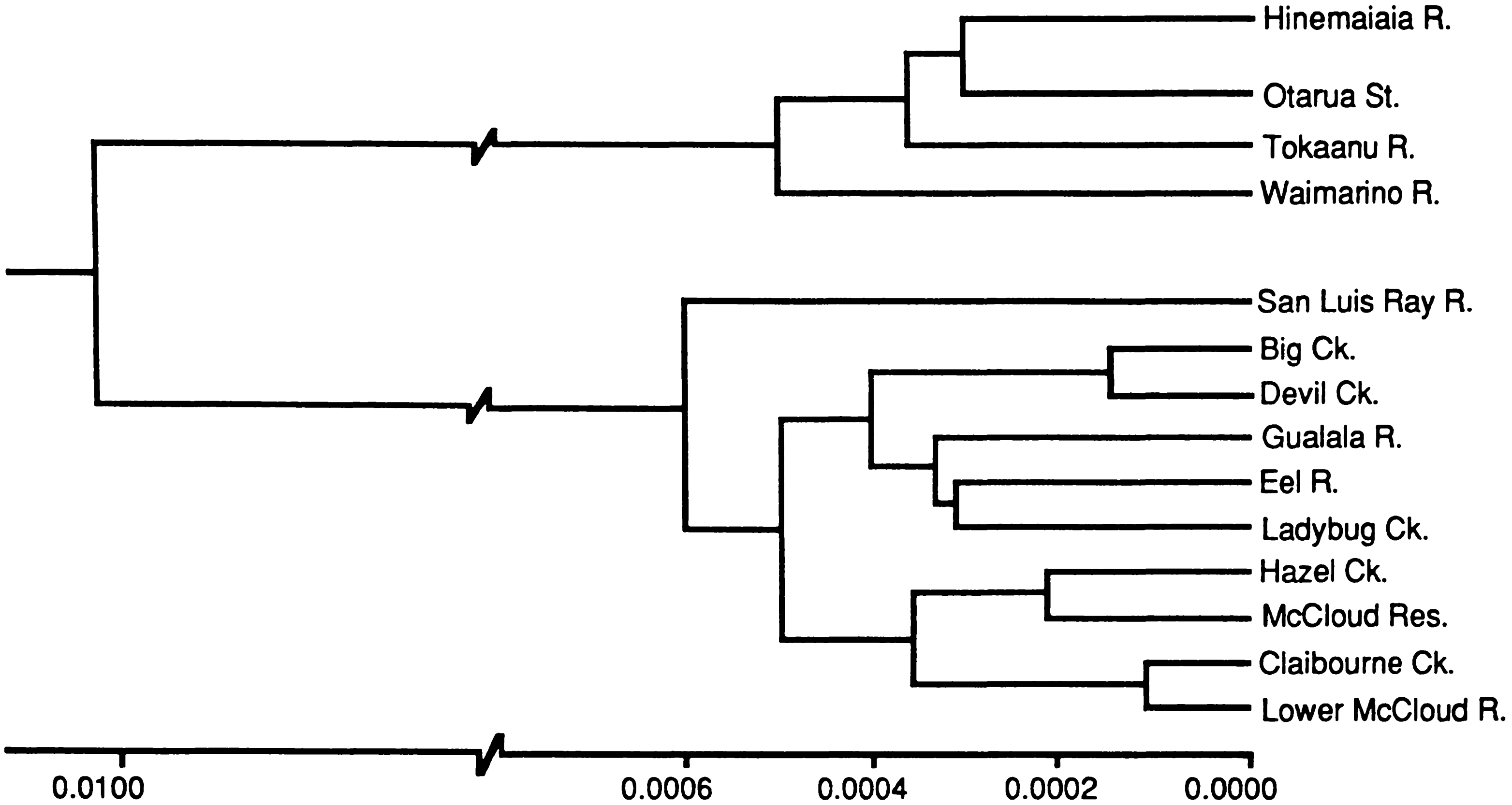


Fig. 3.--Flow in the study streams.

Fig. 4.-- UPGMA dendrogram showing cluster analysis of genetic distances (Nei's D), measured from allele frequencies, among four Lake Taupo populations of rainbow trout, and compared with the 10 nearest Californian populations from Berg (1987).



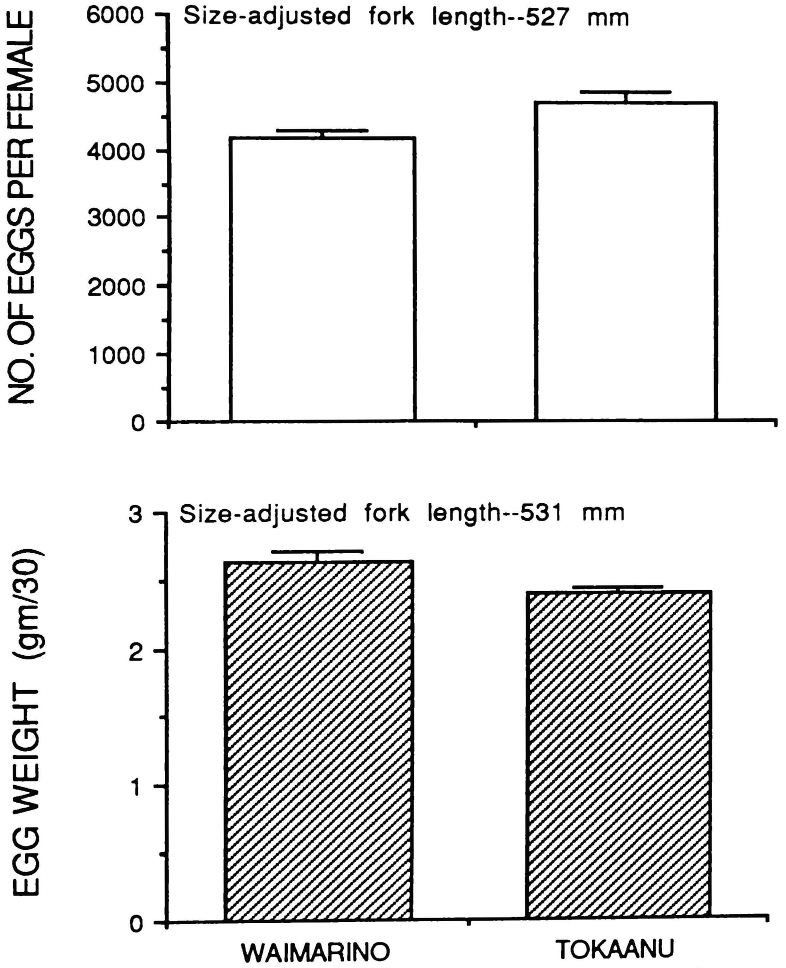
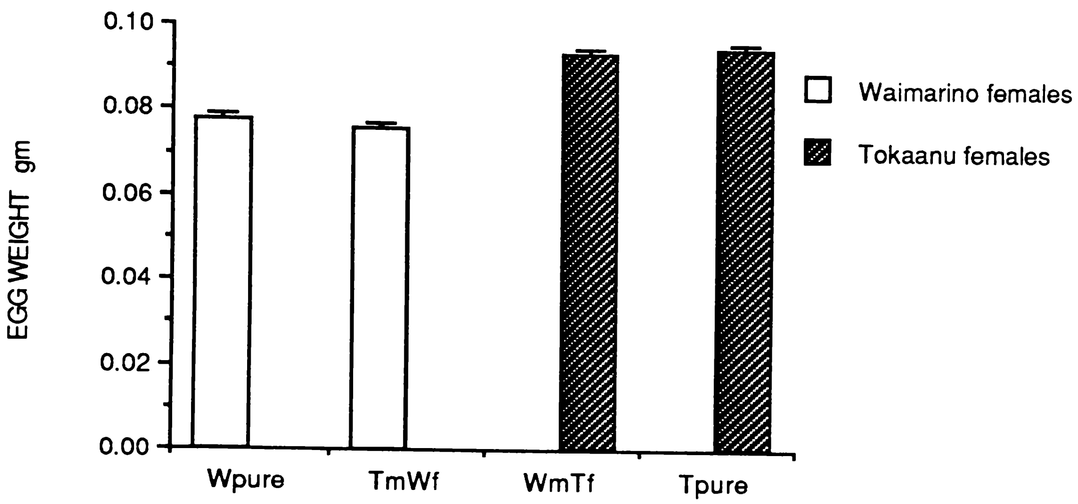


Fig. 5.--Egg-weight and fecundity comparisons. With SE's.



Size of incubation eggs--with SE's

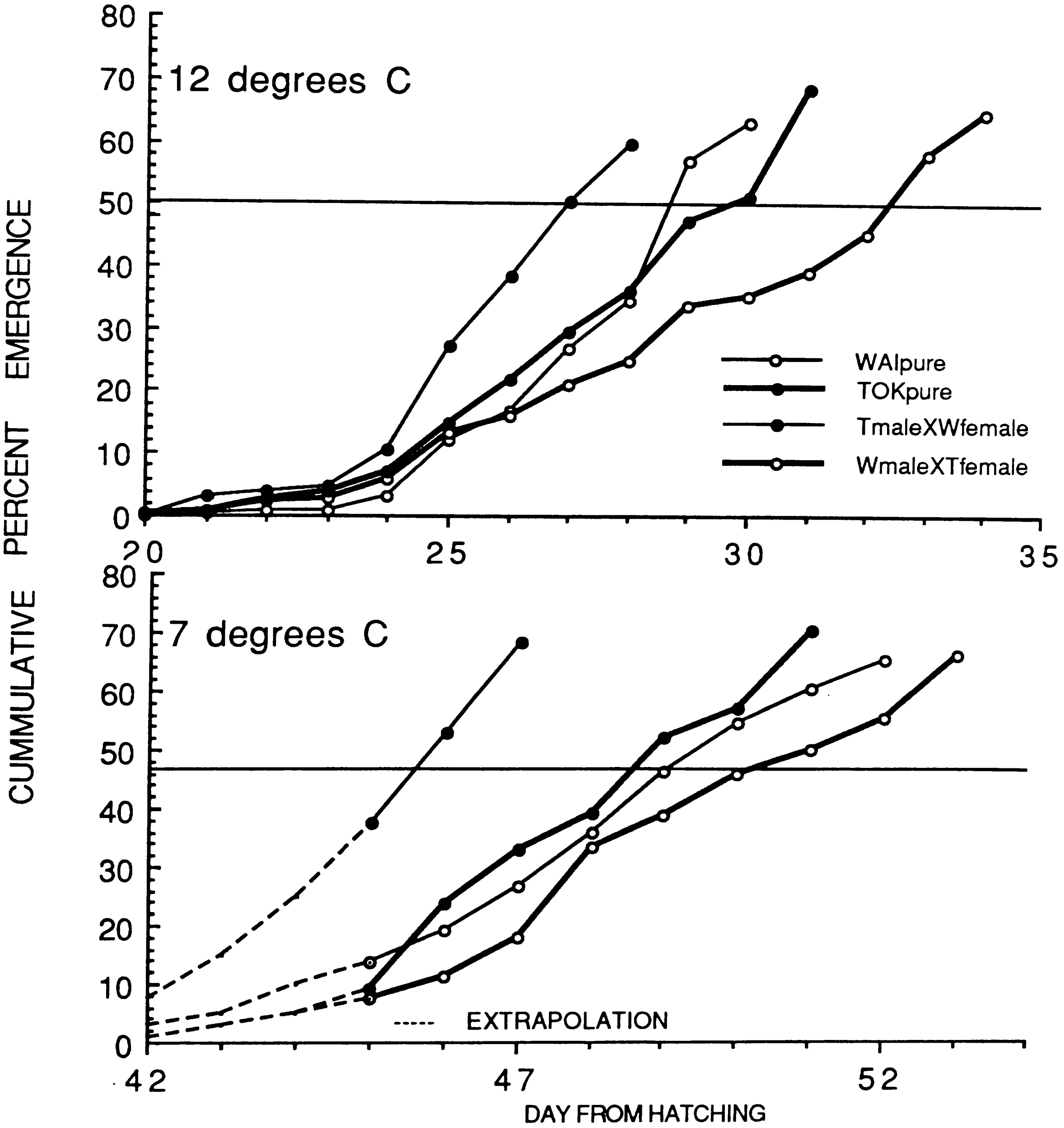


Fig. 6.--Cummulative emergence from hatching day.

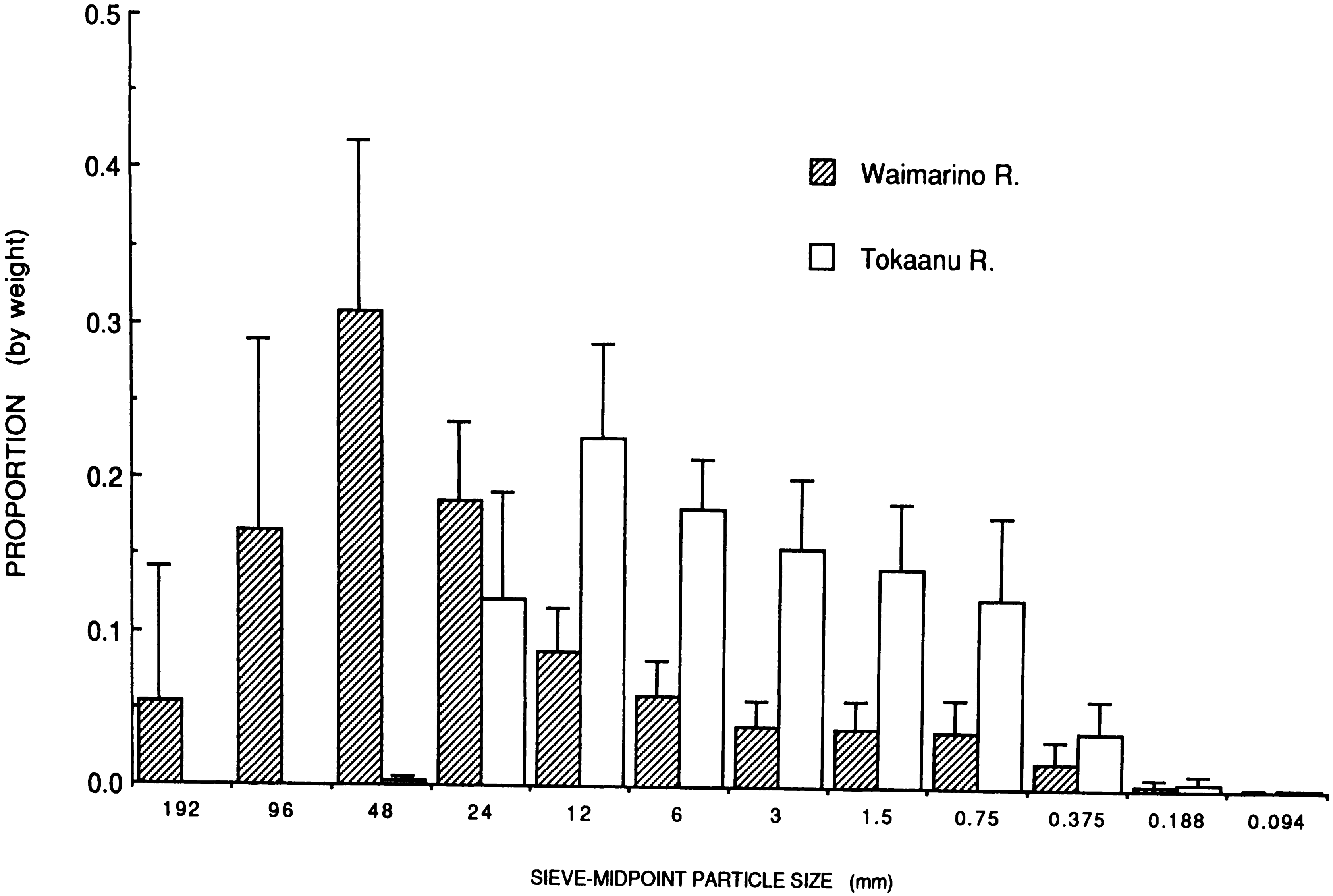


Fig. 7.--Particle-size distribution of the study redds. With SD's, n=10.