LIFE HISTORY OF
FLUVIAL AND LACUSTRINE LAND-LOCKED KOARO
(*Galaxias brevipinnis*) Günther (Pisces: Galaxiidae)
IN THE TARAWERA LAKES

A thesis

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Abstract

Biological diversity in New Zealand has been seriously degraded as a result of human induced disturbances which include the introduction of many exotic species. Freshwater ecosystems have not escaped damage, with the introduction of primarily sports fish suspected to be a significant contributing factor in diminished native biological freshwater values. This is reflected by range and population reductions of several native fish species.

One of these species is koaro (*Galaxias brevipinnis*), for which abundance in land-locked populations in the central North Island lakes has significantly declined. Koaro were once abundant in these lakes, and pre-European harvest in both its juvenile (whitebait) and adult (kokopu) form, comprised an important food resource for inland Maori. Since the introduction of recreational trout species to these lakes in the late 1880s, followed by the introduction of common smelt (*Retropinna retropinna*) in the early 1900s, the abundance of koaro has dramatically declined to the extent that, in these lakes, the species is now considered rare.

To date, the interactions between recreational trout species, common smelt, and koaro populations have not been established, and the life-history of land-locked koaro is not fully understood. In particular, the extent of movement between lake and stream habitats remains unclear. However, a collaborative project between the indigenous people of the Rotorua Lakes (Te Arawa) and the Department of Conservation to restore a koaro population in one Rotorua lake, has driven a need to gain a better understanding of the biology and ecology of land-locked koaro. This includes identifying threats to important life-history stages and understanding the role of tributary streams.

During July 1999 to February 2001, lacustrine and fluvial koaro were studied in Lake Tarawera and Lake Okareka and their tributary streams. Both lakes are part of the Tarawera lakes group, a subgroup of the Rotorua lakes situated in the central North Island. Fyke netting was used to sample lacustrine koaro on a monthly basis from January 2000 to February 2001, and seasonal two-pass reduction electric fishing at five sites in the tributary streams took place in April, July and November 2000 and February 2001. All fish larger than 70 mm total length were tagged with a passive implant transponder. Spawning season and location, together with size and growth of lake and stream fish were determined. Movement of lake fish within the littoral zone was also investigated.

The study found that lake and stream koaro may belong to two sub-populations indicated by differences in size, growth rate, spawning time and locality, and return of lake and stream koaro to natal habitats. The life-history of stream koaro has remained similar to that of its diadromous counterparts. Stream fish were found to spawn and hatch in stream environs, rear as larvae in the lake environs, and return to tributary streams as juvenile fish. Lake fish by contrast, most likely spawn in the lake itself, and results suggest that no juvenile migration of lake spawned fish to tributary streams occurs. Consequently, it was concluded that tributary streams may play little role in the life-history of lacustrine koaro.

Abundance of lacustrine koaro in both Lake Tarawera and Lake Okareka was low in comparison to lakes where trout species or common smelt are absent, and abundance of post-whitebait koaro (greater than 45 mm total length coloured and patterned) in both tributary streams studied was also low where rainbow trout (*Oncorhynchus mykiss*) were proportionally present in greater abundance. Important life-history stages were found to be subject to competition and predation by a combination of rainbow trout and common smelt in both lakes and streams.

Given the above, restoration programmes for land-locked koaro will need to be undertaken at the population level to enhance the survival of larval and juvenile life-history stages. This will need to occur at an ecosystem scale, and include the management of the combined effects of trout and common smelt in both lake and respective tributary stream environs.

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Section one
Introduction

1.1 Background

Biological diversity has been severely degraded in New Zealand as a result of 35 species of introduced mammals (Atkinson 1989). Furthermore, at present 50% of New Zealand flora is naturalised (Webb at al. 1988), and the same statistic is true for New Zealand freshwater fish (McDowall 1990c). Consequences for ecosystems, communities and populations of species have been dramatic, for example, many species now have only restricted and fragmented distributions (Towns & Daugherty 1994). Freshwater ecosystems have not escaped damage with introductions of primarily sports fish (see McDowall 1990c) suspected to be a significant contributing factor in diminished native biological freshwater values. For instance, many of the New Zealand's freshwater native fish have suffered range and population reductions to the extent that, of the 37 native species described, nearly half of the native freshwater fish fauna is considered threatened (Allibone and McIntosh 1999). Ecologically and evolutionary-wise, the freshwater fish fauna includes species that are every bit as unique as New Zealand's ratite birds like the kiwi and moa (Allibone and McIntosh 1999), but how can protection of New Zealand's unique biological features such as its freshwater fish fauna proceed in the face of ongoing threats as highlighted above?

Conceptually, biological conservation should be directed at an ecosystem level through minimising threats or more particularly minimizing human-induced disturbances, followed by mimicking ecological processes that have been impeded (Ferreira & Towns 2001). This translates to restoration of biological features and/or key populations at specified sites, as specified in New Zealand's Department of Conservation ten year strategic plan (Anon. 2001). Many instances exist where single species conservation programmes will augment the approach suggested above (Ferreira and Towns 2001), and accordingly a large component of New Zealand's freshwater native fish species will require population level restoration approaches to successfully ensure the persistence of these species. To this end, specific recovery plans are currently being prepared by the Department of Conservation for twenty native freshwater fish species.

One of these species is the koaro (*Galaxias brevipinnis*) for which land-locked populations are present in many inland lakes of New Zealand, including Lake Waikaremoana, Lake Taupo, and the Rotorua lakes in the central North Island, and Lakes Alexandrina, Wanaka, Christabel, and Chalice in the South Island. These populations contain both lacustrine and fluvial koaro. Diadromous populations are relatively secure with most populations stable, reflected by their wide distribution and major contribution to the country's whitebait fishery (McDowall 1996). This is partly because the larval stage of the lifecycle is borne out at sea where the effect of human induced disturbances such as competition and predation by exotic fish, are presumably less concentrated. In contrast, the maintenance of land-locked populations requires an understanding of inherent dynamics and factors likely to impede on those dynamics. Since crucial life-history stages are severely affected by human-induced disturbances, it is expected that land-locked populations will have a higher probability of local extinction. Understanding those factors which affect land-locked population persistence will significantly contribute to the maintenance of these populations.

Koaro are a member of the galaxiid family, a family of primitive fish found only in the southern hemisphere and which date back to the Mesozoic times (> 65 million years ago) (McDowall 1970, McDowall and Pole 1997). Koaro are native to New Zealand and are found in rivers, streams, and lakes. When access is freely available to the sea, koaro form diadromous sea-going populations with a larval marine phase (McDowall 1990a). In these populations, adults reside in freshwater habitats where they spawn (Allibone and Caskey 2000). Upon hatching larvae are washed out to sea (McDowall and Suren 1995) where they spend approximately six months rearing into juvenile fish (McDowall and Eldon 1980) before returning to freshwater in spring as part of mixed-species migratory shoals collectively known as "whitebait". Whitebait shoals comprise the juveniles of five galaxiid species, including koaro. Where access to the sea is denied, koaro form land-locked populations and the larvae of these populations rear in the surface water of lakes (McDowall 1990a).

The biology and ecology of diadromous koaro populations is relatively well understood from studies regarding diet; (eg; Main and Winterbourn 1987, Glova and Sagar 1989, West 1989, Hayes 1996), habitat preferences; (eg; McDowall 1978, Taylor 1988), spawning; (eg; Duffy 1996, O'Connor and Koehn 1998, Allibone and Caskey 2000) and general life history; (eg; McDowall and Eldon

1980, McDowall and Suren 1995). In contrast, studies relating to the life history of land-locked non-diadromous fluvial and lacustrine koaro populations are limited. In particular, the extent of movement between open water lake habitats and their associated tributary streams is not known.

Rowe et al. (2001 in press) provides an account of the population structure, distribution, reproduction, diet, and relative abundance of koaro in Lake Rotoaira, situated in the central North Island, and the biology and ecology of fluvial koaro in the tributaries of Lake Taupo was described by Kusabs (1989). Several smaller surveys and studies have also been undertaken, such as the biology of koaro in Lake Alexandrina (Naylor 1983); a survey of koaro in Lake Christabel (Johnson et al. 1976); and a survey of koaro in Lake Chalice (Meredyth-Young and Pullan 1977). Consideration of these studies together highlights that land-locked koaro are abundant where trout species are absent, and that there are significant gaps in knowledge regarding the general life history of land-locked koaro populations and the effects of introduced species on koaro at the population level.

Uncertainty surrounds the natural establishment of inland land-locked koaro populations, particularly where lakes are remote, located at high altitude and have no overland surface flow, such as Lake Chalice in the South Island. A discussion by Strickland (1993) regarding the likely role of Maori in the present distribution of New Zealand's freshwater fish, and in particular, in the establishment of an inland fishery in the lakes of the central North Island concluded that Maori transferred fish from one waterbody to another, raising doubt as to the natural origin of land-locked populations. However, koaro are prodigious climbers often found above large inland waterfalls (McDowall, 1996) and diadromous populations have been found to land-lock relatively easily (in one generation) such as the now land-locked population of koaro found in Lake Mahinerangi formed by a dam in 1911 (McDowall 1990a). It is therefore possible that some land-locked populations naturally established as the result of the removal of access to the sea for existing fluvial diadromous populations following catastrophic events such as dam formation from volcanic activity or landslides. Evidence suggests that the koaro population in Lake Waikaremoana established in this way as a result of a landslide 2000 years ago (McDowall 1990a).

McDowall (1990a) considers that land-locked populations of koaro have retained a life-history pattern similar in most respects to that of diadromous stocks. This is consistent with Kusabs (1989) suggestion that lacustrine koaro spawn in the lower reaches of Lake Taupo tributaries. Similarly, Rowe et al. (2001) concluded that spawning of lacustrine koaro occurred mainly in tributary streams of Lake Rotoaira. Reconnaissance surveys for this study of seven streams and two lakes belonging to the Tarawera lakes group during early 1999, revealed that while large koaro (> 160 mm total length) were present in the lakes, they were absent in tributary streams. This could provide further support for the migration of mature lake fish into tributary streams for spawning purposes only, with a subsequent emigration back to lake environs, or alternatively could suggest that there are distinct lake and stream koaro populations. From the above discussion it follows that successful restoration of a land-locked koaro population will require, in the first instance, an understanding of inherent population dynamics and, in particular, the movement and survival of key life-history stages.

Prior to the introduction of trout to the lakes of the central North Island, koaro were commonly encountered and comprised an important component of an inland indigenous Maori fishery (Buck 1921, Best 1929, Armstrong 1935, Phillips 1940). However, since the European introduction of rainbow trout (*Oncorhynchus mykiss*), and in some cases brown trout (*Salmo trutta*) to these lakes in the 1880s (Burstall 1980), the abundance of koaro declined to the extent that they are now considered rare and are only occasionally encountered. Although there is limited data available which shows that introduced trout preyed extensively on koaro (McDowall 1990c), the species comprised an important forage food for trout during the establishment of the now world renowned, rainbow trout fishery in these lakes. Indeed, the collapse in the koaro fishery in the early 1900s coincided with a decline in size and condition of trout in the central North Island lakes (Strickland 1993), and therefore fisheries managers at that time, attempted stocking the lakes with alternative forage species suitable for trout such as the freshwater shrimp (*Paratya curvirostris*) and other fish species (Strickland 1993).

It is generally accepted that common smelt (*Retropinna retropinna*) were introduced into the Rotorua lakes from the lower Waikato River from 1906 – 1909 to replace the diminishing koaro food source (Burstall 1980, McDowall 1990b). In contrast to this view however, Strickland (1993) argues that common smelt were already present in Lake Rotorua before European introduction, possibly introduced by Maori many years prior. Despite these conflicting viewpoints, the introduction of common smelt to two Tarawera lakes, a subgroup of the Rotorua lakes, is far more certain with records documenting the liberation of common smelt into Lake Tarawera and Lake Okataina in 1931 by the Department of Internal Affairs (Burstall 1983, Stephens 1984). In addition, following the successful restoration of trout size in Lake Tarawera and Lake Okataina (Burstall 1983), subsequent transfers of common smelt to Lake Taupo from the Rotorua Lakes occurred, and are well documented (see Burstall 1950).

Regardless of how common smelt became established in the central North Island lakes it is clear that some establishment of this species to places where they did not previously exist can be attributed to European transfers undertaken solely for the purpose of trout management, with little regard for the maintenance or restoration of the previously existing koaro fishery. Consequently, research on the demise of koaro in these lakes has received little attention from fisheries managers beyond their diminishing contribution as a food resource for trout. The interactions between trout, common smelt, and koaro populations have not been studied, even though the decline in lacustrine land-locked koaro to the extent that they are now rare, has only occurred where common smelt was introduced as a forage fish for trout and displaced koaro, or where brown trout predominate as in some South Island lakes (Rowe et al. 2001 in press). The total disappearance of koaro from Lake Rotopounamu, a small volcanic lake situated in the central North Island is due solely to the introduction of common smelt (Rowe 1993) and provides strong supporting evidence for the effects of common smelt on koaro. Therefore, to successfully restore a land-locked koaro population, a better understanding in the second instance, of the threats to various stages of the life history of the species is required.

Koaro are a category C threatened species in the priority ranking system for conservation of New Zealand's native species (Tisdall 1994). Under section 6(ab) of the Conservation Act 1987, the Department of Conservation is mandated with the responsibility to preserve as far as practicable freshwater fisheries and their habitats. This has been translated into action through the Department's commitment to New Zealand's biodiversity strategy which seeks to enhance population numbers and ranges of indigenous freshwater species threatened with extinction. A collaborative project between the Department of Conservation and the indigenous tribal people of the Rotorua lakes (Te Arawa) provides an opportunity for the Department of Conservation fulfil a biodiversity goal while giving effect to its mandated role through the restoration of a population of lacustrine koaro in one Rotorua lake.

Before conservation management decisions to restore koaro can be made, the competitive interactions between trout, common smelt, and koaro, and the biology and ecology of land-locked koaro must firstly be understood. The aim of this study therefore is to remedy part of this information gap, primarily through investigating the role that tributary streams play in important life-history stages of lacustrine and fluvial koaro in the Tarawera lakes.

1.2. Study Questions

The following key questions will be addressed:

1) What is the role of tributary streams with respect to aspects of the biology and ecology of lake and stream land-locked koaro?, including:

   (i) where and when lake fish and stream fish spawn?,

   (ii) what differences exist in the size and growth of fish from the two habitats?, and

   (iii) what is the extent of lake and stream fish movement between habitats?

And,

2) What are the likely impacts of rainbow trout and common smelt on important life history stages and abundance of lake and stream populations?

In addition, the implications of the results for restoration and maintenance of land-locked koaro populations will be discussed.

1.3 Study Area

The Tarawera lakes group comprises eight volcanically formed, hydrologically connected lakes. These lakes and associated tributaries are situated in the central North Island of New Zealand at an elevation of approximately 300 metres above sea level (Figure 1). Lake Tarawera is the largest and lowest lying lake of the group and receives inflow from all other lakes in the complex via overland flow or subsurface drainage.

Lake Tarawera drains by surface outflow through and over a partly subterranean waterfall which forms the start of the Tarawera River. This river flows directly north to discharge to the sea at Matata.

Lake Okareka is a relatively small lake 333.5 hectares in surface area and with a maximum depth of 32 metres. Approximately 20% of the catchment has remained in native vegetation, with the predominant land uses being pastoral farming, limited production forestry, quarrying, and lakeside settlement. Lake Okareka is mesotrophic and regularly experiences deoxygenation of the hypolimnion during summer months (Burns 2001).

The surface area of Lake Tarawera is 4097 hectares and maximum depth is 87 metres. The greater proportion of the immediate catchment of Lake Tarawera has retained its native vegetation cover which has regenerated following the eruption of Mount Tarawera in 1886. Approximately 20 % of the catchment is characterised by predominantly rural land uses such as pastoral farming, production forestry, and lakeside settlement along the western shore. Lake Tarawera is an oligotrophic lake (Burns 2001).

Several wetlands are present on the riparian margins of Lake Tarawera and one wetland is associated with Lake Okareka. The levels of each lake fluctuate according to rainfall and at high lake levels the wetland areas become contiguous with the main body of the respective lakes. The level of Lake Okareka is artificially controlled by a weir and outlet structure which discharges via an open drain and pipeline to the Waitangi Spring and Stream, and then into Lake Tarawera at Waitangi Bay.

In addition to koaro, common smelt, and rainbow trout, other fish species present in both lakes include; common bully (*Gobiomorphus cotidianus*); longfinned eel (*Anguilla dieffenbachii*); goldfish (*Carassius auratus*) and *Gambusia affinis*. Goldfish and *G. affinis* are both exotic species. Koura (*Paranephrops planifrons*) a freshwater crayfish native to New Zealand is also present in both lakes.

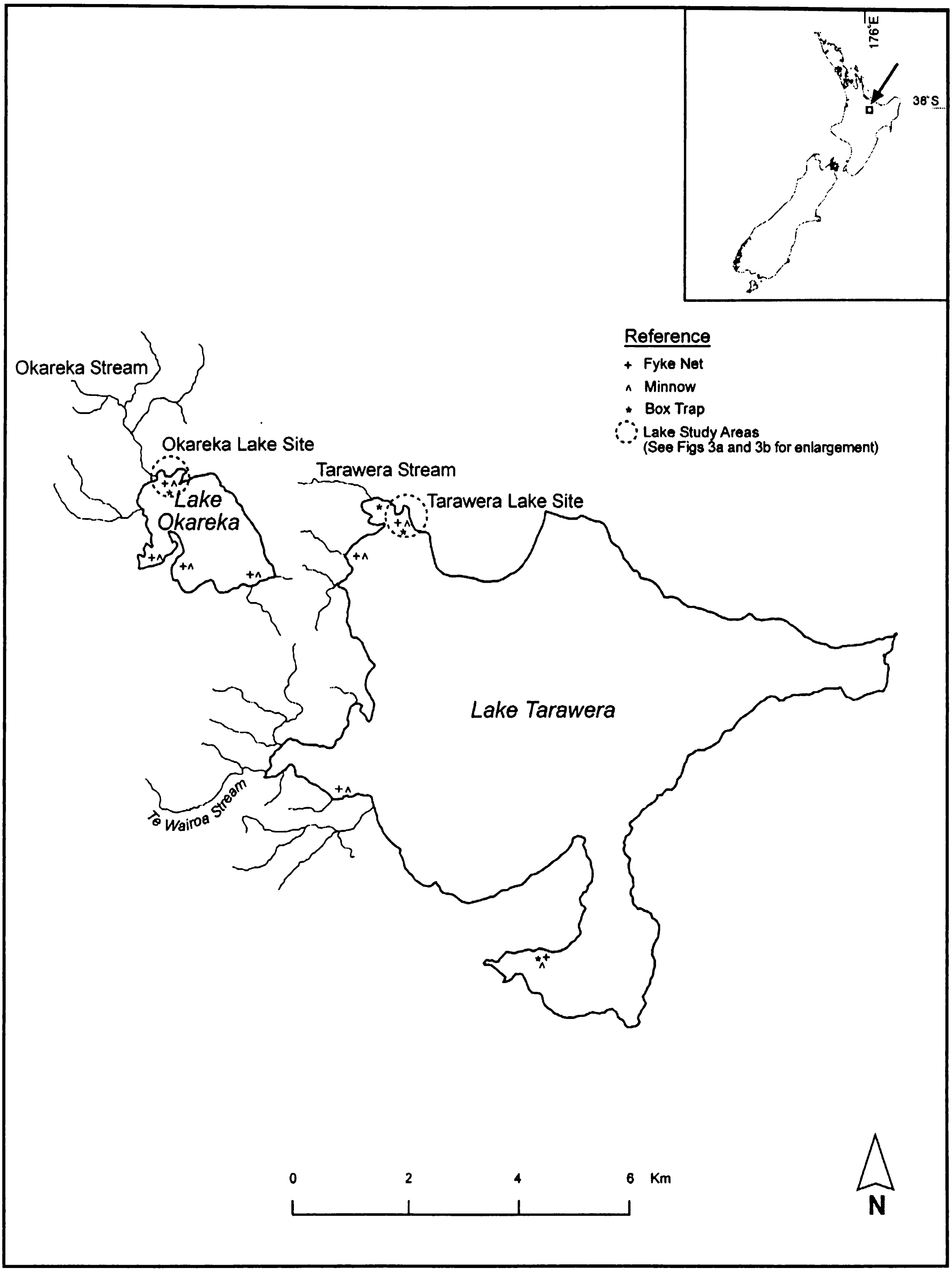


Figure 1 Map of the North Island showing location of the Tarawera Lakes. Lake Tarawera and Lake Okareka were selected as the study lakes due to the existence of tributary streams associated with the main lake body, and the presence of lacustrine and fluvial koaro in the respective lake and stream habitats.

Section two
Methods

2.1 Study sites and sample collection

A study site was chosen in Lake Okareka and Lake Tarawera and a study stream was then chosen which drained into each lake. Lake study sites were selected as the sites with the highest catch per unit effort (CPUE) considered as the mean number of fish per net per night during exploratory netting trials conducted in a range of different habitats and locations in the lakes. All catch rates are expressed as fish net^{-1} night^{-1}. Once lake study sites were selected, the stream draining into each lake in closest proximity to the lake site was selected as the study stream to increase the chances of observing fish movement between the two habitat types (Figures 1, 2 and 3).

2.1.1 Lake sites

Exploratory catch methods were performed in a range of different habitat types during August and September 1999 to determine the best method and location for catching lake-dwelling koaro (Figure 2). Exploratory catch methods included, unbaited gill nets, box traps (1.2 m trap with 20 mm mesh and a 23 m leader with 3.5 cm mesh), fyke nets and baited gee minnow traps (5 mm mesh). Fyke nets set to shore and box traps set in the middle of small bays provided a similar CPUE. No fish were caught in minnow traps and gill nets. Since fyke nets were easier to set than box traps, and provided more opportunity to observe movement within the lake shore environment than box traps, fyke nets were adopted as the regular sampling method.

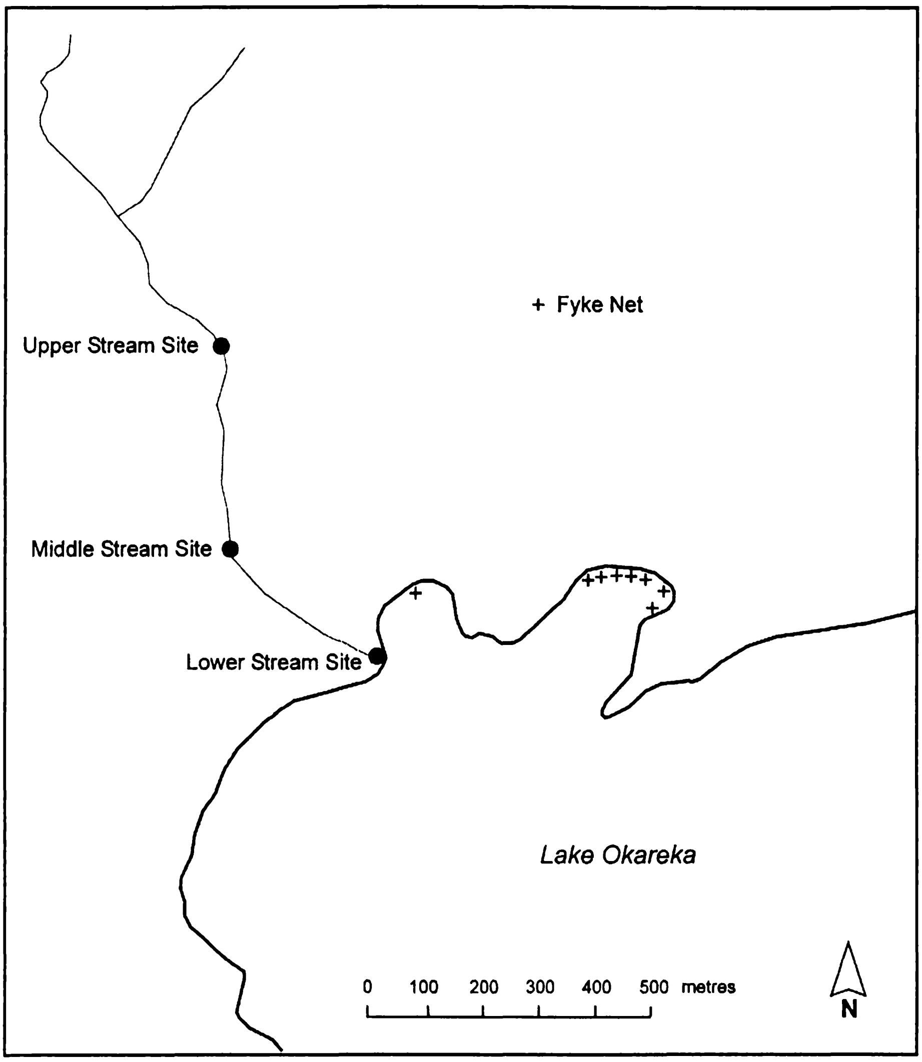


Figure 2 Lake Okareka lake and stream sites.

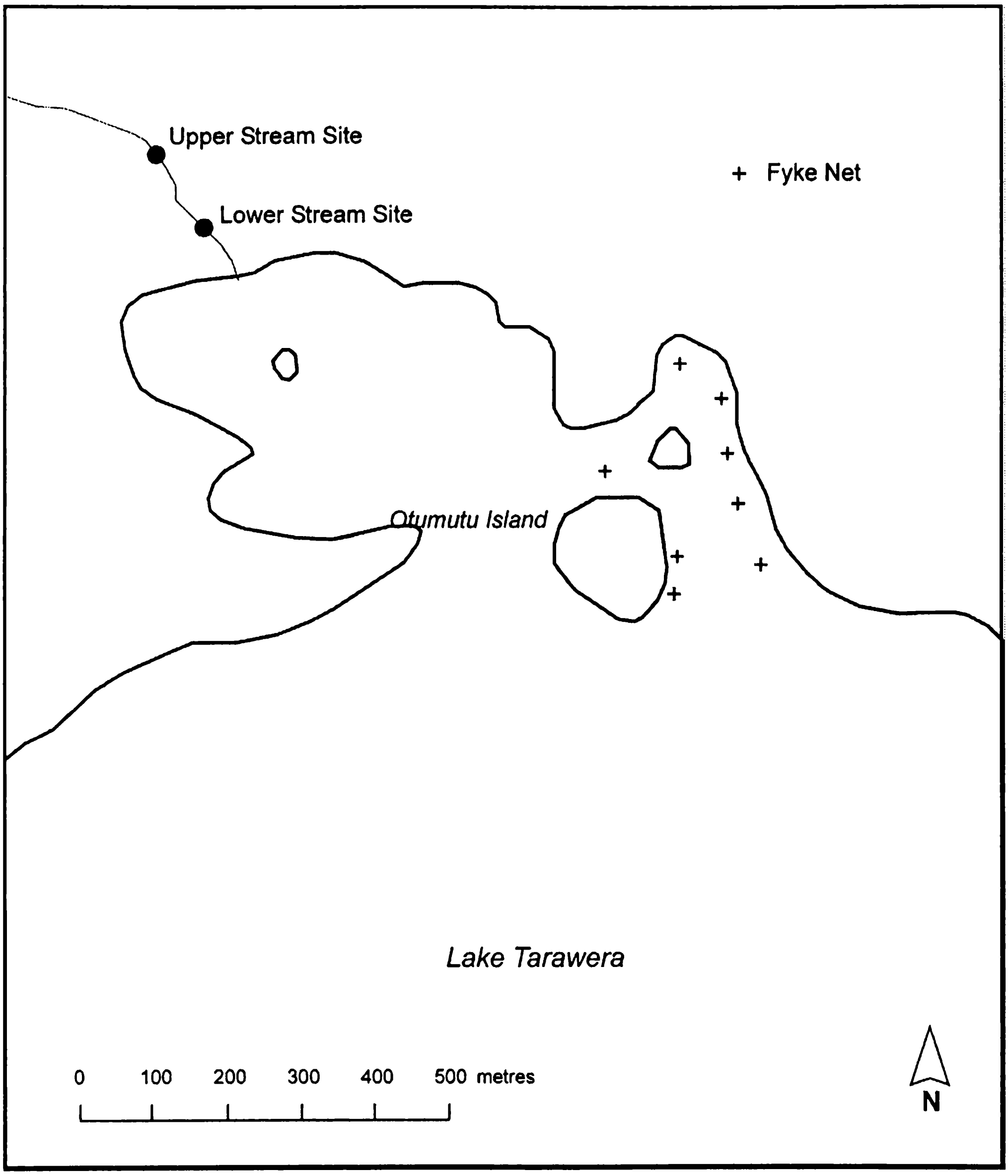


Figure 3 Lake Tarawera lake and stream sites.

Habitat types included substrates with predominantly boulder, silt, gravel or sand in association with various combinations of submerged and emergent macrophyte beds and proximity or otherwise to wetland areas. Trials found that nets set adjacent to a wetland area where reeds and submerged aquatic macrophytes were present provided the greatest CPUE and therefore lake study sites were chosen with these attributes (Figures 2 and 3).

At the completion of trials, eight fyke nets were set in the littoral zone once each month for 14 months from January 2000 to February 2001 inclusive. Nets were set between 1600 and 1800 hours and lifted 16 – 20 hours later. Nets comprised two chambers and a 2.7 m leader wall. Mesh size of the catching chamber and leader was 15 mm by 15 mm. Each net was set perpendicular to the shoreline with the leader set to shore in order to minimise loss of fish around the leader edge (Figures 4 a and b). On each sampling occasion four nets were set at depth (1 – 3 m) and four nets were set in the shallow (< 1 m). All eight nets were set in the same location on every sampling occasion (Figures 2 and 3).

The mesh size of the fyke nets selected against the capture of small fish, and therefore fish < 84 mm total length (TL) are not represented in the lake samples. An additional three fyke nets with small mesh (5 mm by 5 mm) set in October 2001 caught five small koaro between 49 – 56 mm TL confirming that small fish were present in the lake.

Figure 4a Shallow set fyke net. Net set less than 1 metre deep in Lake Tarawera adjacent to a wetland area on a gravel substrate.

Figure 4b Deep set fyke net. Net set at a depth greater than 1 metre over a macrophyte bed of oxygen weed (*Lagarosiphon major*) and adjacent to stand of raupo (*Typha orientalis*) in Lake Okareka.

Due to markedly lower catch rates in Lake Tarawera in comparison to Lake Okareka, nets were set for three nights at two additional sites on Lake Tarawera (Figure 3) to investigate the possibility that the low catch rates were the result of site choice. This additional sampling was undertaken three nights immediately following relatively high CPUE in Lake Okareka.

All fish caught on the final sampling occasion were retained for laboratory analysis. In addition, 55 koaro caught from Lake Tarawera by the Acclimatisation Society in the early 1980's and preserved in formalin were also included in vertebral count analysis. These fish were caught using gill nets set at depths of between 5 – 20 m (Phil Kirk, pers comm. 1997).

2.1.2 Stream sites

Three study sites where chosen in the Okareka study stream (lower, middle and upper) (Figure 2) and two study sites (lower and upper) were chosen in the Tarawera stream (Figure 3). Sites were representative of different habitats as defined by substrate, riparian cover and stream structure (Table 1) (Figures 5 and 6). Each site was 100 m^2.

Table 1. Physical characteristics of Okareka and Tarawera stream study sites.

				Stream structure (approx %)			Substrate (approx %)		
Site	Mean depth (m)	Mean water width (m)	Riparian vegetation (descriptive)	Run	Riffle	Pool	Sand	Silt	Gravel
Okareka									
Lower	0.5	1.75	Rank grasses, willows and secondary native vegetation	50	10	40	40	45	15
Middle	0.3	1.25	Willows, blackberry, gorse and secondary native vegetation	80	0	20	20	25	55
Upper	0.4	1.2	Combination of secondary native vegetation and planted native trees and flax	50	30	20	0	30	70
Tarawera									
Lower	0.6	2.5	Lawn grass and planted flaxes	15	35	60	15	80	5
Upper	0.4	1.2	Native secondary vegetation	55	20	25	0	20	80

Two-pass reduction electro-fishing using a backpack battery powered electric fishing machine (NIWA Kainga 300 series) was undertaken to determine relative abundance and estimate population density at each site during April, July and November 2000 and February 2001.

Electro-fishing was chosen as the sampling method due to the ability to flush fish out from undercut banks and overhanging vegetation and quantify CPUE. Electro-fishing involves the passing of a pulsed direct current through the water body via a positive (anode) and negative (cathode) electrode. The current either stuns fish causing them to lose swimming ability and float to the surface and/or downstream, or causes them to swim towards the anode due to an involuntary nervous muscular response. Stunned fish were retrieved in a downstream catching net and fish attracted to the anode were scooped out of the water with a hand-held dip net.

Figure 5 Lower Tarawera Stream site.

Figure 6 Typical upper stream site (Tarawera stream).

Reduction electro-fishing involves the removal of all catch on each pass as described in Armour et al. (1983). Stop nets were placed at the upper and lower ends of each site to restrict movement of fish in and out of sampling sites during fishing. All fish from each pass were sorted to species level and size class, counted and returned to the sampling site.

Fish smaller than 45 mm TL that were uncoloured (transparent) and un-patterned (no distinct marking) were classed as whitebait. Fish greater than 45 mm TL that were coloured and patterned were classed as post whitebait.

All fish over 70 mm were internally fitted with an AVID© passive implant transponder (PIT) tag prior to return. The size of the tag was either 12 mm or 14 mm depending on the fish size. Fish were anaesthetised using clove oil as described by Peake (1998) with the addition of aloe vera aquarium solution to reduce the potential for fungal infection. Once anaethestised, fish were held upside down in the palm of the hand, tail end facing outwards, and the PIT tag was inserted via hypodermic needle and syringe into the abdominal cavity in the direction away from the anal vent. Fish were held in an aerated bucket until they had regained full swimming ability (up to five minutes) before being released. No fish died during the tagging procedure or during recovery and observations of recaptured tagged fish revealed that insertion wounds had healed over well with no noticeable scarring or damage to external tissues. However, mortality associated with the tagging procedure post release was not measured.

Each tag contains a unique 9 character alphanumeric identification code. Tags were read in situ through the abdominal wall using an AVID© PIT tag reader (Power tracker II) held approximately 100 mm away from the fish.

All post whitebait fish caught on the last sampling occasion (February 2001) were retained for laboratory analysis. Further post whitebait samples were collected in an additional sampling occasion at the Okareka middle site during early April 2001 and from the Tarawera stream mouth site during September 2001.

2.2 Ripeness

All lake and stream fish greater than 60 mm TL were assessed in the field for ripeness by the application of gentle pressure to the abdominal flank in the direction of the anal vent. Extrusion or absence of reproductive products was noted and fish were also checked for inflammation about the genital aperture (anal vent area) for indication of recent spawning. Where milt or eggs were extruded the sex of the fish was recorded and the fish was considered running ripe (ripe). Where the genital aperture was protruding and inflamed, but where no eggs or milt were extruded, the fish was recorded as a spent female.

Gonadal maturity of fish retained for laboratory analysis at the end of the study was assessed visually under dissection according to the six stage classification described by Nilkosky (1963) as follows:

1) Immature – Fish sexes indistinguishable.
2) Resting – Developing virgin or resting adult. Eggs visible under 25x magnification.
3) Maturation stage 1. Developing/eggs visible to the naked eye.
4) Maturation stage 2. Gonads filling body cavity. Testes white, ovaries yellow, eggs 1 mm in diameter.
5) Reproduction – Ripe, eggs or milt extruded by light pressure.
6) Spent – gonads in spent condition.

2.3 Size

Maximum natural total length (TL) from the nose to the tip of the tail as described by Anderson and Gutreuter (1983) was measured to the nearest millimetre for all lake fish and post whitebait stream fish using a measuring board or similar. All lake and stream post-whitebait fish were weighed using portable scales (Jadever Snug 300) to the nearest 0.01 g. Whitebait were not measured or weighed.

2.4 Age

Sagittal otoliths were extracted from fish retained at the end of the study. Otoliths were dissected from the fluid filled sac located slightly below the brain by a vertical section between the eyes extending just behind the rear edge of the eye region. Both right and left otoliths were removed, gently wiped clean of all remaining tissue and placed in a labelled container to dry for a minimum of three days.

Once dry, otoliths were mounted onto glass slides convex side up using an epoxy resin mounting compound and then left to fix for several days. Care was taken to avoid the capture of air bubbles between the otolith and glass slide. Mounted otoltihs were then ground using wet and dry sandpaper and polished with aluminium oxide powder. A circular motion was used to expose the widest section while still maintaining the nucleus in view.

Ground otoliths were viewed under reflected light on a black background as described by West (1989) with a Leica DMRE Research Photo-microscope using a 5x, 10x, 20x or 40 x objective depending on size. Images were generated by a Dage-MTI DC-330 1/3" 3 chip colour video camera and electronically captured with a Scion CG7 colour frame grabber using Image Pro Plus software (Cybernetics).

Using the calibration feature of Image Pro Plus software, the radius of each otolith from the nucleus to the outer edge was measured to the nearest 0.0001 mm along the axis identified as providing the strongest relationship between total length and otolith radius by McCaughan (1995) (Figure 7).

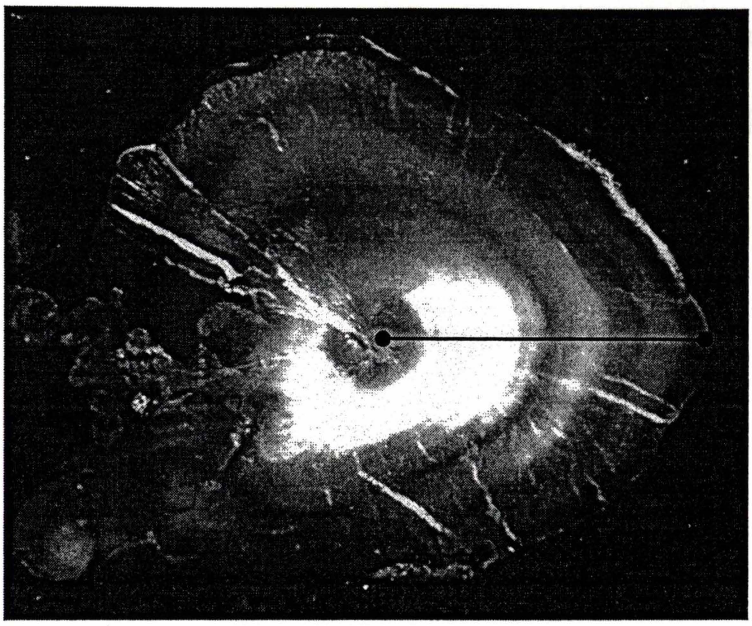


Figure 7 Sagittal otolith from a three year old stream fish from Okareka Stream collected in April 2000. Imposed line shows axis with the strongest relationship between total length and otolith radius (McCaughan 1995) and dark bands represent winter growth and opaque bands summer growth.

Under reflected light, it was assumed that layers laid down during slow growth periods (usually the autumn and winter months) would appear as dark or translucent hyaline bands (zones) and layers making up the spring and summer months of active growth would appear as white opaque zones as described for other fish species (see Jearld 1983). Under this assumption, a light and dark band were counted as one year of growth (Figure 7).

2.5 Growth

Von Bertalanffy growth curves (von Bertalanffy 1938) were fitted to the mean lengths for each otolith age group using a Walford plot (Walford, 1946) for stream and lake fish according to the equation from Tesch (1971):

$$l_t = L_\infty (1-e^{-K(t-t_0)})$$

Where l_t = the length at age t

L_∞ =the asymptotic length predicted by the equation

e = the base of the natural log

t = age in years

t_0 = time in years when length would theoretically be zero

K = the Brodie growth coefficient (instantaneous rate)

Walford regressions (Walford 1946) were fitted to the mean lengths data, the parameters L_∞, K and t_0 were estimated for lake and stream fish from the regression (see Hopkins 1979 and Kusabs 1989).

Growth for lake fish was also determined from measurements taken from recaptured fish. Each fish was ascribed a primary growth season according to whether it was at large for one season or for a combination of seasons between recaptures. Mean daily growth was calculated for spring and summer growth fish combined and autumn and winter growth fish combined.

Instantaneous rate of growth was calculated as the natural log of total length at second capture minus the natural log of total length at first capture divided by the number of days between captures.

2.6 Movement of fish between habitat types

Several approaches were used to investigate whether fish moved between habitat types. Of particular interest was whether lake fish moved into streams for spawning.

Direct observations of fish movement were made through the recapture of tagged fish. The distance moved between captures was calculated for each recaptured fish as the shoreline distance between capture locations. The mean distance moved was compared between male and female fish.

Differences between spawning place for lake and stream fish were examined using vertebral counts. The relationship between vertebral number and temperature is negative in most cases (Lindsay 1988) and therefore provides a clue as to where the parent fish spawned. Lake and stream specimens included fish retained at the final sampling. Lake specimens were augmented by fish caught by the Acclimatisation Society in the early 1970s and preserved in formalin. Stream specimens were augmented by fish caught during an additional sampling occasion in early April 2001 (Okareka Stream) and September 2001 (Tarawera Stream).

Fish were x-rayed laterally or dorsally depending on their shape. Fish which were laterally compressed were x-rayed laterally and fish which were dorso-ventrally compressed were x-rayed dorsally. Fish < 100 mm TL were x-rayed using a GE Senograph 800T mammogram unit. Fish > 100 mm TL were x-rayed by a Toshiba

KXO-15E x-ray unit. Counts were of all centra between, but not including, the bassioccipital and urostylar half vertebra (Figure 8).

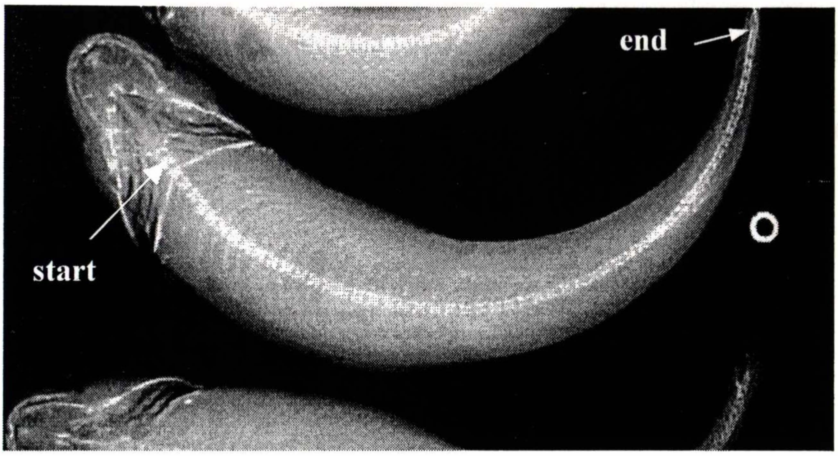


Figure 8 Dorsal X-ray of vertebrae in a preserved fish from Lake Tarawera with start and end vertebra counted as shown.

Difference in spawning time between lake and stream fish was further explored using the measurement of otolith nucleus to first winter band. Otoliths form during the embryonic period and reflect all life history events Jearld (1983). Therefore, the measurement from the nucleus to the inside edge of the first winter (hyaline) band provides an insight into the length of time spent growing before the onset of the first winter period and hence indicates the season in which the fish hatched.

Measurements were made at 5x and 20x magnification using a graticule eyepiece and micrometer to the nearest 0.001 mm along the axis identified by McCaughan (1995) for providing the largest r^2 value for total length and otolith radius relationship.

2.7 Data Analysis

Differences between total length of male and female lake fish, lake and stream fish and fish caught from deep and shallow sites were explored using a two sample t-test on natural log transformed data. Comparison between lake and stream fish was limited to ripe male fish due to lake sampling selecting against the capture of small fish.

Comparison of mean shoreline distance moved between male and female tagged lake fish was undertaken using a Kruskall-Wallis non-parametric comparison of means on non-transformed data. Comparison of mean distance between nucleus and first winter band on sagittal otoliths was undertaken using a two sample t-test on natural log transformed data.

Relationships between total length and weight between lake and stream fish and male female fish were explored using a linear regression on natural log transformed data and analysis of covariance (ANCOVA) was performed on natural log transformed data to establish whether any difference existed between the relationship according to habitat types.

Relationship between otolith radius and total length was explored using linear regression on non-transformed data and between otolith radius and age using non-transformed data. ANCOVAs were performed to establish whether any difference existed between the relationships according to habitat types.

Comparison of mean number of vertebrae between fish from each lake and stream not combined, were undertaken using a one way ANOVA, and means groups were established using the Bonfferoni post hoc pairwise multiple comparison.

All ANOVA and linear regression analyses were undertaken using SPSS Base 10 statistical software package. All ANCOVAs were performed on SYSTAT version 10 statistical software package (SYSTAT Inc).

Section three
Results

3.1 Abundance

3.1.1 Lake sites

Exploratory netting trials found that fyke nets and box traps provided a similar catch per unit effort (CPUE measured as mean number of fish net^{-1} night^{-1}) (Table 2). Since box traps took considerably longer to set than fyke nets, and a series of fyke nets provided more ability to study movement within the lake shore environment, fyke nets were selected over box traps as the monthly sampling method. All fish were caught from sites with weed or gravel substrates overlain with silt and no fish were caught from sites with substrates comprising sand, boulders or pure silt. In Lake Okareka, fish were only caught at sites that were immediately adjacent to the only wetland area associated with the lake.

The CPUE in Lake Okareka was almost 20 times greater than that found in Lake Tarawera. This was observed for all sampling, despite the addition of three sampling nights in Lake Tarawera (Table 3).

Other species commonly captured included common bully (*Gobiomorphus cotidianus*) and goldfish (*Carrasius auratus*) (Table 4). Rainbow trout were occasionally encounted, and one longfinned eel (*Anguilla dieffenbachii*) was caught in Lake Okareka and two in Lake Tarawera. Koura (*Paranephrops planifrons*) freshwater crayfish, were also a common by-catch in deep set nets

(1 – 3 m). Although common smelt are present in both lakes, none were caught in the fyke nets.

Table 2 Catch rates of koaro for different trapping methods. Lake Tarawera and Lake Okareka data combined from exploratory netting trials in July and September 1999.

Method	Total number	Trap/netting nights	Total number of fish caught	Catch per unit effort (fish net $^{-1}$ night $^{-1}$)
Box trap	4	2	3	0.37
Fyke net	12	2	8	0.33
Gill net	2	2	0	0.00
Minnow	24	2	0	0.00

Table 3 Overall catch rates of koaro from fyke nets. Fish were caught in eight fyke nets set monthly from January 2000 to February 2001.

Lake	Number of nights	Number of net nights	Total number of fish caught	Catch per unit effort (fish net $^{-1}$ night $^{-1}$)		
				Mean	95% confidence interval	
					lower	upper
Tarawera	17	136	5	0.04	0.01	0.07
Okareka	14	112	87	0.78	0.51	1.04

Table 4 Catch rates for species other than koaro caught in Lake Okareka and Lake Tarawera from fyke netting from eight fyke nets set monthly from January 2000 to February 2001.

Species	Mean catch per unit effort (fish net $^{-1}$ night $^{-1}$)	
	Okareka	Tarawera
Common bully	0.06	1.59
Goldfish	0.41	1.26
Longfinned eel	0.01	0.03
Rainbow trout	0.05	0.01
Koura	5.45	2.86

In Lake Okareka CPUE of koaro was lower than average during cooler months from May to October 2000 and higher than average during the warmer months of January, November, December 2000 and February 2001 (Figure 9). Ripe males dominated the catch in autumn (86% of total catch). Ripe females were most abundant in late spring and summer (28% of total catch), in contrast to autumn and winter when ripe females were virtually absent (5% of total catch). Of the five fish caught in Lake Tarawera, three were caught in January, one in May, and one in September.

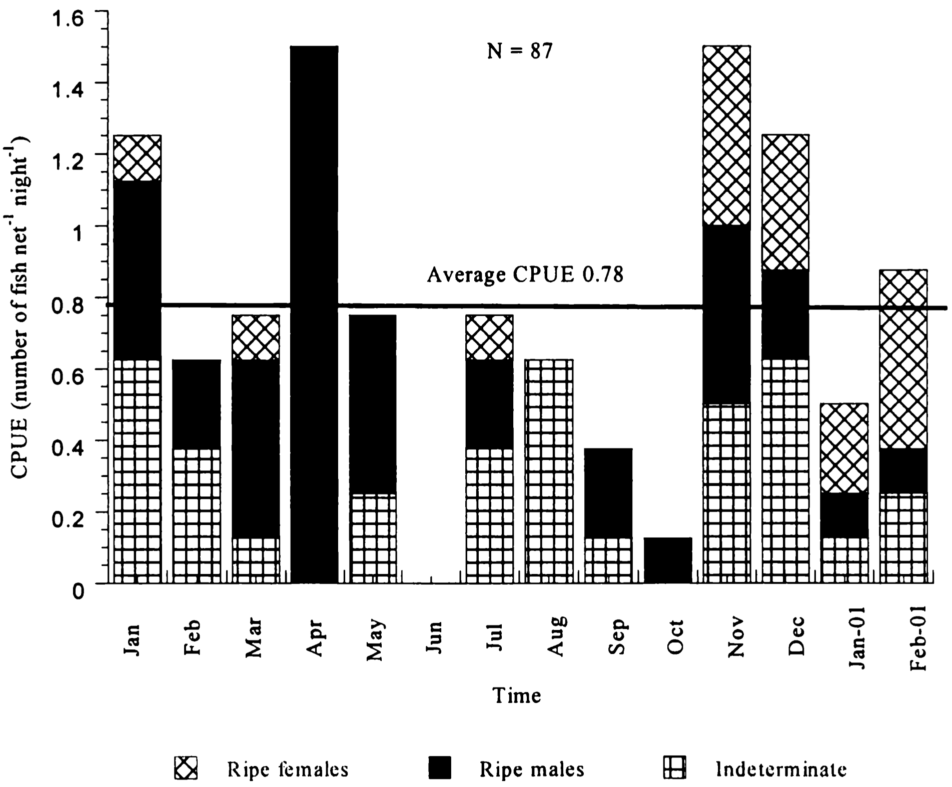


Figure 9 Variation in catch rate in Lake Okareka across months with changes in proportion of ripe male and ripe female fish. Data from 8 fyke nets set monthly from January 2000 to February 2001 and once in September 1999. Average CPUE is shown from all 14 sampling months. (N = total number of fish from all months combined).

3.1.2 Streams

3.1.2.1 Koaro

Koaro whitebait and post whitebait life-stages were found in both study streams along with juvenile and adult rainbow trout, common bully, common smelt and koura (freshwater crayfish). Catch rates for streams were considered as the total sum of fish caught in the 100 m^2 site. Catch rates for whitebait and post-whitebait koaro are reported separately. Catch rates of koaro whitebait at the lower study sites of both the Tarawera and Okareka streams were highest during summer (February) and autumn (April) (Table 5 a and b). A small increase in the catch rate of whitebait was observed in the middle and upper sites of both streams during winter (July) and spring (November). Catch rates of post-whitebait koaro (>45 mm coloured and patterned) in both streams were low on all sampling occasions ranging from 0 to 0.16 fish m^{-2} (Table 5 a and b).

Table 5 (a) and (b) Change in catch rates of koaro in streams according to season. Total catches from (a) Tarawera stream sites, and (b) Okareka stream sites of 100 m^2 are provided for whitebait (w) and post-whitebait (pw) koaro separately. Data are from two-pass electrofishing in April, July, November 2000 and February 2001. Note that whitebait were fish < 45 mm TL that were uncoloured and post-whitebait were fish > 45 mm TL that were coloured and patterned.

(a) Tarawera Stream

	Total sum of fish			
Month	lower site		upper site	
	w	pw	w	pw
April	292	0	0	2
July	14	0	0	4
November	0	0	4	2
February	8	4	0	2

(b) Okareka Stream

	Total sum of fish					
	lower site		middle site		upper site	
Month	w	pw	w	pw	w	pw
April	96	0	0	4	0	2
July	0	0	2	0	12	2
November	0	0	4	2	0	0
February	160	16	0	0	0	0

Only 26 post-whitebait koaro were found in the Okareka Stream in total, and only 14 were found in total in the Tarawera Stream. No increase was observed in the catch rate of post-whitebait koaro in streams corresponding to the winter months of low abundance in lakes (Figure 9).

3.1.2.2 Rainbow trout

Catch rates of juvenile rainbow trout changed markedly according to season peaking in spring (November) (Table 6 a and b). Unfortunately, catch rates of trout were not recorded in winter due to an oversight during sampling and therefore no quantitative winter data is available, however a peak in abundance of adult trout would be expected during this season and was observed in the field. The catch rate of adult trout was similar in autumn, spring and summer (Table 6 a and b).

Catch rates of juvenile and adult rainbow trout combined, was considerably higher than koaro whitebait and juveniles combined in the middle and upper stream sites during spring, summer and autumn. During summer and autumn, catch rates of koaro were higher than those of trout in the lower stream sites.

Table 6 (a) and (b) Change in catch rates of rainbow trout in streams according to season. Total catches from (a) Tarawera stream sites, and (b) Okareka stream sites of 100 m^2 are provided for juvenile and adult rainbow trout separately. Data are from two-pass electrofishing in April and November 2000 and February 2001.

(a) Tarawera Stream

	Total sum of fish			
	lower site		upper site	
Month	juvenile	adult	juvenile	adult
April	1	0	12	3
November	8	1	23	5
February	6	1	16	4

(b) Okareka Stream

	Total sum of fish					
	lower site		middle site		upper site	
Month	juvenile	adult	juvenile	adult	juvenile	adult
April	2	1	9	1	12	7
November	7	3	10	0	25	6
February	10	0	16	0	6	4

3.2 Koaro ripeness

In Lake Okareka ripe male fish were found throughout the year (except in June when no fish were caught) with higher proportions present during autumn (March, April, May 2000) and spring (October 2000) (Figure 10). In contrast, ripe female fish were found in greater proportion during the summer period, peaking in January. Three out of four previously unsexed female fish caught and retained in February 2001 were at an advanced stage of gonadal maturation. One fish caught during July was in early stages of maturation. No ripe female fish were found during winter or spring. In Lake Tarawera, changes in gonad ripeness were not compared due to the low number of fish caught.

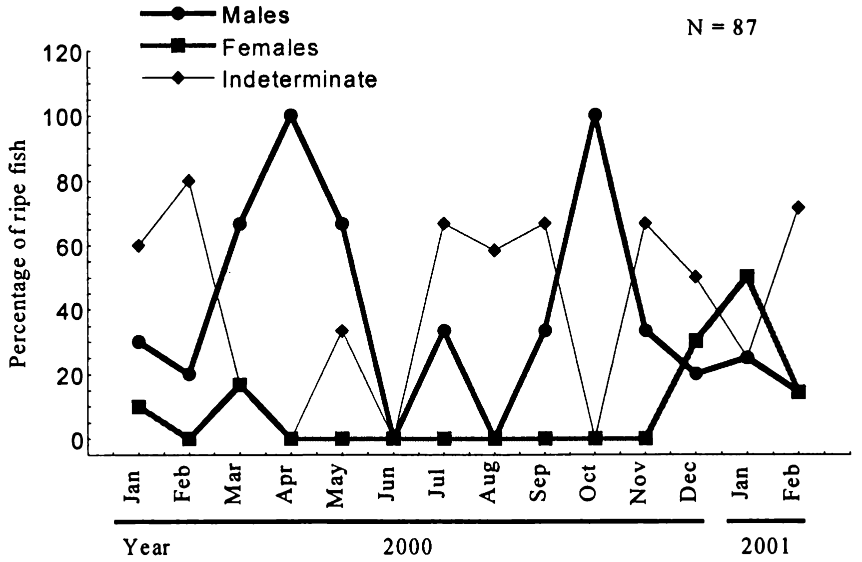


Figure 10 Change in percentage of ripe fish in relation to time. Data are from 8 fyke nets set monthly in Lake Okareka from January 2000 to February 2001 inclusive.

At all sites from both streams, the only ripe fish caught were male. These fish were all caught during the autumn sampling period and no ripe males were found during any other sampling occasion (Table 7). Additional sampling in early April 2001 revealed that female fish were present in the streams (*N* = 4) with gonads in moderate to advanced stages of maturation (Nilkolsky stages 2, 3 and 4) as described in Nilkolsky (1963). Males found during this additional autumn sampling occasion (*N* = 3) were also found to be in moderate to advance stages of gonadal maturation (Nilkolsky stages 2 and 4 respectively).

Table 7 Change in number of post-whitebait ripe and non-ripe male, female and indeterminate sex koaro according to season in Tarawera and Okareka streams combined, from two-pass electric fishing of five 100 m^2 sites in April, July and November 2000 and February 2001.

Month	Indeterminate	Ripe male	Ripe female
April	3	5	0
July	6	0	0
November	4	0	0
February	22	0	0

3.3 Size, age and growth of lake and stream koaro

3.3.1 Length distributions

Lake koaro were 68% larger than stream koaro with total length (TL) of lake fish ranging from 84 to 226 mm (155 mm ± 5.5, mean ± 2SE) and total length of post whitebait stream fish ranging from 49 to 123 mm (92 mm ± 7.5) (Figure 11). Aside from one very small fish (84 mm TL) in the lake samples there was little overlap in length of fish between the two habitat types. An exploratory netting trial using three fine mesh fyke nets in Lake Okareka in October 2001 caught five small koaro between 49–56 mm TL. This confirmed small fish were present in the lake, and that the large mesh of the fyke nets selected against their capture. The lack of large fish in the stream samples can only be attributed to their absence since the electric fishing machine is considered more effective at catching larger fish than smaller fish (Zalewski and Cowx 1990).

The difference in length between lake and stream fish was significant ($F_{1,49} = 47.0$, $P < 0.001$) when mean total lengths of ripe male fish were compared (Table 8). Analysis was limited to ripe male fish to ensure comparison of fish from the two habitat types at the same life stage in the absence of small fish in the lake samples.

Table 8 Range and mean of ripe male lake and stream fish total lengths. Fish were from 8 fyke nets set monthly in Lakes Okareka and Tarawera from January 2001 to February 2001, and two pass electric fishing in tributary streams in April, July and November 2000, and February and April 2001.

	Total length (mm)		
Habitat type	Mean	Minimum	Maximum
Lake	145	84	185
Stream	91	80	105

A difference in mean total length between sexes of lake fish was also found with female lake fish 20% longer than male lake fish. Total length of females ($N = 17$) ranged from 123 to 225 mm (mean 173 mm ± 15.5) and males ($N = 50$) from 84 to 185 mm (mean 145 mm ± 5.5). This difference was significant ($F_{1,65} = 16.0$, $P < 0.001$ on natural log transformed data). Due to the low number of known female ($N = 4$) and male ($N = 7$) fish found in all the stream sites combined, no analysis of difference between male and female stream fish was undertaken.

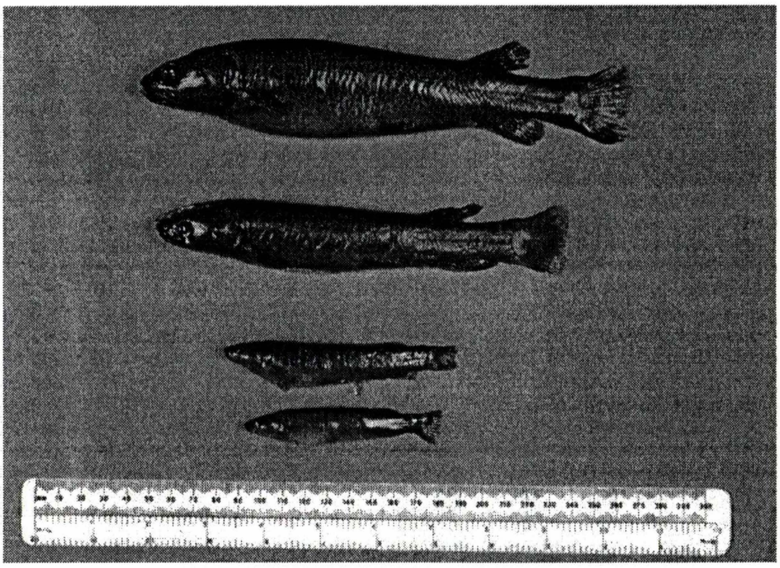
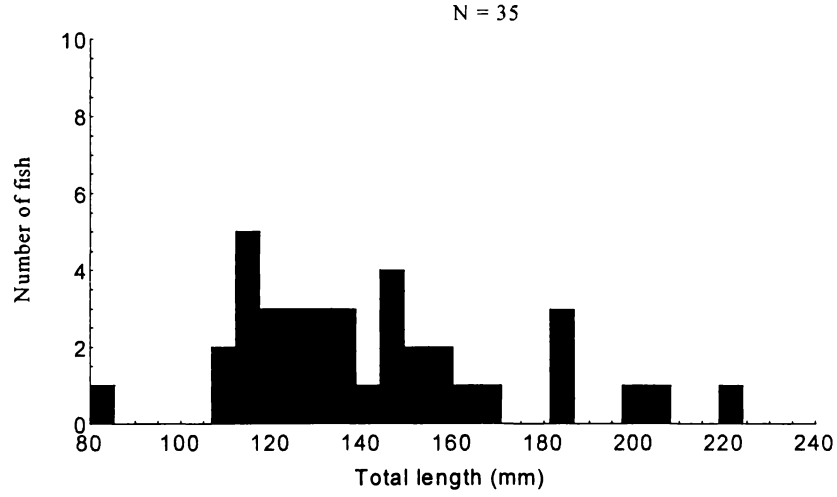


Figure 11 Koaro from Lake Okareka and Okareka Stream caught during February and April 2001. Lake fish above and stream fish below.

Lake fish caught from deep and shallow environments also differed in mean total length. Fish caught in deeper sites (1-3 m) (mean 161.2 mm ± 6.4) were 11% longer than lake fish caught in shallow sites (<1 m) (mean 145.3 mm ± 10.01) ($F_{1,95} = 5.2$, $P = 0.02$ on natural log transformed data) (Figure 12 a and b).

(a) Shallow (< 1 m)



(b) Deep (1-3 m)

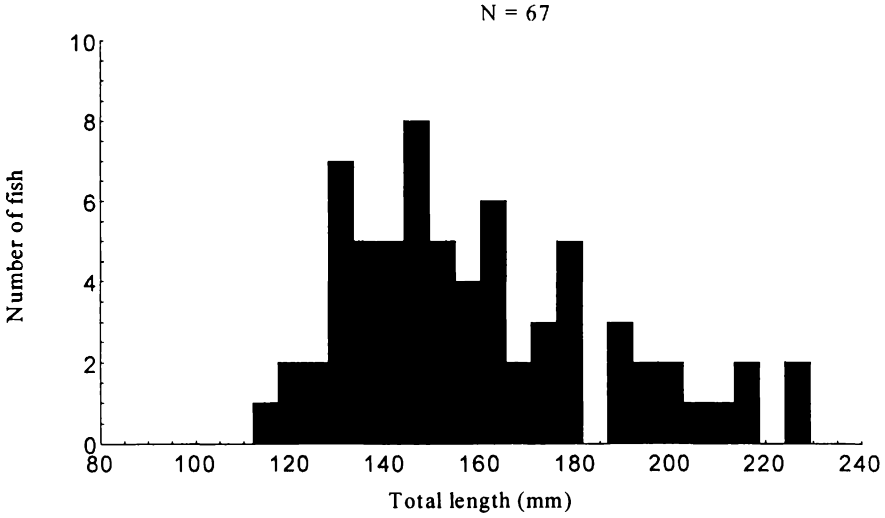


Figure 12 a and b Length distributions of Lake Okareka koaro caught in shallow and deep waters. Fish were from four deep (1-3 m) and four shallow (< 1 m) placed fyke nets set monthly from January 2001 to February 2001 and September 1999.

3.3.2 Length to weight relationships

3.3.2.1 Stream and lake fish

Stream fish ranging from 80 to 120 mm were heavier for length than lake fish of equivalent length (Figure 13). The relationship for stream fish was $Y = -13.0 + 3.3 * X$, where Y is the natural logarithm of weight in g, and X is the natural logarithm of total length in mm ($r^2 = 0.92$). The relationship for lake fish was $Y = -15.0 + 3.8 * X$ ($r^2 = 0.9$).

The slopes of the two regression lines were different, as the interaction term of the ANCOVA for natural log transformed data was significant ($F_{1,128} = 864.0$, $P < 0.001$).

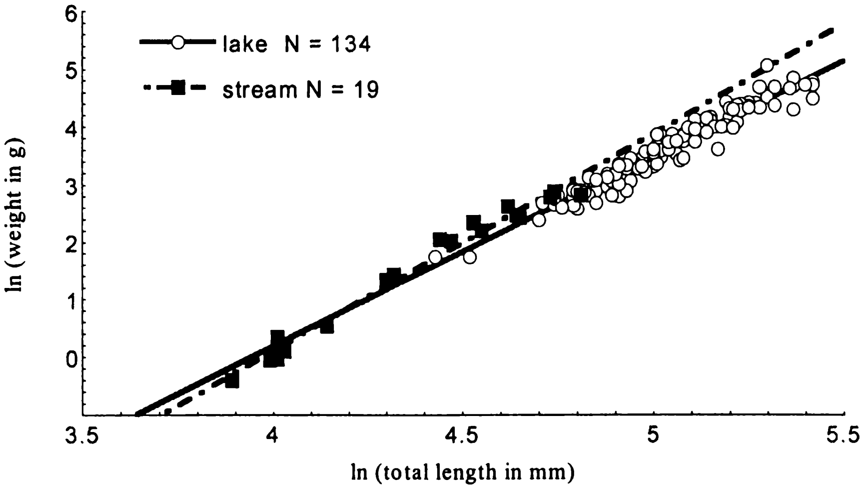


Figure 13 Relationship between total length (mm) and weight (g) for lake and stream koaro. Koaro from Tarawera and Okareka tributary streams were combined, and koaro from Lakes Okareka and Tarawera were combined.

3.3.2.2. Male and female lake fish

The relationship between length and weight for male and female lake fish combined was *W* = -13.2 + 3.3 * *L* where *W* is the natural logarithm of weight in g, and *L* is the natural logarithm of total length in mm ($F_{1,65} = 607.9$, $r^2 = 0.9$, $P < 0.001$; Figure 14). Outliers included one spent female that was lighter than expected, and one ripe female that was heavier than expected according to the regression equation.

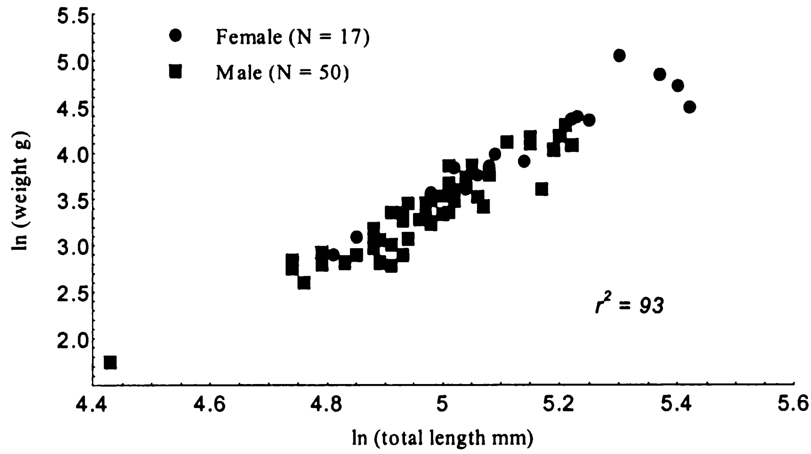


Figure 14 Relationship between length and weight of male and female koaro in Lake Okareka. Data are from combined samples of fish from 8 fyke nets set monthly from January 2000 to February 2001 and once in September 1999 in Lake Okareka and Lake Tarawera.

3.3.3 Growth

3.3.3.1 Measured growth of tagged fish

A total of 20 fish were recaptured in Lake Okareka, providing direct measurement of growth for a known time period. Fish that had the spring and summer growth season between recaptures grew slightly faster than fish which had grown between recaptures in autumn and winter. Average daily growth rate for spring and summer growth fish combined was 0.030 mm day^{-1} with a very large 95% confidence interval (-0.002, 0 062, $N = 9$) compared with the average winter daily growth of autumn and winter growth fish of 0.025 mm, again with a large 95% confidence interval (-0.007, 0.057, $N = 10$).

There was substantial variation in growth rates. Some fish grew large amounts between recaptures while others grew at much slower rates. Two fish actually shrank from one capture to the next (Table 9). These variable growth rates are reflected in weak linear regressions when absolute growth is plotted against time between captures. While a significant relationship for spring/summer growing fish combined was revealed ($F_{1,7} = 7.0$, $P = 0.03$) with a low r^2 value of 0.5, no relationship was found for autumn/winter growing fish ($F_{1,8} = 2.0$, $P = 0.20$, $r^2 = 0.2$). Only one stream fish was recaptured during the study which had grown at a rate of 0.19 mm day $^{-1}$ over the summer season.

Table 9 Summary of total lengths and growth of recaptured fish from Lake Okareka. Fish were caught in 8 fyke nets set monthly from January 2000 to February 2001 (inclusive) and in September 1999 and from Okareka Stream caught by two pass electrofishing in April, July and November 2000 and February 2001.

			Total length (mm)			Growth (mm day^{-1})	
Sex	Season at large between recaptures	Time between recaptures (days)	Marked	Recaptured	Increase	Absolute growth rate	Instantaneous rate of increase
Lake Okareka							
Female							
	winter	163	226	215	-3.66	-0.022	-0.00031
	winter spring	196	225	225	0	0.000	0.00000
	spring	37	160	160	0	0.000	0.00000
	summer	63	155	157	1	0.016	0.00020
Male							
	summer	190	128	138	10	0.053	0.00040
	whole year	447	132	152	20	0.045	0.00032
	summer	41	144	149	5	0.122	0.00083
	autumn	14	138	140	2	0.143	0.00103
	winter	129	135	135	0	0.000	0.00000
	winter	129	139	139	0	0.000	0.00000
	winter	120	135	150	3.75	0.031	0.00088
	winter	120	155	160	1.25	0.010	0.00026
	winter	124	140	156	4	0.032	0.00087
	spring	95	139	144	5	0.053	0.00037
	spring	75	150	154	1.33	0.018	0.00035
Indeterminate							
	autumn	94	215	225	3.33	0.035	0.00048
	winter spring	124	200	212	3	0.024	0.00047
	spring	95	196	204	2.6	0.027	0.00042
	spring	37	148	148	0	0.000	0.00000
	summer	92	166	160	-1.6	-0.017	-0.00040
Okareka stream							
	summer	126	74	100	24	0.190	0.00239

3.3.3.2 Growth estimated from otolith ages

Age was determined for 11 lake fish and 11 stream fish. Where available right and left otoliths of each fish were read independently. Total lengths of lake and stream fish were then grouped into year classes and mean total length for each year class calculated (Table 10). Okareka and Tarawera stream fish were smaller for a given age class than those determined by Kusabs (1989) for stream populations of koaro in Lake Taupo tributaries, and considerably smaller than those determined by West (1989) for sea-going populations in Waikato streams (Table 10). No comparable data are available for age and length of lake fish, however in comparison to diadromous koaro in Waikato streams, lake fish were larger for any given age (Table 10).

Table 10 Mean lengths of lake and stream koaro according to age class. Fish in this study were from Lake Okareka and Lake Tarawera combined (*N* =12), and Okareka and Tarawera streams combined (*N* = 11). Fish from Lake Taupo streams and Waikato streams from other studies are also shown.

	This study			Lake Taupo tributary streams (Kusabs 1989)		Waikato streams derived from data provided in West (1989) for two streams combined	
Age	Number in age class	Mean total length (mm)	SE	Number in age class	Mean total length (mm)	Number in age class	Mean total length (mm)
Lake							
3	4	134	5				
4	3	160	5				
5	4	168	9				
Stream							
1	3	50	2	2	74		
2	3	64	6	3	89	1	100
3	3	92	2	5	112	6	121
4	2	93	8	1	146	2	143
5						4	157
6						6	176

Measurements of distance on the otolith from the nucleus to the first winter band were also taken for 24 otoliths from 12 lake fish, and 22 otoliths from 11 stream fish. Otoliths from lake fish had a shorter distance between the nucleus to first winter band ($F_{1,44}$ = 286.1, $P < 0.001$) and there was no overlap in distance between the two habitat types (Figure 15). Mean length of lake fish nucleus to first winter band (4.1 μm ± 0.13) was considerably larger than mean length for stream fish (35.0 μm ± 0.40).

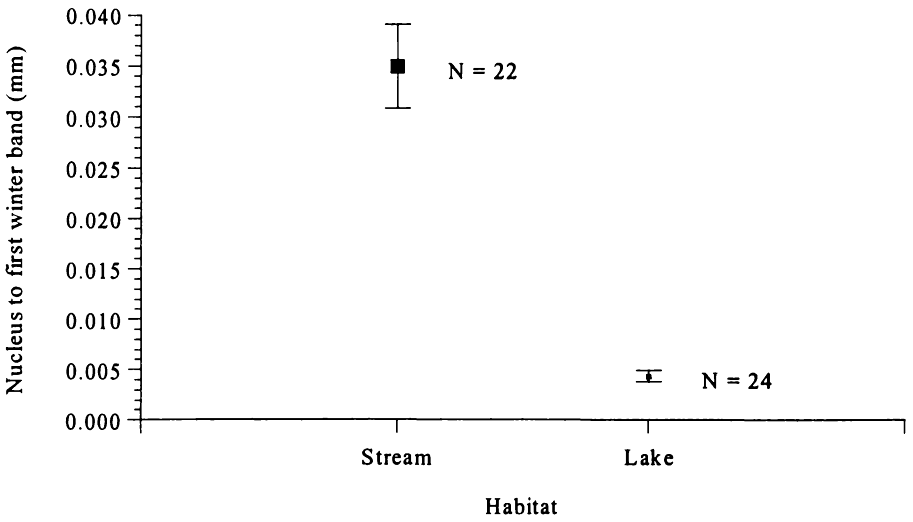


Figure 15 Comparison between mean distance from nucleus to inside edge of first winter band on sagittal otoliths for Okareka and Tarawera stream fish combined collected during February to April 2001 and Lake Okareka fish collected during February 2001. Error bars represent 95% confidence interval for the mean.

Measurements of otolith radius from the nucleus to the outermost edge along the longest axis were obtained for 22 otoliths from 12 lake fish from Lake Okareka and 20 otoliths from 11 stream fish from Okareka and Tarawera streams combined. The relationship between otolith radius and total length was significant (N = 42 for lake and stream fish combined, $r^2 = 0.94$, $P < 0.001$), explained by the equation: $R = 3.97 + 0.79 * L$, where; R = the natural logarithm of radius and L = the natural logarithm of total length (mm). The continuity of the data suggests that total length and otolith radius are directly related regardless of different growth rates (Figure 16). This was confirmed by ANCOVA which found no significant difference between the relationship of otolith radius and length between lake and stream fish ($F_{1,34} = 0.54$, $P = 0.47$). In contrast to the relationship between otolith radius and length, the relationship between otolith radius and age was different between the two habitats (ANCOVA $F_{1,20} = 69.5$, $P < 0.001$). Otolith growth rate in stream fish slowed down after 3 years compared to lake fish in which otoliths continued steady growth until at least year 5 (Figure 17).

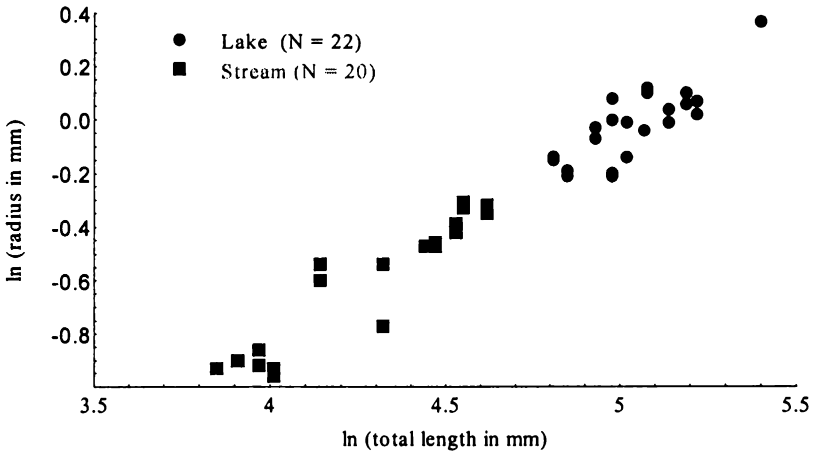


Figure 16 Relationship between total length and otolith radius. Fish were from Lake Okareka, and Okareka and Tarawera streams combined, collected in February 2001, and February and April 2001 respectively.

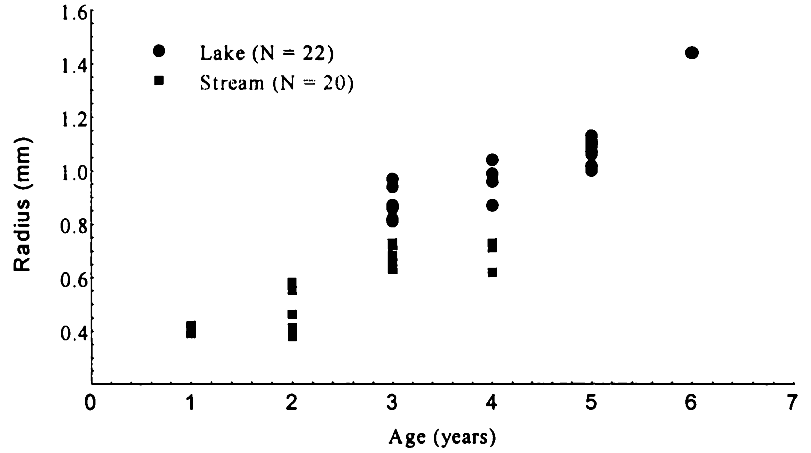


Figure 17 Relationship between otolith radius and age in years (derived from annual bands on sagittal otoliths) for lake and stream fish. Fish were from Lake Okareka collected in February 2001, and from Okareka and Tarawera streams combined, collected in April 2001.

3.3.3.3 Von Bertalanffy growth model

When mean total lengths calculated from otolith year class groupings were graphically fitted to the von Bertalanffy growth equation, it is apparent that growth rates for lake and stream fish were markedly different (Figure 18). Lake fish had a greater L_{∞}, and smaller K value than stream fish (Table 11). The L_{∞} value of 230 mm for lake fish is consistent with the observed maximum TL of 226 mm in field samples.

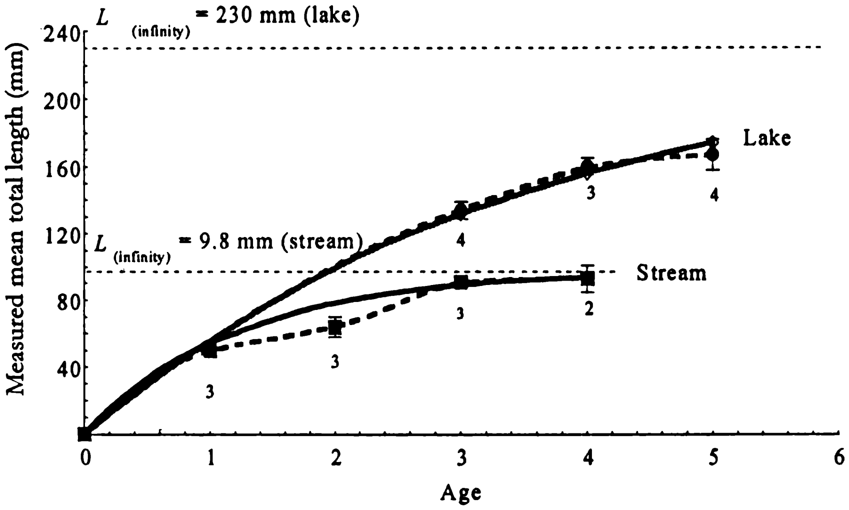


Figure 18 Von Bertalanffy growth curves for lake and stream fish. Fish were from Okareka and Tarawera streams combined collected during February to April 2001, and from Lake Okareka collected during February 2001. Mean measured total lengths are represented by dotted lines with markers and SE bars. Error bars are one standard error for mean total lengths derived from age class groupings according to sagittal otoliths.. Estimated total lengths are represented by solid lines without markers. Numbers by markers are *N* for each age group.

Table 11 The graphically derived parameters L_{∞}, K and t_0 for von Bertalanffy growth curves. Parameters are from Figure 18 for fish from Lake Okareka, and Okareka and Tarawera streams combined. For both lake and stream fish the t_0 value was assumed to be zero.

Site type	Total number of fish	$L_{(\infty)}$ (mm)	K	t_0 (years)
Lake	12	230	0.28	0
Stream	11	98	0.82	0

3.4 Interaction between lake and stream fish and movement between habitat types

3.4.1 Movement of lake koaro

A total of 102 fish were caught in Lake Okareka during the study, including fish caught during the exploratory capture trials in September 1999. Of these, 20 fish were previously tagged (19.6%) with mean shoreline distance for each sex shown in Table 12. Four fish (3 males and one female) were recaptured twice. Female fish moved a greater mean distance than male fish. One ripe female fish and two spent female fish moved shoreline distances of more than 200 m (Table 12).

All male fish were recaptured in either exactly the same location or in close proximity (within 100 m) to their previous capture. This included three male fish that were captured three times in exactly the some location (Table 12). The difference between sexes in distance moved was not significant (Kruskal-Wallis $P = 0.47$) presumably due to the small sample size.

Of the five indeterminate sex fish recaptured, three relatively large fish (> 190 mm TL) (Table 9) had moved shoreline distances ≥ 100 m (Table 12).

Only two fish were recaptured in Lake Tarawera, both of which were of unknown sex. One had moved a shoreline distance of 151 m while the other was caught in exactly the same location. One stream fish was recaptured from the Okareka stream sites. This was an unripe female fish captured in the same location as first capture. Over the whole study period, no tagged lake fish were captured from stream sites, and no tagged stream fish were captured from lake sites.

Table 12 Shoreline distance moved and ripeness of recaptured fish from Lake Okareka from 15 sampling occasions. Fish were captured using eight fyke nets set monthly from January 2000 to February 2001, and September 1999.

Sex	First capture		Second capture		Distance moved (m)			
	Month	Ripeness	Month	Ripeness	Total	Mean for each sex	95% confidence interval for each sex	
							lower	upper
Female	Mar-00	not ripe	Aug-00	spent	546	362.5	-98.9	823.9
	May-00	not ripe	Dec-00	spent	647			
	Nov-00	not ripe	Dec-00	ripe	10			
	Nov-00	not ripe	Jan-00	ripe	247			
Male	Sep-99	ripe	Mar-00	ripe	58	63.2	23.2	103.2
	Sep-99	ripe	Nov-00	ripe	97			
	Jan-00	ripe	Feb-00	not ripe	0			
	Apr-00	ripe	Aug-00	ripe	90			
	Apr-00	ripe	Aug-00	ripe	0			
	May-00	ripe	Sep-00	not ripe	97			
	May-00	not ripe	Sep-00	ripe	6			
	Jul-00	ripe	Nov-00	ripe	100			
	Aug-00	ripe	Nov-00	ripe	189			
	Sep-00	not ripe	Dec-00	ripe	0			
	Mar-00	ripe	Apr-00	ripe	58			
Indeterminate	Feb-00	not ripe	May-00	not ripe	647	181.0	-151.5	513.5
	Jul-00	not ripe	Nov-00	not ripe	100			
	Aug-00	not ripe	Nov-00	not ripe	148			
	Nov-00	not ripe	Dec-00	not ripe	10			
	Nov-00	not ripe	Feb-01	not ripe	0			

3.4.2 Vertebral count

Mean number of vertebrae in lake fish from Lake Tarawera and Lake Okareka was lower than stream fish (ANOVA $F_{3,75} = 7.3$, $P < 0.001$) (Table 13). A Bonferroni post hoc pairwise multiple comparison revealed no significant difference between number of vertebrae of fish between the two streams ($P = 0.98$) or between the two lakes ($P = 0.44$), giving rise to the means groups shown in Table 13.

There was no relationship between number of vertebrae and total length when a regression was undertaken on fish from all sites combined ($F_{1,44} = 3.6$, $P = 0.065$).

Table 13 Vertebral number in fish from Lake Tarawera, Lake Okareka, Okareka and Tarawera streams with mean groups at $P < 0.05$ shown.

Site	Number of fish	Mean vertebral number	95% Confidence limits		Means groups at $P < 0.05$
			Lower	Upper	
Lakes					
Okareka	9	53.9	52.9	54.9	a
Tarawera	55	55.0	54.8	55.3	a
Streams					
Okareka	9	56.0	55.1	56.9	b
Tarawera	7	56.1	55.8	56.5	b

Section Four
Discussion

Successful population restoration in New Zealand relies on fulfilment of two key information requirements before restoration programmes can be soundly developed; firstly, an understanding of the demography of the population including age-specific fecundity, survival, immigration and emigration, and secondly an understanding of how human-induced threats alter these demographic variables. The restoration of a koaro population is no exception and will require an understanding of inherent population dynamics and threats to important life stages. In this discussion the demographic variables and the threats that impinge on them are considered, together with a discussion of the implications of these variables and threats in relation to the restoration of a land-locked koaro population.

4.1 Abundance

4.1.1 Lake koaro

Koaro in this study were in low abundance compared to a number of South Island lakes where trout species are absent. In Lake Cristabel, Johnson et al. (1976) observed immature koaro being widespread and abundant throughout the lake, and in Lake Chalice the mean catch rate of koaro > 80 mm total length (TL) during winter of 1.87 fish net^{-1} night^{-1} (from Meredyth-Young and Pullan 1977), was higher than Lake Okareka in this study where mean catch rate was 0.78 fish net^{-1} night^{-1}. Catch rates in Lake Tarawera were even lower (mean 0.04 fish net^{-1} night^{-1}).

4.1.2 Stream koaro

Catch rates of post-whitebait koaro were low throughout all seasons in both the Okareka and Tarawera tributary streams. Whether this reflects the sparse lake populations or the poor habitat provided by the streams is not clear, however, during sampling of the Okareka and Tarawera streams an almost complete absence of benthic macroinvertebrate fauna was noted and attributed to the highly mobile bed of the streams and scouring by frequent flash floods. The lack of benthic fauna in the streams would render the streams poor habitat, since benthic prey is the dominant component of the koaro diet (Main and Winterbourn 1987, Kusabs 1989, Glova and Sager 1989).

4.1.3 Factors influencing abundance of koaro

Prior to the introduction of rainbow trout and brown trout to the lakes of the central North Island in the late 1800s (see Burstall 1983), land-locked koaro were abundant (Buck 1921, Best 1929, Phillips 1940). Juvenile koaro were caught "by the hundred weight" (approximately 50 kg lots) and formed an important and staple food and barter item for Maori. Koaro were so abundant that in storm conditions they were washed up in "cartloads" on the shores of Lake Taupo (Armstrong 1935), and many lake shore landmarks of the Rotorua Lakes area are named after prized fishing grounds for this species (Buck 1921).

Following the establishment of trout in the central North Island lakes, a major collapse in the native koaro fishery occurred (account of Makereti Papakura in Penniman 1938), and in 1877 official complaints were made to the Rotorua Town Board of the day by Maori regarding the loss of their valued food supply (Strickland 1993). By 1912, the reduced abundance of juvenile koaro caused deterioration in the establishing trout fishery in Lake Taupo (Burstall 1950). Documented evidence of juvenile koaro comprising a large component of the diet of rainbow trout (Fletcher 1919a, Phillips 1924, Armstrong 1935) has lead current researchers to suggest that trout predation and competitive displacement was responsible for the demise of koaro in the lakes of the central North Island (eg, McDowall 1990a, Rowe 1990).

The presence of trout species on their own, however, may not fully account for the low abundance of koaro in Lakes Okareka and Tarawera. Common smelt were introduced as a forage fish for trout stocks into Lake Tarawera in 1931, and into Lake Taupo from 1934 – 1940 (Burstall 1983), as well as to several other central North Island lakes and may also have contributed to the low abundance of koaro found in these lakes today. The total extinction of koaro from Lake Rotopounamu on the central North Island volcanic plateau is attributed solely to the introduction of common smelt (Rowe 1993), and the decline of lacustrine land-locked koaro to the point where they are now rare, has only occurred in lakes with both common smelt and trout, or in South Island lakes where brown trout predominate (Rowe et al. 2001). In addition, koaro are still commonly found in lakes where rainbow trout are present but common smelt are absent, such as in Lake Pukaki and Lake Alexandrina in the South Island (Rowe et al. in submission).

Brown trout are not present in Lake Tarawera or Lake Okareka, but common smelt are common in both study lakes and are regularly observed during spring in large shoals around the lake margins. In Lake Rotoaira, also situated on the central North Island volcanic plateau, where rainbow trout are present but common smelt are not, the mean catch rate of koaro > 80 mm TL of 1.06 fish net^{-1} night^{-1} (from Rowe et al. 2001 in press) was higher than catch rates in Lake Okareka (mean 0.78 fish net^{-1} night $^{-1}$) and Lake Tarawera (mean 0.04 fish net^{-1} night $^{-1}$), but slightly lower than in Lake Chalice (mean 1.87 fish net^{-1} night $^{-1}$) (from Meredyth-Young and Pullan 1977) where neither trout or common smelt are present.

The mechanism for common smelt displacement of koaro has not been established. Interspecific competition for food provides a plausible explanation for competitive exclusion as discussed by Rowe (1993), since juvenile koaro and larval and juvenile common smelt are both limnetic planktivourous feeders (Jolly 1967, Naylor 1983, Stephens 1984). In addition, koaro assume a benthic existence following its larval and juvenile lifestage (McDowall 1978), while post-juvenile (1+) common smelt remain limnetic feeders and also become surface feeders (Stephens 1984), and since adult common smelt become mainly piscivorous from the age of two years (Stephens 1984), it is likely that direct predation of koaro larvae and possibly small juveniles occurs.

Within streams similar interactions exist. Added to poor stream habitat, already discussed, koaro are likely to face competition and predation from rainbow trout in these streams. In a review of sports fish and native fish interactions Allibone and McIntosh (1999) found that distributional studies of non-migratory galaxiids in Otago (eg, Allibone and Townsend 1995, Allibone and McDowall 1997 and Townsend and Crowl 1991), have provided a body of evidence for galaxiid displacement by salmonids, and have shown that non-migratory galaxiid species, rarely if ever, coexist with salmonids. In this study, the catch rates of juvenile rainbow trout during all seasons, ranged from *c.*2 – 8 times higher than catch rates of post-whitebait koaro in the upper Tarawera stream site, and *c.* 2 – 12 times higher in the middle and upper stream sites in the Okareka stream. On the basis of Kusabs and Swales (1991) finding that a significant dietary overlap existed between juvenile rainbow trout and koaro in Lake Taupo tributaries, and that in autumn and summer juvenile koaro comprised 87% by weight of the juvenile rainbow trout diet, it is suspected that juvenile rainbow trout directly compete with and predate on juvenile koaro in the streams in this study. The virtual absence of koaro where juvenile rainbow trout were abundant, and the abundance of koaro where rainbow trout were absent in the tributaries of Lake Rotoaira, provides support for the effects of trout depression of koaro abundance. In addition, a similar distribution pattern of galaxiid abundance in the absence of trout occurred in the Ruamahunga River system in the Wairarapa where the non-migratory dwarf galaxias (*Galaxias divergens*) was only found above waterfalls that posed barriers to upstream trout movement (Hopkins 1971).

It is therefore likely that the introduction of rainbow trout, in combination with the presence of common smelt, has significantly contributed to the low abundances of both lake and stream koaro found in this study. Competition with, and direct predation on, important koaro life-history stages in both lake and stream habitats are considered to be the most likely mechanisms.

4.2 Life history - the role of tributary streams and interactions between lake and stream koaro

The role of tributary streams in the life history and maintenance of land-locked koaro populations is poorly understood, and in particular the extent of movement between habitats is unknown. McDowall (1990a) considered that the life history of land-locked koaro was similar in most respects to that of their diadromous counterparts, and that land-locked koaro most likely spawned in associated river habitats. Support for this view is provided by Rowe et al. (2001) who concluded that in Lake Rotoaira, lacustrine fish migrate into inlet streams during summer to spawn. In addition, Kusabs (1989) suggested that gravid koaro migrated into the lower sections of tributary streams of Lake Taupo to spawn.

Aside from whitebait migrations from the lake to tributary streams, no direct observations of movements between habitats by lake and stream fish have been made in this or any other study on land-locked koaro. Therefore, implications from differences between lake and stream fish with respect to size, growth, spawning period and spawning place are discussed together within the context of the insight they provide regarding; firstly, the use of tributary streams for important life stages by lake and stream fish, and secondly, the level of interaction between lake and stream fish.

4.2.1 Size and growth

Genetic analysis undertaken for 20 stream fish and 12 lake fish found no evidence of difference between lake and stream fish based on three polymorphic microsatalite loci (Keith King pers comm. 2001). Therefore, differences in environmental variables such as temperature, food availability, space, and direct and indirect inter and intra specific competition between habitats provide the most likely explanations for any differences in size and growth of lake and stream fish. It follows therefore, that size and growth can reveal the period of occupation of lake and stream fish in their respective habitats, as well as possibly revealing whether movement between habitats occurred for a length of time sufficient to affect growth rate.

The study found that post-whitebait lake fish were 68% larger (mean 155 mm TL) than stream fish (mean 92 mm TL). Although little overlap in length of fish between the two habitat types was observed, the presence of fish between 45–55 mm TL in the lake during October 2001 confirmed that small fish are present in the lake, but that the mesh size of the monthly fyke nets selected against their capture. Since the electric fishing machine selects for large fish (Zalewski and Cowx 1990), the small size of koaro in streams appears to be real.

Difference in size is supported by a difference in comparative growth rates in fish from each habitat. Von Bertalanffy growth curves showed that lake fish grew faster and larger (L_∞ = 230 mm) than stream fish (L_∞ = 9.8 mm) (Figure 18). Stream fish reached a maximum total length at or around age three when growth rate slowed in comparison to lake fish, which continued to grow past the age of three to at least five years (Figure 18).

The absence of lake fish less than three years old in the samples provides no ability to comment on growth of lake fish prior to this age. It is however apparent that from the age of three years lake and stream fish grow at different rates, and therefore any time spent in non–respective habitats from this age must be short enough to have no influence on the pattern of growth. Measurements from sagittal otoliths support this suggestion.

Otolith growth was linearly related to total length regardless of habitat type. A significant relationship between total length and radius of sagittal otoliths of lake and stream fish was found with no significant difference between the relationship for habitat types (Figure 16). This is consistent with McCaughan (1995) finding that somatic and otolith growth within species was closely related for nine species of native fish regardless of the location of the population. By contrast, a significant difference in relationship of age and otolith radius between lake and stream fish (Figure 17) was found. Otolith growth rate in stream fish slowed after three years in comparison with lake fish, where otolith growth remained steady until at least the age of five years. Of particular note is the lack of overlap in otolith radius for fish of three years and older. This, combined with the linear relationship between total length and otolith radius, confirms that any movement between habitats for periods of time long enough to influence otolith growth rate must occur before the age of three years.

No growth data for lacustrine koaro from other studies are available for comparison with this study, however, data from West (1989) and Kusabs (1989) for diadromous and land-locked fluvial koaro provide some useful comparisons. Okareka and Tarawera stream fish were smaller for a given age than land-locked fluvial koaro from Lake Taupo tributaries, and diadromous koaro from Waikato streams. In addition, they were considerably smaller than the size classes of 160–180 mm commonly found in New Zealand rivers and streams (McDowall 1990a). The largest post-whitebait koaro caught in the Okareka and Tarawera streams measured 128 mm TL, 45% smaller than the largest fish caught from a Lake Taupo tributary measuring 186 mm TL. Mean total length of fish from ages two to four inclusive from Okareka and Tarawera streams ranged from 48-56% smaller than fish from Lake Taupo tributaries, and 53-56% smaller than diadromous koaro from Waikato streams.

Reasons for the reduced size may be due to the poor habitat provided by the Tarawera and Okareka tributary streams as previously discussed, compounded by competition with rainbow trout. Trout were absent from those sections of Waikato streams where koaro were collected (D. West pers comm. 2001). In addition, in Lake Taupo tributary streams, Kusabs (1989) found koaro in better condition throughout the year where trout numbers were low, in contrast to poorer and fluctuating condition where trout numbers were high.

Lacustrine koaro in this study were larger for any given age than diadromous koaro from the Waikato streams. The largest documented koaro specimens have been found in lake environments, and it is interesting to speculate whether koaro do better in still water environments. To date, the habitat preference of koaro has been described as rapidly flowing tumbling rocky streams (McDowall 1990a) with greater abundance found in riffle areas (McDowall 1978, Taylor 1988). However, Hayes (1996) documents observations of approximately 15 large (150–250 mm TL) stream dwelling koaro surface feeding from the drift in a large slow moving pool in a South Island stream in the absence of trout, and suggests that koaro are confined to riffle and cascade areas as a result of competitive displacement by rainbow and brown trout. This supports the suggestion that in rivers and streams koaro may only be limited to benthic feeding when coexisting with drift feeding competitors such as juvenile salmonids (Glova and Sagar 1989).

The L_∞ value of 230 mm for lake fish in this study is consistent with the observed maximum TL of 226 mm caught in Lake Okareka, but smaller than the largest recorded koaro found in New Zealand to date (271 mm TL) from Lake Chalice where trout are absent (Meredyth –Young and Pullan 1977), and the next largest from Lake Pukaki (270 mm TL) where trout are present but common smelt are absent (Rowe 1999). It is possible that prior to the introduction of trout and common smelt, larger fish were once present in the central North Island lakes. Historical Maori fishing nets from Lake Taupo were reported to have a mesh size of 40 mm (Burstall 1983) suggesting that large fish were present.

Extrapolation of the von Bertalanffy growth curve in Figure 18 for lake fish shows that at the L_∞ value of 230 mm TL a lake fish would be approximately eight years old. Attainment of eight years seems realistic, given that an eight year old and several seven year old koaro were found in a tributary of the Waikato River

(West 1989), and that banded kokopu (*Galaxias fasciatus*), a closely related species has been reported reaching at least nine years of age (Hopkins 1979).

The L_∞ value of 9.8 mm derived for stream fish was less than the maximum of 128 mm TL observed in field samples. Some explanation is provided by noting that the L_∞ value is derived from mean measured values and therefore some variance is also expected for the L_∞ value. Further explanation is provided by the absence in laboratory samples of larger fish that were observed in field samples.

4.2.2 Spawning season

Distinct spawning seasons for lake and stream fish are indicated from changes in the proportion of ripe fish and differences in sagittal otolith measurements of fish from the two habitats. The occurrence of distinct spawning seasons suggests that interaction at the reproductive level for lake and stream fish is limited, and further that lake and stream fish may belong to two sub-populations.

Changes in the proportion of ripe fish provide a clue as to when fish are likely to spawn. In Lake Okareka ripe female fish were more abundant during the summer months of December, January, February, and to a lesser extent in March. By contrast, an extended period of male ripeness from April to October with peaks not aligned with peaks in female ripeness (Figure 10) provides a confusing picture. However, spawning is by necessity dictated by the presence of ripe females, and these were only found during summer, suggesting that summer is the spawning season. A very similar period of extended male ripeness was observed in koaro in Lake Rotoaira, where male koaro were ripe from September to April, but where ripe females also peaked during summer (Rowe et al. 2001 in press). In Lake Coleridge, the appearance of larval koaro in the lake from November to February with a peak in January (Taylor et al. 2000) indicates that some summer spawning and hatch of koaro occurs in this lake. Whether these larvae were derived from lake or stream fish is unknown. In Lake Taupo, the presence of juvenile koaro of 31-47 mm TL in the littoral zone during winter (R.T.T Stephens unpublished data 1983 Appendix 1) also indicates that some summer spawning of koaro must occur, followed by a summer or early autumn hatch, given that at 45–55 mm TL, diadromous koaro are approximately 6 months old (McDowall and Eldon 1980).

The summer spawning of lacustrine koaro in this study, and in Lake Rotoaira, represents a shift in spawning season between land-locked koaro and diadromous koaro. Diadromous koaro spawn in autumn to early winter (West 1989, Duffy 1996, O'Connor and Koehn 1998, Allibone and Caskey 2000). While no speculation is made on the mechanism responsible for this shift, it supports the suggestion that a shift in spawning season is a consequence of loss of diadromy due to land-locking (McDowall 1988). It is interesting to note that similar shifts have occurred in other species such as in land-locked populations of inanga (*Galaxias maculatus*) in Australia (Pollard 1971), and in land-locked common smelt populations in the central North Island lakes (Stephens 1984).

In contrast to the summer spawning period of lake fish, koaro from the Okareka and Tarawera streams appear to spawn in autumn. Relative abundance of ripe males in streams peaked during autumn, and no ripe male fish were encountered during any other season. During field sampling, no ripe female fish were found in streams, however laboratory analysis of fish retained at the end of sampling in autumn, revealed the presence of both male and female fish in moderate to advanced stages of gonadal maturation. This suggests a late autumn or early winter spawning period. Autumn or early winter spawning is consistent with observations of fluvial lake-locked koaro in a tributary stream belonging to Lake Cristabel on the west coast of the South Island, where gravid female koaro were found in early to mid June (Johnson et al. 1976). It is also partially consistent with observations of koaro in Lake Taupo tributaries, which displayed the greatest spawning activity in late summer or early autumn (Kusabs 1989).

Annual deposition of hyaline otolith rings has not been validated for koaro and therefore results must be treated with caution. However, it appears that differences in sagittal otolith measurements between lake and stream fish reveal different hatching seasons for fish from the two habitat types, supporting the existence of different spawning seasons. Otoliths form during the embryonic period and reflect all life history events; concentric growth zones form around a central nucleus and represent distinct seasonal bands (Jearld 1983). The distance from the nucleus to the first winter band on the sagittal otolith can indicate the season in which a fish hatched, and therefore when the parent fish spawned. Since spring and summer are the primary growth seasons for fish (Jearld 1983), it follows that the smaller this distance, the less primary growth season experienced before the first distinct winter band appears on the otolith structure.

Mean distance between nucleus and first winter band for lake fish (4.1 µm ± 0.13, mean ± 2SE) was significantly smaller than that of stream fish (35 0 µm ± 0.39). The scale of this difference (Figure 15) indicates that fish caught from lakes and streams hatched in different seasons. The comparatively small distance from lake fish otoliths is consistent with summer spawning, followed by a late summer or autumn hatch, and limited growth before the onset of winter. The comparatively large distance from stream fish otoliths, indicates an autumn or early winter spawning, followed by hatch in winter, and growth throughout the whole spring and summer season before the onset of the following next winter.

The different hatching seasons suggested for lake and stream fish may have implications for survival and growth of larval and juvenile life-stages and therefore population abundance. For example, in Lake Taupo, larval common smelt appear in the epilimnion during summer (Stephens 1984). If the same is true for the Tarawera lakes, koaro larvae which hatch during late summer may experience more intense competition for food resources with larval common smelt during this period. Also, seasonal changes in lake productivity may positively or negatively affect summer or winter hatched fish. For example, Stephens (1984) considered that in Lake Taupo, maximum zooplankton biomass occurred in October following the maximum period of productivity in the lake. Therefore, if the seasonal zooplankton biomass pattern is similar in the Tarawera lakes, then winter hatched stream fish may take advantage of higher food availability during this time.

4.2.3 Spawning place

Distinct spawning locations for lake and stream fish are apparent from movement observations, and are supported by a difference in vertebral counts between lake and stream fish. Lake and stream fish remained in their respective environments to spawn, and no evidence was found to suggest that any migration from lakes to the streams occurred. Difference in spawning locations strengthens the argument for emerging lake and stream sub-populations. This is indicated by the different spawning seasons and suggests that tributary streams are most likely not important for the spawning of lake fish.

Female fish in Lake Okareka moved 474% greater shoreline distance between recaptures (mean 362.5 m) than male fish (mean 63.2 m). All male fish were captured in exactly the same location or in close proximity (< 100 m shoreline distance away) to their previous location, despite being ripe on some capture occasions. This included three male fish which were captured more than once. The limited movement of male fish suggests a degree of male residency in a relatively small area of the lake (< 100 m^2). This is analogous to site fidelity observed in diadromous populations of koaro and a closely related species the shortjawed kokopu (*Galaxias postvectis*). In Waikato River tributaries, West (1989) found that 58% of recaptured tagged fish were within the site where they were previously tagged over a one year period. Over a two year study period of streams draining Mt Taranaki, Allibone et al. (2001) found that of 78 tagged shortjawed kokopu a substantial proportion (75% R. Allibone 2001, pers. comm.) were found in the exact same pool or run where the fish had been previously been captured.

In contrast to male fish in Lake Okareka, two spent female fish and one ripe female fish moved comparatively large shoreline distances (> 500 m), in a direction away from the Okareka Stream to where ripe male fish were present. Since the Okareka Stream is the largest of only two perennial streams discharging into the lake, these observations suggest that female fish migrate to spawning sites located in the littoral zone of the lake itself, as opposed to in tributary streams.

Changes in seasonal abundance in Lake Okareka, may provide support for a migration of female fish to spawning sites in the littoral zone. Koaro were 131% more abundant during seasonally warm months (November to April), when ripe female fish were found in the samples, in comparison to seasonally cool months (May to October) (Figure 9) when ripe female fish were virtually absent. Female fish were 20% longer than male fish, and length distributions of fish caught from deep and shallow sites may provide a clue as to the absence of female fish during winter.

Length distributions in Figure 12 (a and b) show that large fish (> 160 mm TL) were more abundant in deep water in comparison to shallow water. Since female fish were larger than male fish, it follows that unripe female fish could be more abundant in deeper water. If so, female fish may reside in deeper waters until ripe when they move into the littoral zone to spawn. This could also explain why ripe female fish comprised only 14.3 % of the total catch, in comparison to ripe male fish which comprised 42%.

In the absence of direct observation of spawning migrations, spawning or deposited eggs, the migration of ripe lake fish to other parts of the lake or tributary streams for a short period of time to spawn cannot be completely discounted. However, the patterns of movement of ripe fish strongly suggest that spawning takes place in the lake itself either in the littoral zone or lake margin. Support for the possibility of lakeshore spawning is provided by the presence of viable populations of land-locked koaro in several New Zealand lakes with no inflowing tributaries, such as in Lake Henrietta situated in Te Urewera National Park in the central North Island (Chris Ward, Department of Conservation, pers. comm.).

Diadromous koaro are known to spawn on the flooded margins of normal adult habitat and deposit eggs in dry riparian gravels above normal stream base flows during rapid rises in water level known as “spates”, caused by storm events (West 1989, Duffy 1996, O Conner and Koehn 1998, Allibone and Caskey 2000). In contrast to fluvial environs, changes in lake levels and inundation of lake margins due to flood events do not occur as rapidly as stream spates. Lake levels can remain high for extended periods of time, for example, in July 1998 a storm event caused water levels in Lake Okareka to rise by approximately 0.42 m which lasted three months until October 1998 before steadily receding (Wallace 1999). Koaro eggs take between 30-70 days to develop and hatch (O’Connor and Koehn 1998). Therefore eggs deposited during periods of high lake levels in riparian margins, would be immersed throughout their whole development period in contrast to the drier environment of the riparian margin where their fluvial counterparts develop.

Complete immersion however, may not compromise egg viability to hatch. O'Connor and Koehn (1998) found that completely immersed koaro eggs held in aquaria successfully completed development after 12 days and hatched 28 days after fertilisation when agitated. In addition, in experiments of koaro egg viability at different moisture levels, West (1989) found that only fully immersed koaro eggs remained viable and developed to hatch. Therefore, despite being immersed, development and successful hatch of eggs spawned in the lake itself, or on an inundated lake margin, is biologically possible.

In contrast to lake koaro, it appears that stream koaro spawn within stream environments. In the mid reaches of the Okareka Stream, both male and female stream fish in advanced stages of gonadal maturation, or ripe, were present, suggesting that spawning occurs in the vicinity of normal adult habitat. This is consistent with spawning of koaro in the vicinity of, or in close proximity to normal adult habitat, as found in other studies (Kusabs 1989, West 1989, Duffy 1996, Allibone and Caskey 2000).

Differences in vertebral number in lake and stream fish provide further support for distinct spawning places. Vertebral number is fixed during the early part of the embryonic period (Fahy 1976), and thereafter remains unchanged (Lindsay 1975). Both heredity and environmental factors can affect vertebral number in fish populations and are hard to disentangle (Lindsay 1988). Environmental factors can positively or negatively affect the number of vertebrae formed during the embryonic development stage, including but not limited to; temperature, oxygen, salinity and radiation exposure (sunlight) (Lindsay 1988).

In this study, the mean number of vertebrae in stream fish (Okareka 56.0 ± 0.94, Tarawera 56 ± 0.35, mean ± 2SE) was higher than in lake fish (Okareka 53.9 ± 96, Tarawera 55 ± 0.25). Since no genetic distinction between fish from the two habitats was found (Keith King, pers. comm. 2001) it is likely that differences in vertebral number are due to environmental factors. Salinity is not expected to differ markedly between the surface lake waters and stream water since waters are derived from the same catchments. Temperature however, substantially differs between habitats with streams remaining cooler than the surface waters of the lakes year round. Stream temperatures range from 8.2 °C – 15.9 °C and lake temperatures range from 10.5°C–20.9 °C (EBOP Monitoring dataset, November 2001).

In most cases the relationship between vertebral number and rearing temperature is negative, and cooler temperatures typically produce fish with a higher number of vertebrae (Lindsay 1988). Temperature ranges during the identified autumn and early winter spawning period for stream fish (range 8.2 – 11.4 °C) are considerably lower than the lake surface water temperature range (12.0 - 20.9 °C) during the identified summer spawning period for lake fish. When differences in vertebral count between lake and stream fish are considered comparatively, the higher mean vertebral number in stream fish is consistent with their development in the cooler stream environment, and the lower mean vertebral number of lake fish is consistent with development in the warmer lake environment.

The movement observations combined with the differences in vertebral number support different spawning locations and limited migration of reproductively mature fish between lakes and streams giving rise to sub-populations. However, the lack of genetic distinction found between lake and stream fish implies that if sub-populations have developed, a level of reproductive mixing still occurs between lake and stream fish.

4.2.4. Migration of whitebait to tributary streams

Migration of juvenile koaro (whitebait) from the sea to freshwater is the critical recruitment phase for maintenance of fluvial diadromous populations. Having left the marine environment, koaro whitebait migrate upstream in pursuit of suitable habitat and remain in freshwater (McDowall 1900a). In land-locked populations, migrations of juvenile koaro from lake environs into tributary streams have been commonly observed. For example, in Lake Wanaka, large migrations of whitebait enter the Matukituki River during April (McDowall 1990a) and in Lake Taupo tributaries, a migration of whitebait occurs during August to March each year (Kusabs 1989). Whether koaro whitebait migrations in land-locked populations comprise only stream spawned fish returning to their natal habitat type, and/or whether migrated whitebait remain in tributary stream environments like their diadromous counterparts, are two questions of prime relevance to the role of tributary streams and to the possibility of lake and stream sub-populations.

The results suggest that the peak migration period of whitebait to tributary streams occurred from summer to autumn, due to the relatively high abundance of koaro whitebait in the lower Okareka and Tarawera stream sites during these seasons, in contrast to a substantially lowered abundance during winter. This migration period is consistent with summer and autumn migrations to tributary streams in the land-locked populations mentioned above, but is inconsistent with migrations of diadromous koaro whitebait into river and stream mouths which occur during spring each year (Saxton et al. 1987, Stancliff et al. 1988, McDowall and Eldon 1980, McDowall 1990a, Young 2001). Diadromous koaro are approximately six months old at migration and measure between 44–55 mm TL (McDowall and Eldon 1980). In this study, whitebait caught in tributary streams fell within or slightly below this length range, and the same inference can be drawn from the size at migration and the timing of the run. The summer to autumn run, and lack of a second run during winter or spring suggests that migrating whitebait mainly comprise stream-spawned fish returning to their natal habitat type. After hatching in late autumn or early winter, stream spawned fish would be seven to eight months old at migration, only slightly older than their diadromous counterparts of six months. By contrast, lake spawned fish which were found to hatch in summer or early autumn would either be approximately two months old (if hatched in mid to late summer) or one year old (if hatched by early autumn), by the following summer to autumn whitebait migration. Since the size class of migrating whitebait observed ranged between 40-45 mm it is difficult to accept that a two month old fish would have already attained this length, or that a one year old fish could still have been recorded as whitebait in the summer/autumn migratory run. McDowall (1990a) considers that soon after entering freshwater, diadromous koaro become a dark olive green colour and much more slender in shape. If we cautiously assume that land-locked koaro follow similar timing in colouration, we could speculate that a lake spawned fish should be well coloured and possibly patterned by the age of one year.

The previously discussed difference in sagittal otolith measurements from nucleus to first winter band between lake and stream fish provides convincing support for fish from the two different habitats either returning to, or as in the case of lake spawned fish remaining in, their respective hatching environs. Figure 15 shows that the difference in measurement range between lake and stream fish was so large that no overlap between data sets existed. This indicates that all 24 otoliths from lake fish most likely came from summer spawned fish that either returned or remained in the lake habitat where they were caught. Similarly all 22 otoliths from stream fish most likely came from autumn or winter spawned fish that returned from the lake to stream habitats where they were caught.

Differences in mean vertebral number between lake and stream fish also supports a return to respective hatching environs. As discussed, the higher number of vertebrae in stream fish compared to lake fish is most likely attributed to differences in temperature in embryonic development environs. Therefore, a complete lack of overlap in upper 95% confidence interval for lake fish, and lower 95% confidence interval for their respective stream fish (Table 13), strongly indicates that there is little mixing of fish from the two habitat types.

4.3 General discussion and implications for restoration of land-locked koaro

The use of several approaches, which included determining spawning site, spawning place, and size and growth of lake and stream fish, provided a means to unravel aspects of the life history of land-locked koaro in the Tarawera lakes. It appears that that separate lake and stream sub-populations may exist or be developing, and that the life histories of the two sub-populations are dissimilar. In particular, it appears likely that lake koaro have a solely lacustrine life history.

The life history of lake koaro differed markedly from stream koaro and their diadromous counterparts. The shift from spawning in stream environs to lakeshore or littoral zone spawning, combined with an absence of a migratory phase into tributary streams, suggests that tributary streams do not play a major role in important life-stages of lacustrine koaro.

In direct contrast, stream koaro appear to have maintained a similar life history to diadromous koaro in terms of timing and place of spawning, and retention of a main whitebait recruitment phase to stream populations. Tributary streams are therefore important habitats for stream koaro populations throughout most life-stages except for the larval stage which is spent in the lake.

The possible existence of lake and stream sub-populations within the land-locked environs poses an interesting evolutionary scenario that warrants further research.

The lack of genetic difference between lake and stream fish suggests that speciation has not occurred between the two sub-populations, possibly indicating that differences in life history may have developed relatively recently.

The mechanism for why two life histories have developed is not immediately apparent and no speculation is made here. However, regardless of their origin, it is clear that restoration programmes aimed at the population level cannot focus on management of tributary streams alone. This is because the combination of competition and predation by rainbow trout and common smelt most likely exerts pressure on the important larval and juvenile life-stages of both lake and stream populations.

The larval stage of both lake and stream koaro are likely to be subject to competition with, and predation by, common smelt in the lake itself. Juvenile koaro are probably subject to predation by rainbow trout in the lake, and predation by juvenile rainbow trout in streams. In addition, post-whitebait stream fish must also compete with juvenile rainbow trout for food resources.

Therefore, to restore land-locked populations of lake and stream koaro in the Tarawera lakes, management must be applied at the ecosystem scale, which encompasses the body of the lake itself and its associated tributary streams. Management at this scale is particularly important given that tributary streams appear to play little role in the life history of lacustrine koaro, but do play a large role in the life history of fluvial koaro. At the ecosystem scale, restoration can be targeted at the population level to improve survival of important life-history stages of both lake and stream populations. To a large extent, this will most likely involve management of the effects of trout and common smelt.

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