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ORIGINAL ARTICLE

The significance of past interdrainage connectivity for studies of diversity, distribution and movement of freshwater-limited taxa within a catchment

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ABSTRACT

Aim Historical connectivity between drainages may represent an underappreciated contributor to the biodiversity within a catchment. First, we tested whether an isolated population of freshwater-limited galaxiids represents a contribution by past interdrainage connectivity to this system's biodiversity, rather than reflecting intracatchment dispersal or speciation. Second, we sought to distinguish between possible geomorphic processes that could have allowed any past connectivity.

Location The Clutha and adjacent Southland region drainages on the South Island of New Zealand.

Methods We estimated the phylogeographical relationships among 466 cytochrome *b* sequences from 'roundhead' *Galaxias* populations throughout the Southland region and the Clutha drainage, using three different methods. Subsequently, possible geomorphic mechanisms of interdrainage connectivity were examined concurrently with genetic population divergence time estimates obtained by coalescent analysis.

Results All samples obtained in the lower Clutha system were genetically attributable to *G. gollumoides* and reflected at least a third, independent colonization event from Southland involving this species, rather than intradrainage dispersal or speciation by pre-existing Clutha populations. Geomorphological inferences and divergence time estimates of less than 7 ka are consistent with headwater connections across low divides between the lower Clutha and the Catlins region of Southland, rather than anastomosing of main channels during low sea stands.

Main conclusions The observation of at least three interdrainage connectivity events influencing the diversity and distribution of *G. gollumoides* lineages within the Clutha system highlights the potential significance of these processes as contributors to the magnitude and distribution of biodiversity within catchments.

Keywords

Dispersal mechanisms, fish, freshwater biodiversity, *Galaxias*, geomorphology, interdrainage connectivity, New Zealand, phylogeography.

INTRODUCTION

The diversity and distribution of freshwater-limited taxa within a catchment can be influenced most obviously via *in situ* speciation (Waters *et al.*, 2001a; Barluenga & Meyer, 2004), extinction (Bermingham & Martin, 1998), and the abilities of taxa to disperse throughout the catchment (Gomez-Uchida *et al.*, 2009; Carrea *et al.*, 2013). However, the contribution made by the colonization of novel lineages from adjacent catchments following changes in drainage geometry, or during episodic tributary connections (Craw *et al.*, 2007), is less well appreciated. Although historical connectivity of freshwater-limited taxa presently isolated by terrestrial barriers (catchment boundaries) has been increasingly reported in

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regions of varying geological histories, e.g. New Zealand (Waters *et al.*, 2001b; Burridge *et al.*, 2006, 2007, 2008a), Australia (Unmack, 2001), South Africa (Chakona *et al.*, 2013), North America (Mayden, 1988) and South America (Ruzzante *et al.*, 2011), the prevalence of such connectivity, and hence its likely contribution to present-day catchment biodiversity, is yet unknown.

Possible mechanisms for historical connectivity of freshwater-restricted lineages occupying presently isolated catchments include drainage rearrangements or dispersal across low relief drainage divides (Craw *et al.*, 2007). Changes in drainage geometry can occur during river capture events, when a section of a stream – and its resident biota – is displaced from one catchment to another (Bishop, 1995). Likewise, catchments can become physically connected and then isolated from each other in response to glacio-eustatic sea-level fluctuations (Craw *et al.*, 2007). Episodic tributary connections can also occur in low relief drainage divides, depending on sediment accumulation, erosion or inundation (Craw *et al.*, 2007), providing freshwater-restricted species with a chance to disperse. Studies combining genetically inferred relationships of freshwater-limited fish species and geomorphological observations have confirmed the influence of historical catchment connectivity on contemporary species distributions (Wallis *et al.*, 2001; Burridge *et al.*, 2006, 2007; Hughes *et al.*, 2009) and the types of mechanisms involved are related to the species' ecology (Hughes, 2007; Burridge *et al.*, 2008b).

The South Island of New Zealand holds a unique assemblage of freshwater-limited fish species, the *Galaxias vulgaris* complex, which has been particularly informative for studies of freshwater biogeography and drainage evolution (Craw *et al.*, 2007). These species exhibit strong biogeographical structure, with a major division of lineages marked by the divide between the Clutha system and the Southland region drainages (Fig. 1a) (Waters *et al.*, 2001b). In Southland rivers (e.g. Waiau, Aparima, Oreti and Mataura), *G. gollumoides* and *G.* 'southern' are widely represented (Waters *et al.*, 2001a; Burridge *et al.*, 2007). In the neighbouring Clutha River system, other members of the *G. vulgaris* complex occur, including *G. anomalus*, *G. pullus*, *G.* sp. 'D' and *G.* 'teviot' (Waters & Wallis, 2001a). However, in two tributaries of the Clutha River, localized drainage rearrangements displaced Southland lineages into the Clutha system. Specifically, the Nevis River contains a divergent lineage of *G. gollumoides*, reflecting its original orientation into Southland drainages (Waters *et al.*, 2001b). Likewise, the Von River has Southland-derived lineages of both *G. gollumoides* and *G.* 'southern' (Burridge *et al.*, 2007). Consequently, past changes in drainage connectivity have already made a contribution to species diversity and distributions within the Clutha.

During a recent survey of the lower Clutha system, we obtained samples of a 'roundhead' *Galaxias* morphotype that could potentially correspond to any one of three species: *G. gollumoides*, *G. anomalus* or *G. pullus*. Importantly, the Southland 'roundhead' *Galaxias* (*G. gollumoides*) is phylogenetically distinct from *G. anomalus* and *G. pullus*, which inhabit the Clutha system (Waters & Wallis, 2001b). The lower Clutha 'roundhead' *Galaxias* could potentially represent offshoots of lineages that occur upstream in the Clutha,

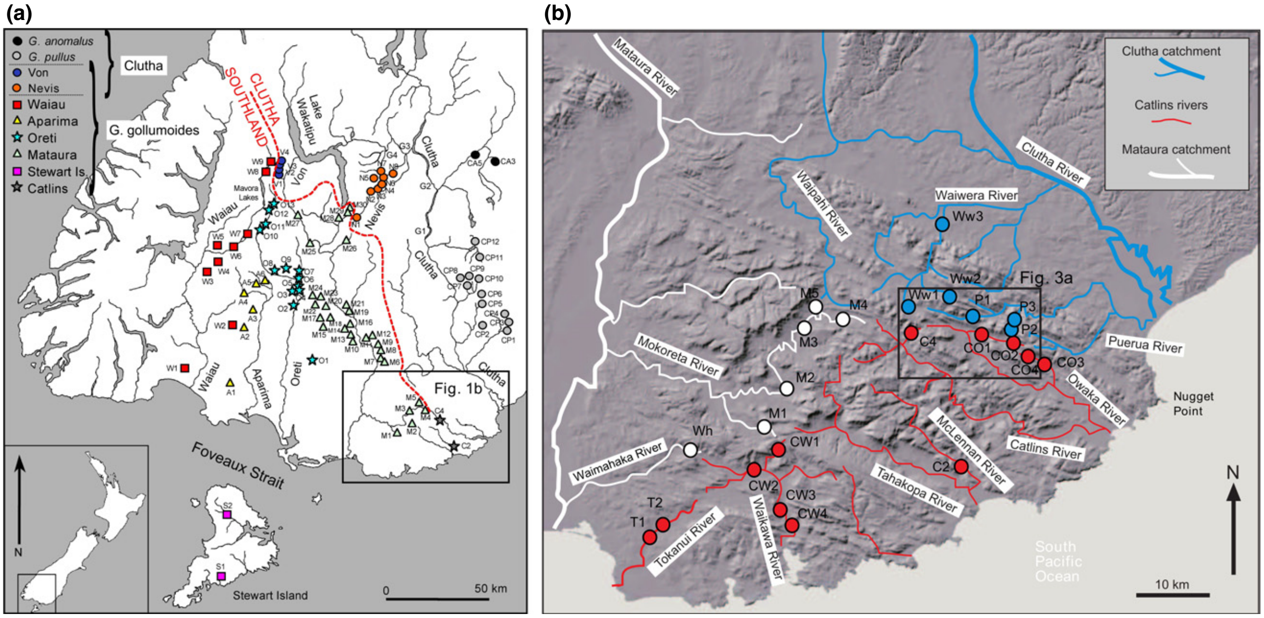

Figure 1 (a) Map of southern South Island, New Zealand, showing the regional drainage divide between the Clutha River catchment and Southland, and sampling sites from previous studies of 'roundhead' *Galaxias* incursion into the Clutha catchment in the Von River (Burridge *et al.*, 2007) and the Nevis River (Waters *et al.*, 2001b). Gorges are indicated as G1–G4. (b) Digital elevation model (from http://geographx.co.nz/) of the Catlins block, showing sampling sites on the principal groups of river catchments discussed in this study, including the *G. gollumoides* samples new to this study. The large black rectangle shows the location of Fig. 3a.

either *G. anomalus* or *G. pullus*, or the Von or Nevis river lineages of *G. gollumoides*, although the presence of lakes and gorges in the upper Clutha make such dispersal by *G. gollumoides* unlikely (Fig. 1a; Burridge *et al.*, 2007). Alternatively, the lower Clutha 'roundhead' population could be a distinct Southland-derived lineage of *G. gollumoides* that originated in adjacent catchments in the Catlins region (Fig. 1b). This would represent the third colonization of this catchment by *G. gollumoides*, and therefore indicates a greater contribution by past intercatchment connectivity on the distribution of 'roundhead' *Galaxias* lineages in the Clutha than either *in situ* speciation or intracatchment dispersal. If such is the case, the geomorphologic mechanism of past connectivity is also of interest (Bishop, 1995; Unmack, 2001; Smith & Bermingham, 2005; Burridge *et al.*, 2008b).

Any close relationship of lineages between the lower Clutha system and adjacent catchments in the Catlins region of Southland by freshwater-limited taxa could involve dispersal across low relief drainage divides, a mechanism called 'episodic tributary or swamp connections' (Craw *et al.*, 2007), or movements of drainage divides themselves by processes such as river capture and glacio-eustatic sea-level changes. The Catlins region is dominated by NW–SE trending ridges that are likely to restrict gene flow between adjacent river systems, although some breaches between them are possible due to low relief drainage divides in their headwaters (Fig. 2a) which may have allowed past connectivity. Alternatively, glacio-eustatic sea-level fluctuations could have allowed coastal connections that induced interdrainage connectivity, followed by vicariant isolation, in which case the genetic divergence between populations from presently isolated catchments should reflect the time since the last lowstand. Finally, river capture may also have been influential. Therefore, geological and topographical analysis of the potential for such connections between the lower Clutha River and adjacent rivers in the Catlins region is important to determine the processes that could have facilitated the movement of freshwater-limited taxa between what are presently isolated catchments.

In this study we examine the phylogeographical relationships among 'roundhead' *Galaxias* populations throughout Southland, the Catlins region, and the Clutha catchment, with the specific aim of identifying the origins of the 'roundhead' *Galaxias* population recently discovered from the lower Clutha River. Genetic affinities of this population with *G. pullus*, *G. anomalus* or *G. gollumoides* from either the Von or Nevis would imply movement within the Clutha system. If the newly discovered 'roundhead' population was sufficiently distinct from other lineages, *in situ* speciation may be favoured. On the contrary, a close relationship with *G. gollumoides* from the adjacent Catlins region would indicate another contribution of past interdrainage connectivity to the biodiversity of this system, involving either low relief divide-crossing, river capture, or low sea-stand connections, which can be distinguished based on a combination of both the age of lineage divergence and a geological examination of the region.

MATERIALS AND METHODS

Sample collection

'Roundhead' *Galaxias* individuals ($n = 38$) were obtained using electrofishing and pole-nets from two lower Clutha River tributaries: Puerua and Waiwera (Fig. 1b). In order to identify the potential origin of those individuals, 63 'roundhead' galaxiids were sampled in three catchments of the

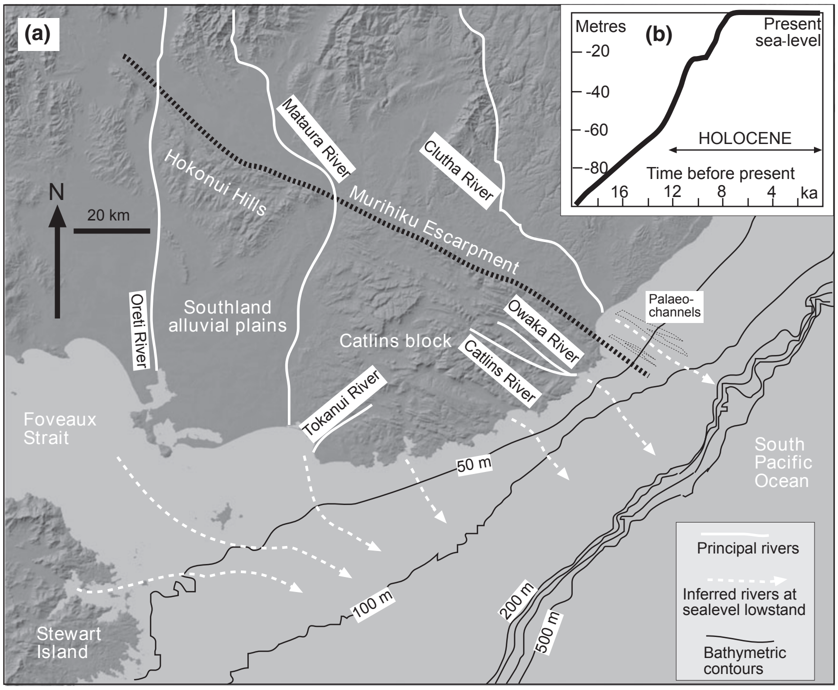

Figure 2 (a) Digital elevation model (from http://geographx.co.nz/) of the SE South Island, New Zealand, showing principal geological and topographic features of the Catlins block and adjacent areas. Clutha River palaeochannels (after Carter & Carter, 1986) and inferred river drainage directions on the shallow continental shelf during sea-level lowstands are indicated. (b) Generalized sea-level curve since the Last Glacial Maximum lowstand (after Gibb, 1986).

Catlins region (Owaka, Waikawa and Tokanui), and 45 individuals in two catchments of the Southland Region (Mokoreta and Waimahaka). In addition, 320 ‘roundhead’ galaxiid samples comprising *G. gollumoides* identified by Burridge *et al.* (2007) and Waters *et al.* (2001b) from Southland and the upper Clutha (Nevis and Von rivers), as well as *G. anomalus* and *G. pullus* from the mid Clutha (Burridge *et al.*, 2007), were included in the analyses in order to cover all possible origins (see Appendix S1 in Supporting Information for details on sites and sample sizes). In total, 466 ‘roundhead’ *Galaxias* from 102 sites in 14 different catchments were analysed (Fig. 1).

Geological framework of the study area

The Catlins block, which is the principal geological focus of this study (Fig. 2a), is a distinctive topographic feature in the south-east corner of the South Island, and forms a rugged wedge between the lower Clutha catchment and the Southland alluvial plains (Fig. 2a). The block has been uplifted along bounding faults, the most prominent of which has resulted in a steep north-east margin, the Murihiku Escarpment (Fig. 2a; Turnbull & Allibone, 2003). Uplift of the block began about 20 Ma, but many of the bounding faults are still active (Turnbull & Allibone, 2003; Stein *et al.*, 2011). The Catlins block consists of uplifted Triassic–Jurassic sandstones and shales whose prominent WNW-striking bedding features dominate the topography (Figs 1b & 3a). Sandstones are relatively resistant to erosion and form prominent ridges, whereas shales are more readily eroded and form valleys, so river drainage patterns follow the underlying geological structure, with occasional short narrow gorges cutting across sandstones and connecting longer river reaches in shales (Figs 1b & 3a).

To the west of the Catlins block, the landscape is dominated by the Southland alluvial plains, which have been formed by the Mataura and Oreti rivers, both of which have breached the Murihiku Escarpment (Fig. 2a). These rivers have migrated across the plains throughout the Quaternary, and have been variably interconnected (Craw *et al.*, 2007). Further connections between these rivers occurred during sea-level lowstands, when Foveaux Strait was an alluvial plain as well (Fig. 2a; Cullen, 1967; Craw *et al.*, 2007). The Foveaux Strait alluvial plain facilitated river connections to Stewart Island, the most recent of which were cut by a rise in sea level starting *c.* 20 ka (Fig. 2b; Gibb, 1986; Craw *et al.*, 2007). The lower Clutha River has been constrained by the Murihiku Escarpment, and currently enters the sea on its northern side (Fig. 2a).

Mitochondrial DNA sequence analysis

Genomic DNA extraction and amplification of the complete cytochrome *b* gene with primers cyt b-Glu and cyt b-Thr followed Waters & Wallis (2001a). A 768-bp segment was sequenced with cyt b-Glu and sequence alignments were performed manually. The sequence alignment can be downloaded from the Dryad database (see Data Accessibility). Phylogenetic relationships were estimated by means of three

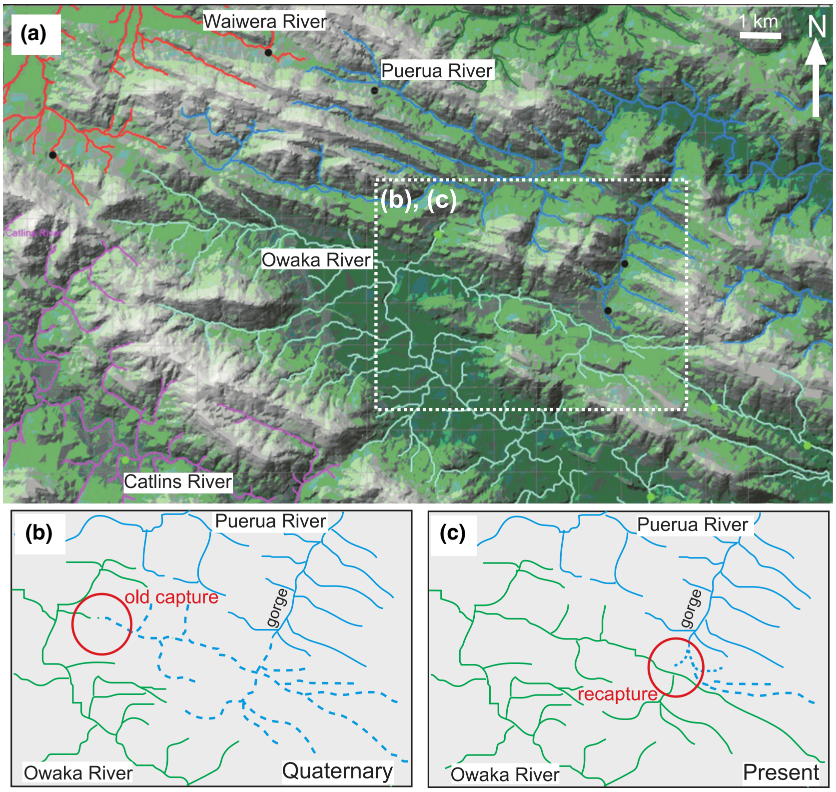

Figure 3 Stream geometry in the Catlins block near the drainage divide between Clutha catchment (Puerua and Waiwera rivers) and the Catlins–Owaka River catchment, showing the strong geological control on drainage patterns. (a) Aerial photograph of the area indicated in Fig. 1b, with principal stream tributaries overlain. (b) Geological sketch map showing inferred location of past river capture point (red circle) of Puerua tributary headwaters during the Quaternary, leaving a deep gorge underfit. Puerua tributary streams that were captured by the Owaka in this event are dashed. (c) Geological sketch map of the area at the present time. The location of ongoing erosional and projected future recapture by the Puerua tributary is indicated, with the present drainage divide in Quaternary alluvium, which may constitute an episodic wet connection between catchments. Tributaries that may have already been recaptured by the Puerua are dashed.

different methods: maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI). Analysis under the parsimony criterion was performed by PAUP* 4.0b10 (Swofford, 2003) using the heuristic search algorithm with 10 replicates of random sequence addition, to recover a maximum of 5000 equally most-parsimonious topologies. All character state transformations were equally weighted. Parsimony bootstrap analysis (Felsenstein, 1985) also employed 10 heuristic searches for each of 500 bootstrap replicates, with up to 500 equally most parsimonious topologies retained per heuristic replicate.

Our ML analysis was conducted using PhyML 3.0 (Guindon *et al.*, 2010; available at http://www.atgc-montpellier.fr/phyml). The best-fit model of nucleotide substitution was the one proposed by Tamura & Nei (1993), which was selected from 56 candidates using Modeltest 3.7 (Posada & Crandall, 1998). The starting tree topology was the majority-rule consensus obtained from MrBayes 3.2.1 (Ronquist & Huelsenbeck, 2003) analysis. Bootstrap support was based on 500 replicates.

Two types of Bayesian analyses were performed with MrBayes 3.2.1. First, data were treated as a single partition as the small number of variable characters available can hinder the parameterization of a large number of partitions. Second, data were partitioned by codon position in order to assess the potential influence of evolutionary model heterogeneity among codon partitions. For the single partition analysis a reversible jump-Markov chain Monte Carlo (RJ-MCMC) procedure was used, allowing the MCMC sampling to jump across different substitution models. A proportion of nucleotide sites were considered invariant, with a gamma-shaped distribution of rates across sites. For the partitioned analysis, each codon position was treated under a different substitution model as determined by Modeltest 3.7. The first codon position was treated under the F81 model (Felsenstein, 1981), the second codon position was treated under the K80 model (Kimura, 1980), and for the third position a RJ-MCMC procedure was used as the TrN model (Tamura & Nei, 1993) was not available.

Both analyses were performed using the MrBayes default prior probability distributions for the model parameters, and duplicate MCMC searches were conducted with four chains of 2,000,000 generations and a tree sampling frequency of 500 generations in each case. Three of the chains were heated according to 'Temp = 0.1'. The first 25% of the samples from the cold chain were discarded as 'burn-in' if the search had attained stationarity by that point. Stationarity and adequate mixing of the chains was assessed using Tracer 1.5 (Rambaut & Drummond, 2009) to establish the attainment of asymptotes for the values of ln*L* and substitution model parameters in the trace plots and ensure effective sample sizes greater than 200. Convergence was determined when the average standard deviation of split frequencies was lower than 0.005. The tree was rooted using two lineages closely related to *G. gollumoides*: *G. anomalus* (sister species) and *G. pullus* (Waters *et al.*, 2010).

Estimation of population divergence time

In order to help distinguish between possible mechanisms of interdrainage connectivity we used IMa (Hey & Nielsen, 2007) to generate posterior probabilities for population divergence time between the lower Clutha 'roundhead' population and its sister lineage. This program applies the Isolation with Migration model (Nielsen & Wakeley, 2001), which assumes selective neutrality, no recombination within a locus, no population structure and no genetic exchange with unsampled populations. Although the last two assumptions are difficult to test in natural systems, it has been found that violations to these assumptions do not to lead to significant bias in the parameter estimates for simulated data sets (Strasburg & Rieseberg, 2010). Neutrality was tested using Tajima's D (Tajima, 1989) as implemented in DnaSP 5 (Librado & Rozas, 2009). The Hasegawa–Kishino–Yano (Hasegawa *et al.*, 1985) nucleotide substitution model was applied. Preliminary runs were used to assess sufficient mixing of the chains. The absence of trends in the parameter's trendline plots, and high effective sample size (ESS) values (the lowest value of ESS among the parameters was > 1500) indicated that a burn-in of 500,000 iterations followed by a run of 2,500,000 iterations provided a large sample from the stationary distribution. Four runs were performed in order to test for the convergence of estimated parameters.

Two different approaches were implemented in order to interpret the model estimate t in terms of years. Firstly, we placed the t parameter in the chronosequence of coalescent t estimates obtained by Burridge *et al.* (2008a) for galaxiid fishes where population divergence times were constrained based on geological evidence. In order to validate this extrapolation, a linear regression analysis between the geological divergence ages and the coalescent t estimates was performed using Matlab 7.0.1 (Mathworks, Natick, MA, USA). Secondly, we converted the splitting time parameter t into units of years using $t = T \times \mu$, where T is the time since population splitting and μ the mutation rate estimated by Burridge *et al.* (2008a) for cytochrome *b* in galaxiid fishes using calibration points younger than 200 ka. Burridge *et al.* (2008a) observed a range of 0.031–0.125 changes/site/Myr. In order to obtain an estimate of time since divergence in units of ka, we used μ = 0.059 changes/768 bp/kyr.

RESULTS

Phylogeographical relationships

Partitioned Bayesian analysis revealed that mitochondrial DNA (mtDNA) sequences obtained from the 'roundhead' samples in the lower Clutha River were genetically similar to Catlins *G. gollumoides*, confirming that a third lineage of this species has colonized the Clutha system (Fig. 4). Specifically, this lineage is clearly phylogenetically distinct from other 'roundhead' lineages found in the upper Clutha system: *G. anomalus*, *G. pullus* and *G. gollumoides* lineages found in

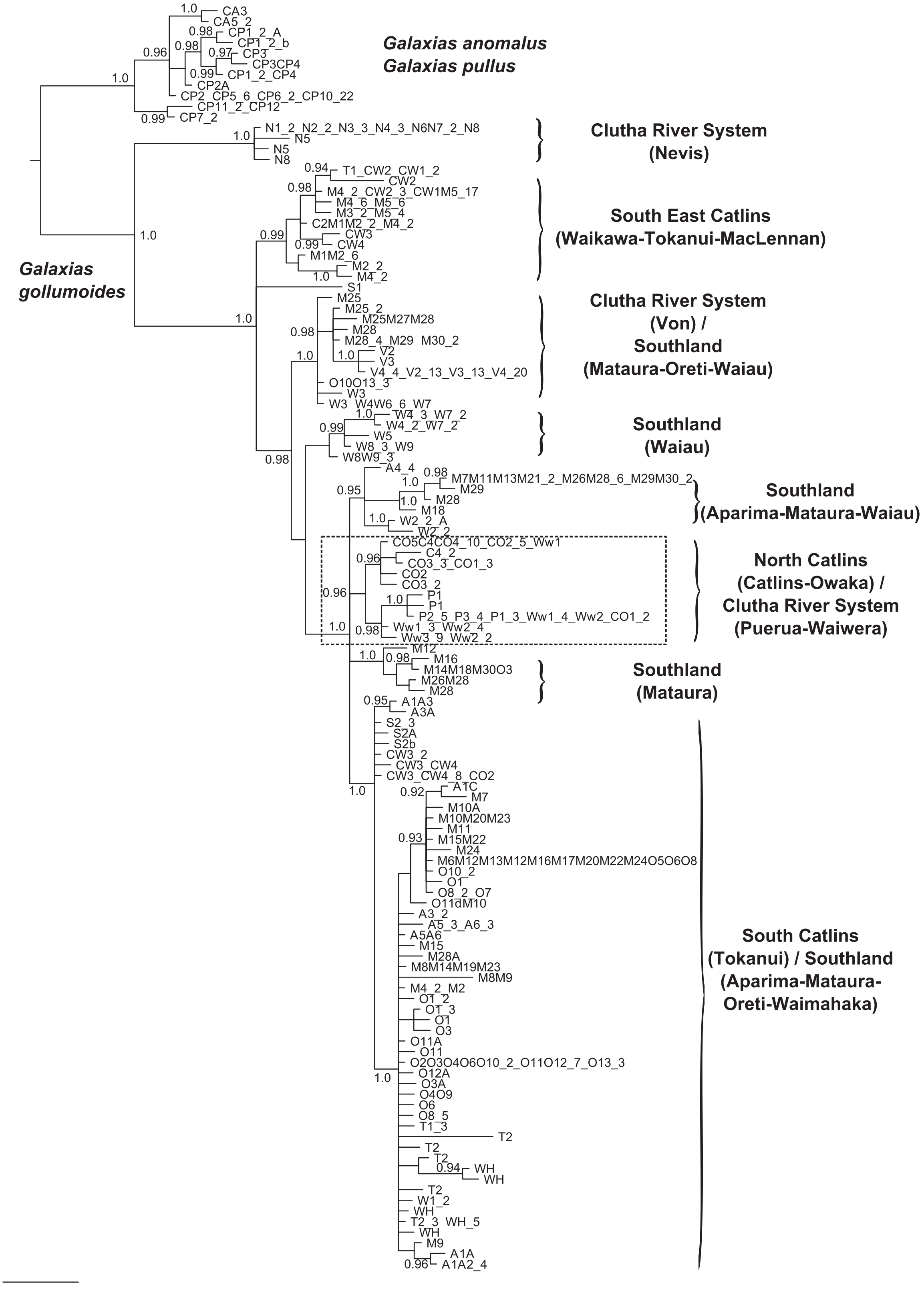

Figure 4 Bayesian inference majority-rule consensus topology derived from partitioned analysis of cytochrome *b* mitochondrial DNA sequences of 'roundhead' *Galaxias*. Values at nodes indicate posterior probabilities. The dashed box indicates the genetic affinities between *G. gollumoides* from Waiwera and Puerua, in the lower Clutha system, and *G. gollumoides* from Catlins and Owaka rivers, in the Catlins region. See Appendix S1 and Fig. 1 for collection localities codes and geographical location. Locality codes followed by an underscore indicate the number of individuals from that locality with identical sequences, when greater than one.

the Von and Nevis rivers. *Galaxias gollumoides* individuals from both the Waiwera and Puerua rivers (lower Clutha River) showed close genetic affinities with individuals from the adjacent Owaka and the Catlins rivers in the Catlins region [North Catlins clade, posterior probability (PP) = 0.96, Fig. 4]. The topologies obtained from maximum parsimony, maximum likelihood and non-partitioned Bayesian analyses were consistent with the partitioned Bayesian analysis topology (not shown), with identical geographical structuring of intraspecific genetic variation with respect to the major clades. Bayesian inferences, by treating data as a single partition or partitioned by codon positions, resulted in identical topologies. However, we chose to show the results from the partitioned analysis as node support was slightly higher. The number of variable sites (VS) and parsimony informative variable sites (PIVS) by codon position were VS = 15 and PIVS = 12 (position 1), VS = 27 and PIVS = 7 (position 2), and VS = 101 and PIVS = 23 (position 3).

Geological inferences

The geological controls on topography of the Catlins block has resulted in a set of SE-draining river catchments that do not flow into either the Clutha or the Southland (Mataura) rivers, but currently discharge directly into the sea (Fig. 1b). These WNW-trending valleys, controlled by the underlying geology, presumably continued beyond the present coastline during sea-level lowstands on to the continental shelf (Fig. 2a). A sediment-filled Quaternary channel, up to 30 m deep and 1 km wide, trends south-east from the Clutha River mouth across the shelf towards prominent canyons in the shelf edge, and this is the probable path of the Clutha River during sea-level lowstands (Fig. 2a; Price *et al.*, 1982; Carter & Carter, 1986). Offshore-trending remnants of the Murihiku Escarpment at Nugget Point (Fig. 2) apparently formed a southern edge to the offshore Quaternary Clutha River channel (Price *et al.*, 1982; Carter & Carter, 1986), and therefore separated the Owaka–Catlins river catchment and other adjacent Catlins rivers from the Clutha River on the shelf during the Holocene (at least for the past *c.* 10 kyr; Fig. 2).

Any freshwater connections between river catchments on the shallow shelf ceased more than 8000 years ago, as sea level rose towards present levels (Fig. 2b). Subsequent wet connections between catchments must have involved inland drainage divides (Craw *et al.*, 2007). In the Catlins block, the most widespread wet connections are of two types: river capture with associated episodic wet connections (e.g. Fig. 3b,c), and continuous wet connections via swamps or lakes on topographic divides (e.g. Fig. 5). The complex drainage patterns of the Catlins block suggest that river capture was widespread throughout the topographic evolution of the block. However, uplift and erosion rates are low, and the area was not glaciated during the Pleistocene, so most capture events occurred prior to the Holocene, or even the Pleistocene. The relatively low rates of erosion support long-term low relief areas on topographic divides in which variably swampy terrain facilitates continuous and interconnected streams and pools that drain into both catchments simultaneously (Fig. 5; Craw *et al.*, 2007).

Examples of two inter-related river capture events at a divide between the Clutha catchment (Puerua River) and the Owaka–Catlins catchment are depicted in Fig. 3. Pre-Holocene capture of extensive headwaters of a tributary of the Puerua River by the Owaka River (Fig. 3b) is indicated by the now underfit Puerua tributary remnants in a deep gorge. Capture was apparently facilitated by build-up of a pile of Quaternary alluvium immediately upstream of the Puerua gorge (Fig. 3b,c). Recent headwater erosion by the Puerua tributary into this alluvium pile has nearly connected with the previously captured Owaka tributary, and recapture by the Puerua tributary is possible in the near future (Fig. 3c).

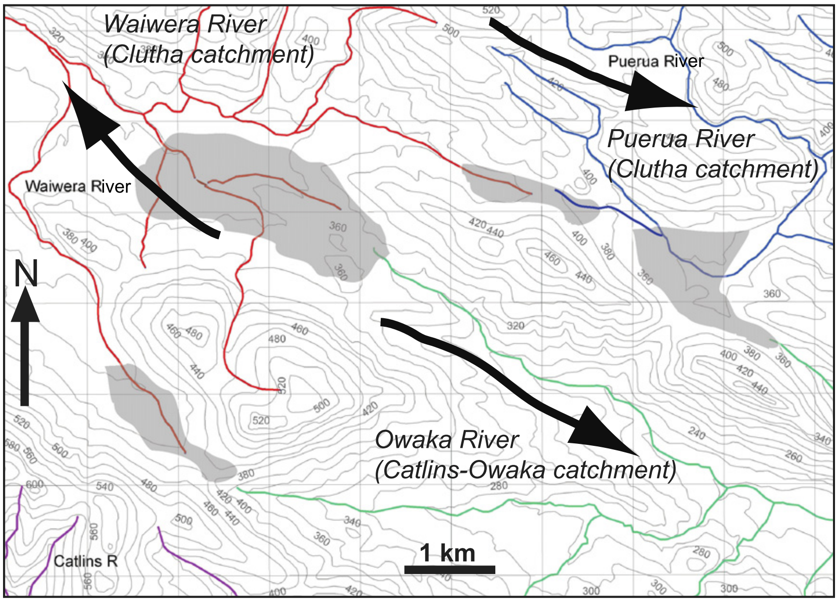

Figure 5 Examples of low relief topographic divides between river catchments. Variably swampy areas at divides between the Clutha catchment and the rivers of the Catlins region that may constitute continuous wet connections are indicated in grey.

Some recapture of small streams draining into the Puerua tributary may have occurred already (dashed blue lines, Fig. 3c). The present drainage divide at this point is only *c.* 100 m wide on a flat alluvial terrace, and simultaneous surface water discharge down both sides of this divide is highly probable during large rain events.

Estimation of population divergence times

The neutrality hypothesis could not be rejected (Tajima's $D = -1.05$, $P > 0.1$). Preliminary IMa runs indicated that the genetic data set did not contain enough information to identify all parameters in the full Isolation with Migration model; therefore a simpler model (excluding post divergence migration rates) was run. Marginal posterior distributions for θ_1, θ_2, θ_A and population divergence time (t) are shown in Appendix S2. Replicates across four independent MCMC runs resulted in nearly identical posterior distributions, suggesting convergence on the stationary distribution given the model, and appeared insensitive to reasonable variation in priors. The estimated divergence time between *G. gollumoides* from the lower Clutha system (Puerua and Waiwera) and those in the Owaka and Catlins corresponded to $t = 0.275$ (0.07–0.725) [mode and 90% highest posterior density (HPD)].

The correlation between independent estimations of divergence time, geological and coalescent (Table 1) obtained from Burridge *et al.* (2008a), was significant ($R^2 = 0.91$, $P < 0.01$), indicating that an extrapolation of the geological age of isolation for the present t parameter is possible. When placed in the chronosequence of t parameters obtained for nine galaxiid population divergence events (Burridge *et al.*, 2008a) with geologically constrained ages of population divergence (Table 1), the divergence time estimate obtained in the present study indicates a relatively recent population split (< 7 ka). Congruently, the conversion of the t parameter into ka, by $t = T \times \mu$, resulted in a population divergence time of 4.7 ka. Previous to the Puerua–Waiwera colonization, two independent *G. gollumoides* colonization events of the Clutha River system from Southland are shown in Table 1: the Von River (12 ka) and the Nevis River (300–500 ka).

DISCUSSION

The present study indicates that 'roundhead' *Galaxias* in the lower Clutha system reflect a third colonization of this catchment by *G. gollumoides* from adjacent catchments in the Southland region, rather than (1) *in situ* speciation or (2) movement through or reliction within the Clutha system by pre-existing Clutha 'roundhead' *Galaxias*. Furthermore, the presence of *G. gollumoides* in both the Puerua and Waiwera (lower Clutha tributaries), but its apparent absence in the intervening streams, including the Clutha main channel (NZ Freshwater Fish Database, http://www.niwa.co.nz/), suggests the possibility that these tributaries were colonized independently from adjacent Southland catchments. Therefore, there may have been as many as four colonizations of the Clutha by *G. gollumoides* in total. Alternatively, one of the Clutha tributaries could have acted as an intermediary (e.g. Owaka to Puerua, then Puerua to Waiwera). It is also possible that these populations were previously more widespread and connected through streams or the Clutha main channel, but the species has now been excluded by introduced salmonids (e.g. *Salmo trutta* and *Oncorhynchus mykiss*) that are present in high densities in the Clutha River (Teirney & Jowett, 1990). These introduced species are aggressive competitors (McIntosh *et al.*, 1992) and voracious predators of galaxiid fishes (Townsend, 2003). Regardless of whether there were three or four colonization events by *G. gollumoides*, our findings indicate that past interdrainage connectivity had a greater impact on the diversity and distribution of

Table 1 Chronosequence of population divergence time parameters (t) derived from coalescent analysis under the 'Isolation with Migration' framework for geologically dated galaxiid divergence events (from Burridge *et al.*, 2008b). That for the lower Clutha–Owaka/Catlins river population divergence (this study, bold), is smaller than that observed for any of the geologically dated divergence events.

Event (location and mechanism)	Species	Geological age of isolation (ka)	Population split (t), mode and 90% HPD
Lower Clutha–Owaka/Catlins divergence	***G. gollumoides***	**?**	**0.28 (0.07–0.73)**
Pelorus–Kaituna, valley drowning	*G. divergens*	7	0.63 (0.16–2.04)
Von–Oreti, river capture	*G.* 'southern'	12	0.67 (0.27–1.57)
	G. gollumoides	12	1.11 (0.67–1.75)
Lochy–Matuara, river capture	*G. paucispondylus*	<20	1.19 (0.31–5.57)
Clarence-Wairau, river capture	*G.* 'northern'	10–20	1.17 (0.86–5.16)
	G. divergens	10–20	2.96 (1.43–5.84)
	G. paucispondylus	10–20	0.96 (0.29–2.01)
Kaituna–Wairau, river reversal	*G. divergens*	70–130	8.53 (4.23–13.23)
Mararoa–Oreti, river capture	*G. paucispondylus*	140–240	6.03 (1.01–8.81)
	G. 'southern'	140–240	8.13 (4.35–21.39)
Nevis–Matuara, river reversal	*G. gollumoides*	300–500	17.37 (4.97–24.67)
Chatham Is, island formation	*Neochanna rekohua*	<1000	44.15 (13.49–52.95)
Southern Alps, mountain uplift	*G. divergens*	2000–5000	73.72 (5.77–86.62)

HPD, highest posterior density.

'roundhead' *Galaxias* lineages in the Clutha than intracatchment speciation or dispersal.

Significant inroads into the understanding of biodiversity-generating processes in freshwaters are required given that projected biodiversity loss is high in these systems (Jenkins, 2003), and these require both a consideration of deterministic (e.g. biotic and abiotic conditions), neutral and historical factors, with study into the latter increasingly advocated (Wiens & Donoghue, 2004; Cavender-Bares *et al.*, 2009; Vamosi *et al.*, 2009). For example, while Muneepeerakul *et al.* (2008) observed a good fit of neutral model predictions to the spatial distribution of fish diversity within the Mississippi–Missouri basin, the higher diversity observed in the east almost certainly contains a historical contribution from lineages that colonized the basin by crossing the Appalachian Drainage Divide (Mayden, 1988). Ignorance of interdrainage movement in studies of ecology and evolution of freshwater taxa is surprising, given that the geological processes which facilitate such movement have long been recognized (Darwin, 1872; Banarescu, 1990), and provide not only a mechanism through which existing species can be added to a catchment, but also initiate allopatric distributions between catchments, potentially leading to speciation (Burridge *et al.*, 2006, 2008b). Indeed, in many instances local biodiversity may increase more rapidly through movement than speciation (Donoghue, 2008; Cavender-Bares *et al.*, 2009).

Another important implication of our observation of multiple colonizations of the Clutha by *G. gollumoides* is the possibility that other studies may overestimate the dispersal capabilities of taxa within catchments based on contemporary distributions alone, and underestimate the influence of features such as lakes, gorges and waterfalls, if interdrainage connectivity events have occurred but are unrecognized. Studies of intracatchment movement by freshwater biota therefore also need to control for this possibility by sampling lineages from adjacent catchments (e.g. Taylor *et al.*, 2003; Poissant *et al.*, 2005). Indeed, in some instances it appears easier to move between catchments than within them, as has been the case for *G. gollumoides* in the Clutha. The hydrological characteristics of the Clutha main channel (e.g. depth, water velocity, substrate size) represent habitat better suited for introduced *Salmo trutta* and *Oncorhynchus mykiss* (Jowett & Davey, 2011) than for a swamp-dwelling species such as *G. gollumoides*. Thus, it seems likely that the combination of high predation risk by introduced salmonids and the lack of suitable habitat restricts the dispersal capabilities of *G. gollumoides* within the catchment.

A potential limitation regarding the analysis of the present study should be noted. The accuracy of mtDNA gene trees can be compromised by various mechanisms, including introgressive hybridization or incomplete lineage sorting (Bossu & Near, 2009). Regardless, introgression between invading *G. gollumoides* and resident Clutha taxa would not alter the inference that the former lineage has recently invaded the lower Clutha from the Catlins. Incomplete lineage sorting seems an unlikely explanation for the *G. gollumoides* lineage in the lower Clutha, as there appears to be complete correspondence of the morphotype with the gene tree throughout its Southland range.

Estimates of the timing of past intercatchment connectivity (and severance thereof), along with geological observations from the region, enable the range of candidate mechanisms for this connectivity to be assessed. The divergence time estimate obtained between the lower Clutha *G. gollumoides* population and its sister lineage in the Owaka and Catlins rivers (< 7 ka; Table 1) appears too recent to be explained by glacio-eustatic sea-level fluctuations given the chronology of these fluctuations (Fig. 2b). Likewise, the inferred drainage routes for these rivers on the shallow continental shelf during sea-level lowstands appear incompatible with past connectivity (Fig. 2a). Similarly, evidence for past connectivity via river capture between these systems, involving the capture of a tributary of the Puerua River by the Owaka (Fig. 3b), is likely to pre-date the age of the population connectivity, and would favour intercatchment movements in the opposite direction (Puerua into Owaka) than inferred. On the other hand, observed evidence of a continuing recapture process (Fig. 3c) suggests that the recent recapture of a few Owaka tributaries by the Puerua (dashed blue lines, Fig. 3c) could have allowed intercatchment movement in the inferred direction.

In comparison to the processes suggested above, the geological and genetic evidence presented in this study indicates that the interdrainage connectivity of *G. gollumoides* in the lower Clutha is likely to have occurred via low drainage divide crossing (Figs 3a & 4). The Waiwera, Puerua, Owaka and Catlins rivers are separated by low divides with eroded breaches and variably swampy areas in their headwaters (Fig. 5) that may have allowed for the multiple *G. gollumoides* colonization events suggested by the observed phylogeographical relationships and distribution of the lower Clutha populations. This form of dispersal has been previously inferred for *G. gollumoides* in a system of two adjacent rivers in western Southland, the Mararoa and Oreti rivers (Burridge *et al.*, 2008b). *Galaxias gollumoides* populations in the Mararoa and Oreti systems exhibit paraphyletic relationships across their drainage divide, in contrast to the obligate riverine galaxiids that exhibit reciprocally monophyletic relationships between these catchments. The ability of *G. gollumoides* to occupy swamps, slow-flowing streams and steep headwaters seems to have allowed the species to exploit episodic connections between the Mararoa and Oreti rivers (Burridge *et al.*, 2008b) and may have facilitated interdrainage connectivity among populations in the Owaka–Puerua–Waiwera system as well.

While a range of mechanisms have been proposed for the distribution of freshwater-limited taxa across catchments presently isolated by terrestrial barriers (Craw *et al.*, 2007), greatest attention has been given to those that can be related to explicit mechanisms in place and time, such as river captures (e.g. Waters *et al.*, 2001b; Burridge *et al.*, 2006, 2007), or anastomosing of adjacent catchments during low sea stands (Ruzzante *et al.*, 2011). However, evidence is accumulating for interdrainage connectivity by freshwater-restricted taxa via low relief divide crossing events, which may represent an important mechanism of range expansion for freshwater-limited taxa and a contributor to intracatchment biodiversity (Thacker *et al.*, 2007; Burridge *et al.*, 2008b; Chakona *et al.*, 2013). For example, interdrainage connectivity across the continental drainage divide have been suggested for a large number of Australian taxa (e.g. Thacker *et al.*, 2007, 2008; Faulks *et al.*, 2008, 2010; Jerry, 2008), despite sentiment that river capture has been rare given the geological stability of this system (Nott & Horton, 2000; Holdgate *et al.*, 2008). Consequently, other studies should consider the possibility of interdrainage connectivity even where obvious geomorphological signatures are lacking.

In conclusion, our observation of a third independent colonization of the Clutha system by *G. gollumoides* indicates the high frequency with which interdrainage movement can occur for freshwater-limited taxa, even into a single catchment. Although evidence for interdrainage movements by freshwater-limited taxa has been accumulating, their contribution to biodiversity within a catchment, and their potential impacts on studies of species movements and distribution within catchments, have been rarely considered. For example, while the Clutha presently houses the highest diversity of freshwater-limited galaxiid fishes of any catchment in the world (seven species), the majority of these could have been contributed by past interdrainage connectivity, rather than *in situ* speciation; the Von River population of *G.* 'southern' was founded from Southland (Burridge *et al.*, 2007), and sister lineages of Clutha populations of *G. paucispondylus* (two lineages), *G. anomalus*, *G. pullus* and *G.* sp. 'D' are each distributed in adjacent catchments (Waters *et al.*, 2010; Craw *et al.*, 2012). Similarly, in the Murray–Darling system – one of the largest catchments in Australia – 21 out of 29 freshwater-limited species are also distributed in adjacent coastal catchments, and molecular studies suggest that for several of these shared species the Murray–Darling was a sink, rather than a source (Faulks *et al.*, 2008, 2010; Jerry, 2008), although from other studies movement in either direction appears equally supported (Thacker *et al.*, 2007, 2008). Our study highlights the fact that interdrainage connectivity provides the opportunity to increase not only the diversity of species within a catchment but also the number of lineages within species and their distribution within the catchment.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Details on sampling sites and sample sizes.
Appendix S2 Plots of the marginal posterior densities for the estimated model parameters obtained with IMa.

DATA ACCESSIBILITY

The cytochrome *b* sequence alignment can be downloaded from the Dryad Digital Repository at http://dx.doi.org/10.5061/dryad.25kc1.

BIOSKETCH

This paper emerged from C. Carrea's visit to C. Burridge's Lab at the School of Zoology, University of Tasmania. C.C.'s research interests are in phylogeography and conservation genetics of both freshwater and marine species.

Author contributions: C.C. and C.B. led the writing, J.W. and D.C. were involved in subsequent versions of the manuscript; C.B., J.W. and D.C. conceived the ideas; L.V.A. collected the data and C.C. analysed the data.

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