

Influence of open and closed river systems on the migrations of two northern New Zealand populations of banded kokopu (*Galaxias fasciatus*)

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Abstract

Otolith microchemical analysis by laser ablation inductively coupled mass spectrometry (ICP-MS) was used to investigate the migratory life histories of banded kokopu (*Galaxias fasciatus*) in two streams on the North Island of New Zealand. Known differences in marine and freshwater chemistry were used as a premise to document the migratory life strategies of banded kokopu between these environments. More specifically, temporal trends in high and low strontium/calcium ratios (Sr/Ca) identified in fish otoliths were used to determine evidence of migration between fresh and saltwater environments. Trace element analysis of fish captured above the Whau Valley Reservoir reflected non-migratory life histories and exhibited consistently low Sr/Ca ratios across the entire otolith. However, one fish from above the reservoir indicated unusually high Sr/Ca ratios in early adulthood. These high Sr levels were attributed to localised inputs from mineral-rich seepages associated with past mining practices in the region and low calcium availability within the Pukenui Stream. Otoliths from banded kokopu collected from Komiti Stream were shown to be migratory with a marine larval stage (high Sr/Ca ratio levels at the otolith nucleus), followed by a freshwater adult phase (low Sr/Ca ratio levels towards the edge) indicating their amphidromous origins. The study provides further evidence of non-diadromous recruitment for banded kokopu as a consequence of a large in-stream barrier and will add to the known distribution of landlocked species in New Zealand.

Key words: Banded kokopu – *Galaxias fasciatus* – diadromy – otolith microchemistry – landlocked – laser ablation ICP-MS

Introduction

The amphidromous lifecycle of banded kokopu (*Galaxias fasciatus*) is representative of life history patterns

followed by ten of New Zealand's eighteen diadromous fish species (McDowall 1993; 1995). Typically, strategies involving fish movement between fresh and saltwater environments are termed 'diadromy'

(McDowall 1988; 1990; 1996). More specifically, an amphidromous life strategy is characterised by spawning and egg development in freshwater followed by a marine growth phase (as hatchlings) returning several months later as upstream migrant juveniles to mature in freshwater (McDowall 1995; 2007). For researchers, the task of documenting movement patterns of this type can be difficult, particularly where fish may range over large temporal and spatial scales. Furthermore, such life strategies preclude conventional tagging methods due to size limitations in tagging technology, costs and the inability to effectively track larval fish throughout time and space (Thorrold. *et al.* 1998; Munro 2004).

However, microchemical analysis of fish otoliths offers another approach as otoliths act as natural tags recording in chronological sequence daily growth increments composed of trace elements present in the water throughout a fish's life (Campana 1999; Campana & Thorrold 2001). Furthermore, once chemical elements are deposited in the otolith they are neither resorbed nor re-metabolized, resulting in a permanent chemical record of the fish's life history (Campana 1999; Campana & Thorrold 2001). For this reason, the ratio of Sr over Ca (Sr/Ca), can be used to describe fish movements between fresh and saltwater environments particularly as Sr concentrations are higher in seawater (0.088 ppm), than freshwater (0.00018 ppm), (Tzeng 1996; Tzeng *et al.* 2005).

In New Zealand, a growing number of studies have used Sr/Ca ratios to elucidate diadromous life histories for several freshwater fish species. David *et al.* (2004) used Sr/Ca ratios to identify the princi-

ple forms of larval recruitment in giant kokopu (*Galaxias argenteus*) collected from the lower Taieri and Mataura River catchments in Southland Otago. Aside from identifying typical diadromous movements in fish, their study indicated that non-diadromous recruitment may also play an important role in sustaining coastal populations of giant kokopu in the region (David *et al.* 2004). Similarly, otolith chemical analysis of common bully (*Gobiomorphus cotidianus*) by Closs *et al.* (2003) collected from the same general sample locations as David *et al.* (2004), provided further evidence of diadromous and non-diadromous recruitment. This was later shown to be the case for common bully in Lake Tarawera and the Tarawera River on the North Island of New Zealand (Michel *et al.* 2008). In the present study, we set out to expand the current information on the migratory life strategies of banded kokopu caught within an open and closed river system using otolith microchemistry techniques. More specifically, we compare $^{88}\text{Sr} : ^{43}\text{Ca}$ ratios in otoliths of fish taken above a large 65 m high dam near Whangarei City (with no upstream access from the sea) with fish from a small stream in the Kaipara Harbour (with sea access) on the North Island of New Zealand.

Methods

Fishing sites

Banded kokopu were collected from the Pukenui Stream located above the Whau Valley Reservoir near Whangarei on the east coast and from Komiti Stream in the Kaipara Harbour on the west coast of northern New Zealand (Figure 1). The Whau Valley Reservoir (25 ha)

was constructed in the early 1950s by the Whangarei District Council as the main water supply for Whangarei residents. Three headwater streams feed into the Pukenui Stream before entering the reservoir from the Pukenui Forest Reserve (NZMS260 Topographic Map, 1:50,000 Q07, Q08). From the reservoir outlet the Pukenui Stream descends 65 m into the Waiarohia Stream and the Whangarei Harbour. Fish species above the reservoir include banded kokopu (*Galaxias fasciatus*), rainbow trout (*Oncorhynchus mykiss*) and the longfin eel (*Anguilla dieffenbachii*), (Manning 1996). However, in the Waiarohia Stream immediately below the reservoir banded kokopu are not present. Instead a population from Komiti Stream in the Kaipara Harbour was sampled (Figure 1). The surrounding catchment of Komiti Stream is primarily pine forest (*Pinus radiata*) with a small residential area leading to the river mouth. We selected this stream because it had no in-stream barriers (waterfalls or culverts and dams) that would prevent fish passage from the sea. Eight fish from Pukenui Stream above the reservoir and seven from Komiti Stream were collected on 1 July and 10 October 2006 (Table 1), using minnow traps (4 mm mesh), baited with Kraft Vegemite®, and by spotlighting. For each day of sampling, traps were set before sunset along the Pukenui Stream and in the Komiti Stream. Within the first hour after sunset, spotlighting was carried out along shallow (< 600 mm depth) stream reaches and banded kokopu identified by spotlight were carefully scooped up by dip net (5 mm mesh). Fish captured (by both methods) were anaesthetised in benzocaine until dead, measured to the nearest mm total length (TL), and placed

in labelled containers in 70% ethanol for transport to the lab.

Otolith extraction and polishing

Sagittal otolith pairs were extracted from fifteen banded kokopu (Table 1). The head of each fish was sectioned with a scalpel along the midline dorsal surface (from the head to the mouth), and separated to expose left and right cranial cavities. Brain tissue was carefully flushed out with distilled water using a pipette, exposing the brain cavity and inner ear. Left and right otolith pairs were then removed from both cavities using fine-tip tweezers under a compound microscope. Excess tissue was removed and otoliths were rinsed thoroughly in distilled water before being stored in labelled vials to air-dry for 24 h. Otoliths were then embedded in thermosetting glue (Crystalbond, Aremco Products, Inc, USA) and mounted on glass slides (3 per slide), labelled by date and stream site using a glass etching drill and left overnight to dry. Otolith polishing was carried out systematically using firstly 1200, 2000, and then 4000 grain wetted carborundum sand paper to expose the otolith nucleus (area representing the larval growth phase in fish) for chemical analysis.

Laser ablation ICP-MS

Chemical analysis of fish otoliths was conducted at the University of Waikato's Mass Spectroscopy Suite using a Perkin Elmer Elan SCIEX DRCII inductively coupled mass spectrometer (ICP-MS) with a New Wave Research Nd: YAG 213 nm wave length laser. Only six otoliths from Komiti Stream and six from Pukenui Stream were suitable for analysis after sustaining damage during

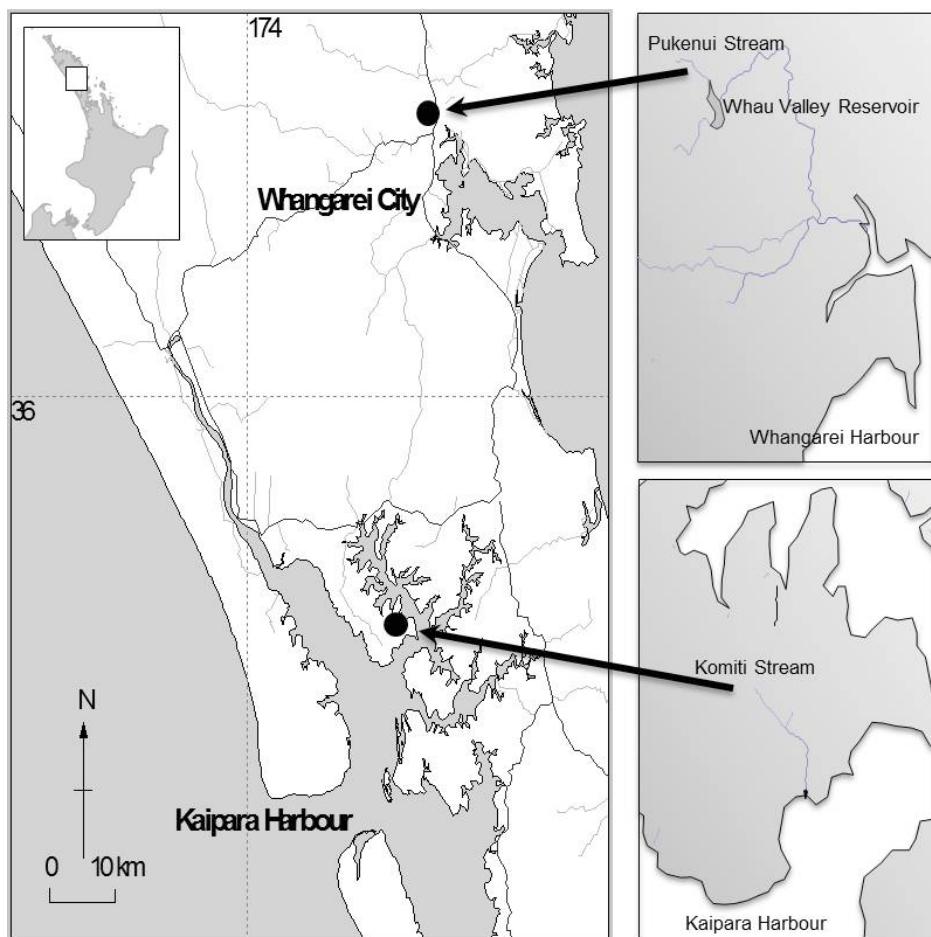


Figure 1. Location of banded kokopu fishing sites in the Pukenui Stream above Whau Valley Reservoir near Whangarei on the east coast and Komiti Stream in the Kaipara Harbour on the west coast of northern New Zealand.

the polishing and ablation process. To minimise the need to repeatedly open the laser ablation chamber, three otoliths mounted on a single glass slide were loaded into the chamber and purged by an argon carrier gas for 15 minutes to remove any residual material in the chamber, lines and ICP. Prior to and after sample analysis National Institute of Standards and Technology (NIST) 612 standard reference material (SRM) for which concentrations of 50 elements are known, was ablated. In between

standards, a single line of spots across the otolith growth axis starting from the nucleus to the edge of the otolith was ablated. The core was identified with transmitted light through an ablation chamber viewing screen. Spot diameter was 30 µm, and the laser was fired at a repetition rate of 20 Hz; grid spacing ranged between 50-75 µm because larger and smaller otolith sizes influenced the amount of spots which could be placed on the otolith. The laser was fired at 50% output power and a 10 s inter-site

pause to allow for background noise from the previous firing point to dissipate. Similarly, prior to ablation of each sample, argon gas blanks were flushed through the sample chamber alongside normal purge procedures when starting a new sample. The mean counts of blanks were subtracted from the sample counts per second (cps) to determine if any polyatomic interferences were present in the carrier gas and to provide baseline measures to show where true laser data were being recorded and completed.

Although a broad range of elements were measured only three isotopes ^{88}Sr , ^{43}Ca , and ^{137}Ba were of interest in this study based on the effectiveness of these isotopes in documenting diadromous migrations in New Zealand (Closs *et al.* 2003; David *et al.* 2004; Hicks *et al.* 2005) and overseas (Arai *et al.* 2006; Limburg 1995; Tzeng 1996; Tzeng *et al.* 2005). Elemental data for otoliths are presented as mean counts per second for each isotope (ratioed to calcium) as a consequence of the lack of matrix-matched standards (Morales-Nin *et al.* 2005).

Water sample analyses

Ten water samples from each stream were collected at separate fishing sites at the same time as fish were collected using 15 mL acid-washed Falcon tubes. In the field, the sampling tubes were rinsed thoroughly in the stream then filled completely and sealed with the cap while submerged. Samples were then stored in a chilled thermos at about 4°C for transport to the laboratory. In the laboratory, water samples were filtered through disposable 0.45 μm millipore filters and transferred back into sterile 15 mL falcon tubes at a set volume of 9.8 mL then topped off with 0.2 mL nitric

acid (HNO_3) and shaken. Water samples collected from both fish sampling sites were analysed using ICP-MS in aqueous mode. The water sample transport lines were rinsed before and after each sample with Type-1 water and HNO_3 (2 %), to clean the lines for the next sample. The ICP-MS was calibrated at two levels of sensitivity using Merck XXI standards. A calibration blank was run for specified elements at low sensitivity 50 ppb and compared with a separate standard with known elements of 50 ppb, to indicate how close the readings were to the standards. The process was also repeated at high sensitivity 330 ppb, to determine the level of calibration one to the standards. Mean differences (\pm SD), in stream water chemistry for ^{88}Sr and ^{43}Ca between the ten fishing sites were evaluated by small-sample t-tests (unequal variances) and are presented as elemental concentrations in ppb.

Results

Otolith Sr/Ca ratios

Banded kokopu from both sample streams showed varying levels of Sr/Ca and Ba /Ca ratios (cps) from the nucleus (larval growth zone) to the otolith edge (maturing growth zone), (Figures 2 & 3). Otoliths extracted from fish in Komiti Stream all showed peak Sr/Ca ratios 14-19 at the otolith nucleus indicating a marine rearing growth phase (Figure 2). Similarly, from the nucleus edge noticeable decreases in Sr/Ca ratios were shown for all fish otoliths from Komiti Stream and were generally the same as low level Sr/Ca ratios from above the reservoir < 2-5 with the exception of one individual fish (Figure 2A, Table

Table 1. Summary information of fish collection dates, identification codes and location of fishing sites Komiti Stream (KS) and Pukenui Stream (PS) along with fish size (TL, mm) and otolith condition (after polishing) for laser ablation ICP-MS analysis.

Date collected	Fishing site	Identification code	Otolith condition	Length (TL) (mm)
1-Jul-06	KS	WHUBKOO1	good	175
1-Jul-06	KS	WHUBKOO2	good	169
1-Jul-06	KS	WHUBKOO3	good	134
1-Jul-06	KS	WHUBKOO4	good	138
1-Jul-06	KS	WHUBKOO5	good	95
1-Jul-06	KS	WHUBKOO6	damaged	118
1-Jul-06	KS	WHUBKOO7	good	166
10-Oct-06	PS	PLUBKOO1	good	142
10-Oct-06	PS	PLUBKOO2	damaged	92
10-Oct-06	PS	PLUBKOO3	good	85
10-Oct-06	PS	PLUBKOO4	good	81
10-Oct-06	PS	PLUBKOO5	damaged	79
10-Oct-06	PS	PLUBKOO6	good	88
10-Oct-06	PS	PLUBKOO7	good	75
10-Oct-06	PS	PLUBKOO8	good	78

1) which showed a slight increase in Sr/Ca ratios at the edge of the otolith. In addition, fish from Komiti Stream were smaller (81mm to 142mm) than fish from above the Whau Valley Reservoir (95-175 mm), suggesting there were a number of recent recruits (Figure 2B-F), as well as a resident adult (Figure 2A). Ba/Ca ratios generally demonstrated an inverse relationship to Sr/Ca with ratios being lower near the otolith nucleus and slightly higher towards the otolith edge (Figure 2).

Otoliths of fish taken from the Pukenui Stream above the reservoir showed consistent trends in otolith chemistry with only slight variations in Sr/Ca ratios at distance from the nucleus. Generally, Sr/Ca ratios followed relatively low uniform trends across all otolith growth

zones reflective of permanent freshwater residency (Figure 3A-E). Trends in Ba/Ca ratios were more variable and typically ranged around 0.008-0.032 across otolith growth zones. However, a large 175mm adult fish (Figure 3F) indicated unusually high Sr/Ca ratios. Most notably, these high Sr levels were not observed at the nucleus (larval growth zone) but midway between the otolith edge and nucleus fringe existing over a relatively large proportion of the otolith before decreasing back to original nucleus Sr/Ca ratio levels 4 (Figure 3F). In addition, all fish taken from above the reservoir were mature adults 95-175 mm (Table 1; McDowall 1990). Concentrations of Ca in water samples from Komiti Stream (30163 ± 11213 ; mean \pm 1 SD ppb), were significantly higher ($P < 0.001$) than in

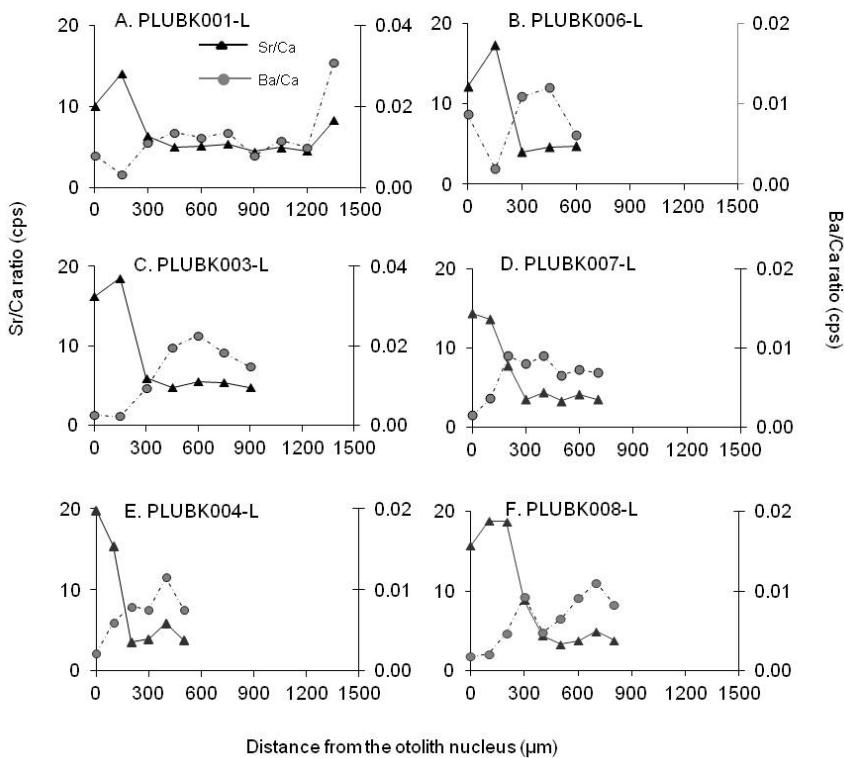


Figure 2. Elemental ratios of Sr/Ca and Ba/Ca (cps) in sequence from the otolith nucleus (μm) to the otolith edge of banded kokopu collected from Komiti Stream in the Kaipara Harbour.

the Pukenui Stream (6983 ± 2551 ; mean \pm 1 SD ppb), small sample t-test, $N=10$ for each stream. Similarly, elemental concentrations of Sr were also significantly higher ($P < 0.001$), in Komiti Stream (341 ± 139 ; mean \pm 1 SD ppb), than in the Pukenui Stream (101 ± 22 ; mean \pm 1 SD ppb).

Discussion

All banded kokopu collected from Komiti Stream were shown to have marine phase life histories as larvae (indicated by high Sr/Ca ratios at the core). Probably the most important determinator of these migrations was the absence of large in-stream barriers such as dams, waterfalls or culverts. With

clear access to and from the sea, marine phase life strategies for banded kokopu in this site were expected. Similarly, all developmental trends associated with the recruitment of juveniles from the sea suggest maturation in freshwater habitats. Banded kokopu populations above the Whau Valley Reservoir appear to be non-migratory (Figure 3). Banded kokopu typically have a larval marine growth stage (Charteris *et al.* 2003, McDowall 1995), subsequently low Sr/Ca ratios in otoliths of fish collected from above the reservoir suggests that the recruitment of fish within this watershed occurred entirely within freshwater.

The propensity of banded kokopu to

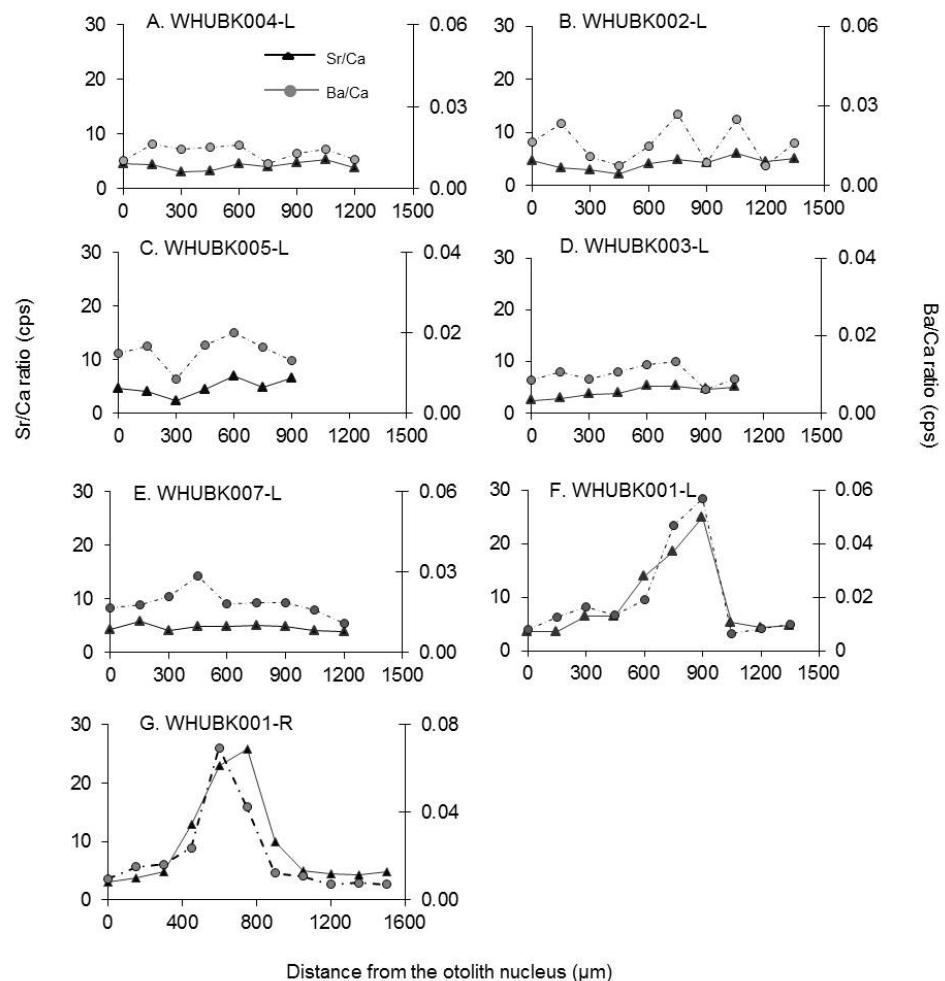


Figure 3. Elemental ratios of Sr/Ca and Ba/Ca (cps) in sequence from the otolith nucleus (μm) to the otolith edge of banded kokopu collected from Pukenui Stream above the Whau Valley Reservoir. NB: Plots F and G are left and right otolith analyses from the same fish.

adopt non-diadromous recruitment strategies as a consequence of impeded access to the sea is widely recognised and has been shown to occur throughout much of New Zealand. Schipper (1979) was the first to document landlocked banded kokopu in Lake Ototoa on the westcoast of Northland New Zealand. However, in more recent years landlocked banded kokopu have been recorded in Lake Kaihoka northwest of Nelson, Lake Hochstetter in Westland, and

Lake Okataina in the Rotorua District of northeastern New Zealand (Rowe & Graynoth 2002). Additionally, a number of small reservoirs (Waitakere and Hunua reservoirs near Auckland), are also known to contain landlocked banded kokopu (Rowe & Graynoth 2002). While much of the evidence supporting landlocking has been based on identifying major in-stream barriers to migration, in the present study we

used an alternative line of evidence to address this question based on high or low Sr/Ca ratios.

For banded kokopu collected above the Whau Valley Reservoir, the Sr/Ca ratios suggest that fish have not been to sea. However, one banded kokopu (Figure 3F, 3G), had high Sr/Ca ratios in midlife 29 which not only exceeded ratios of other fish from the same location 5 but also surpassed the marine ratios reflected in fish from Komiti Stream 19. This may be due to several factors the most obvious being that the fish was flushed over the reservoir, down into a marine environment as a juvenile where it spent a substantial amount of time before returning back over the reservoir as a larger fish sometime later. Although banded kokopu are widely recognised as being excellent climbers as post larvae-juveniles, with increasing size the climbing ability of larger adults would have been greatly reduced (Boubée *et al.* 2000; McDowall 2000), making this highly unlikely. For this reason we processed the right sagittal otolith using the same preparation methods and laser ablation settings, which resulted in the general ratios and trends (Figure 3G), indicating that they were a true reflection of the fish's life history. We suggest the reason for these high Sr/Ca ratios maybe due to localised variations within the reservoir and its draining catchment. In this study, we observed the presence of several iron-rich seepages scattered throughout the same sample catchment including a small tributary stream which was covered in iron flocculent. Similarly, there is a prior history of mining in the general area (Manning 1996). The high presence of dissolved ions as a result of iron-rich seepages may accompany elevated Sr levels, which have been shown to occur

in lake and freshwater catchments with geothermal and spring fed groundwater inputs (Muller, 1969).

This would seem a likely answer to increased Sr/Ca uptake although given this particular fish was a large adult and the proportion of high Sr/Ca relative to time (approx, 280 µm growth), the high Sr/Ca levels would have to be relatively constant at that level and time period to be incorporated. These high Sr counts may therefore be compounded by fluctuations in available calcium within the stream (McDonald *et al.* 1983), which would limit calcium's uptake and therefore facilitate Sr and Ba uptake in fish otoliths in the absence of calcium (De Vries *et al.* 2005). Similarly, given that Ba forms a carbonate structure that is isostructural with aragonite, it like Sr can substitute for calcium within the otolith crystalline matrix when calcium is in low abundance (Campana 1999; Munro 2004). This was indicated at least for the water samples collected from the Pukenui Stream with calcium concentrations (6983 ± 2551 ppb), significantly lower ($P < 0.001$) than in Komiti Stream (30163 ± 11213 ppb). Similarly, low calcium in fish may also be the product of disease or injury resulting in calcium deficiencies (Kulczykowska *et al.* 2004). However, in some cases fish may recover from deficiency problems when calcium once again becomes readily available in the system (McDonald *et al.* 1983). In this study low calcium availability, coupled with the presence of iron-rich seepages within the Whau Valley Reservoir may explain why the indifferent Sr/Ca ratio of the fish above the reservoir fluctuated over time (Figure 2A) before returning to similar ratios as was indicated in its early rearing stage. Overall, this study illustrated that banded

kokopu are flexible in their migratory life strategies regardless of in stream barriers, with fish collected from above the reservoir indicating permanent freshwater resident life histories, while banded kokopu collected from Komiti Stream, exhibited early marine life histories indicative of their diadromous origins. The study provides further evidence of non-diadromous recruitment for banded kokopu as a consequence of a large in-stream barrier and will add to the current information on the known distribution of landlocked species. Future management and conservation impetus will need to build on and include a broader understanding of the extent of diadromy for a range of species throughout New Zealand.

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References

- Arai, T., Yang, J., & Miyazaki, N. (2006). Migration flexibility between freshwater and marine habitats of the pond smelt *Hypomesus nipponensis*. *Journal of Fish Biology* 68: 1388–1398.
- Boubée, J. A. T., Richardson, J., & Williams, E. (2000) Fish Passage: Review and Guidelines for the Auckland Regional Council. Auckland, NIWA Client Report ARC.
- Campana, S.E. & Neilson, J.D. (1985). Microstructure of fish otoliths. *Canadian Journal Fish Aquatic Science*. 42: 1014–1032.
- Campana, S. E. (1999). Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Review. *Marine Ecology Progress Series* 188: 263–297.
- Campana, S. E. & Thorold, S. R. (2001). Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations? *Canadian Journal Fish Aquatic Science* 58: 30–38.
- Charteris, S. C., Allibone, R. M., & Death, R. G. (2003). Spawning site selection, egg development, and larval drift of *Galaxias postvectis* and *G. fasciatus* in a New Zealand stream. *Journal of Marine and Freshwater Research* 37: 493–505.
- Closs, G.P., Smith, M., Barry, B., & Markwitz, A. (2003). Non-diadromous recruitment in coastal populations of common bully *Gobiomorphus cotidianus*. *New Zealand Journal of Marine and Freshwater Research* 37: 301–313.
- David, B., Chadderton, L., Closs, G.P., & Markwitz, B. (2004) Evidence of flexible recruitment strategies in coastal populations of giant kokopu *Galaxias argenteus*. DOC Science Internal Series 160, New Zealand Department of Conservation Wellington, pp.1–23.
- De Vries, M .C., Gillanders, B. M., & Elsdon, T. S. (2005) Facilitation of barium uptake into fish otoliths: Influence of strontium concentration and salinity. *Geochimica et Cosmochimica Acta* 69: 4061–4072.
- Hicks, A.S., Closs, G.P., & Swearer, S.E. (2008). Otolith microchemistry of

- two amphidromous galaxiids across an experimental salinity gradient: A multi-element approach for tracking diadromous migrations. *Journal of Experimental Marine Biology and Ecology* 394: 85-97.
- Hicks, B .J., West, D.W., Barry, B.J., Markwitz, A., Baker, C.F. & Mitchell, C. P. (2005). Chronosequences of strontium in the otoliths of two New Zealand migratory freshwater fish, inanga *Galaxias maculatus* and koaro *G. brevipinnus*. *International Journal of PIXE*, 1-7.
- Kalish, J. M. (1990). Use of otolith microchemistry to distinguish the progeny of sympatric anadromous and non- anadromous salmonids. *Fishery Bulletin (US)* 88: 657-66.
- Kulczykowska, E., Sokolowska, E., Gozdowska, M., & Kalamarz, H. (2004). Disruption of the melatonin rhythm in wild and farmed fish: a consequence of prolonged thyroxine administration and calcium depletion. *Journal of Fish Biology* 65: 331-332.
- Limburg, K.E. (1995). Otolith strontium traces environmental history of sub-yearling American shad *Alosa sapidissima*. *Marine Ecology Progress Series* 119: 25-35.
- Manning, D. (1996). Natural areas of Whangarei Ecological District, Reconnaissance survey report for the Protected Natural Areas Programme. Published by the Department of Conservation Northland Conservancy, Whangarei New Zealand, pp.132-145.
- McDonald, D. G., Walker, R. L., & Wilkes, P. R. H. (1983). The interaction of environmental Calcium and low pH on the physiology of the Rainbow Trout, *Salmo gairdneri*: II. brachial ionoregulatory mechanisms. *Journal of Experimental Biology* 102: 141-155.
- McDowall, R. M. (1972). The species problem in freshwater fishes and the taxonomy of diadromous and lacustrine populations of *Galaxias maculatus* (Jenyns). *Journal of the Royal Society of New Zealand* 2: 325-367.
- McDowall, R.M. (1988). *Diadromy in fishes: migrations between freshwater and marine environments*. Croom Helm, London.
- McDowall, R.M. (1990). *New Zealand Freshwater Fishes: a Natural History and Guide*. Heinemann Reed, Auckland.
- McDowall, R.M. (1993). Implications of diadromy for the structuring and modeling of riverine fish communities in New Zealand. *New Zealand Journal of Marine and Freshwater Research* 27: 453-462.
- McDowall, R.M. (1995). Seasonal pulses in migrations of New Zealand diadromous fish and the potential impacts of river mouth closure. *New Zealand Journal of Marine and Freshwater Research* 29: 517-526.
- McDowall, R.M. (1996). Diadromy and the assembly and restoration of riverine fish communities: a downstream view. *Canadian Journal of Fisheries and Aquatic Sciences*, 53 (Suppl. 1): 219-236.
- McDowall, R. M. (2000). *Hidden treasures exposed: discovering our freshwater fish fauna*. Cawthron Institute Nelson New Zealand, pp. 1-24.
- McDowall, R. M. (2007). On amphidromy, a distinct form of diadromy in aquatic organisms. *Fish and Fisheries*, 8: 1-13.
- Michel C., Hicks, B.J., Stölting, K.N., Clarke, A.C., Stevens, M.I., Tana, R., Meyer, A., & van den Heuvel, M. R.

- (2008). Distinct migratory and non-migratory ecotypes of an endemic New Zealand eleotrid (*Gobiomorphus cotidianus*) – implications for incipient speciation in island freshwater fish species. *BMC Evolutionary Biology* 49: 1-14.
- Morales-Nin, B., Swan, S. C., Gordon, J. D. M., Palmer, M., Geffen, A. J., Shimmield, T., & Sawyer, T. (2005). Age-related trends in otolith chemistry of *Merluccius merluccius* from the north-eastern Atlantic Ocean and the western Mediterranean Sea. *Marine and Freshwater Research* 56: 599-607.
- Muller, G. (1969). High strontium contents and Sr/Ca ratios in Lake Constants waters and carbonates and their sources in the drainage area of the Rhine River (Alpenrhein). *Mineral Deposita* 4: 75-84.
- Munro., A. R. (2004). Identification of life history variation in salmonids using otolith microchemistry and scale patterns implications for illegal introductions and for whirling disease in Missouri River rainbow trout. Fish and Wildlife Biology. Montana State University, pp. 1-218.
- Rowe, D.K. & Graynoth, E. (2002). Lake Managers' Handbook; Fish in New Zealand Lakes. The Ministry for the Environment, Wellington, New Zealand.
- Schipper, C. M. (1979). Landlocked banded kokopu (*Galaxias fasciatus*) from Lake Ototoa. Fisheries Research Division, New Zealand Ministry of Agriculture and Fisheries, Rotorua.
- Thorrold, S. R., Jones, C. M., Campana, S. E., McLaren, J. W., & Lam, J. W. H. (1998). Trace element signatures in otoliths record natal river of juvenile American shad *Alosa sapidissima*. *Limnology and Oceanography* 43: 1826-1835.
- Tzeng, W. N. (1996). Effects of salinity and ontogenetic movement on strontium: calcium ratio in otolith of the Japanese eel *Anguilla japonica* (Temminck and Schlegel). *Journal Experimental Marine Biology and Ecology* 199: 111-122.
- Tzeng, W. N., Severin, K. P., Wang, C. H., & Wickstrom, H. (2005). Elemental composition of otoliths as a discriminator of life stage and growth habitat of the European eel, *Anguilla anguilla*. *Marine and Freshwater Research* 56: 629-635.