

Evidence of flexible recruitment strategies in coastal populations of giant kokopu (*Galaxias argenteus*)

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Evidence of flexible recruitment strategies in coastal populations of giant kokopu (*Galaxias argenteus*)

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ABSTRACT

Diadromy (the movement of organisms between freshwater and marine environments) is an important characteristic of the New Zealand freshwater fish fauna. This feature is often epitomised by the five galaxiid species whose larvae, when returning from the sea, make up the whitebait fishery. Diadromous life history patterns are undergoing renewed scrutiny as advances in otolith (fish ear stone) microchemistry have allowed larval and juvenile fish movement to be tracked between marine and freshwater environments. The potential role of non-diadromous recruitment in coastal populations of New Zealand galaxiids appears to have received little consideration. Among the five whitebait species, four (koaro *Galaxias brevipinnis*, inanga *Galaxias maculatus*, banded kokopu *Galaxias fasciatus*, and giant kokopu *Galaxias argenteus*) are capable of forming non-diadromous populations, whereas larval movement to the sea is thought to be obligatory for shortjaw kokopu *Galaxias postvectis*. In this study we collected otoliths from four distinct giant kokopu populations from the southeast South Island and used otolith Sr:Ca ratios to determine whether diadromy was the principal form of recruitment. Analysis of otoliths indicates that despite open access to the sea, local rather than diadromous recruitment primarily occurs in giant kokopu populations in the lower Taieri / Waipori and Mataura River catchments. These results suggest that local rather than diadromous recruitment of larvae may be important for sustaining coastal populations of giant kokopu in some regions; they highlight the need for further research in other regions, in other stream geomorphologies, and for other diadromous species. If non-diadromous recruitment is more important than previously thought, the implications for the future management of coastal freshwater environments and native diadromous species in New Zealand are significant.

Keywords: diadromy, otoliths, giant kokopu, *Galaxias argenteus*, recruitment, Sr:Ca, otolith micro-chemistry.

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1. Introduction

A feature of New Zealand's native freshwater fish fauna is the high proportion (more than 50%) of diadromous species (McDowall 1996). Diadromous fish undertake migrations between marine and freshwater environments at some points in their life cycles. The high proportion of diadromy in New Zealand fish is unusual, as only about 230 diadromous species are believed to occur globally (McDowall 1988). The influence of diadromy in New Zealand is evident in the wide distribution of most diadromous species throughout both the North and South Islands and their lack of genetic structuring (Allibone & Wallis 1993).

Of the thirty-eight or so freshwater fish species currently identified in New Zealand, members of the family Galaxiidae comprise more than half (McDowall 2000). Of these, five species (giant kokopu *Galaxias argenteus*, banded kokopu *Galaxias fasciatus*, shortjaw kokopu *Galaxias postvectis*, koaro *Galaxias brevipinnis*, and inanga *Galaxias maculatus*) are considered to be diadromous (McDowall 1990). Adults of these species typically spawn in freshwater or estuarine habitats and larvae are thought to 'go' to sea (Ots & Eldon 1975; McDowall & Suren 1995) before returning after several months (McDowall 1990). The shoals of returning larvae are commonly referred to as 'whitebait' and are an important fishery resource in some parts of the country. Recruitment for these species in coastal areas is thought to be overwhelmingly dominated by larvae returning from the sea (McDowall 1990). One of the aspects of a diadromous life history is that individuals of a species may disperse along coastlines to form new populations in other catchments. This dispersal has obvious advantages for the continued existence of a species should a disease or other natural disaster eliminate a population in a particular catchment.

Although diadromous recruitment is undoubtedly important for New Zealand fish, it is not obligatory for all species. Of the diadromous galaxiids, only *G. postvectis* does not appear capable of forming self-sustaining landlocked populations (McDowall 1993). Recruitment flexibility is also exhibited by common bully *Gobiomorphus cotidianus*, and Northcote et al. (1992) found that smelt *Retropinna retropinna* are capable of recruiting locally, even where they have unimpeded access to the sea. Such flexibility in life-history behaviour has also been shown for a number of fish species in other countries (Pender & Griffin 1996; Secor et al. 2001).

The question of whether non-diadromous recruitment could be important for the maintenance of coastal galaxiid populations (given favourable conditions for larval development and growth) has received little attention. If recruitment is reliant upon larvae derived from local freshwater or estuarine environments rather than marine environments, then a re-evaluation of current management strategies for these and, potentially, other diadromous species is required. The New Zealand Biodiversity Strategy (2000) and the New Zealand Large Galaxiid Recovery Plan, which is being prepared at present, include the goals of maintaining and restoring viable representative populations across their natural range. To achieve this goal, a detailed understanding of species' life history, recruitment, dispersal and migration patterns is essential.

This study considers whether non-diadromous recruitment could be important for the maintenance of coastal giant kokopu (*Galaxias argenteus*) populations and, specifically:

- Whether diadromy is the principal form of larval recruitment to coastal populations of giant kokopu in southern New Zealand.
- Whether larval recruitment patterns are potentially influenced by river catchment morphology and / or different system types.
- To use the information gained from this study to provide recommendations and future research directions for the management of giant kokopu and other diadromous fish species.

2. Non-diadromous recruitment in giant kokopu populations

Giant kokopu are endemic to New Zealand and are the largest galaxiid known (McDowall 1990). They have undergone significant range reductions (Bonnett et al. 2000), and are now considered to be chronically threatened and in gradual decline (Hitchmough 2002). Causes of their decline are thought to include habitat loss as a result of land clearance, loss of fish passage, and wetland drainage, as well as predation and / or competition with introduced species (Bonnett et al. 2000; Chadderton & Allibone 2000; David 2001; David et al. 2002). At present, giant kokopu are found on the three main islands of New Zealand, though major populations are centred around the Waikato River, Taranaki, Bay of Plenty, and Wairarapa in the North Island (Fig. 1) and North West Nelson, Westland, and coastal Southland / Otago in the South Island (Fig.1). They tend to favour slow-flowing coastal waters with abundant instream cover (McDowall 1990; Bonnett et al. 2000).

In southern New Zealand (Coastal Southland / Otago and Stewart Island), the largest populations of giant kokopu are associated with coastal floodplains, barrier estuaries, lagoon systems, and inland lakes (Chadderton 1990; Bonnett et al. 2000; David et al. 2002). Giant kokopu populations found in shorter, steeper coastal streams that lack these low water velocity features are usually much smaller, often limited to a few adult fish (David et al. 2002).

Along the east coast of the South Island there are a number of disjunct populations of giant kokopu (David et al. 2002, Fig. 1). This fragmented distribution has been attributed to the absence of suitable adult habitat (Bonnett et al. 2000). Significantly, for these disjunct isolated populations to be maintained, larval and juvenile giant kokopu must:

- Have the capacity to migrate across large oceanic distances and then locate suitable habitats.
- Have the capacity to home in on and return to natal streams.
- Recruit from freshwater or estuarine habitats located within the river / lake catchment in which they were spawned.

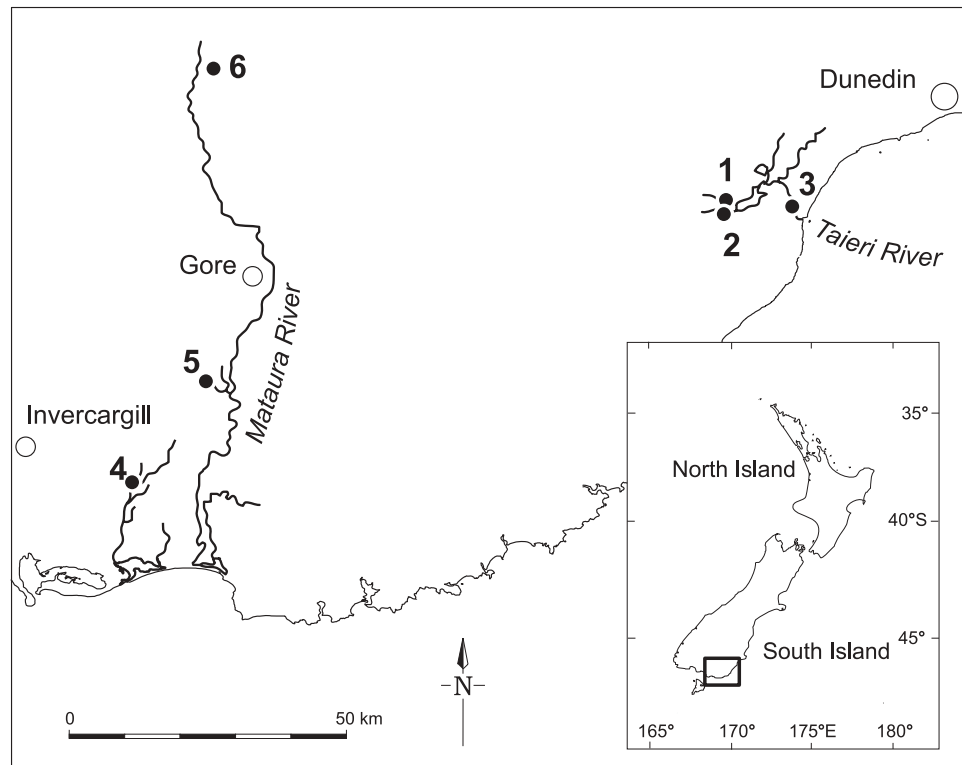
Figure 1. Distribution (○) of giant kokopu (*Galaxias argenteus*) throughout New Zealand. Data obtained from the New Zealand Freshwater Fish Database.



Giant kokopu appear to be readily able to establish landlocked populations. They are found in inland Southland, especially in the upper Waiau and Matuara basins (Fig. 2) where downstream barriers to fish passage prevent present-day diadromous recruitment. They have been found in small lakes or ponds (W.L. Chadderton pers. obs.), including old mining ponds at Round Hill (Lake George), and Waikaia. It seems plausible, and is consistent with inland Southland giant kokopu populations, that lentic (slow-flowing water) habitats prevalent in many coastal floodplains (e.g. lower Taieri, Lake Waihola, Waituna Lagoon) could function as a surrogate marine (pelagic) environment to facilitate larval development and growth, even where passage to the sea is still possible. This may explain observations of giant kokopu larvae migrating into lower Taieri streams several months after localised flooding and well outside the months during which peak whitebait runs occur (B. David pers. obs.). The

Figure 2. Sample sites for giant kokopu and one banded kokopu in southern South Island.

- Site 1 = Alex Creek,
- 2 = Cullen's Creek,
- 3 = Picnic-Gully Creek,
- 4 = Waituna Creek,
- 5 = Ota Creek,
- 6 = Waikaia ponds.



ability of giant kokopu to form non-diadromous populations in relatively small lentic systems (such as the Waikaia Dredge ponds) indicates that slow-flowing low-gradient river systems may also provide environments with hydraulic characteristics that can facilitate non diadromous recruitment.

3. Otolith microchemistry technique

Otoliths are stones found in the ears of fish. They are formed from calcium carbonate (CaCO_3) that is deposited as concentric rings around a central core as the fish grows. There is no turnover of deposited crystalline material and hence a transect across an otolith represents a permanent chemical record of the fish's life history. Recent advances in the analysis of otolith micro chemistry have enabled researchers to determine whether and when individual fish have moved between marine and freshwater environments during their life history (Markwitz et al. 2000; Howland et al. 2001). Ambient environmental concentrations of strontium are consistently higher in seawater (average Sr:Ca ratio 0.0087) than freshwater (average Sr:Ca ratio 0.0019). As a result, layers of otolith formed when a fish is in a marine environment typically exhibit higher strontium to calcium (Sr:Ca) ratios than layers deposited when a fish was resident in fresh water (Kalish 1990; Secor & Rooker 2000). Incorporation of strontium into the otolith (as strontium carbonate) has been shown to be proportional to, and reflective of, ambient environmental concentrations in the

surrounding water (Bath et al. 2000). It should be noted that other factors such as temperature, food, activity and inter-species differences may also play a role in uptake (Kalish 1990; Radtke & Shafer 1992; Secor & Rooker 2000). However, the influence of these other factors appears to be minor relative to the differences in Sr:Ca ratios that occur as a result of residency in either marine or freshwater environments (Bath et al. 2000; Secor & Rooker 2000). Fish that have had a larval / juvenile developmental phase in a marine environment before moving back to fresh water can be expected to have a high core Sr:Ca ratio relative to the otolith edge (Fig. 3A). In contrast, fish that have spent their entire life-cycle in a freshwater environment can be expected to have Sr:Ca ratios that are relatively low and consistent throughout the otolith (Fig. 3B).

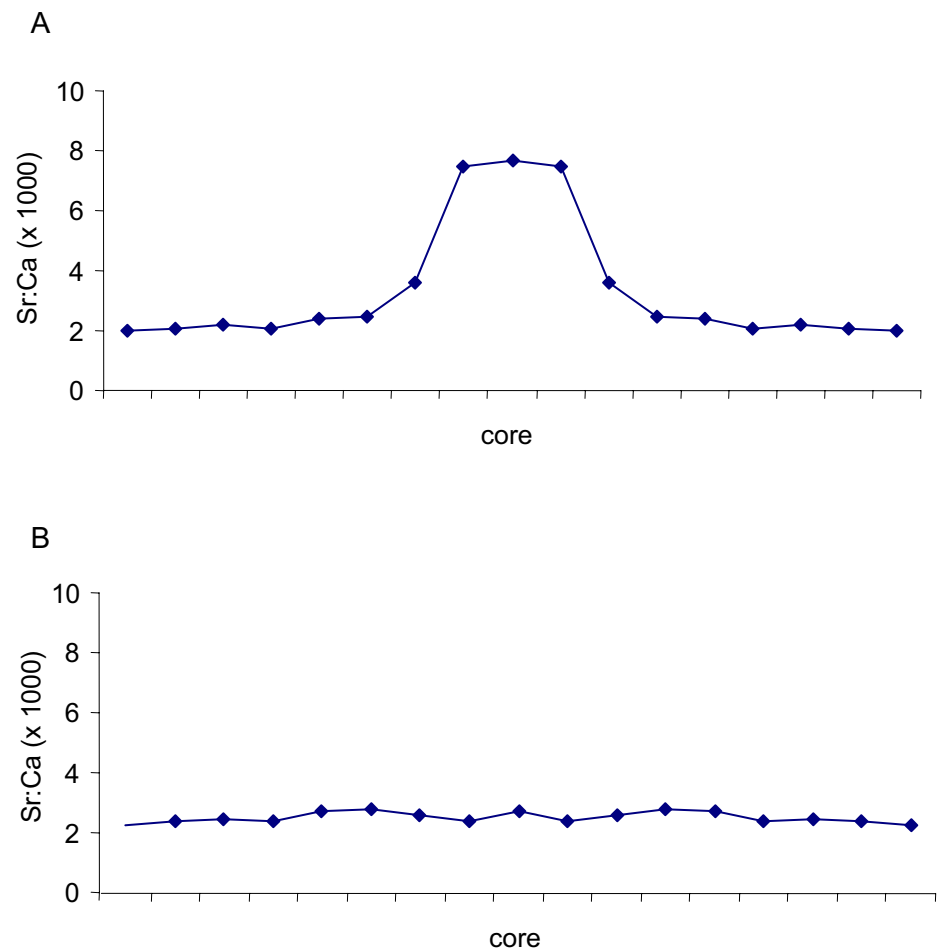


Figure 3. Sr:Ca otolith profiles for hypothetical marine (A) and freshwater (B) recruits.

4. Otolith geochemistry of coastal Otago / Southland giant kokopu

4.1 POPULATIONS EXAMINED

Patterns of strontium deposition in otoliths extracted from giant kokopu from four populations in Southland and Otago were examined. These populations included two with unimpeded access to the sea (lower Taieri catchment, lower Maitara catchment) one with intermittent access (Waituna Lagoon) and one that was known to be landlocked (Waikaia Ponds) (Fig. 2). If diadromy was the principal form of recruitment, we would expect most fish in systems with unimpeded access to the sea to exhibit high Sr:Ca ratios in their otolith cores (i.e. clear evidence of a larval marine life-history stage) relative to those from the landlocked populations.

4.2 SAMPLING DETAILS

Samples were collected as follows:

- Eleven giant kokopu were collected from the lower Taieri catchment. Six of these fish were collected from Alex Creek and five from Cullen's Creek. Both of these creeks are small (2nd and 3rd order respectively) and drain into Lake Waihola, a tidally-influenced water body that receives periodic saltwater intrusions (Schallenberg & Burns in press). Lake Waihola is located 10 km from the sea and salinity levels in the lake water can vary substantially, both seasonally and from year to year. Though variable, maximum salinity levels, based on current records, are always less than one-third of that found in sea water (Schallenberg et al. 2003). Fish have unimpeded passage from Lake Waihola to the sea via the Waipori and Taieri rivers.
- Ten giant kokopu were collected from Ota Creek, a small (2nd order) tributary entering the lower Maitara River (approximately 35 km inland). There is open access to the sea via Toetoes Estuary.
- Six giant kokopu were collected from Waituna Creek which drains into Waituna Lagoon in Southland. Although Waituna lagoon is situated on the coast, passage for fish between the lagoon and sea is intermittent and depends on outlet opening that is artificially maintained. Fish passage between the lagoon and the sea may be denied for indeterminate periods; although, in recent years, extended periods of opening have occurred (Thompson & Ryder 2003). When open, the lagoon is tidal with seawater intrusions (Riddell et al. 1988). When the lagoon is closed to the sea, a saline influence persists. Thompson & Ryder (2003) reported salinities ranging from 1.1 part per thousand in the western lagoon to 2.3-5.1 parts per thousand on the eastern seaward side of the lagoon (seawater = 34 parts per thousand).

- Three giant kokopu were collected from a landlocked population in the Waikaia Ponds at Freshford, 105 km inland. The combination of distance inland, the absence of connection to the Mataura River, and the ponds' location above the Mataura Falls are considered likely to preclude any chance of upstream migration to this site.
- One banded kokopu was collected from a known diadromous population in Picnic-Gully Creek, a small (2nd order) coastal creek which runs through native bush and enters the sea at the mouth of the Taieri River (Fig. 3).

Most fish used in the study were captured in 2002, but some that had been collected and preserved during the period 2000-01 were also sampled (see Table 1).

TABLE 1. SUMMARY OF FISH SAMPLED FOR OTOLITH MICRO-CHEMISTRY INCLUDING SPECIES TYPE (GK = GIANT KOKOPU, BK = BANDED KOKOPU), THE DATE OF COLLECTION FOR EACH INDIVIDUAL, THEIR SIZE AND THE LOCATION OF CAPTURE. THE CODE DEFINING EACH INDIVIDUAL HERE AND IN THE TEXT IS REPRESENTED BY AN ABBREVIATION OF THE CAPTURE LOCATION.

CODE	SPECIES	DATE COLLECTED	SIZE (cm)	LOCATION
A1	GK	29 Feb 00	23.3	Alex Ck
A2	GK	24 Apr 02	16.1	Alex Ck
A3	GK	24 Apr 02	10.1	Alex Ck
A4	GK	24 Apr 02	10.1	Alex Ck
A5	GK	24 Apr 02	10	Alex Ck
A6	GK	24 Apr 02	14.3	Alex Ck
C1	GK	24 Apr 02	13.1	Cullen Ck
C2	GK	19 Nov 99	30.2	Cullen Ck
C3	GK	24 Apr 02	12.4	Cullen Ck
C4	GK	24 Apr 02	6.3	Cullen Ck
C5	GK	24 Apr 02	6.2	Cullen Ck
OT1	GK	21 May 02	25.2	Ota Ck
OT2	GK	21 May 02	27.5	Ota Ck
OT3	GK	21 May 02	7.3	Ota Ck
OT4	GK	21 May 02	6.8	Ota Ck
OT5	GK	21 May 02	11.6	Ota Ck
OT6	GK	21 May 02	12	Ota Ck
OT7	GK	21 May 02	14.5	Ota Ck
OT8	GK	21 May 02	17.5	Ota Ck
OT9	GK	21 May 02	6.4	Ota Ck
OT10	GK	21 May 02	24.1	Ota Ck
WT1	GK	27 Apr 02	6.9	Waituna Ck
WT2	GK	27 Apr 02	7.5	Waituna Ck
WT3	GK	27 Apr 02	7.3	Waituna Ck
WT4	GK	27 Apr 02	6.3	Waituna Ck
WT5	GK	27 Apr 02	6.3	Waituna Ck
WT6	GK	27 Apr 02	6.8	Waituna Ck
WK1	GK	31 Apr 02	7.5	Waikaia Ponds
WK2	GK	31 Apr 02	10.9	Waikaia Ponds
WK3	GK	31 Apr 02	12	Waikaia Ponds
PGBK1	BK	11 Apr 01	11.1	Picnic Gully Ck

4.3 FISH CAPTURE AND OTOLITH REMOVAL

All giant kokopu captured for this study were caught at night using a spotlight and dipnet and killed immediately using an overdose (400 mL/L) of 2 phenoxyethanol before being transferred into 95% ethanol for preservation. Prior to otolith removal in the laboratory, the length of each fish was recorded. Sagittal otoliths were obtained from the fish by first removing the head (immediately anterior to the pectoral girdle) and then, using a scalpel, bisecting the cranium from the dorsal surface precisely along the midline. Otoliths from each cranial half were removed from the small depression located at the posterior end of the brain case. Following removal, otoliths were viewed under a dissecting microscope and, if necessary, cleaned in distilled water to remove any capsule tissue still attached. Otoliths were then placed in a labelled vial to air-dry (overnight) prior to mounting, sanding and polishing.

4.4 OTOLITH PREPARATION

The method used to prepare otoliths depended on their size. For small thin otoliths (from fish < 13 cm in length) the otolith was positioned horizontally on a standard microscope slide and permanently embedded in an epoxy (EPO TEK 301) resin. Once the resin had cured (6 h at 60°C) the otolith was sanded (using 1200 grade carborundum paper) to reach its core. Frequent checks were made under a compound microscope at 1000 × magnification to determine proximity to the core. Once the cut surface was within 25 µm of the core (determined using the mm scale on the fine focus adjustment) the otolith was polished by hand in an aluminium oxide slurry (Diamond Edge) then rinsed in distilled water. For large otoliths (removed from fish > 13 cm in length), it was necessary to first embed the otolith in a thermoplastic resin ('Crystalbond') and then sand and polish one side to remove some of the lateral otolith 'bulk'. The bulk prevented light from penetrating the otolith to reveal the core, thus it was necessary to sand both sides to avoid unknowingly sanding through the core. Once some of the bulk had been removed, the resin holding the otolith was remelted and the otolith removed. Any resin still attached was cleaned off before the otolith was flipped over and set permanently in epoxy. Once set, the unsanded side was sanded back to the core and polished using the same procedure as that used for smaller otoliths.

4.5 OTOLITH ANALYSIS AND INTERPRETATION

The Sr distributions in the otolith sections were examined by micro-PIXE (particle induced X-ray emission) using the nuclear micro-probe system at Geological and Nuclear Sciences, Rafter Laboratory, Wellington. Two line scans of each otolith were performed with the ion beam hitting the samples perpendicularly (for more detailed information see Markwitz et al. 2000). The line scan containing the most data points was selected for analysis. The results of the line scans for each otolith are expressed as a single line graph with each point on the graph representing the Sr:Ca ratio detected at that point in the otolith. Thus, connecting all the points together provides an Sr:Ca ratio 'profile' across the otolith. Sr:Ca ratios are presented in Figs 4–7 as molar ratios × 1000.

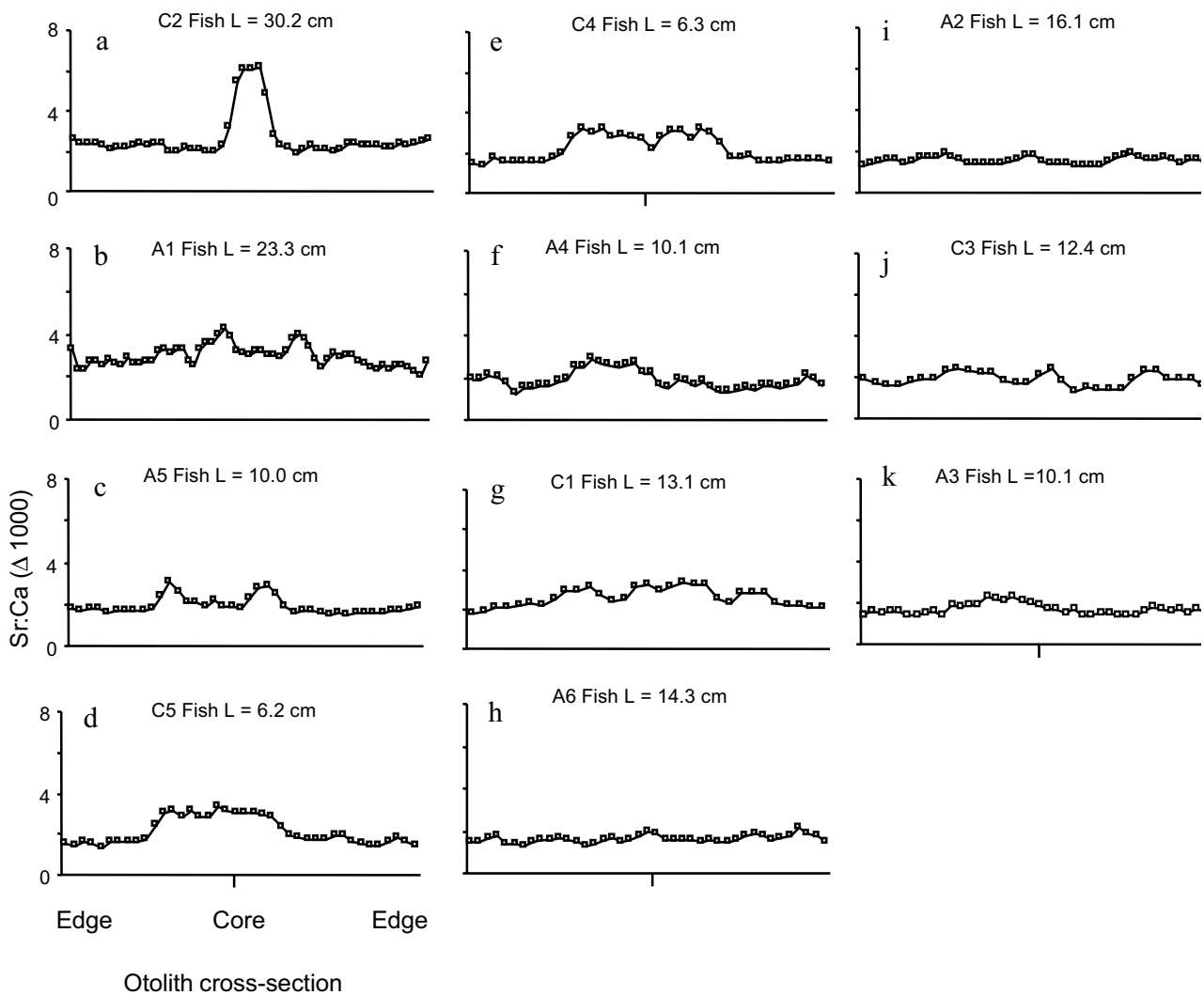


Figure 4. Profiles of otolith molar Sr:Ca ratios $\times 1000$ as defined by the edge (E) core (C) edge (E) cross-sectional line scans for fish collected from Alex's (e.g. A1) and Cullen's (e.g. C1) Creeks (lower Taieri / Waipori River catchment). Lengths indicate total length of each fish.

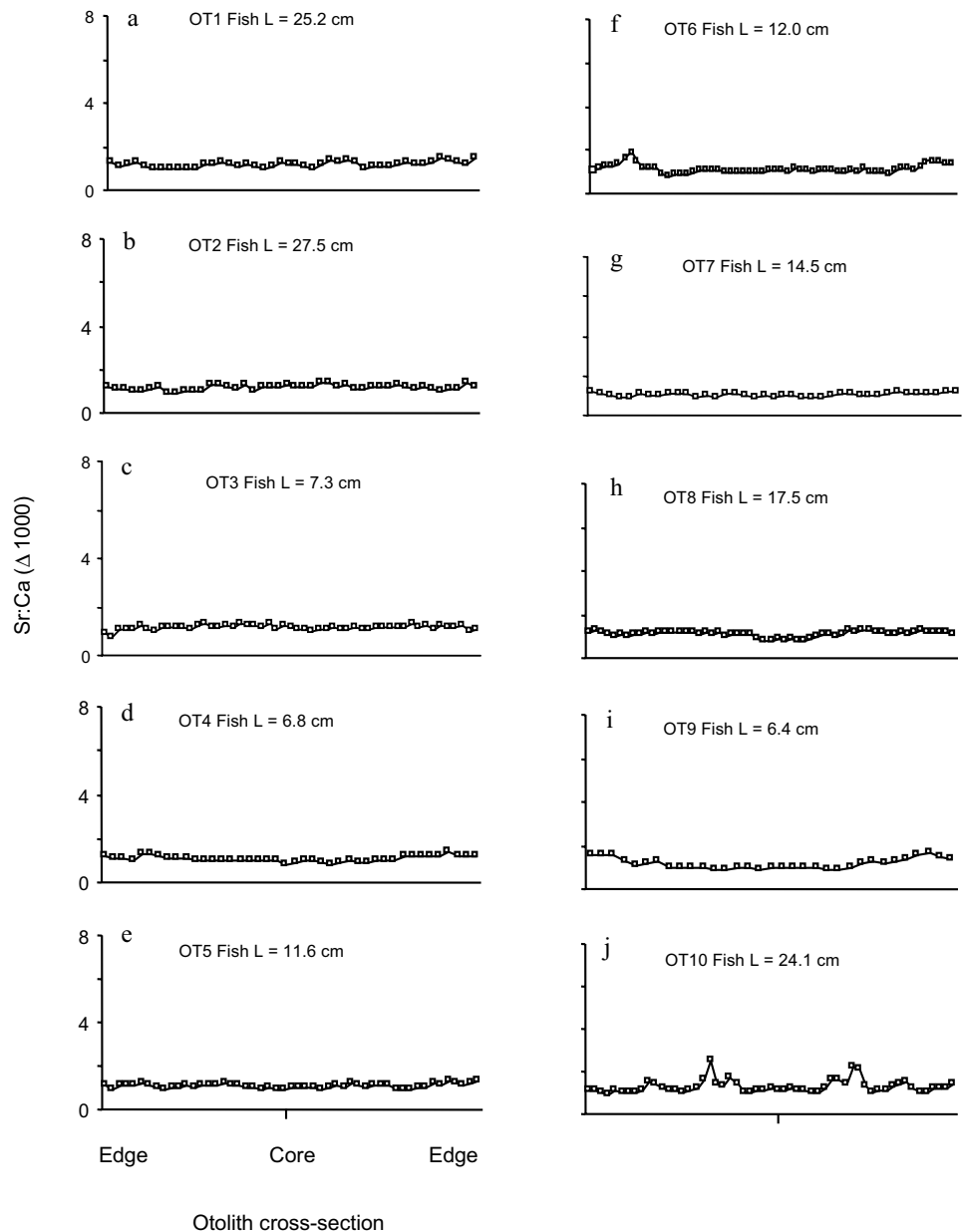
5. Results

Profiles of Sr:Ca ratios fell into three distinct groups:

- High Sr:Ca ratio at the otolith core and a lower ratio either side of the core to the edge suggesting recruitment from a marine environment (e.g. Fig. 4a).
- Relatively low and constant Sr:Ca ratio from one edge of the otolith to the other (e.g. Fig. 5a), suggesting recruitment from a freshwater environment.
- Sr:Ca ratios intermediate between the highest values observed in groups one and two at varying points from otolith core to edge (e.g. Fig. 6a), suggesting recruitment from a brackish or estuarine environment.

Giant kokopu sampled from Cullen's and Alex Creeks ($n = 11$) in the Taieri / Waipori River catchment ranged in length from 6.2 to 30.2 cm (Table 1) and thus represent multiple recruitment years. One otolith (C2) exhibited clear evidence of marine recruitment with a core Sr:Ca ratio of around seven (Sr:Ca $\times 1000$) (Fig. 4a). This core ratio was distinctly higher than core or edge Sr:Ca

Figure 5. Profiles of otolith molar Sr:Ca ratios $\times 1000$ as defined by the edge (E) core (C) edge (E) cross-sectional line scans for fish collected from Ota Creek (e.g. OT1) in the lower Maitaura River catchment. Lengths indicate total length of each fish.

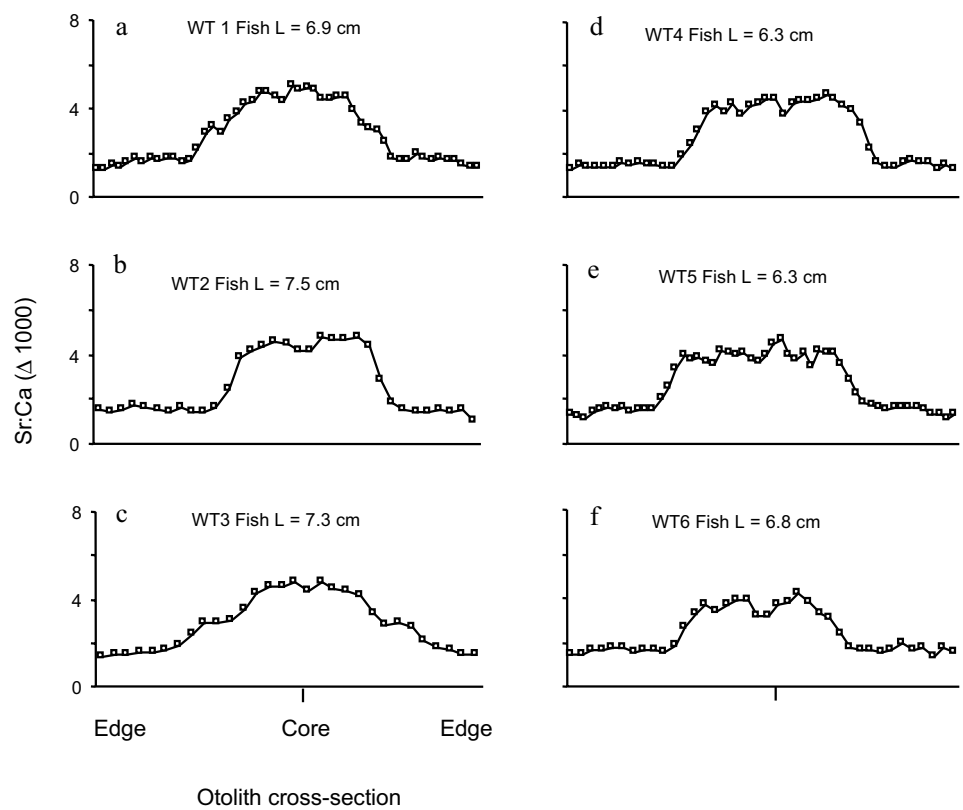


ratios exhibited by any other fish sampled from these streams (Fig. 4a-k). Three individuals had low and relatively stable Sr:Ca ratios from one edge of the otolith to the other suggesting no evidence of marine recruitment (Fig. 4h-k), whereas the remaining individuals exhibited Sr:Ca ratios that were intermediate at the otolith core (Fig. 4b-g) suggesting possible estuarine recruitment.

Giant kokopu sampled from Ota Creek (lower Maitaura) ranged in length from 6.4 to 27.5 cm ($n = 10$, Table 1), again representing fish that had recruited in different years. All otoliths examined from this population exhibited consistently low Sr:Ca profiles, indicating that they had not been to sea (Fig. 5a-j).

Giant kokopu collected from Waituna Creek were all juveniles ranging between 6.3 and 7.5 cm in length ($n = 6$, Table 1), and probably represented a single year class of recruitment. The Sr:Ca ratios and otolith profiles were virtually identical for all fish and were characterised by an intermediate core Sr:Ca ratio $\times 1000$ of 4.5-5.5 with a lower ratio (Sr:Ca $\times 1000 < 2$) on either side of the core (Fig. 6a-f).

Figure 6. Profiles of otolith molar Sr:Ca ratios $\times 1000$ as defined by the edge (E) core (C) edge (E) cross-sectional line scans for fish collected from Waituna Creek (e.g. WT1). Lengths indicate total length of each fish.



Giant kokopu collected from the land-locked population at the Waikaia ponds ($n = 3$) ranged in length from 7.5 to 12.5 cm (Table 1). Otoliths from these fish exhibited low and consistent Sr:Ca ratios across each otolith, indicating entirely freshwater life-cycles (Fig. 7a-c). Sr:Ca ratios and otolith profiles for these fish correspond closely to those of the Ota Creek fish (Fig. 5a-j) and for fish A6, A2 and A3 (Fig. 4h-j) from the lower Taieri / Waipori system.

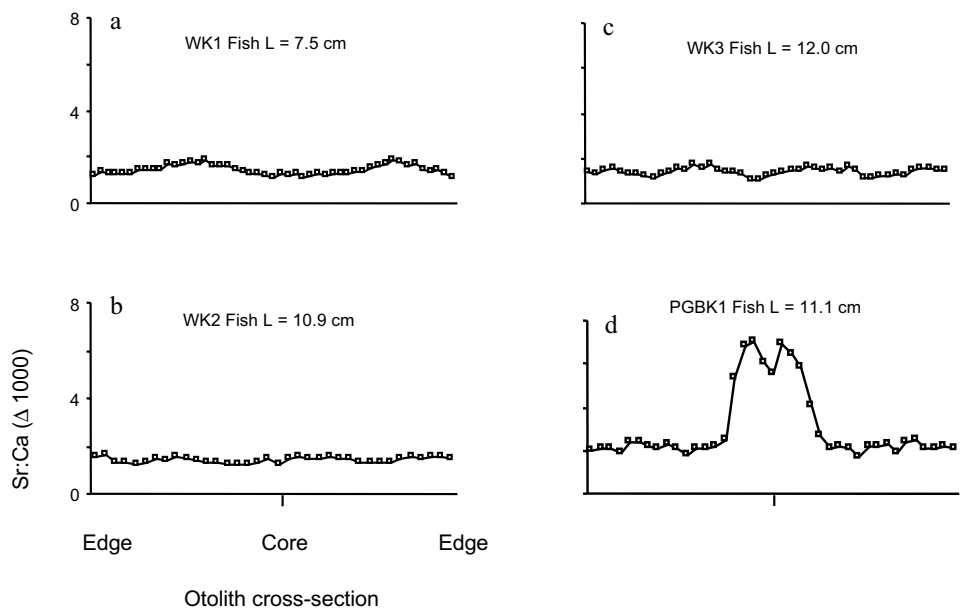
The banded kokopu from Picnic-Gully creek (which enters the sea near the Taieri River mouth) exhibited clear evidence of having been to sea with a Sr:Ca ratio of 7-8 (Fig. 7d). This distinctly higher value and otolith profile is comparable to that exhibited by the giant kokopu sample C2 (Fig. 4a) from Cullen's Creek.

6. Discussion

Our data suggest that freshwater or estuarine recruitment plays a significant role in the maintenance of giant kokopu populations in the southeast of the South Island. In the sampled populations, recruitment of giant kokopu appears to be more dependant upon larvae recruiting from freshwater or estuarine habitats located within the catchment in which they were spawned, rather than from the sea.

Of the 30 giant kokopu otoliths examined, 29 exhibited low or intermediate Sr:Ca otolith profiles. Such ratios suggest that none of these 29 fish spent any significant time in a marine environment at any stage during their lifecycle. This

Figure 7. Profiles of otolith molar Sr:Ca ratios $\times 1000$ as defined by the edge (E) core (C) edge (E) cross-sectional line scans for giant kokopu collected from the landlocked Waikaia ponds (e.g. WK1) and for the banded kokopu (PGBK1) collected from Picnic-Gully Creek at Taieri mouth. Lengths indicate total length of each fish.



is despite most individuals (excluding the three collected from the landlocked Waikaia Ponds and potentially the six from Waituna lagoon) having unimpeded access to and from the sea. Only two fish sampled in this study (the banded kokopu, PGBK1, and a giant kokopu, C2 from the Taieri / Waihola system) exhibited high Sr:Ca ratios that suggest recruitment from the sea.

A number of fish exhibited intermediate Sr:Ca ratios in their otolith cores (neither high or low), including some from the Lower Taieri / Waihola area and all fish collected from Waituna Creek. The profiles and intermediate Sr:Ca ratios observed in the otoliths from these fish (relative to the core values observed for PGBK1 and C2) suggest that they have recruited from the estuarine environments of Lake Waihola and Waituna Lagoon (into which Waituna Creek drains) rather than directly from the sea. Salinities within Lake Waihola are variable (Schallenberg & Burns in press), and the variation observed across all fish may reflect the variations in salinities experienced by fish from different recruitment events. The otolith profiles for Waituna Creek fish (all young of the year juveniles) were particularly consistent, suggesting that all the fish experienced similar rearing conditions. At the time of sampling, Waituna lagoon was closed to fish passage, although it had been open prior to sampling (R. Thompson pers. comm.), and salinities in the lagoon remain slightly elevated (relative to freshwater) even during periods of closure (Thompson & Ryder 2003).

The results of otolith analysis of all fish collected from Ota Creek indicate recruitment from an entirely freshwater environment, and that this has occurred across multiple year classes. Ota Creek is a small creek that flows into the lower reaches of the Mataura River where it meanders across the Southland floodplain. There are no lentic water bodies between Ota creek and the Mataura Estuary, suggesting that Ota Creek fish may have entrained and recruited from riverine habitats. However, lentic recruitment cannot be discounted, as there are many small water bodies in the lower flood plain that contain giant kokopu, and the Ota Creek fish could represent spillover from these habitats.

The results of this study suggest that river catchment morphology and, in particular, the presence of lentic or slow-flowing habitats in the lower reaches of rivers may promote freshwater rather than diadromous recruitment.

Furthermore, these results provide the first evidence that some giant kokopu can maintain non-diadromous life-cycles alongside others with diadromous life-cycles, even where access to the sea is continuously available. Similar findings have been reported for a variety of other diadromous species including barramundi *Lates calcarifer* in Australia (Pender & Griffin 1996), striped bass *Morone saxatilis* in North America (Secor et al. 2001), and common bully *Gobiomorphus cotidianus* and common smelt *Retropinna retropinna* in New Zealand (Northcote et al. 1992; Closs et al. in press). These studies provide increasing evidence that diadromy may be more facultative than obligatory for some species. It seems probable that New Zealand's five diadromous galaxiids represent a gradient from obligate diadromy (shortjaw kokopu) to fully facultative species which will readily recruit within freshwater environments (koaro). Our understanding of why populations sometimes abandon diadromy and the frequency of abandonment is not yet clear. However, the ability for species like koaro to readily form land-locked populations may help explain the radiation and multiple speciation events that have arisen in the *Galaxias brevipinnis* group in New Zealand (Waters & Wallis 2001).

Whilst diadromous recruitment may represent a relatively risky life-history strategy, it is likely to play an important role in the maintenance of giant kokopu populations across large spatial scales. Diadromy provides a mechanism for colonising new stream systems, thus facilitating species dispersal and gene flow between catchments. Annual recruitment of one or two diadromous fish to a population would be sufficient to maintain gene flow (J. Waters pers. comm.).

Our study and these other recent studies indicate that there is a need to re-examine the degree of diadromy among the other large diadromous galaxiids, the Eleotridae (bullies) and other diadromous species in New Zealand. There are significant management implications if non-diadromous recruitment is more frequent and widespread than currently perceived.

7. Management implications

The large galaxiid recovery plan being prepared at present sets the objective to prevent major range contractions or the extinction of genetically distinct local populations. It identifies core populations for protection and monitoring on the basis of current abundance estimates (R. Allibone pers. comm.). Our results indicate that lowland lakes, rivers and estuaries are likely to be important for giant kokopu larval development and growth. Therefore, protection efforts should focus on fish populations that are centred on such systems, including their flood plains, particularly where rivers are still connected to lentic water bodies.

Habitat modification and degradation have led to a significant reduction in the quality and extent of lowland riverine habitats. River straightening, channelisation and constriction of water courses (levees) and snag removal are likely to impact negatively on native fish recruitment by creating conditions that are less likely to favour local larval retention within lowland rivers. Such changes alter stream hydrology to produce higher mean water velocities, higher discharge,

reduced habitat heterogeneity (loss of low-flow areas) and reduced connectivity to floodplain lentic habitats. The persistence of many species within a catchment, irrespective of whether recruitment is local or diadromous, may be reliant on fish having access to such areas for larval development and growth. If this is the case, then protecting and enhancing giant kokopu populations is likely to require the maintenance and restoration of floodplain connectivity.

These results highlight the fact that for our restoration efforts to be successful, we must understand giant kokopu recruitment dynamics. The regional extent of diadromous v. non-diadromous recruitment has implications for projects aiming to re-establish giant kokopu populations. Attempts to do so by simply restoring adult habitat may fail if diadromous recruitment either does not occur or is rare. In regions where diadromous recruitment is rare, translocation of fish may be required to establish populations of adult fish. Further, the sustainability of such populations requires successful long-term recruitment. Consequently, consideration of the recruitment mechanisms likely to operate in areas selected for restoration of giant kokopu is important. If diadromous recruitment is rare, or non-diadromous recruitment is unlikely to be successful, habitat restoration alone will probably fail to establish sustainable populations in the long term.

Finally, whether it is appropriate to treat giant kokopu as a single connected national population needs to be examined. If diadromy is limited in some regions, then disjunct populations may be isolated from gene flow and hence genetically distinct. Populations along the northeast coast of the North Island and the Bay of Plenty appear to be isolated by distance and oceanic currents, both of which are likely to create barriers to dispersal (Schnabel et al. 2000)

8. Research recommendations

Further research is required to improve our understanding of the role and importance of diadromous and non-diadromous recruitment in New Zealand native fish. Future research objectives should include:

1. Determination of patterns and importance of diadromous and non-diadromous recruitment for native fish species in relation to regional abundance, river catchment morphology, and oceanic currents.

The apparent lack of diadromous recruitment seen in this study may not be indicative of recruitment patterns in other populations around New Zealand. Where giant kokopu are more abundant and widespread (e.g. Stewart Island, Westland) diadromous recruitment may be more significant. Such areas differ from those on the east coast of the country in that wetland drainage and land development have been relatively minor. In effect, core populations of giant kokopu tend to be in closer proximity along the coast of Stewart Island and Westland (Chadderton 1990; Bonnett et al. 2000) and thus the potential for larval spillover from these populations to nearby streams and catchments should be greater. Studies of population strongholds in Westland and on Stewart Island where recruitment patterns are unlikely to be influenced by habitat degradation are therefore a priority.

The presence of prevailing onshore winds and longshore currents would be expected to facilitate diadromous recruitment. Equally, enclosed coastal water bodies, inlets and large embayments may also facilitate diadromy, where larvae are entrapped by internal currents / gyres. Hence, we would expect higher levels of diadromous recruitment in streams on the west coasts of the North and South Islands, and those entering Hawkes Bay, Marlborough Sounds and Paterson Inlet, Stewart Island. Populations from areas with a range of coastal current and wind pattern regimes need to be sampled so that the role of larger-scale oceanic influences and coastal geomorphology on larval recruitment can be assessed.

2. Larval physiology and recruitment requirements

We know little about the physiological tolerances, behaviour and swimming capabilities of larval fish in New Zealand. Examining the swimming capabilities and behavior of larvae under a variety of flow conditions would assist in interpreting and understanding patterns of recruitment across a variety of freshwater geomorphologies, and potentially identify limitations for larval entrainment. Simple physiological and animal health trials may also elucidate general tolerance to varying saline and freshwater environments.

3. Determination of the relationships between recruitment dynamics and population structure

Size structure and fish abundance in populations may provide information on recruitment dynamics. For instance, a riverine population comprising primarily medium to large size classes of giant kokopu may indicate poor recruitment in recent years (irrespective of whether larval recruitment is diadromous or non-diadromous), particularly if suitable juvenile habitat is available and unoccupied. The lack of small fish may indicate that conditions required to facilitate diadromous or non-diadromous recruitment are (or have become) unsuitable. Giant kokopu population structure in Mill Stream in the lower Taieri Floodplain, Otago was indicative of recruitment limitations (David et al. 2002).

Similarly, the size structure and abundance of fish within a region may provide further indications of geomorphologies and system types that promote regular recruitment. For instance, in the lower Taieri Floodplain region, giant kokopu are widespread but really only abundant in streams entering Lake Waihola. Populations in these streams are large (all size classes present) and the abundance of small fish indicates high recruitment (for more information see David et al. 2002). Whether the high densities and high recruitment of giant kokopu are linked to the presence of Lake Waihola, into which these streams drain, is uncertain.

4. Determination of inter-regional genetic structure

If non-diadromous recruitment is the principal form of recruitment in some regions, there is increased potential for genetic isolation. If populations are genetically distinct, then to maintain genetic diversity, fish that are translocated for restoration should be sourced locally. A national study that looks at the genetic structure in giant kokopu is recommended.

5. Assessing the role of diadromy in other native fish species

The importance of non-diadromous larval recruitment in other New Zealand fish species which are believed to be diadromous should be re-examined in light

of these and other results (e.g. Northcote et al. 1992; Closs et al. in press). In particular, a closer examination of the three large galaxiids—shortjaw and banded kokopu, and koaro—is a conservation priority.

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