Taonga and mahinga kai of the Te Arawa lakes: a review of current knowledge - Koaro

NIWA Client Report: HAM2007-022
July 2007

NIWA Project: TACF062

Taonga and mahinga kai of the Te Arawa lakes: a review of current knowledge - Koaro

Dave Rowe
Ian Kusabs

Prepared for

Te Arawa Lakes Trust

NIWA Client Report: HAM2007-022
July 2007

NIWA Project: TACF062

National Institute of Water & Atmospheric Research Ltd
Gate 10, Silverdale Road, Hamilton
P O Box 11115, Hamilton, New Zealand
Phone +64-7-856 7026, Fax +64-7-856 0151
www.niwa.co.nz

© All rights reserved. This publication may not be reproduced or copied in any form without the permission of the client. Such permission is to be given only in accordance with the terms of the client's contract with NIWA. This copyright extends to all forms of copying and any storage of material in any kind of information retrieval system.

Contents

Acknowledgements		iv
1.	Introduction	1
2.	Origin of kōaro in the Te Arawa lakes	2
3.	Kōaro in the Te Arawa lakes - past and present	6
4.	Life history, distribution, movements and habitats	11
5.	Prey species, predators and parasites	16
6.	Age, growth, fecundity, maturation and population structure	18
7.	Environmental tolerances	19
8.	Factors affecting kōaro population size in lakes	20
9.	Protection and restoration issues and options	22
10.	Critical knowledge gaps	23
11.	References	25

Reviewed by:

E. Williams

Approved for release by:

D. Roper

Formatting checked

A. Bartley

Acknowledgements

We are grateful for the contributions from the following people:

Roku Mihinui and Hera Smith, Te Arawa Lakes Trust.

Bella Tait, Rotorua District Council.

David Hamilton and Joseph Butterworth, University of Waikato.

Jacques Boubée, John Clayton, Tracey Edwards, Max Gibbs, Chris Hickey, Kristel van Houte-Howes, Clive Howard-Williams, Weno Iti, Mike Martin, Stephanie Parkyn, Ngaire Phillips, John Quinn, David Roper, Apanui Skipper, Charlotte Severne and Thomas Wilding, NIWA.

Willy Emery, Te Arawa.

This project has been funded by FRST/HRC Māori Development under contract C01X0512 “Sustainable Management Framework for Te Arawa Lakes Customary Fishing”.

1. Introduction

The kōaro (*Galaxias brevipinnis*) is a member of the family 'Galaxiidae' and is found only in New Zealand (including the Chatham and Campbell Islands) and in southern Australia, where it is known as the climbing galaxiid, or broad-finned galaxias. It is a relatively small fish (max. length about 300 mm) and has an elongate, tubular body. Like other fish in the Galaxiidae, it has no scales, and its greyish-brown skin is broken with irregular light-coloured blotches providing a typical 'camouflage' pattern (Fig. 1).

Figure 1: Adult kōaro showing typical body-form and camouflage colouration pattern (photo courtesy of S. Moore, Landcare Research Ltd).

The Galaxiidae were present some 80 million years ago in Gondwanaland, and the kōaro has its origins in the Mesozoic era some 65 million years ago (McDowall, 1990a). Whereas some galaxiid species (e.g., inanga or *Galaxias maculatus*) now have a wide circum-Antarctic, southern distribution, and are found in South America as well as in Australia and New Zealand, others (including the kōaro) have a more restricted distribution. The presence of kōaro in only New Zealand and Australia suggests that it evolved in Australia after the geographic isolation of the ancient galaxiid stocks through continental drift, glaciation and/or sea level changes. It then spread eastward to colonise New Zealand by marine dispersal (McDowall, 1990a). This dispersal probably occurred during the Miocene/Pliocene era (Waters and Wallis, 2001). A small but measurable difference in the mitochondrial DNA between Australian and New Zealand stocks reflects the fact that, today, there is little movement of kōaro across the Tasman Sea to New

Zealand, and that the Australian and New Zealand stocks are now more or less genetically isolated.

The life history pattern of kōaro is based on diadromy (i.e., its life cycle involves a freshwater as well as a saltwater or marine phase) with spawning occurring in riverine habitats and larval development occurring at sea. Juveniles migrate from the sea into rivers during spring months and at this time form an important part of the New Zealand 'whitebait' catch. For example, kōaro dominated the whitebait catch in the Motu River between 1981 and 1983 (Rowe et al. 1992). However, kōaro readily form landlocked populations in lakes and, in these populations, the lake acts as an inland sea where larval development occurs before the juvenile kōaro migrate upstream into lake tributaries.

The ability of the kōaro to colonise inland lakes is due largely to the extraordinary climbing ability of the juvenile migrant stage. The pectoral fins of juvenile migrants are relatively large and have special ridges on their undersides (McDowall, 2003). These allow kōaro to stick to and climb vertical rock faces. Not surprisingly, this climbing ability allows kōaro to surmount many large falls and to reach riverine habitats at altitudes up to 1200 m (McDowall, 1993). As a consequence, kōaro and longfin eels (which are also adept climbers) are often the only fish species found at the highest altitude sites in New Zealand river catchments. It is therefore not surprising that kōaro were once common in many inland lakes of New Zealand.

2. Origin of kōaro in the Te Arawa lakes

The Kaharoa eruptions of the early fourteenth century occurred between about 1301 and 1315 with the c.1315 eruption blanketing most of the Te Arawa lakes and their catchments with a thick (30 cm or more) layer of ash over a period of 4-5 years (Johnston et al. 2002; Hodgson and Nairn, 2005). As a consequence, most fish present in these lakes can be expected to have been annihilated at this time (Burstall, 1980).

The Te Arawa canoe arrived in New Zealand around 1350 (Stafford, 1967), some 35 years after the Kaharoa eruptions. Kōaro are likely to have re-colonised at least some of the Te Arawa lakes by this time. For example, when the Te Arawa explorer Ihenga first discovered lakes Rotorua and Rotoiti, 'inanga' (used here to indicate the juvenile stage of kōaro) were already present, but there was no mention of eels or common bullies at this time (Stafford, 1967 & 1986). According to legend, Ihenga was on an inland expedition

from the coast when his dog returned from a brief foray and regurgitated small fish indicating the presence of a waterway nearby (Reed, 1958; Stafford, 1967). This waterway proved to be a 'small lake', hence the name Rotoiti. Later, clarification of the taxonomy of fish in inland New Zealand lakes revealed that the inanga in the Te Arawa lakes were the juvenile form of *Galaxias brevipinnis* (McDowall, 1990a). The story of Ihenga's discovery and the accompanying descriptions of the size and behaviour of these small fish in Reed (1958) and Stafford (1967) indicate that the inanga caught by Ihenga were juvenile *G. brevipinnis*. This fish species was later given the common name 'kōaro', which was originally used for this species in the Taupō lakes (Stokell 1955; McDowall 1990a). Today, fish fitting the taxonomic description of *G. brevipinnis* are known as kōaro throughout New Zealand.

Given that kōaro were present in Lake Rotoiti when this lake was first discovered by Ihenga, two scenarios for the establishment of kōaro in Lake Rotoiti (and the adjoining Lake Rotorua) are possible. Natural colonisation could have occurred as a consequence of upstream migrations of kōaro from the sea via the Kaituna River after 1315 but before about 1350 (i.e., after the Kaharoa eruptions but before the arrival of Te Arawa). Because these lakes are at relatively high altitudes (i.e., 280 m) the only fish species likely to have been able to ascend the Kaituna River and enter them will have been those capable of long upstream migrations and able to surmount rapids and small falls (i.e., eels and kōaro). Both these species have similar climbing abilities and they are able to penetrate inland to distances of over 300 km (McDowall, 1993) as well as altitudes up to 1200 m (New Zealand Freshwater Fish database). If kōaro can reach an inland lake, then eels, particularly longfin eels, would also be expected to, and vice versa. However, only kōaro can form landlocked populations in lakes (i.e., maintenance of their population in a lake does not depend on annual migrations of juveniles from the sea). Hence, any subsequent barrier to the upstream access of these fish species caused by a change in channel structure (e.g., through faulting or landslides) would affect the recruitment of eels into lakes, but not kōaro. Without annual recruitment from the sea, eels would die out within approximately 50-80 years (the life span of large eels in some New Zealand lakes), leaving a landlocked population of kōaro. This means that both eels and kōaro could have potentially reached Lake Rotoiti from the sea between 1300 and 1350 with eels then dying out because of the formation of a barrier to juvenile migrants of both species in the Kaituna River. Such a barrier exists today and historically it could have been formed by the effects of land movements (e.g., faulting, subsidence, landslides) and/or failure of sediment-based dams in the Kaituna River following the Kaharoa eruptions (c.f. Hodgson and Nairn, 2005). Similar landlocked populations of kōaro could well have developed at

the same time in Lake Tarawera (and colonised the lakes connected to it, i.e., Rotokākahi, Ōkareka) because Lake Tarawera is accessible from the sea via the Tarawera River. Jolly (1959) stated that Tarawera is the only lake to contain a permanent population of eels. This statement is presumably based on hearsay as there is no hard evidence to substantiate natural recruitment of eels to this lake. Nevertheless, her statement may reflect observations by Māori prior to the Tarawera eruption, and they imply that eels (and hence kōaro) could ascend the Tarawera River and reach this lake. If so, natural colonisation of this lake by kōaro was even more likely than for Lake Rotoiti and Rotorua.

An alternative explanation is that kōaro were stocked into Lake Rotorua/Rotoiti by early inhabitants living beside the lakes. Māori legend indicates that Hatupatu stocked Lake Rotorua with kōaro from Lake Rotoaira (Mair, 1923; Stafford, 1967), but this seems unlikely as kōaro were already present in the lake when Ihenga (a contemporary of Hatupatu) first discovered it. Ihenga later returned to the lakes district and discovered Lake Rotorua ('second lake') where he found that other Māori were already settled around the lake edge, fishing for inanga with large nets (Stafford, 1967). These people were descendants of Ika and hence also of Te Arawa origin (Hiroa, 1921; Stafford, 1967), and they may have conceivably stocked the lake with kōaro before its discovery by Ihenga. However, it seems unlikely that Hatupatu would have been able to stock Rotorua with kōaro before its discovery and settlement by Ika and later Ihenga. Hatupatu was a contemporary of Ihenga and was the youngest of 3 brothers who were all on the Arawa canoe (Stafford, 1967). Nevertheless, there is little doubt that after the discovery and settlement of lakes Rotorua and Rotoiti, both Hatupatu and Ihenga stocked the lakes with a range of fish species in order to improve and extend the fisheries. For example, there are several stories of attempts by Hatupatu to stock eels into Lake Rotorua (Stafford, 1967). One experiment even involved snapper. Another story tells how Ihenga brought inanga (most probably juvenile *Galaxias maculatus*) from Kawakawa to Maketu and thence to Lake Rotorua in a gourd of water (Stafford, 1967). Mair (1923) indicated that Hatupatu stocked Lake Rotorua with kōaro from Rotoaira, where a subterranean stock of kōaro occurred (Phillipps, 1924a). It is therefore possible that Lake Rotorua contained a lacustrine (i.e., lake-dwelling) stock of kōaro, and that Hatupatu added a 'subterranean' stock to this lake. This would account for the kōaro that migrated into and out of the Hamurana Spring each year, and the unique fishery that developed at the spring's mouth (see Section 3). This localised, seasonal fishery emulated that present at Lake Rotoaira's underground springs (Rowe et al. 2002a).

None of the Te Arawa legends indicate that fish were absent in lakes Rotorua and Rotoiti at the time they were first settled. It seems more likely that kōaro were already present and landlocked in these lakes in pre-Arawa times. Such a natural, land-locked population of kōaro (either in Lake Rotorua/Rotoiti or Lake Tarawera) would have provided the stock for liberations elsewhere, and would have been readily spread by early Māori settlers to other lakes, such as Rotomā, Rotoehu, and Ōkataina, which lack connections to the sea and would therefore have been fishless. Māori soon became highly experienced at fish stocking (Sherrin, 1886; Hobbs, 1948; Stafford, 1967), and it is apparent that early Māori settlers will have ensured that kōaro were placed in most, if not all, the Te Arawa lakes.

The common bully is not a good climber and would not have been able to reach these lakes naturally. However, it too readily establishes self-perpetuating, land-locked populations in lakes when stocked into them. In contrast to kōaro, the presence of the common bully in the Te Arawa lakes will have depended entirely on stocking by Māori. Only Lake Ngāpouri lacks common bullies today (Rowe, 1984), and this may reflect a conscious decision not to stock it. The occurrence today of populations of another galaxiid species (*Galaxias fasciatus*) in certain streams in Lake Ōkataina (New Zealand Freshwater Fish Database) may be a consequence of such early stocking experiments as this species would not have occurred in this lake naturally.

McDowall (1996) dismissed the potential for natural colonisation of the Te Arawa lakes by native fish, but the presence of landlocked kōaro in lakes Rotorua and Rotoiti at the time of their first discovery by Te Arawa around 1350, and the absence of prior colonists around these lakes (Stafford, 1967) who could have stocked kōaro into them, argues against this. In reality, the origin of kōaro in the Te Arawa lakes is most likely to be due to a combination of natural recruitment from the sea to some lakes, coupled with the spread of these land-locked stocks by early Māori settlers to other local lakes not connected to the sea. The likely hypothetical sequence of natural colonisation and artificial stocking is shown in Figure 2. Analysis of mitochondrial DNA may help untangle and resolve the relative origins and affinities of the kōaro in these lakes and hence throw more light on their origin.

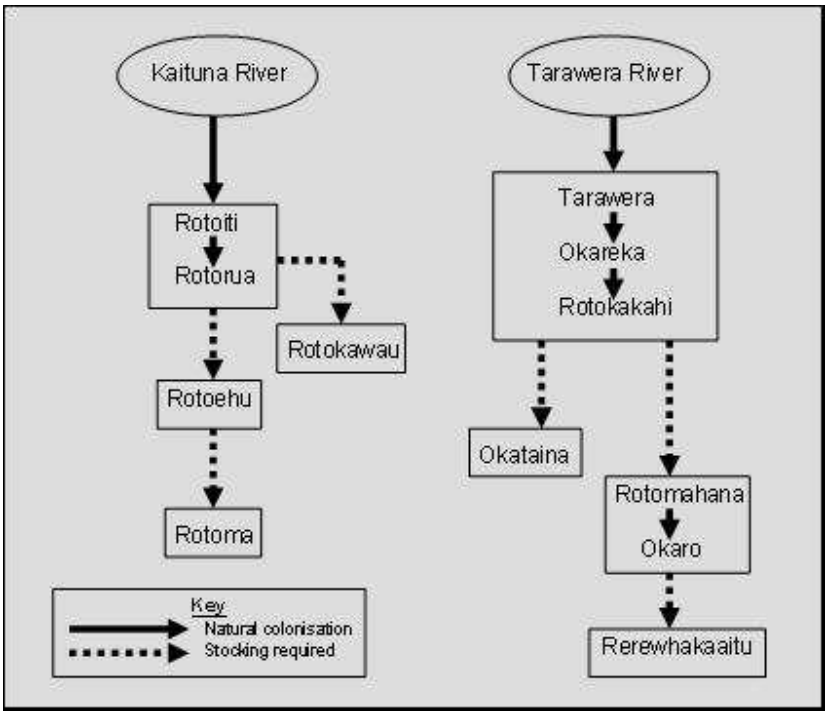

Figure 2: Hypothetical origin of kōaro in the Te Arawa lakes based on access to the sea (via a river system) for natural colonisation and then spatial proximity for stocking by Māori. Boxes indicate lakes where stocks may be genetically similar because of natural movement between lakes.

The eruption of Mount Tarawera in 1886 will have probably annihilated any kōaro present in lakes centred around Lake Rotomāhana (e.g., Ōkaro, Rerewhakaaitu, Tikitapu, Rotokākahi, Ōkareka), but remnant populations in the northern streams of Lake Tarawera may well have survived and recolonised Rotokākahi and Ōkareka. It is also possible that migrants from the sea accessed Lake Tarawera at this time, even if migrations past the outlet are not possible today.

3. Kōaro in the Te Arawa lakes - past and present

Hiroa (1921) provides an account of the fisheries for kōaro, primarily in Lake Rotorua, and Stafford (1994 & 1996) documented the fishing grounds for kōaro in Rotorua, Rotoiti, Rotoehu and Rotomā. Some years after the introduction of trout to Lake Rotorua, Gilbert

Mair, in a letter to his friend Arthur Iles (dated 14th March 1922), described the fishery situation as follows:

> 'Re native trout or kōkopu. These used to be caught by baiting small circular nets with crushed "kōura" in deep water in Rotoiti in very large numbers. They were very fat and delicious eating. A rare species was taken on certain nights coming up out of the Awahou and Hamurana springs. It is entirely a lake fish in these parts, but elsewhere are found in small streams – I mean the kōkopu, not the one found at Hamurana. In Taupō, the kōkopu used to abound in large quantities and grow to a foot or more. They were affected by a thin red worm which coiled up under the skin and eventually caused its death, or at least caused them to rise to the surface when the wind eventually drifted them onshore. After two or three days strong westerly winds they used to pile up on the east coast of Taupō in cart loads and were eagerly collected for food by the natives….The only fish in our lake are the kōkopu, inanga or whitebait, toitoi and the rare fish which used to come out of the Waititi, Awahou and Hamurana Springs called "kōaro".'
>
> 'Re Shags. There have always been a fair number in all these lakes since I knew them in 1865…..I believe that the introduction of trout has had the effect of increasing the shags at least fourfold. Formerly it was a great rarity to find a shag away from the lake, but now they are to be seen in the very small streams – in fact wherever trout are found. I think that the largely increased number of shags has had an appreciable effect on the diminished kōura supply.'

Mair (1923) later described the capture of adult 'kōaro' coming out of the Hamurana Stream in Lake Rotorua in the 1860s in more detail:

> 'a long funnel-shaped net with a pocket was stretched across the river ….the net was lowered into position and pegged to the bottom with forked sticks at about 8 pm; then a 50 ft canoe was moored to a stake at the lower end. Two hours then elapsed, when the pocket was lifted, the end untied and several hundredweight of the fat little fish were emptied into the canoe. This process was repeated several times during the night till quite a ton of weight had been obtained….Of course the introduction of trout was the death-knell of the kōaro and I very much fear they will be destroyed utterly in Rotoaira Lake in like manner.'

This method of capture is now known as 'fyke netting', and was also used to catch kōaro in Lake Rotoaira when they exited and entered the lake from subterranean springs at night from November to January (Phillipps, 1924a). However, large seine nets 50-100 yards long (45 – 91m) and 6-8 ft (1.8 – 2.4m) deep were also used to catch kōaro along the shores of the lakes (Hiroa, 1921; Angas, 1847; Best, 1929). These nets would have needed relatively fine mesh (<5 mm) to catch the smaller (40-50 mm long), slim (4-5 mm wide) inanga (or juvenile kōaro), and so would have involved considerable time and effort to make. Hiroa (1921) stated that net-making was continuous and went on day and night ('…at night the width of the mesh was measured by the fingernail…'). Some of the larger nets apparently took three years to complete. This huge effort no doubt explains why the large seine nets were highly prized, stored in special places, and wherever possible taken or stolen by raiding parties as described by Stafford (1967). The 'pouraka' trap was used to capture the larger kōkopu present close to the lake bottom in deeper (20-80 m) waters (Best, 1929; McDowall, 1990a). The final method of harvest was to collect the kōkopu when they were washed ashore onto beaches by strong onshore winds and wave action as in Lake Taupō (Fletcher, 1919a; Armstrong, 1935; Grace, 1959) and Lake Rotoaira (Rowe et al. 2002a).

The tau method was also used to catch large kōaro in some lakes, particularly in Lake Taupō (Fletcher, 1919b). It is probable that large kōaro were a by-catch from the tau kōura in the Te Arawa lakes. Fletcher wrote:

> 'In February/March, large bundles of fern (*Pteris esculenta*) would be cut and left to dry. While the fern was drying, a long flax rope some 70-90 m in length would be plaited. Along its length would be tied branch ropes at intervals of about a fathom until as many as 30 branches were in place…. This method of catching the large kōaro was practised from April to September.'

It is now apparent that the once abundant kōaro populations present in many of the Rotorua and Taupō lakes have declined drastically over the past century, and that a number of factors including trout predation, displacement by smelt and land-use changes affecting spawning habitats in streams have combined to reduce them (McDowall, 1990a; Rowe, 1990; Rowe 1993b). The current knowledge of the past and present status of kōaro in each of the Te Arawa lakes is summarised in Table 4.1. The pre-1900 status is inferred from comments in the early literature relating to the netting of 'inanga', except in the case of Lake Ōkataina and Ōkareka. Kōaro are still present in these two lakes today and,

despite the lack of early records of netting 'inanga' here, kōaro can be expected to have been as historically abundant in these lakes, as in lakes Tarawera and Rotoiti.

Table 1: Past and present status of kōaro in the Te Arawa lakes.

Lake name	Access to sea (river name)	Kōaro status in the Te Arawa lakes*	
		Pre-1900	Current-2005
Rotorua	Yes (Kaituna R.)	Abundant [4, 5, 9,11]	Rare, confined to streams [15,16]
Rotoiti	Yes (Kaituna R.)	Abundant [5, 9,12,14]	Present in bush-clad streams, some in lake [10,15,16]
Rotoehu	No	Abundant [3, 7, 9,12,14]	Extinct [15,16]
Rotomā	No	Abundant [9,12]	Extinct [15,16]
Rotokawau	No	Abundant [6,15]	*Status unknown*
Ōkataina	No	Abundant [16]	Present in bush-clad streams, some in lake [15]
Ōkareka	Yes (Tarawera R.)	Abundant [13,14,15]	Present in bush-clad streams, some in lake [13,15]
Tarawera	Yes (Tarawera R)	Abundant [2, 8]	Present in bush-clad streams, some in lake [13,15]
Rotokākahi	Yes (Tarawera R.)	Abundant [8]	*Status unknown*
Tikitapu	No	No records	Not present [15,16]
Rotomāhana	No	Abundant [1, 9, 14]	*Status unknown*
Rerewhakaaitu	No	Abundant [14]	Extinct [15,16]
Ōkaro	No	Abundant [14]	Extinct[16]
Ngahewa	Yes (Waikato R.)	No records	*Status unknown*
Ngāpouri	Yes (Waikato R.)	No records	*Status unknown*

*Sources: [1]Dieffenbach (1843), [2]Bates (1870), [3]Talbot (1882), [4]Hiroa (1921), [5]Mair (1923), [6]Cowan (1926), [7]Pomare and Cowan (1930), [8]Papakura (1986), [9]Stafford (1967), [10]Rowe(1993a), [11]Stafford (1994), [12]Stafford (1996), [13]Young (2002), [14]Habib (2001), [15]New Zealand Freshwater Fish Database, [16]Rowe unpublished data.

The status of kōaro in the Te Arawa lakes today depends mainly on lake depth and the presence of small, trout-free tributary streams. For example, in shallow lakes such as Rotoehu and Rotorua, kōaro are now very rare and to all intents and purposes are extinct in most tributary streams. It is not known whether kōaro historically occurred in the other shallow lakes (i.e., in Tikitapu, Ngahewa and Ngāpouri) but they are not present there now. They will have gained access to Lake Ōkaro via its outlet into Lake Rotomāhana, but are no longer present in Ōkaro. In contrast, small, relict populations of kōaro still occur in many of the smaller (and hence trout-free), bush-clad streams of the deeper lakes such as Rotoiti, Ōkataina, Ōkareka and Tarawera (Figure 3).

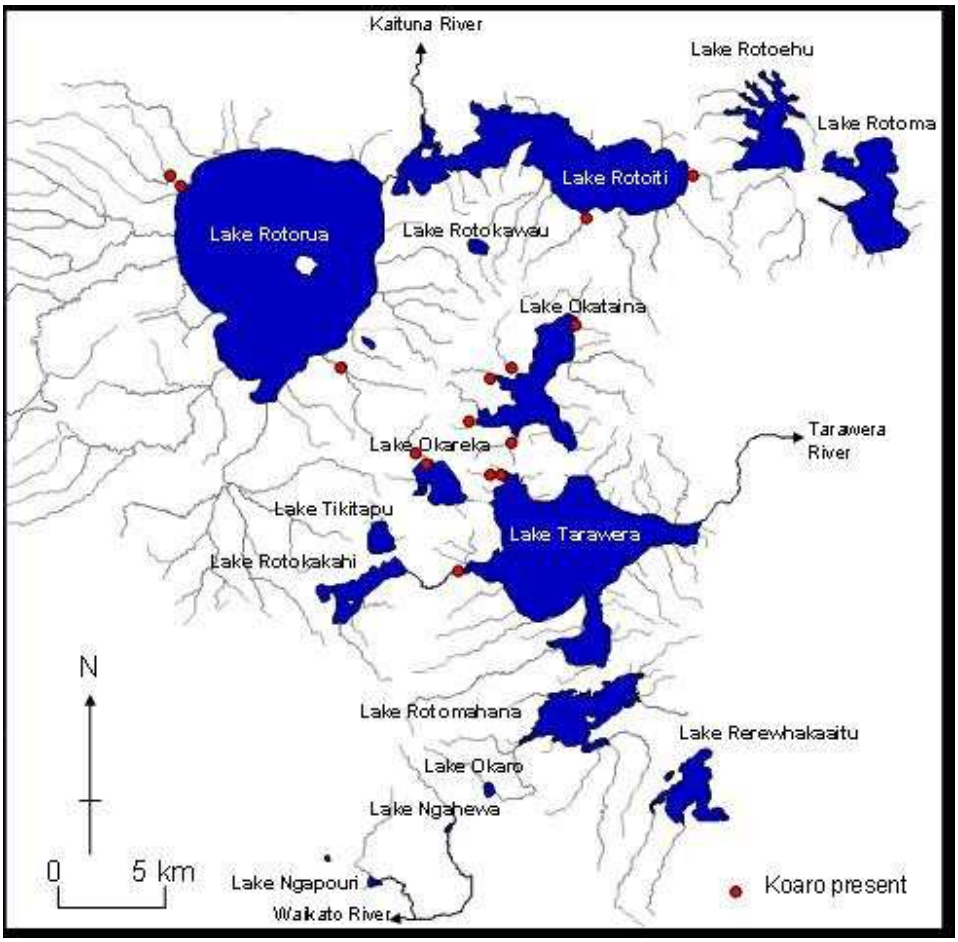

Figure 3: Distribution map for recent (>1980) records of kōaro in tributary streams of the Te Arawa lakes. Data from the New Zealand Freshwater Fish database.

These stream populations are probably responsible for the continued recruitment of kōaro to these lakes, and as a consequence, some adult kōaro (also referred to as kōkopu) still occur in low numbers in deep water close to the lake bottom (Rowe, 1994). An exception is provided by Lake Rotomā. Although many fishing grounds were reported to be historically present in Lake Rotomā (Stafford, 1996), the koaro is not present in this lake today. This is also a deep lake, but unlike the other deep lakes, it lacks any stream large enough to support a resident population of kōaro. Kōaro were also once present in lakes Rotokawau, Rotomāhana, Rotokākahi, Ōkaro and Rerewhakaaitu and relict populations can be expected in some of these lakes as well. Kōaro may have been annihilated in Lake

Rotomāhana, Ōkaro and Rerewhakaaitu by the Tarawera eruption in 1886. Although remnant populations still exist in some of the inlet streams of some of the deeper lakes (i.e., in Rotoiti, Ōkataina, Tarawera), these populations are highly vulnerable to land-use changes that reduce riparian vegetation (e.g., logging) or that allow invasion of trout through increased flows or removal of barriers to upstream movement by trout.

4. Life history, distribution, movements and habitats

The stream resident populations of adult kōaro in lake inlets have been well studied by Kusabs (1989) in Lake Taupō. His studies describe the movements, spawning, diet, growth rate and population structure of this species in these environments. Studies on the biology of kōaro in lakes have been carried out by Meredyth-Young and Pullan (1977), Naylor (1983), Rowe et al. (2002a) and Young (2002).

Diadromous *G. brevipinnis* lay their eggs in reaches of streams where riparian trees provide shade and where eggs can be deposited in the interstices among small pebbles and gravels on the stream bank. This egg deposition occurs at the stream edge when such sites are inundated by high flows following heavy rain (O'Connor and Koehn, 1998; Allibone and Caskey, 2000). As a consequence, once the flood waters recede, the eggs remain out of the water and only hatch when another flood inundates them. This spawning habitat is consistent with observations related to spawning in lacustrine kōaro (Kusabs, 1989) as well as other closely-related, lacustine galaxiids (Rowe and Graynoth, 2002). Such spawning habitats are also consistent with the known downstream drift of kōaro larvae in New Zealand rivers (McDowall and Suren, 1995), with the location of large ripe kōaro (Duffy, 1996), and with observations on lacustine populations of kōaro. For example, Kusabs (1989) found ripe kōaro in the cobbly-bottomed streams of Lake Taupō, and Rowe et al. (2002a) noted that the historic migration of large numbers of adult lacustrine kōaro into and out of springs in Lake Rotoaira occurred at the time when these fish spawned. These observations all indicate that kōaro spawn primarily in small streams where there is heavy shading from riparian trees and where rocky substrates predominate. However, a preference for spawning sites in the cobble habitats of bush-clad streams does not preclude the use of other habitats for spawning in lakes where stream spawning habitat is scarce, or even absent. For example, Stokell (1955) noted that kōaro occurred in Lake Marymere (Canterbury) where there are no permanent stream inlets or outlets. Similarly, kōaro were once abundant in Lake Rotopounamu where the only inlet stream is too small to support a stream-resident kōaro population. Other galaxiids (e.g., landlocked inanga in

Northland lakes) do not require streams for spawning and use other lacustine habitats. Similarly, rainbow trout will spawn along lake edges and/or among the gravels on lake margins when their preferred stream spawning sites are limited (Penlington, 1983). Thus, it would not be surprising to find that kōaro can also spawn along the rocky shorelines of some lakes. Some evidence for this is provided by Young (2002). She found that lacustrine and stream-dwelling kōaro in Lake Ōkareka differed in terms of both vertebral number and time of hatching (as indicated by otolith growth patterns), indicating the presence of discrete spawning stocks.

The time of spawning for diadromous kōaro will depend on seasonal factors (e.g., declining water temperatures and shorter day lengths), as well as on shorter term temporal factors such as floods. In Australian streams, spawning occurred mainly at times of high flows in autumn (O'Connor and Koehn, 1998). Fresh eggs were found among pebbles and cobbles about 1 m from the water's edge, and in some cases up to 7 m beyond the water's edge. These observations indicate that spawning occurs mainly when streams flood. Hatching requires heavy rain and rising water levels to re-inundate the eggs, and larvae are mainly captured following freshets (e.g., McDowall and Suren, 1995). However, lacustrine populations of fish often spawn at different times to diadromous stocks, and in the colder South Island lakes kōaro can be expected to spawn later than in the warmer North Island ones. This is because the spawning season is adjusted (through natural selection) to ensure that larvae enter the sea or lakes at a time when the probability of larval growth and survival is greatest (i.e., when food supplies for larvae in the lake are maximal). Thus, gravid kōaro have been found in South Island lakes during June (Johnson et al. 1976), but spawning of kōaro stocks in Lake Taupō and Rotoaira occurs mainly over summer and early autumn (Kusabs, 1989; Phillipps, 1924a; Rowe et al. 2002a). Young (2002) indicated a summer spawning season for lacustrine kōaro in Lake Ōkareka, and an autumn season for kōaro inhabiting its tributary streams.

The kōaro is an iteroparous species. That is, once fish are mature, they spawn each year for a number of years (possibly up to 20 in lakes) before eventually dying. This strategy ensures that should poor climatic conditions in one or even over several years result in the failure of eggs to hatch or larvae to survive, the population will persist. In this respect, kōaro differs from semelparous species, such as the smelt, which tend to spawn over a single season and then die.

Kōaro eggs remained viable after 12 days incubation in moist, damp surroundings, but the larvae could only be stimulated to hatch by agitating the water (O'Connor and Koehn, 1998). A longer incubation time may therefore be required to ensure hatching on flood flows. Once the eggs hatch, larvae are carried downstream to the sea or lake. At this stage they are likely to be 7-9 mm long and transparent (McDowall and Suren, 1995; O'Conner and Koehn, 1998).

In lakes, larvae occur mainly in the limnetic (mid-water) zone. Larvae were caught at depths down to 18 m in Lake Rotoiti in September, but not in deeper waters (Rowe, 1993a). Taylor et al. (2000) found kōaro larvae at depths of 25-45 m in Lake Coleridge in early summer, but they occurred in shallower depths (<20 m) in January and February. Preferred depth may therefore decrease as the larvae increase in size. In Lake Rotoaira, larvae were caught in surface nets during the night, but not during the day (Rowe et al. 2002a). Larvae may therefore move closer to the lake surface at night. There are no studies on the diet of larvae, so important food species for this life history stage are unknown.

Once they reach about 30 mm in length, juvenile kōaro begin to aggregate in small schools near the lake surface. The schooling, juvenile kōaro feed primarily on zooplankton in the surface waters (Naylor, 1983; Rowe et al. 2002a). At this stage in their life cycle, the kōaro are a major prey for trout. Once they are about 40 mm long, the kōaro become slightly pigmented and migrate into the inlet streams of lakes as 'whitebait'. This migration is akin to the migration of whitebait into New Zealand rivers from the sea in spring. In Lake Taupō, these migrations occur mainly in spring (Kusabs, 1989). In Lake Rotoaira, migrations of kōaro 'whitebait' up the Wairehu Canal also occurred in spring (Rowe et al. 1999). However, in Lake Wanaka, the migrations of 'matukituki' whitebait (i.e., kōaro) occurred mainly in autumn (McDowall, 1990a), indicating either a longer larval growing time in this lake, or later spawning. Historically, large migrations of juvenile kōaro will have occurred in the Ohau Channel between lakes Rotoiti and Rotorua (Kusabs, 1989). These schooling fish will have reacted to the large inflow of water into Lake Rotoiti, as they would to a large river entering the sea.

Kōaro over about 50 mm lose their tendency to school and migrate and quickly become benthic. Moffat (1984) found that adult kōaro taken from stream habitats could not maintain a horizontal position in still water without extensive tail movements as well as finning because they were negatively buoyant. They could not cope with high water

velocities, and in a flume tank, remained on the tank floor, arching their bodies and using their fins to maintain their position at the bottom when water velocities increased from 2 to 4 body lengths per second. It appears that adult kōaro are not powerful swimmers and so prefer benthic rather than limnetic habitats. However, they have a well developed air bladder and in lakes will no doubt use this to adjust their buoyancy and move from deep to shallow waters and vice versa.

Some of the kōaro that enter streams as whitebait can be expected to reside in these streams, completing their entire life-cycle (growth and spawning) within them. However, others can be expected to emigrate back to the lake, especially when population density is high in the stream and food is scarce, leading to intraspecific competition. But many juvenile kōaro may not enter any inlet stream and instead remain in the lake, completing their entire life-cycle there. Most adult kōaro in the lake are expected to spawn in inlet streams but some may spawn along the rocky lake margins in some lakes. A wide variety of life history patterns are clearly possible for lacustrine kōaro, but to date none of these have been described in any New Zealand lake, let alone the Te Arawa lakes.

In Lake Rotoaira, adult kōaro occurred primarily around the lake edge down to 12 m and they were found over a range of substrates (e.g., rock, sand, macrophytes). However, kōaro in lakes also occur in much deeper waters. Highest catches around the lake edge occurred at a depth of about 30 m in Lake Tekapo (Rowe et al. 2003). In Lake Rotoiti, a layer of relatively strong echoes occurred from fish just above the lake bottom at depths of 40-60 m. Sampling indicated that these fish were mainly adult kōaro rather than trout (Rowe, 1993a & 1994). This is consistent with observations of kōaro distribution by pre-European Māori. For example, Fletcher (1919a) describes how adult kōaro were traditionally trapped in Lake Taupō (using the ‘pouraka’) at depths down to 30 fathoms (approximately 60 m). This method was also used in Lake Rotoiti (Hiroa, 1921). It is apparent that adult kōaro can occupy a wide range of habitats in lakes. The fact that they do not do so today is mainly because of the combined effects of predation by trout and displacement by smelt.

The versatility of kōaro in exploiting lacustrine habitats in lakes is exemplified in their ability to burrow into the substrate and to enter underground springs. In Lake Rotoaira, kōaro were known to migrate into underground springs (Phillipps, 1924a; Rowe et al. 2002a) during summer months. This behaviour is consistent with spawning migrations into and out of surface tributary streams which flow beneath the ground for a small

distance before entering the lake as an underground spring (Rowe et al. 2002a). However, kōaro also enter true subterranean springs (no surface flow). For example, Mair (1923) observed large numbers of kōaro being caught as they exited the Hamurana Stream in Lake Rotorua. Such summer migrations of kōaro into and out of springs coincide with the spawning season for lacustrine kōaro (Kusabs, 1989; Rowe et al. 2002a), but they also coincide with warm-water conditions in these lakes. In some North Island lakes, summer temperatures may prove to be too hot for kōaro. As they are a cold-water fish (Richardson et al. 1994), they may move into the cold-water springs *en masse* during summer and, like trout, use them as a temporary thermal refuge. However, migration into springs for spawning seems more likely.

There is no doubt that kōaro are also capable of burrowing through lightly packed material such as pumice sand. An 8-9 cm long kōaro once appeared in the ground-water of a large hole that was being excavated for a septic tank some 3-5 m away from the edge of the nearest watercourse (pers comm. G. Konui, ranger, Lake Rotoaira). The kōaro had presumably penetrated fissures in the compacted pumice below the soil layer and was disturbed by the excavation of overlying sand and pumice. Another story of the burrowing ability of kōaro comes from Peter Lawlor, a trout angler from Rotorua.

> 'I was fishing off the lake-edge at the eastern end of Lake Rotoiti and as dawn approached, saw a small fish swimming close to the lake bed as it moved past me towards the shore. It disappeared under a piece of wood lying on the sand in shallow water. Later, I gently lifted the wood and to my surprise found that the kōaro had vanished. I was sure that it had not re-emerged as I had watched the wood carefully. I probed the sand beneath the log with my fingers and located the fish about 40 cm below the surface of the sand. An hour later it was still there and to all intents and purposes appeared to be asleep.'

As with the mudfish (cousins of the galaxiids that are capable of hibernating in the muddy substrates of drains and wetlands when their watercourses dry up), the kōaro clearly has an ability to bury itself in the coarse substrates of watercourses where it can avoid both predators and seasonal water temperature extremes (i.e., both hot or cold water).

5. Prey species, predators and parasites

Nothing is known about the feeding habits of larval kōaro in lakes. However, the juvenile schooling stage is primarily planktivorous and feeds on zooplankton in surface waters. The main prey species for juvenile kōaro (30-40 mm long) in lakes Rotoaira (North Island) and Alexandrina (South Island) was the waterflea, *Daphnia* (Naylor, 1983; Rowe et al. 2002a).

Kōaro over about 50 mm long in Lake Rotoaira fed on a wide range of benthic invertebrates. The main prey by weight were caddis larvae (*Paroxythira* and *Triplectides*), but snails and dragonfly larvae were also important (Rowe et al. 2002a). The largest fish (90-120 mm) fed mainly on small snails but also ate small common bullies. In Lake Chalice, a small, oligotrophic, alpine lake in the South Island, a sample of relatively large (120-255 mm) kōaro was found to be primarily carnivorous, with terrestrial insecta supplementing juvenile kōaro as the main prey (Meredyth-Young and Pullan, 1977). This was probably because aquatic prey such as snails and insect larvae were scarce in this lake, and the absence of trout allowed the kōaro to feed in surface waters where terrestrial insecta and juvenile kōaro occur. Similar feeding strategies have been described for kōaro in the large pools of rivers where trout are absent (Hayes, 1996).

Whereas the schooling juvenile stage of kōaro is primarily limnetic and feeds mainly on zooplankton, adults can feed throughout the water column and so have a much wider range of foods. In productive lakes, and in deep lakes containing trout, kōaro are primarily benthic and their main prey species are benthic. However, in shallow lakes lacking trout, kōaro are likely to feed on terrestrial insecta at the lake surface as well as on benthic prey.

Kōaro are reported to be nocturnal feeders in streams (Glova and Sagar, 1989), but this may be related to avoidance of predators during the day (Hayes, 1996). Most accounts of Māori fishing for adults in lakes indicate that the kōaro is more active during the night than during the day (Mair, 1923; Phillipps, 1924a; Best, 1929).

Sapsworth (1945) noted that kōaro fed on the eggs of common bullies in Lake Taupō, and suggested that they may exert some control over bully numbers in this lake. Support for this contention is provided by the increase in bully numbers observed in both lakes Rotopounamu and Rotoaira soon after kōaro declined in these lakes (Rowe, 1993b; Rowe et al. 2002a). This assumes that bullies were present in these lakes before the decline of

the kōaro, but it is possible that bullies were stocked into both lakes soon after the decline of the kōaro. Cadwallader (1975) found that interactive segregation occurred as a consequence of competition and/or predation between bullies and galaxiids, resulting in the displacement of bullies. As the adults of both kōaro and common bullies are benthic, and can be expected to feed on similar prey (i.e., small benthic invertebrates), competition for food and space is likely among these two species. Armstrong (1935) noted that both adult kōaro and bullies in Lake Taupō sought cover under stones. Large kōaro (100-250 mm long) would be able to feed on adult common bullies, such that simultaneous competition and predation could develop within the same food chain. This has been shown to be an unstable ecological situation in lakes leading to the decline of one of the species involved (Rowe, 1993b). It is therefore theoretically likely that kōaro will exert a degree of control over common bully numbers in lakes as suggested by Sapsworth (1948).

The main predator of kōaro in the Te Arawa lakes is now the rainbow trout (Phillipps, 1924b; Rowe et al. 2000). Shags are also a significant predator of kōaro in lakes (Stokell, 1941; Armstrong, 1935), and eels can also be expected to feed on small kōaro in lakes. Before the introduction of trout to the Te Arawa lakes, shags will have been the main natural predator of kōaro. Rainbow trout feed primarily on the juvenile, schooling stage, whereas shags prey mainly on the larger, benthic kōaro. Large smelt (>50 mm long) are known to feed on larval fish in lakes (Jolly, 1967; Stephens, 1984; Forsyth and James, 1988), and Rowe (1993b) indicated that smelt predation on kōaro larvae may be significant in shallow lakes such as Lake Rotopounamu.

Kōaro are likely to be significant vectors in the life cycle of some parasitic species in lakes. For example, the shagworm (*Eustrongyloides ignotus*) was once a major parasite of trout in the Te Arawa lakes, and high infestation rates reduced the condition of trout in Lake Ellesmere (Stokell, 1936). The shagworm is a reddish worm about 50-60 mm long and forms unsightly, pea-sized cysts in trout. The life cycle of the shagworm involves an egg/larval stage which occur on the lake bed and which infests small, benthic fish such as bullies and kōaro. The worm grows and forms small cysts within the body tissues of these fish which are then eaten by shags, herons and bitterns. The worms enter the bird's intestine where they produce eggs. These are later voided into the lake with the faeces and settle on the lake bottom so the life cycle can begin again. This parasite is rarely found in limnetic fish such as smelt (McDowall, 1990a; D. Rowe, pers. obs.), but it commonly occurs in benthic fish such as kōaro and bullies. Up until the mid 1970s, it was relatively common in trout from Lake Rotoiti (pers. obs.) but it now occurs infrequently, perhaps

because the trout now feed more on limnetic fish (smelt) than on benthic fish (bullies and kōaro) and so depend on a limnetic rather than a benthic food chain (Rowe, 1984; McDowall, 2000). This change in prey therefore broke the benthic food web on which the parasitation of trout depended.

Kōaro also play a major role in the life cycle of the freshwater mussel or kākahi (*H. menziesi*) in the Te Arawa lakes. The larval stage of the mussel (glochidia) has an obligate relationship with fish and uses a tiny hook on its shell to fix onto the fins or gills of benthic fish. The glochidia has little control over its movement. One function that this relationship may serve is to transport the glochidia to suitable substrate for settling. Interestingly, kākahi population surveys fail to record juvenile mussels, with population skewed to larger sizes. The distribution of adult kākahi varies and is influenced by factors including substrate, depth, slope and wave action. Although common bullies are now a major host for glochidia in the Te Arawa lakes, kōaro are likely to have been the main host in the past.

6. Age, growth, fecundity, maturation and population structure

The largest kōaro in Lake Chalice was 271 mm, and a 270 mm long, all-white (albino) kōaro was found in Lake Pukaki (Rowe, 1999a). These are the largest kōaro recorded in lakes to date. In rivers, the largest kōaro recorded is 288 mm long (Duffy 1996). This species is therefore unlikely to exceed 300 mm in length. The length-frequency distribution of 65 kōaro from Lake Chalice revealed three modes, at 50 mm, 120 mm and 230 mm, respectively, indicating three cohorts in this population of relatively large-sized fish. These modes may reflect age cohorts, but the implied growth rate of 50-100 mm/year is faster than expected for this species, and so the modes may reflect years when recruitment was high.

Naylor (1983) aged a sample of 83 kōaro from Lake Alexandrina using otoliths, and found that 0+ fish were 35-55 mm, 1+ fish 60-70 mm, and 2+ fish 90-130 mm. This implies a growth rate of 45 mm in the first year of life, 20 mm in the second year, but 45 mm in the third year. The latter rate is unlikely, because fish growth per year generally decreases with age. Young (2002) estimated the growth rate of both lacustrine and stream-dwelling kōaro in lakes Ōkareka and Tarawera. Lengths were 50 mm (in both environments) at age 1, 60 mm and 98 mm for stream and lake-dwelling fish, respectively, at age 2, then 90 mm

and 130 mm at age 3, and 95 mm and 160 mm at age 4, for the stream and lake-dwelling fish respectively. Hence, lake-dwelling kōaro that are 200 mm long are expected to be much older than 5+ years. Studies on the closely related banded kōkopu indicate that fish of approximately 200 mm long could be as old as 10 years (West et al. 2005), and an age of 10+ for a 200 mm long kōaro seems more likely.

The sex ratio of kōaro in Lake Rotoaira changed from female dominance in September to male dominance in April, mainly because of the absence of females in the lake over summer (Rowe et al. 2002a). In Lake Taupō tributary streams, where most kōaro were stream-resident, the sex ratio was close to 1:1 (Kusabs, 1989).

Kōaro in Lake Rotoaira ranged in size from 50-135 mm, and fish as small as 60 mm long (1+ years old) were mature (Rowe et al. 2002a). This means that reproduction starts at an early age/size for kōaro and continues annually for up to at least 5 years, if not more, for the larger/older fish.

The fecundity of mature kōaro is reported to be several thousand eggs (McDowall, 1990a). However, fecundity increases with fish size and may vary between lacustrine and riverine stocks. Kusabs (1989) determined that kōaro obtained from a Lake Taupō tributary ranged in length from 101-175 mm contained 3,600-19,800 eggs, respectively.

7. Environmental tolerances

Kōaro are essentially a cold water fish species. Taylor (1988) found that the 'probability of occurrence' for kōaro increased as water temperature decreased. Main (1988) found that the temperature (at which 50% of test fish died) for kōaro was 27ºC and, on the basis of temperature relationships for New Zealand native species developed by Richardson et al. (1994), this indicates a preferred temperature of close to 15ºC. This is colder than for the other native fish species tested to date but is consistent with the mean January air temperature predicted from habitat-based models of kōaro distribution (Leathwick et al. 2005). The preference of kōaro for cold-water may help explain why adults migrate into cold underground springs of lakes during summer months. However, such movements may also facilitate spawning and incubation of eggs.

Adult kōaro are associated with a high pH (alkaline waters) in Southland rivers (Taylor, 1988), and this may reflect a preference by adults for alkaline versus acid waters (Rowe, 1991). For example, Minns (1990) found a strong association between the amount of limestone/marble in catchments, which contributes to a high pH, and kōaro occurrence. Furthermore, kōaro are not generally found in acid lakes. Although West et al. (1996) found no preference by juvenile kōaro for pH between 5-10, adults may be more sensitive to low pH and prefer neutral or slightly alkaline waters as generally occurs in large inland lakes. There are no data on the tolerance of kōaro to oxygen or ammonia, and their responses to heavy metals and pesticides are also unknown.

8. Factors affecting kōaro population size in lakes

It is clear that the once abundant populations of kōaro in New Zealand's inland lakes, including the Rotorua and Taupō lakes, no longer occur, and that this species is now largely confined to a few small, tributary streams in these lakes. It is also clear, from the accounts of several early observers, that kōaro abundance declined markedly in these lakes following the introduction of trout (Fletcher, 1919a & b; Mair, 1923; Phillipps, 1924b; Armstrong, 1935). Both brown and rainbow trout were voracious predators of juvenile kōaro and they soon decimated the kōaro populations to the point where the Māori fisheries for them collapsed. However, kōaro were soon to face another major threat - the introduction of smelt. Although predation by rainbow trout decimated the kōaro, it did not completely reduce their populations. In fact, kōaro were still abundant enough to be a major seasonal prey for rainbow trout in a number of lakes many decades after trout had been introduced (Rowe, 1990; Rowe et al. 2000). It appears that kōaro, though much reduced, stabilised at a new population level that was in balance with trout predation. Further evidence that kōaro can remain common (if not abundant) in lakes containing rainbow trout is provided by their long-term persistence in lakes Rotoaira, Alexandrina and Waikare-iti, all of which have contained self-recruiting rainbow trout populations for nearly a century.

The introduction of smelt to Lake Rotorua in the late 1920s, and to the other Te Arawa lakes in the 1930s, caused a further decline in kōaro. Competition between juvenile smelt and kōaro for food and space, coupled with predation of kōaro larvae by large smelt, is likely to have resulted in the decline of kōaro to the point where they are now rare in these lakes and largely confined to either tributary streams in shallow lakes, or to the deeper waters (>40 m) of the larger lakes (Rowe, 1993b). Field evidence that the introduction of

smelt can result in the demise of kōaro, independently of trout, is provided by the disappearance of kōaro from Lake Rotopounamu shortly after the introduction of smelt. This shallow lake contained no trout, and the introduction of smelt alone was enough to eliminate the kōaro (Rowe, 1993b). A similar fate is likely to have occurred to the kōaro population in Lake Rotokawau (near Rotorua). Kōaro were historically present in this lake (Cowan, 1926, New Zealand Freshwater Fish database), but the limited sampling here over the past 20 years has revealed only smelt and bullies. Nevertheless, its deeper waters (> 50 m) may provide a refuge for some adult kōaro, allowing a relict population to still exist.

In contrast to rainbow trout, the effects of the more piscivorous brown trout on kōaro are likely to have been much more devastating. Brown trout dominate the fish fauna in many South Island lakes, and the decline of kōaro has been more marked in these southern brown trout dominated lakes than in the more northern rainbow trout dominated lakes (Rowe et al. 2003). Smelt are rare in these southern lakes, so are not a major problem for the kōaro. The demise of kōaro in South Island lakes is therefore likely to be related mainly to the prevalence of the more piscivorous brown trout, than to smelt. In comparison, smelt plus rainbow trout were probably required to drive kōaro to the brink of extinction in North Island lakes.

Rowe (1994) found that kōaro occupied the deeper waters (40-60 m) of Lake Rotoiti in summer, but were excluded from these depths in autumn. De-oxygenation of the hypolimnion (the water volume below the thermocline) in this lake now occurs each autumn (Rowe, 1994; Rowe and Chisnall, 1995), and the lack of oxygen below about 25 m in Lake Rotoiti forces all adult kōaro (along with all other fish and crustacea) into shallower waters. This shift in kōaro distribution can be expected to increase both inter- and intra-specific competition for benthic foods. It also increases the risk of predation from both trout and shags.

Another factor influencing the abundance of kōaro in lakes is the damming and diversion of water for hydroelectric power schemes. The large population of kōaro now present in Lake Mahinerangi has been attributed to the damming of the Waipori River in Otago to form a reservoir (McDowall, 1990a). This facilitated the upstream invasion of tributary streams above Lake Mahinerangi by kōaro, and this invasion is thought to have excluded the common river galaxias from these waters (McDowall and Allibone, 1994). In this

case, the amazing climbing ability of juvenile kōaro allowed it to colonise upstream waters and displace another native fish!

In Lake Rotoaira, the migratory ability of the juveniles to swim up-river and to climb barriers may have led to its decline. The Tongariro Power Scheme resulted in the construction of two new major inflows into Lake Rotoaira. The Wairehu and Poutu canals now bring water from the Whanganui and Tongariro rivers, respectively, into this lake through man-made, mainly concrete-lined canals. Schools of kōaro responded to these large, new flows by migrating into the canals and attempting to climb the concrete barriers within them. For example, large numbers of juveniles were photographed climbing the concrete wall of the first barrier in the Wairehu Canal (McDowall, 1990a). Most of these migrants would have either perished in the attempt, or if successful, left the lake. These new inflows will therefore have resulted in greater emigration of juvenile kōaro from Lake Rotoaira and so helped to reduce its adult population (Rowe et al. 1999).

In the Te Arawa lakes, stream connections between some of the lakes will have facilitated the spread of kōaro, whereas large inflows (e.g., Ohau Channel water into Lake Rotoiti) will have encouraged major migrations of juveniles out of Rotoiti into Rotorua. Today any such movements are likely to be minimal, because kōaro are now relatively rare in these lakes (see Section 3)

A final factor that can account for some of the decline of kōaro in lakes is the removal of forest cover, particularly the riparian vegetation along the margins of inlet streams. Adult kōaro are rarely found in streams where the forest canopy has been removed and where the stream is now exposed to direct sunlight (McDowall, 1990a; Rowe, 1981). Forest removal was an integral part of the development of the catchments of many of the Te Arawa lakes for farming and there is no doubt that ‘stream habitat’ for kōaro was greatly reduced by this land-use change. This will have contributed to the decline of kōaro in some lakes by reducing stream populations, but more significantly by reducing stream spawning habitats for lacustrine fish.

9. Protection and restoration issues and options

Restoration of kōaro populations in the Te Arawa lakes has been proposed by Young and Smale (2003). They identified many of the major factors to consider and developed a

method for prioritising lakes for kōaro restoration. But the feasibility and cost of restoration are yet to be determined. Young and Smale (2003) proposed restoration of kōaro in Lake Ōkataina, even though this implies the eradication of both trout and smelt. Although trout numbers could be reduced by blocking access to spawning streams, rainbow trout are well able to adapt quickly to such changes and will spawn on lake shores. For example, lake-shore spawning currently accounts for a large proportion of the wild rainbow trout in Lake Rotomā (Penlington, 1983). It is highly likely that trout in Ōkataina would also spawn around the lake shore. Therefore, removing trout access to all spawning streams would reduce trout numbers, but may not reduce them to the point where predation on kōaro is significantly reduced. Removal of all smelt in such a large lake would be logistically impractical.

A more realistic goal would be to restore kōaro in some of the tributary streams of the large lakes and to restore lake-dwelling stocks to small lakes, especially those that are of limited value for trout fishing and where trout and smelt removal would be feasible. Such lakes could include Rotokawau and Ngahewa. Rotokawau formerly contained large numbers of kōaro, its water quality is high, no trout are present, and removal of smelt is the main management action required. This could theoretically be accomplished using a piscicide. However, the depth of this lake (80 m) provides a technical challenge. The piscicide would not be easily mixed to all depths and some smelt may remain in deep water and so evade its effects. However, smelt egg survival might be drastically reduced by shoreline application of a suitable piscicide, and this option may be more viable. Lakes Ōkaro, Ngāpouri, and Tikitapu are also potential sites for kōaro restoration, but the trout fisheries here have some value and the poor water quality in the former two lakes, and a lack of adequate koaro spawning grounds in the latter, may prove to be insurmountable barriers.

10. Critical knowledge gaps

There are a number of key ‘gaps’ in our knowledge of the variables that influence kōaro life history and habitats in lakes. The most important of these is whether or not kōaro spawn within lakes, and if so, what physical conditions (depth, substrate etc.) are needed for this. If spawning is only possible in inlet streams, loss of stream spawning habitat may prove to be a significant limiting factor in lakes where most of the catchment has now been converted to pasture. Clearly, this is not the case with lakes such as Ōkataina, where the catchment is still covered in relatively pristine native forest. Here, the major and only

limiting factors for kōaro are trout predation and displacement/predation of juvenile/larval kōaro by smelt. However, evidence for the role of smelt in the decline of kōaro in lakes is still circumstantial. More conclusive proof of this is required too. Although there are no data on the foods of larval kōaro, the range of micro-floral and faunal species in lakes is generally large, and fish rarely depend on just one species as prey. Therefore, this gap is not of major concern at present.

The habitats and seasonal movements of adult kōaro in lakes are poorly understood. It is clear that they once made use of subterranean springs, but whether this was for spawning or to find refuge from hot summer water temperatures in lakes is not yet clear. Similarly, adults were captured from specific "fishing grounds" in lakes, implying that they concentrated in certain regions and not in others. The basis for such differences in catchability is not known, and research is required to determine whether adult habitat (or just fishing) is restricted to certain locations in lakes. If habitat is restricted to certain locations, then the area of habitat (or food supply associated with this) may now prove limiting.

The observation (Mair, 1923; Best, 1921) that kōaro catchability changes with the seasons (and with changes in wind/wave action) implies that kōaro change their behaviour and distribution in response to short term changes in wind direction and strength. The further observation (from a number of central North Island lakes) that kōaro wash ashore in large numbers when strong winds occur and when onshore wave action is high (Fletcher, 1919a; Armstrong, 1935; Grace, 1959; Rowe et al. 2002a) indicates that kōaro may be highly susceptible to wave action and avoid areas where strong water currents occur. Alternatively, high mortality may have occurred shortly after spawning and sustained winds at this time may have concentrated dead, floating fish on the exposed shorelines.

The current distribution of kōaro in the Te Arawa lakes is also poorly understood. The number of extant stream populations of adults is unknown and surveys are required to identify the streams where tributary populations are still present and can be secured (e.g., through removal of trout, protection of riparian vegetation, and/or maintenance of stream habitat) to provide safe sanctuaries for this species.

11. References

Allibone, R.M.; Caskey, D. (2000). Timing and habitat of kōaro (*Galaxias brevipinnis*) spawning in streams draining Mt Taranaki, New Zealand. *New Zealand Journal of Marine and Freshwater Research 34*: 593-595.

Angas, G.F. (1847). The New Zealander illustrated. McLean, London. *Savage Life and Scenes in Australia and New Zealand*. Smith Elder, London.

Armstrong, J.S. (1935). Notes on the biology of Lake Taupō. *Transactions and Proceedings of the New Zealand Institute 65*: 88-94.

Bates, L. (1870). Lieutenant Bates returns to Napier from pink and white terraces in 1860. *Historical Journal No. 16*, Auckland-Waikato, April 1970.

Best, E. (1929). Fishing methods and devices of the Māori. *Dominion Museum Bulletin No 12*. 92 p.

Burstall, P. (1980). The introduction of freshwater fish into the Rotorua lakes. In. Stafford, D.; Steele, R.; Boyd, J. (eds.). *History of Rotorua 1890-1990*. Rotorua and District Historical Society Inc., Rotorua.

Cadwallader, P.L. (1975). A laboratory study of interactive segregation between two stream-dwelling fish. *Journal of Fish Biology 44*: 865-875.

Carpenter, S.R.; Kitchell, J.F.; Hodgson, J.R. (1985). Cascading trophic interactions and lake productivity. *BioScience 35*: 634-639.

Cowan, J. (1926). Travel in New Zealand: the island dominion, its life and scenery, pleasure-routes and sport. Whitcombe and Toombes Ltd., Auckland.

Dieffenbach, E. (1843). Travels in New Zealand. Murray Press Ltd, London.

Duffy, C.A.J. (1996). Pre-spawning mortality of kōaro (*Galaxias brevipinnis*) in Apias Creek, north-east Ruahine Range, North Island, New Zealand (Note). *New Zealand Journal of Marine and Freshwater Research 30*: 403-405.

Fletcher, H.J. (1919a). The edible fish of Taupō-nui-a-Tia. *Transactions of the New Zealand Institute 51*: 259-264.

Fletcher, H.J. (1919b). Lake Taupō and its trout. *New Zealand Journal of Science and Technology 2*: 367-370.

Forsyth, D.J.; James, M.R (1988). The Lake Ōkaro system 2: Production of the chironomid *Polypedilum pavidus* and its role as food for two fish species. *New Zealand Journal of Marine and Freshwater Research 22*: 327-335.

Glova, G.J.; Sagar, P.M. (1989). Feeding in a nocturnally active fish, Galaxias brevipinnis, in a New Zealand stream. *Australian Journal of Marine and Freshwater Research 40*: 231-240.

Grace, J. Te H. (1959). Tuwharetoa: the history of the Māori people of the Taupō district. Reed Press, Wellington.

Habib, G. (2001). Commercial freshwater fishing rights of Te Arawa. Unpublished report prepared for the Volcanic Interior Plateau Project Directorate and Te Arawa Māori Trust Board. 142 pp.

Hayes, J.W. (1996). Observations of surface feeding behaviour in pools by kōaro, Galaxias brevipinnis. *Journal of the Royal Society of New Zealand 26*: 139-141.

Hiroa, Te R. (1921). Māori food supplies of Lake Rotorua, with methods of obtaining them and usages and customs appertaining thereto. *Transactions of the New Zealand Institute 53*: 433-451.

Hobbs, D.F. (1948). Trout fisheries in New Zealand, their development and management. *Fisheries Bulletin No. 9.* New Zealand Marine Department, Wellington.

Hodgson, K.A.; Nairn, I.A. (2005). The c. AD 1315 syn-eruption and AD 1904 post-eruption breakout floods from Lake Tarawera, Haroharo Caldera, North Island, New Zealand. *New Zealand Journal of Geology and Geophysics 48*: 491-506.

Johnston, D.; Nairn, I.; Martin, R. (2002). Proximal impacts of the 1305AD Kaharoa eruption on modern day New Zealand. *Institute of Geological and Nuclear Sciences Report 2002/18*. 28 pp.

Jolly, V.H. (1959). The trout are smelting. *Science Records 9*: 33-35.

Jolly, V.H. (1967). Observations on the smelt *Retropinna lacustris* Stokell. *New Zealand Journal of Science 10*: 330-355.

Kusabs, I.A. (1989). The biology and general ecology of the kōaro (*Galaxias brevipinnis*) in some tributary streams of Lake Taupō. M. Phil. Thesis, University of Waikato.

Leathwick, J.R.; Rowe, D.K.; Richardson, J.; Elith, J.; Hastie, T. (2005). Using multivariate adaptive regression splines to predict the distributions of New Zealand's freshwater diadromous fish. *Freshwater Biology 50*: 2034-2052.

Main, M.R. (1988). Factors influencing the distribution of kōkopu and kōaro (Pisces: Galaxiidae). MSc Thesis, University of Canterbury.

Mair, G. (1918). Fishing places in Rotorua and other observations on traditional fishing, from evidence given by Gilbert Mair in Native Land Court Hearing, October to November 1918, in Rotorua, application for investigation of title of bed of Rotorua Lake. In Habib (2001).

Mair, G. (1923). Reminiscences and Māori stories. Brett Printing and Publishing, Auckland.

McDowall, R.M. (1987). Impacts of exotic fishes on the native fauna. In: Viner, A.B (ed.). Inland Waters of New Zealand. *DSIR Bulletin 241*.

McDowall, R.M. (1990a). New Zealand freshwater fishes - a natural history and guide. Heinemann Press, Auckland.

McDowall, R.M. (1993). Implications of diadromy for the structuring and modelling of riverine fish communities in New Zealand. *New Zealand Journal of Marine and Freshwater Research 27*: 453-462.

McDowall, R.M. (1996). Volcanism and freshwater fish biogeography in the north-eastern North Island of New Zealand. *Journal of Biogeography 23*: 139-148.

McDowall, R.M. (2000). The Reed field guide to New Zealand freshwater fishes. Auckland, Reed.

McDowall, R.M. (2003). The key to climbing in kōaro. *Water and Atmosphere 11(1)*: 16-17.

McDowall, R.M.; Allibone, R. (1994). Possible competitive exclusion of common river galaxies (*Galaxias vulgaris*) by kōaro (*Galaxias brevipinnis*) following impoundment of the Waipori River, Otago, New Zealand. *Journal of the Royal Society of New Zealand 24*: 161-168.

McDowall, R.M.; Suren, A.M. (1995). Emigrating larvae of kōaro *Galaxias brevipinnis* Günther (Teleostei: Galaxiidae), from the Otira River, New Zealand. *New Zealand Journal of Marine and Freshwater Research 29*: 271-275.

Meredyth-Young, J.L.; Pullan, S.G. (1977). Fisheries survey of Lake Chalice, Marlborough Acclimatisation Society District, South Island, New Zealand Ministry of Agriculture and Fisheries, Fisheries Technical Report No. 150.

Minns, C.K. (1990). Patterns of distribution and association of freshwater fish in New Zealand. *New Zealand Journal of Marine and Freshwater Research 24*: 31-44.

Mitchell, C.P. (1989a). Environmental assessment of the Lake Rotorua control structure. *New Zealand Freshwater Fisheries Miscellaneous Report 24*.

Moffat, R. (1984). Aspects of spatial segregation of adult kōaro (*Galaxias brevipinnis*) and juvenile trout (*Salmo trutta* and *Salmo gairdnerii*) in the Ryton River. MSc Thesis, University of Canterbury.

Naylor, J.R. (1983). The relative abundance, age structure and diet of *Gobiomorphus cotidianus* (Pisces: Eleotridae) and *Galaxias brevipinnis* (Pisces: Galaxiidae) in Lake Alexandrina. MSc Thesis, University of Canterbury.

O'Connor, W.G.; Koehn, J.D. (1998). Spawning of the broad-finned Galaxias, *Galaxias brevipinnis* Günther (Pisces: Galaxiidae) in coastal streams of southeastern Australia. *Ecology of Freshwater Fishes 7*: 95-100.

Papakura, M. (1986). The old-time Māori. New Woman's Press, Auckland.

Penlington, P.B. (1983). Lake-shore spawning of rainbow trout at Lake Rotomā, New Zealand. *New Zealand Journal of Marine and Freshwater Research 17*: 349-355.

Phillipps, W.J. (1924a). The kōaro: New Zealand's subterranean fish. *New Zealand Journal of Science and Technology 7*:190-191

Phillipps, W.J. (1924b). Food supply and deterioration of trout in the thermal lakes district, North Island, New Zealand. *Transactions and Proceedings of the New Zealand Institute 55*: 381-391.

Pomare, Hon. Sir M.; Cowan, J. (1930). Legends of the Māori. Fine Arts (NZ) Ltd., Wellington.

Reed, A.W. (1958). Legends of Rotorua. Reed Books, Auckland. 163 p.

Richardson, J.; Boubée, J.A.T.; West, D.A. (1994). Thermal tolerance and preference of some native New Zealand freshwater fish. *New Zealand Journal of Marine and Freshwater Research 28*: 399-407.

Rowe, D.K. (1981). Fisheries investigations in the Motu River. *Fisheries Environmental Report 11*. Fisheries Research Division of the New Zealand Ministry of Agriculture and Fisheries. 46 p.

Rowe, D.K. (1984). Factors affecting the foods and feeding patterns of lake-dwelling rainbow trout (*Salmo gairdnerii*) in the North Island of New Zealand. *New Zealand Journal of Marine and Freshwater Research 18*: 129-141.

Rowe, D.K. (1990). Who killed the kōaro? *Freshwater Catch 43:* 15-18.

Rowe, D.K. (1991). Native fish distribution and habitat. *Freshwater Catch 46*: 4-6.

Rowe, D.K. (1993a). Identification of fish responsible for five layers of echoes recorded by high frequency (200 kHz) echosounding in Lake Rotoiti, North Island New Zealand. *New Zealand Journal of Marine and Freshwater Research 27: 87-100.*

Rowe, D.K. (1993b). Disappearance of kōaro, *Galaxias brevipinnis*, from Lake Rotopounamu, New Zealand, following the introduction of smelt, *Retropinna retropinna*. *Environmental Biology of Fishes 36: 329-336.*

Rowe, D.K. (1994). Vertical segregation and seasonal changes in fish depth distributions in lakes of contrasting trophic status. *Journal of Fish Biology 45:* 787-800.

Rowe, D.K.; Chisnall, B.L. (1995). Effects of oxygen, temperature and light gradients on the vertical distribution of rainbow trout, *Oncorhynchus mykiss* in two North Island, New Zealand lakes differing in trophic status. *New Zealand Journal of Marine and Freshwater Research 29*: 421-434.

Rowe, D.K.; Cudby, E.J; Turner, D.J. (2000). Prey species and the food web for rainbow trout in Lake Rotoaira, (1972-1974). NIWA Client Report GPL00233. National Institute of Water and Atmospheric Research, Hamilton.

Rowe, D.K.; Graynoth, E. (2002). Lake Managers' Handbook: fish in New Zealand Lakes. Ministry for the Environment, Wellington. 110 pp.

Rowe, D.K.; Graynoth, E.; James, G.; Taylor, M.; Hawke, L. (2003). Influence of turbidity and fluctuating lake levels on the abundance and depth distribution of small benthic fish in alpine, New Zealand lakes. *Ecology of Freshwater Fish 12*: 216-227.

Rowe, D.K.; Konui, G. (2003). Review of the present and future status of kōaro in Lake Rotoaira. NIWA Client Report No. HAM2003-074. National Institute of Water and Atmospheric Research, Hamilton.

Rowe, D.K.; Konui, G.; Christie, K. (1999). Kōaro (*Galaxias brevipinnis*) in Lake Rotoaira. NIWA Client Report ELE90232/2. National Institute of Water and Atmospheric Research, Hamilton.

Rowe, D.K.; Konui, G.; Christie, K. (2002a). Population structure, distribution, reproduction, diet and relative abundance of kōaro (*Galaxias brevipinnis*) in a New Zealand lake. *Journal of the Royal Society of New Zealand 32*: 275-291.

Rowe, D.K.; Saxton, B.A.; Stancliff, A.G. (1992). Species composition of whitebait fisheries in 12 Bay of Plenty rivers, New Zealand: evidence for river mouth selection by juvenile *Galaxias brevipinnis* (Gunther). *New Zealand Journal of Marine and Freshwater Research 26:* 219-228.

Sapsworth, D.D. (1945). The food of trout. A brief account of the food in New Zealand waters. *Salmon and Trout Magazine 113*: 68-70.

Sherrin, R.A.A. (1886). Handbook of the fishes of New Zealand. Wilson and Horton, Auckland.

Stafford, D.M. (1967). Te Arawa - a history of the Arawa people. Reed Books, Auckland.

Stafford, D.M. (1986). The founding years in Rotorua. A history of events to 1900. Ray Richards, Auckland.

Stafford, D.M. (1994). Landmarks of Te Arawa Volume 1: Rotorua. Reed Books, Auckland.

Stafford, D.M. (1996). Landmarks of Te Arawa. Volume 2: Rotoiti, Rotoehu, Rotomā. Reed Books, Auckland.

Stephens, R.T.T. (1984). Trout smelt interactions in Lake Taupō. D. Phil. Thesis, University of Waikato, Hamilton.

Stokell, G. (1936). The nematode parasites of Lake Ellesmere trout. *Transactions and Proceedings of the Royal Society of New Zealand 66*: 80-96.

Stokell, G. (1941). Wildlife control. Defects in the present scheme exposed. Some constructive suggestions. Blundell, Wellington.

Stokell, G. (1955). Freshwater fishes of New Zealand. Simpson and Williams, Christchurch. 145 pp.

Talbot, T. (1882). The new guide to the lakes and hot springs and a month in hot water. Wilson and Horton, Auckland.

Taylor, M.J. (1988). Features of freshwater fish habitat in South Westland, and the effect of forestry practices. *Fisheries Environmental Report 97.* New Zealand Ministry of Agriculture and Fisheries.

Taylor, M.J. Graynoth, E.; James, G.D. (2000). Abundance and daytime vertical distribution of planktonic fish larvae in an oligotrophic South Island lake. *Hydrobiologia 421*: 41-46.

Waters, J.M.; Wallis, G.P. (2001). Cladogenesis and loss of the marine life-history phase in freshwater galaxiid fishes (Osmeriformes: Galaxiidae). *Evolution 55*: 587-597.

West, D.W. Boubée, J.A.T.; Barrier, R.F.G. (1996). Responses to pH of nine fishes and one shrimp native to New Zealand freshwaters. *New Zealand Journal of Marine and Freshwater Research 31*: 461-468.

West, D.W.; Jowett, I.J.; Richardson, J. (2005). Growth, diet, movement and abundance of adult banded kōkopu (*Galaxias fasciatus*) in five Coromandel, New Zealand streams. *New Zealand Journal of Marine and Freshwater Research 39*: 915-929.

Young, K.; Smale, S. (2003). Restoration of kōaro (*Galaxias brevipinnis*) in a New Zealand lake - integrating traditional indigenous resource management with contemporary conservation biology. *In* Beumer, J.P.; Grant, A.; Smith, D.C. (eds.). Aquatic protected areas – what works best and how do we know? World Congress on Aquatic Protected Areas, Cairns, Australia, August 2002.

Young, K.D. (2002). Life history of fluvial and lacustrine land-locked kōaro (*Galaxias brevipinnis*) Gunther (Pisces: Galaxiidae) in the Tarawera Lakes. M. Phil. Thesis, University of Waikato.