

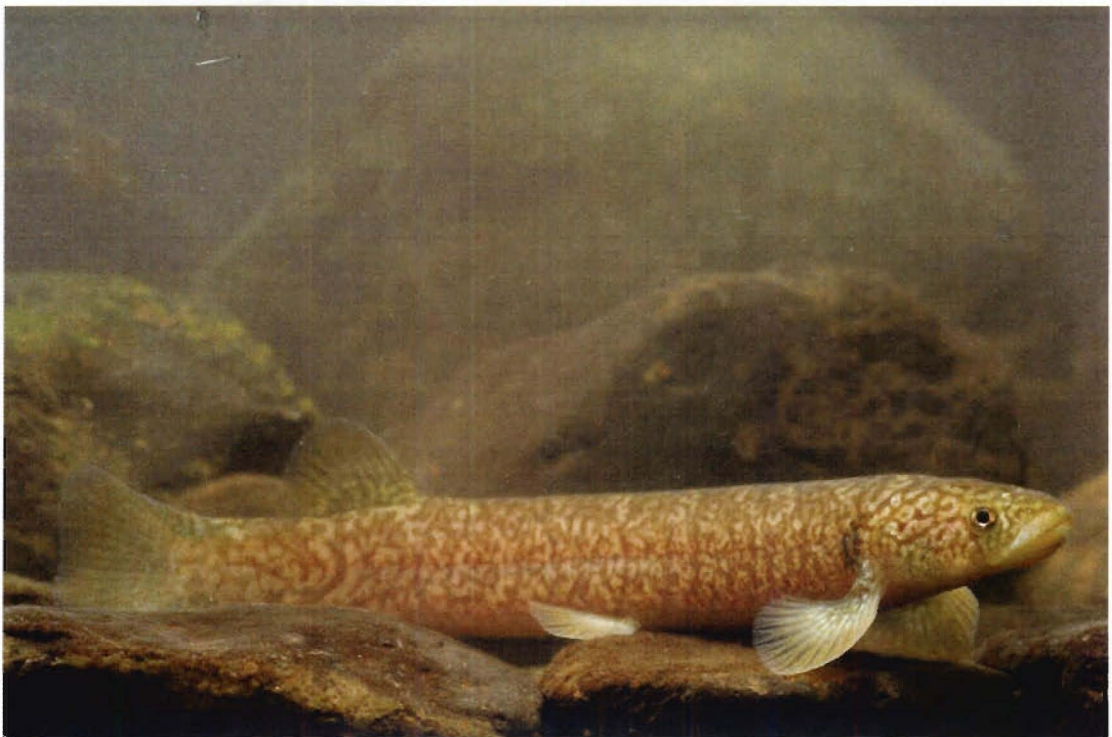
**THE EFFECT OF HABITAT FRAGMENTATION ON
NEW ZEALAND NATIVE FISH: A GIS APPROACH**

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submitted in partial fulfilment
of the requirements for the Degree
of
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Frontispiece



Top: the banded kokopu (*Galaxias fasciatus* Gray).
Bottom: the koaro (*Galaxias brevipinnis* Günther).
(Fish capture: Hans S. Eikaas. Photo: Angus R. McIntosh)

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Abstract

Land use change is likely to have influenced the distributions of adults of the New Zealand galaxiid fishes (family Galaxiidae) with life histories involving a juvenile migratory 'whitebait' stage. The influence of interactions between these diadromous migrations, terrestrial habitat fragmentation, migratory barriers and local habitat conditions on the distribution of koaro, inanga, and giant, shortjaw and banded kokopu were investigated using a geographical information system approach.

A catchment-scale analysis of Banks Peninsula streams with riparian forest indicated position and extent of forest explained 65.7 % of koaro occurrence. When riparian forest was lacking koaro were rare and catchment variables had no influence. A site-scale analysis using logistic regression predicted koaro and banded kokopu presence at > 80 % of sites using land use-related variables. Hindcast and forecast models showed that both species likely occupied over 85 % of available stream habitat in 1860. Reforestation would have differential effect on koaro and banded kokopu depending on forest position. Banded kokopu, a forest specialist, was affected by edge effects of forest fragmentation, occurring in larger numbers and sizes in forested streams, whereas koaro was affected by catchment forest cover.

A large-scale study of migratory galaxiid occurrences on South Island's West Coast indicated maximum slope encountered during upstream migrations was a good predictor of fish occurrence, and species had different slope-thresholds. A hierarchical analysis that differentiated between abiotic barriers, migratory passage, and land use impacts on fish occurrence showed that land use impacts on the migratory passage was the major factor limiting migratory fish distributions.

This research shows that migratory galaxiids are sensitive to the configuration of landscape elements and migratory barriers, factors that can be used in predictive models to differentiate and quantify distribution limitations due to migratory passage, catchment land use, and local habitat conditions. The approach is useful for managers because it is robust, feasible, and transferable to other migratory fish species.

Chapter 1. Introduction

1.1. Introduction

Following European colonisation of New Zealand, populations of native freshwater fish, in particular native Galaxiidae, have undergone extensive declines (McDowall 1990). This has in some instances been attributed to the introduction of exotic species such as trout and salmon, but also to the conversion of native forest cover to various types of other land uses. Many large-bodied galaxiid fish are highly mobile, strong swimmers, which could potentially navigate a watercourse to remote inland locations to reach suitable habitat in headwater streams. However, in catchments where most forest cover has been removed, large galaxiids are frequently absent, whereas in other more forested catchments, they co-occur even where introduced trout are present (McDowall 1990). In this thesis I investigated how changes to catchment land use interacted with migratory behaviour to influence the distributions of New Zealand diadromous galaxiids.

1.2. General effect of humans on stream ecosystems

River and stream ecosystems are significantly modified by human activities, possibly more so than any other type of ecosystem (Allan & Flecker 1993). Changes in the landscape due to deforestation, grazing, farming, water abstraction, impoundment, and the introduction of exotic species have influenced catchments and their waterways directly and indirectly for several millennia around the world (Allan *et al.* 1997). Although we have a growing understanding of the tight coupling of the stream and its valley (Hynes 1975), knowledge of how large-scale spatial patterns in terrestrial ecosystems affect stream communities is limited.

1.3. Habitat fragmentation

Modern land-use practices may have caused various degrees of habitat fragmentation that affect streams. When habitats are fragmented, or destroyed, species come to exist in discrete habitat patches that may only be suitable for a limited range of species or may limit population sizes (Hanski 1994, Hanski 1999). Hence current and future distribution of a species may reflect past and present land use.

Habitat fragmentation is a scale-dependent process. When describing fragment attributes and fragment isolation, the size, shape and aggregation of the patches should be considered. As

the density of habitat fragments decrease, the isolation of patches increase geometrically. Also, with decreasing patch size, the proportion of edge habitat increases geometrically. This may be of particular importance to riverine fish that are constrained to stream corridors, where the fragmentation in the terrestrial landscape may actually have a disproportionate effect on stream inhabitants.

1.4. Link between terrestrial and stream habitat fragmentation

One feature of streams is that they derive most of their energy from uphill. The energy input can be in the form of dead plant material which undergoes a series of processes in the water that make it available as food for benthic invertebrates, bacteria, and fungi (Cummins 1974, Hynes 1975). The invertebrates in turn comprise the food material for the stream fish fauna.

In forested catchments litterfall from the trees is well known to be several tonnes per hectare annually (Hynes 1975), some of which falls directly into the stream, with more entering via runoff and windfall. The amount of litterfall into streams is also dependent on vegetation type (Gregory *et al.* 1991), as different tree species give rise to different amounts of leachate and thus influence on the chemical characteristics of the water. With the conversion of forested areas to pasture-land, the amount of litterfall entering streams declines, resulting in decreased food subsidies to stream fish from the terrestrial environment.

Interactions between terrestrial and aquatic ecosystems include modification of microclimate (e.g., light and temperature) (Barton *et al.* 1985), alteration of nutrient inputs from hillslopes, contribution of organic matter to streams and floodplains, and retention of inputs (Gregory *et al.* 1991). Woody debris from riparian vegetation also provides important invertebrate and vertebrate habitat in streams, and strongly influences the formation of pools and lateral habitats (Gregory *et al.* 1991). In view of the above, fragmentation of the terrestrial riparian and catchment vegetation should affect in-stream habitats as well (Scarsbrook & Halliday 1999) because the structure and trophic processes of lotic ecosystems are determined by their interface with adjacent terrestrial ecosystems (Hicks & McCaughan 1997, Inoue & Nakano 1998, Urabe & Nakano 1998, Nakano & Murakami 2001).

1.5. The New Zealand situation

With its rich and varied assortment of rivers, streams, lakes and wetlands, New Zealand is home to a modest yet fascinating freshwater fish fauna (McDowall 1990, McDowall 2000).

Despite New Zealand's fresh 'clean and green' image, the abundance of native freshwater fish species is sparse (Table 1.1), the majority of them being represented by the family Galaxiidae. Ironically, the best-known species are probably the salmonids, exotic species introduced to New Zealand over a hundred years ago (McDowall 1990).

Table 1.1 Freshwater fishes of New Zealand, indicating life history patterns and conservation status by the Department of Conservation (Hitchmough 2002). Table adapted from McIntosh and McDowall (2004).

Native species				
Family	Species (common name)	Life history	Conservation status	
Geotriidae (lamprey)	<i>Geotria australis</i> (lamprey)	Anadromous	Sparse	
Anguillidae (eels)	<i>Anguilla dieffenbachii</i> (longfin eel)	Catadromous	Gradual decline	
	<i>A. australis</i> (shortfin eel)	Catadromous		
	<i>A. reinhardtii</i> (spotted eel)	Catadromous		
Retropinnidae (smelts)	<i>Retropinna retropinna</i> (common smelt)	Anadromous		
	<i>Stokellia anisodon</i> (Stokell's smelt)	Anadromous		
Prototroctidae (grayling)	<i>Prototroctes oxyrhynchus</i> (grayling)	Unknown	Extinct	
Galaxiidae (galaxiids)	<i>Galaxias argenteus</i> (giant kokopu)	Amphidromous	Gradual decline	
	<i>G. fasciatus</i> (banded kokopu)	Amphidromous		
	<i>G. postvectis</i> (shortjaw kokopu)	Amphidromous	Gradual decline	
	<i>G. brevipinnis</i> (koaro)	Amphidromous		
	<i>G. vulgaris</i> (Canterbury galaxias)	Non-migratory		
	<i>G. depressiceps</i> (flathead galaxias)	Non-migratory	Gradual decline	
	<i>G. pullus</i> (dusky galaxias)	Non-migratory	Gradual decline	
	<i>G. eldoni</i> (Eldon's galaxias)	Non-migratory	Gradual decline	
	<i>G. anomalus</i> (roundhead galaxias)	Non-migratory	Gradual decline	
	<i>G. gollumoides</i> (Gollum galaxias)	Non-migratory		
	<i>G. maculatus</i> (inanga)	Catadromous		
	<i>G. gracillis</i> (dune lake galaxias)	Non-migratory	Serious decline	
	<i>G. divergens</i> (dwarf galaxias)	Non-migratory	Gradual decline	
	<i>G. paucispondylus</i> (alpine galaxias)	Non-migratory		
	<i>G. prognathus</i> (upland longjaw)	Non-migratory	Sparse	
	<i>G. cobitinis</i> (lowland longjaw)	Non-migratory	Nationally critical	
	<i>G. macronasus</i> (bignose galaxias)	Non-migratory		
	<i>Neochanna burrowsius</i> (Canterbury mudfish)	Non-migratory	Nationally endangered	
		<i>N. apoda</i> (brown mudfish)	Non-migratory	Gradual decline
		<i>N. diversus</i> (black mudfish)	Non-migratory	Gradual decline
	<i>N. heleioides</i> (burgundy mudfish)	Non-migratory	Nationally endangered	
	<i>N. rekohua</i> (Chatham mudfish)	Non-migratory	Range restricted	
Pinguipedidae (torrent-fish)	<i>Cheimarrichthys fosteri</i> (torrentfish)	Amphidromous		
Gobiidae (bullies)	<i>Gobiomorphus huttoni</i> (redfin bully)	Amphidromous		
	<i>G. cotidianus</i> (common bully)	Amphidromous		
	<i>G. gobioides</i> (giant bully)	Amphidromous		
	<i>G. hubbsi</i> (bluegill bully)	Amphidromous		
	<i>G. breviceps</i> (upland bully)	Non-migratory		
	<i>G. basalus</i> (Cran's bully)	Non-migratory		
	<i>G. alpinus</i> (Tarnedale bully)	Non-migratory	Range restricted	
Pleuronectidae (flounder)	<i>Rhombosolea retiaria</i> (black flounder)	Catadromous		

New Zealand is an island nation, so one would not expect to have as many species as a mainland nation. Today, about 59 species of freshwater fish are recognised in New Zealand, of

which 21 are introduced (McIntosh & McDowall 2004). This compares to the United Kingdom, also an island nation, that has 51 species, 13 of which are introduced (McDowall 1990). In comparison, the Zambezi River in Africa has 166 species, 9 of which are introduced (McDowall 1990).

With the arrival of European settlers, New Zealand landscapes were also extensively modified and large areas of native forests were converted to pasture, so that today few areas of unmodified forest remain (Jowett *et al.* 1998). Intensive pastoral practices (e.g., dairy and sheep farming), draining of swamps and wetlands, discharge of effluents and fertilisers into lakes and waterways, impounding and abstracting water from rivers for water supply, electricity generation, and irrigation of farmland, have also impacted riverine ecosystems in New Zealand in the century following European colonization (McDowall 2000).

1.6. Fragmented distribution of native Galaxiidae

Many of the larger native fishes have become much rarer in recent years, and it appears that introduced trout, to some extent, have replaced them (Townsend & Crowl 1991, McIntosh *et al.* 1992, McIntosh *et al.* 1994), especially in localities where forest cover has been removed from the streams (McDowall 1990). Additionally, in isolated rivers, particularly where forest cover remains and land development has been minimal, the native fishes may still be found in large numbers (McDowall 1990).

Most of New Zealand native freshwater fish species are highly secretive, typically resting in concealment during the day and emerging to feed at night (Cadwallader 1975). With conversion of forest to yield land for agriculture and farming, much of the original forest cover has disappeared, and brown trout (*Salmo trutta* L) have successfully invaded these streams (McIntosh *et al.* 1992). Native galaxiids such as koaro (*Galaxias brevipinnis* Günther) and banded kokopu (*G. fasciatus* Gray) are rarely found in pastoral streams, and their decline has been attributed to conversion of native forest to pasture (Hanchet 1990, McDowall 1990, Rowe *et al.* 1992, Rowe *et al.* 1999, Rowe & Smith 2003). Main and Winterbourn (1987) also noted that indigenous forest, such as podocarp and beech forest, was present at all eleven sites in their study of diet of koaro in South Westland streams and that terrestrial derived invertebrates dominated koaro diet, demonstrating the importance of native vegetation. A change in land use from forest to pasture affects some native fish species, but the mechanisms involved, and generality of the effect, and the species affected are unknown (Rowe *et al.* 1999). Also, other native fish such as the

shortjawed kokopu (*G. postvectis* Clarke) appear to prefer native podocarp/hardwood forest streams over streams with exotic forest types (McDowall *et al.* 1996, McDowall 1997b).

1.7. Thesis objectives

1.7.1. Objective One – Catchment forest cover and site occupancy by koaro and kokopu

Five species of New Zealand native galaxiids undergo diadromous migrations and have access to a variety of freshwater habitats. However, koaro, shortjaw kokopu, banded kokopu and giant kokopu appear to occur in habitats associated with predominantly native forest cover (McDowall 1990, McDowall *et al.* 1996, McDowall 1997b). There must be some factor associated with native vegetation that these galaxiids detect and subsequently base their choice of site occupancy on. It is possible that native forest cover provides better cover and refugia, more food subsidies from streamside vegetation, and more stable water temperature and water quality than other cover types.

Past studies, in which the association of galaxiids with native forest cover has been assessed (McDowall 1997b), have been undertaken at small spatial scales involving individual streams in the same catchment, or sub-catchment, treating them as replicates, when in fact they are pseudo-replicates. One large-scale study by Minns (1990) attempted to contribute land use changes to the distribution of native fish species. This study was based on the presence/absence data from the New Zealand Freshwater Fish Database (NZFFD). Minns expected to find positive linkages between land use changes on native species, but concluded that patterns and linkages could be coincidences of geography. The varying degrees of sampling intensity and methods, inaccurate site and catchment descriptions, and mixture of historical and recent records held in the NZFFD mean that a more spatially explicit sampling may be useful. No study has treated the entire catchment as a replicate, so knowledge of the influence of large scale processes on diadromous fish distributions. I suggest that there is a positive correlation between the proportion of the total catchment area covered with forests, regardless of type, and the proportion of sites occupied by kokopu and koaro.

1.7.2. Objective Two – Effects of forested riparian stream margins on koaro and kokopu site occupancy

Riparian corridors should enhance connectivity between suitable habitats for forest-dwelling stream fish, because they moderate catchment influences on instream conditions and provide some forest association for the fish. Forested stream corridors also provide in-stream debris for refugia, allochthonous food subsidies, and moderation of fluxes in the thermal regime of streams. Therefore, I hypothesise that having forested stream margins will provide for suitable habitat for koaro and kokopu even where the overall proportion of catchment forest cover is low.

1.7.3. Objective Three – The effect of the location of forest cover in the catchment on kokopu and koaro

Streams situated in upland locations generally have a disproportionately large influence on lowland streams due to the unidirectional flow of water. If upland areas are devoid of a protective forest cover, the effects of surface runoff (i.e., fine sediment input, lack of attenuation of overland flow) may negatively influence the water quality throughout the catchment, providing for unfavourable conditions for migratory stream fish that utilise the entire watercourse through their life cycle. Where the predominant forest position is in lowland reaches, a lack of forest cover along stream margins is likely to preclude occupancy by stream fish with a preference for forested streams. However, where forests are situated in upland reaches, because forested headwaters ameliorate water quality, koaro and kokopu may still be present in high proportions, even though they had to navigate an unfavourable environment to reach this suitable habitat.

I hypothesise that having forest patches situated in upland areas significantly increases the proportion of sites occupied by koaro and kokopu throughout the catchment.

1.7.4. Objective Four – Edge effects of terrestrial habitat fragmentation on forest stream-dwelling fish

For many organisms it has been found that larger habitat patches generally support more individuals, and this has often been used as an argument in favour of single large reserves as compared to several small reserves (Diamond 1975, Soule & Simberloff 1986). For galaxiids it is possible that larger forest patches provide more allochthonous food subsidies than smaller patches. It is also possible that edge mediated effects influence kokopu populations, and the stream in the immediate area of two adjacent cover types provides sub-standard habitat for forest

dwelling stream fish. Thus, if koaro and kokopu are indeed influenced by edge mediated effects, then larger patches with more stream length in forest interior may support more fish. I hypothesise that edge effects due to terrestrial habitat fragmentation may negatively influence kokopu distributions.

1.7.5. Objective Five – Steep stream gradients and distance inland as limits to the distribution of diadromous fish

The presence of steep coastal cliffs, multiple geologic fault lines, and large mountain ranges in New Zealand likely compromise the use of river distance inland and elevation as premium gauges for the distribution of native diadromous fish. Fish may encounter steep stream gradients that may prove to be barriers to further upstream migration at irregular intervals within stream networks. Thus, in some catchments, the distribution of native diadromous fish may appear disjunct, and large areas of apparently premium fish habitat may not be inhabited by fish expected to occur in such environments. I predict that the use of a new variable, the maximum stream slope a fish encounter during upstream migration, will be a better predictor variable for the presence of native diadromous stream fish.

1.7.6. Objective Six – The spatial location of barriers to fish migration and site occupancy by native diadromous fish

Inland insinuation of diadromous fish in river systems is a gradual process, often taking several years for some species (Jellyman 1977). During this upstream migration, migratory fish grow, and their ability to overcome steep stream gradients change. For salmonids that jump to overcome small waterfalls, larger fish are more adept to migrate upstream over small waterfalls. Galaxiids and anguillids, however, use their pectoral fins to climb the wetted perimeters of waterfalls, using surface tension between their ventral surfaces, pectoral fins, and the substrate to overcome steeper stream gradients and waterfalls (Jellyman 1977, McDowall 2003b). Thus, larger fish in inland locations may have a weight-to-surface ratio that inhibits upstream migration above steep stream gradients. This means that the location of steep stream gradients in the riverscape may be of importance to native diadromous stream fish. In coastal areas close to the sources of migrant juvenile fish, I expect to find all species of native diadromous fish. In locations further inland, I expect that species, such as inanga, giant kokopu, and banded kokopu, being weaker climbers, may not occur above steeper stream gradients.

1.7.7. Objective Seven – Hierarchical effects of physical barriers to upstream migration, impacts of catchment deforestation and intensive land uses on migratory passage, and local land use characteristics on kokopu habitat availability

With species having different migratory drives and abilities to overcome physical barriers to upstream migration, such as steep stream gradients, it may be that pristine habitats in inland locations are not occupied because they are beyond the threshold for that species. Additionally, different species have different tolerances when it comes to various types of land use impacts on streams. Migrating juveniles of banded kokopu are sensitive to suspended sediments (Rowe & Dean 1998, Rowe *et al.* 2000, Richardson *et al.* 2001, Baker 2003a), and can be expected to avoid catchments with little forest cover where suspended sediment levels may be higher. Koaro, a strong swimmer and able climber, may access habitats inaccessible to other species, but would also be sensitive to landuse impacts that affect the migratory passage and local habitats. I use a hierarchical analysis approach to differentiate and quantify the amount of habitat loss due to the effects of physical barriers to upstream fish migration, impacts on migratory passage by intensive land uses along the migratory passage and catchment deforestation, and local land uses and habitat characteristics.

1.8. Thesis outline

This thesis examines the distribution of large galaxiid fish in catchments covering a range of landuse types on Banks Peninsula, South Island, New Zealand, as well as the Department of Conservation's West Coast Conservancy. The main focus of this thesis deals with aspects of terrestrial fragmentation of forest cover and physical barriers to upstream migration and how these influence the distribution of five species of New Zealand's native migratory Galaxiid fish. The species studied, koaro, banded kokopu, shortjaw kokopu, giant kokopu and inanga, comprise an economically and culturally important commercial and recreational fishery in New Zealand called the 'whitebait' fishery. Although both commercial and recreational catches fluctuate yearly, a general trend of declining catches has been reported (McDowall 1996b). This decline has been attributed to a multitude of factors, including the introduction of exotic species, such as trout and salmon, as well as conversion of native forests to pasture land.

Using existing data from the New Zealand Freshwater Fish Database for two regions, Banks Peninsula and the Department of Conservation's West Coast Conservancy, supplemented by a

targeted sampling regime in data deficient areas, this thesis aims to elucidate the effects of terrestrial habitat fragmentation and changes in land use on forest dwelling stream fish.

Banks Peninsula represents a severely fragmented terrestrial landscape, where local land uses comprise the major impacts on fish distributions, but physical barriers to dispersal are not an issue. The Department of Conservation's West Coast Conservancy, on the other hand, represent some of New Zealand's least modified landscape, although some catchments are fragmented by various land uses. This area lends itself to study the broader effects of physical barriers to dispersal and edge effects. This area also allows one to control for the effect of physical barriers to dispersal to examine the effects of catchment- and site-scale effects on the migratory passage and local land uses. To start, interactions between factors that influence on the distribution of native fish, such as the amount and specific location of forest cover, operating at catchment and site scales, objectives 1-3, were investigated on Banks Peninsula (Chapter Two). The findings of this study were then incorporated into a predictive model for the distribution of two large galaxiid fish, the koaro and the banded kokopu on Banks Peninsula (Chapter Three). This model also accounts for specific commercial land use practices within catchments and how these impact on fish distributions. The model used contemporary data on fish occurrences, and extrapolates to several scenarios, past and future, illustrating what the distribution of koaro and banded kokopu might have looked like in the past, as well as giving an indication of future distributions under different management regimes. Both Chapter Two and Chapter Three highlight the importance of forest cover along stream margins, as well as the location of forest cover in catchments, to native large-bodied galaxiid fish.

Chapter Four further investigates objective 4, whether forest edge-mediated effects influence populations of native species, with a study of banded kokopu on the West Coast, South Island. This particular study took place within the West Coast Conservancy, where anthropogenic catchment modification is less severe. Chapter Five considered objective 5 by investigating abiotic factors such as river distance inland from all sources of migrant fish, elevations above these sources, and the maximum downstream slopes fish would have encountered during migration to these locations within the riverscape. These effects may cause the appearance of a fragmented distribution of native fish, but operate relatively independently of modifications to the terrestrial landscape. Chapter Six investigates objectives 6 and 7. Here, a hierarchical analysis approach was used to differentiate between limitations to species distributions due to physical barriers in the riverscape, anthropogenic impacts on the migratory

passage and catchment deforestation, and local land uses and habitat characteristics. This chapter highlights how impacts of intensive land uses on the migratory passage restrict migratory fish distributions. Furthermore, it illustrates that accessible habitats may not be occupied by galaxiid fish because of local land uses. Finally, a summary of major findings is given in Chapter Seven.

The thesis is constructed as a series of independent papers, either submitted, or finalised for publication in peer reviewed journals (except Chapter One and Chapter Seven) (Table 1.2). A single reference section is provided to make the thesis easy to read. Although some of the chapters are in press, a consistent format style has been maintained throughout the thesis and each is written in the first person singular although multiple authors are associated with the publications.

Table 1.2 Thesis chapters, authorship, target journals, and current publications status.

Chapter	Title	Authors	Journal	Status
2	Catchment- and site-scale influences of forest cover and longitudinal forest position on the distribution of a diadromous fish	Hans S. Eikaas Angus R. McIntosh Andrew D. Kliskey	Freshwater Biology	50, 527-538
3	Spatial modelling and habitat quantification for two diadromous fish in New Zealand streams: a GIS-based approach with application for conservation management	Hans S. Eikaas Andrew D. Kliskey Angus R. McIntosh	Environmental Management	In press
4	Connections between terrestrial habitat fragmentation and stream inhabitants: edge-effects on fish that occupies forested streams in New Zealand	Hans S. Eikaas Angus R. McIntosh Andrew D. Kliskey Jon S. Harding	NZJMFR	Submitted
5	Patterns in diadromous fish distributions: testing the roles of altitude, distance, and maximum downstream slope	Hans S. Eikaas Angus R. McIntosh Andrew D. Kliskey	Transactions in GIS	Under review
6	An assessment of the relative influence of access barriers, conditions in migratory passage, and local land uses on the distribution of diadromous fish using a hierarchical GIS analysis	Hans S. Eikaas Angus R. McIntosh	Ecological Applications	Submitted

Chapter 2. Catchment– and site–scale influences of forest cover and longitudinal forest position on the distribution of a diadromous fish.

2.1. Summary

The hydrologic connectivity between landscape elements and streams means that fragmentation of terrestrial habitats could affect the distribution of stream faunas at multiple spatial scales. I investigated how catchment- and site-scale influences, including proportion and position of forest cover within a catchment, and presence of riparian forest cover affected the distribution of a diadromous fish.

The occurrence of koaro (*Galaxias brevipinnis*) in 50-metre stream reaches with either forested or non-forested riparian margins at 172 sites in 24 catchments on Banks Peninsula, South Island, New Zealand was analysed. Proportions of catchments forested and the dominant position (upland or lowland) of forest within catchments were determined using geographical information system spatial analysis tools.

Multivariate analysis of variance indicated forest position and proportion forested at the catchment accounted for the majority of the variation in the overall proportion of sites in a catchment with koaro.

Where forest was predominantly in the lower part of the catchments, the presence of riparian cover was important in explaining the proportion of sites with koaro. However, where forest was predominantly in the upper part of the catchment, the effect of riparian forest was not as strong. In the absence of riparian forest cover, no patterns of koaro distribution with respect to catchment forest cover or forest position were detected.

These results indicate that landscape elements, such as the proportion and position of catchment forest, operating at catchment-scales, influence the distribution of diadromous fish but their influence depends on the presence of riparian vegetation, a site-scale factor.

2.2. Introduction

Biotic interactions and movement patterns such as diadromous migrations can have major influences on fish spatial distribution (Gilliam *et al.* 1993, McDowall 1996a, McDowall 1998a, McDowall 1998b), but abiotic factors operating at large spatial scales should not be ignored (Matthews 1998). Over a quarter of a century ago, Hynes (1975) argued that, in every respect, the valley rules the stream, emphasising the link between terrestrial and aquatic environments. Although still not completely understood, the impact of historical catchment-scale land-use practices and local modifications to the landscape on streams are becoming clearer (Hynes 1975, Naiman 1992, Osborne & Kovacic 1993, Richards & Host 1994). However, much of the current knowledge of the ecology of rivers and streams is based on surveys, observations and experiments on organisms and habitats at small spatial scales. Such small-scale investigations can limit the ecological understanding needed to underpin conservation efforts for stream fish (Fausch *et al.* 2002). Moreover, riverine ecosystems have frequently been degraded by ecosystem-wide activities in the terrestrial environment, and they are rarely bounded by the area selected for study (Nakano *et al.* 1999). These activities, historical and contemporary, include road construction, forest harvesting, mining, water diversion, agricultural, industrial, and municipal uses (Allan & Flecker 1993, Kauffman *et al.* 1997), which in turn influence the timing and quantity of flow within channels (Fahey & Watson 1991, Richards & Host 1994). Degradation of the stream valley ecosystems and the riparian zones that link streams with their catchments are likely to diminish a catchment's capacity to provide critical riverine functions necessary for streams and their biota (Osborne & Kovacic 1993).

Headwater and downstream systems are linked not only by the unidirectional downstream flow of water, but also by the upstream and downstream migration of animals, notably diadromous fish. Headwater streams are generally small and numerous, with high drainage density and numerous land use types and intensities whose roles in terms of upstream-downstream linkages are typically underestimated (Gomi *et al.* 2003). Therefore, to allow for effective research and conservation of fish (Fausch *et al.* 2002), there is a need for a continuous view of rivers and streams. This would not only recognise upstream-downstream linkages, but also incorporate the spatial heterogeneity and connectivity of habitat patches critical for completion of fish life-cycles (Schlosser 1995). Studies of fish populations in New Zealand and elsewhere have typically been undertaken at small spatial scales (but see (Minns 1990). Studies

on the spatial distributions of freshwater fish that link local and landscape scales are needed. The objective of my study was to investigate catchment- and site-scale effects on of forest cover on stream-reach occupancy by a native New Zealand galaxiid, the koaro (*Galaxias brevipinnis* Günther).

New Zealand's landscape reflects the geologic history of the region as well as recent events such as floods, fires, and human-induced environmental changes including deforestation, dam construction, pollution, and introduction of exotic species. In New Zealand, pastoral and production forestry land uses are perceived to be some of the main causes of degradation of inland waters (Scarsbrook & Halliday 1999, Quinn & Stroud 2002). At the catchment scale, conversion of native forest or tussock grassland to plantation forest or pasture has altered hydrologic patterns (Graynoth 1979, Fahey & Watson 1991), and may also have caused a loss of physical habitat and deterioration of water quality and substrate composition. Channel morphology adjustments have increased loads of fine suspended and deposited sediments (Jowett & Boustead 2001, Quinn & Stroud 2002).

The koaro is an amphidromous species (McDowall 2000) whose migratory behaviour takes it through a variety of habitats during its journey from the marine environment back to inland freshwater habitats where adult fish are found. Koaro are exceptional climbers and can even negotiate even steep waterfalls (McDowall 1990). While found in grassland streams at a few locations, koaro favour cobble-boulder substrata in streams with extensive riparian forest vegetation (McDowall 1990). Koaro exhibit an open population structure due to mixing of juveniles from different streams while they are at sea, and the species contributes significantly to a commercial and recreational catch (known as whitebait) in some areas of New Zealand (McDowall 1990). They are generalist predators that feed on a variety of terrestrial and aquatic invertebrate prey (Main & Winterbourn 1987, McDowall 1990). Koaro are common throughout New Zealand and are currently not listed as threatened, although the adult habitat is thought to have been greatly reduced by changes in land use from native forest to pasture (Hanchet 1990, Rowe *et al.* 1999).

I expected to find higher proportions of sites with koaro within catchments with greater proportions of their surface covered by forests and of sites with riparian forest on their banks, as the species prefers forested streams (McDowall 1990). Because forest cover attenuates possible negative impacts of detrimental land uses, I also expected to find a higher frequency of koaro occupancy in catchments with higher overall proportions of forest cover compared to catchments

with little forest cover. Finally, I anticipated finding higher site occupancy of koaro in catchments with forested upland reaches, as forested upland areas play a significant role in maintaining overall stream habitat quality even in downstream locations.

My three main objectives were to: (1) elucidate the role of the dominant position of forests within catchments on koaro occurrence in the catchment, (2) to determine the influence of the extent of catchment forest cover on koaro occurrence in the catchment, and (3) to investigate the effect of riparian forest at sites and its effect on the influence of catchment-scale forest cover on koaro distribution.

2.3. Methods

2.3.1. Study area

Banks Peninsula is an 1102-km² promontory feature comprising two extinct shield volcanoes located on South Island, New Zealand (Figure 2.1a). As volcanic activity ceased, the central areas of the volcanoes were eroded out and then drowned to form Lyttelton and Akaroa harbours and the present day terrestrial topography (Weaver *et al.* 1985, Wilson 1992). The Peninsula rises to 919 m a.s.l., and is dissected by more than 100 isolated, short, steep catchments (Harding 2003). The eroded slopes of the craters are mantled by wind-deposited loess derived from the Southern Alps to the west during the glacial periods of the past two million years (Sewell & Weaver 1990). Prior to human habitation, Banks Peninsula was blanketed by forests of totara, matai and kahikatea towering over a sub-canopy of hardwood trees such as mahoe, broadleaf, fivefinger, ribbonwood (Wilson, 1992). Beech forests (*Nothofagus* spp.) dominated the eastern parts of the Peninsula.

Human-mediated deforestation on Banks Peninsula was swift. By the time Europeans arrived, starting around 1850, Maori had already cleared about one third of the forest cover (Petrie 1963). Thereafter, fires and deforestation due to logging cleared another third of the forest cover on the Peninsula within a period of 50 years (Petrie 1963). Kanuka, tussocks, and scrub including the invasive weed gorse, have spread into the cleared land (Wilson 1992, Wilson 1993, Wilson 1994); however, isolated fragments of old growth and regenerating podocarp (*Podocarpus* spp.) forest are found in a few valleys, scenic reserves, and the steeper headwaters of some streams (Harding 2003).

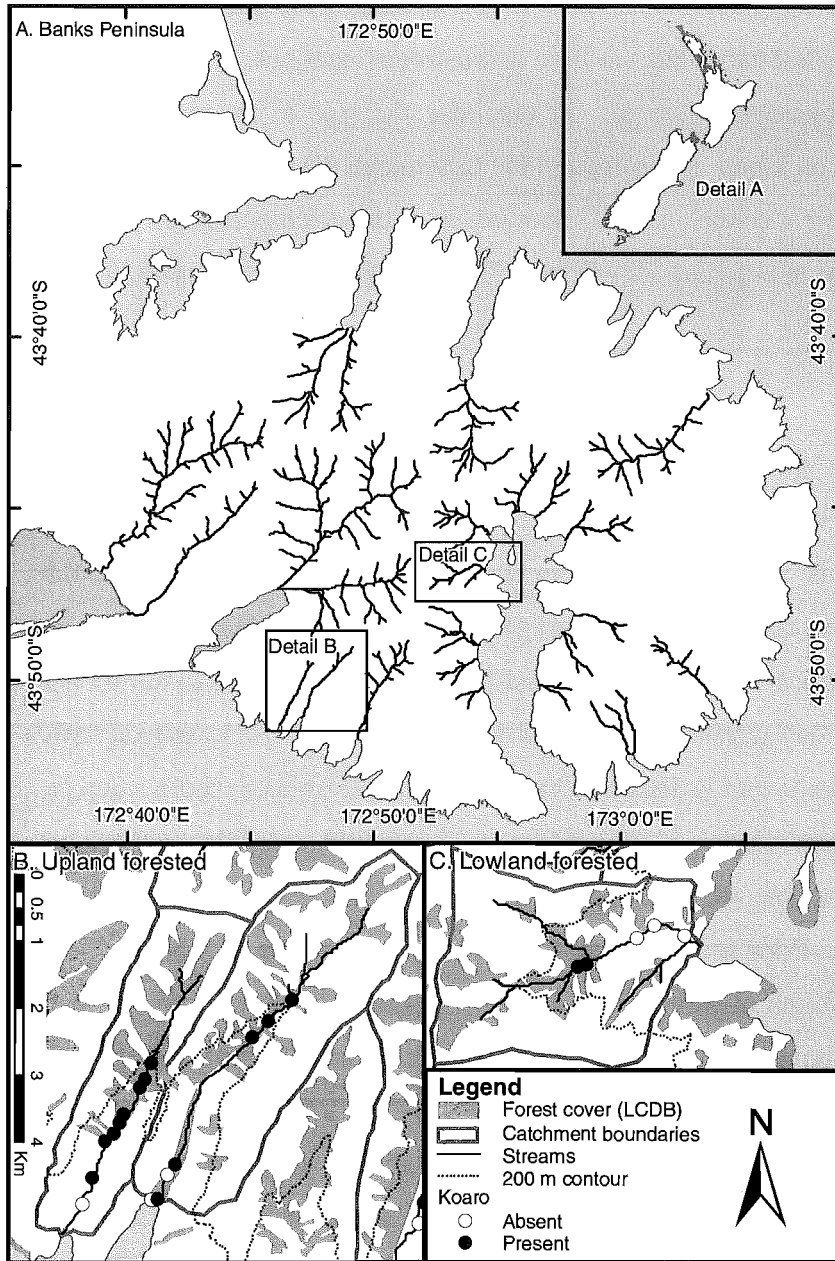


Figure 2.1 (A) Location of the 24 sampled catchments on Banks Peninsula. (B) Two catchments with a greater percentage of forests in upland areas. (C) One catchment with a greater percentage of forest in lowland areas. Forest cover measurements were obtained from the New Zealand Landcover Database (LCDB).

Banks Peninsula has a cool temperate, oceanic, sub-humid climate, and no part is above a potential timberline (Wilson 1992, Wilson 1993). Mean annual rainfall ranges from about 600 mm in the north-west to about 2000 mm in the south-east (Wilson 1992).

The study area is suitable for pursuing my study objectives because the extent of forest cover within study catchments range from almost exclusively open grassland to mostly forested. Also, within my study catchments, about half of the catchments are dominated by upland forest position, and the other half with predominantly lowland forests. Moreover, given the scenario above, open and forested stream reaches are abundant, and in close proximity to one another, providing for an ideal study area.

2.3.2. Catchment and local habitat assessment

Data on the vegetation of sampled sites, riparian vegetation (within 5 m of waters edge), canopy-cover, the presence of barriers to fish migration, and other fish species present were collected from field observations and notes on the New Zealand Freshwater Fish Database (NZFFD; <http://fwdb.niwa.cri.nz>). Percentage of catchment land use (total forest cover, native forest cover, or area of open pasture), altitude, reach slope, maximum downstream slope, and distance from sea of each site were derived from digital data layers (New Zealand Landcover Database 1 Version 2 and South Island 25 m resolution Digital Elevation Model) using ArcView 3.2 (Environmental Systems Research Institute, Redlands, CA, U.S.A.). The maximum downstream slope variable was derived by propagating individual stream segment slopes of the digital hydrology network upstream, so that with increases in stream slopes traversing upstream, the steeper slope value would be retained until an even steeper value was encountered.

2.3.3. Fish sampling and habitat assessment

A total of 172 50-m stream reaches in 24 catchments were sampled by single-pass qualitative daytime electric fishing ($n = 136$), a method that has been demonstrated to effectively detect the presence of most species of native fish (Jowett & Richardson 1996) and night-time spotlighting ($n = 36$) techniques, a method proven especially effective for detecting nocturnal native galaxiid fish (Goodman 2002), during the austral winter and spring of 2001 (Figure 1a). All sites were sampled in an upstream direction, with all available habitat types within a reach (i.e. riffle, pool, backwater, run) being sampled. A Kainga EFM 300 backpack electric fishing machine (NIWA Instrument Systems, N. Z.) was used to produce 400–600 V pulsed DC (pulse width ~ 3 ms, 60 pulses \cdot s $^{-1}$); fish were captured in hand-held stop or dip nets during daytime electric fishing. Where large substratum or overhanging vegetation prevented the use of electric fishing, night-time spotlighting was used. Due to the benthic and nocturnal nature of native galaxiid fish, spotlighting is very effective where water clarity enables all habitats to be observed

(Joy *et al.* 2000). Thirty-three pre-existing post 1990 sampling records available on NZFFD forms were also included in my inventory. Any presence of koaro was converted to binary presence/absence format to avoid bias from different sampling techniques and/or operators.

Because I wanted to assess the influence of factors operating at the scale of whole catchments, a stratified random sampling design was used for sample site selection based on access from roads, land uses within a catchment, and catchment area. To stratify the sampled sites I used a GIS to identify stream segments associated with different vegetation cover classes. Stream sites associated with different vegetation cover classes were then sampled in proportion to the overall percentage cover of that type in the catchment. Actual sampling sites were selected randomly from all sites with the appropriate land cover identified by GIS, with the restrictions that stream segments should have easy access upstream or downstream of roads, and larger catchments should have proportionately more sites. No roads or culverts in the study area were of a nature that would have precluded upstream migration of fish, nor was vegetation cover different near roads compared to far away from roads. The stratified approach allowed for accurate representation of the land uses within the study area, and a representative range of altitudes, slopes, and distances from the sea for each catchment.

2.3.4. Data analysis

Presence/absence of koaro at the 172 sampled sites in 24 catchments on Banks Peninsula were tabulated. Sampled sites were coded according to which catchments they were in (1 to 24) and whether the riparian margins were forested (1) or not (0). The proportions (0.0 to 1.0) of forest cover within the catchments was also calculated after clipping digital land cover data (Map sheet: NZ 262 13) according to topographically delineated catchments.

To differentiate between lowland and upland areas, a histogram analysis of grid cell counts (25*25 m) and their respective elevations was performed using grid analysis in the Spatial Analyst extension of ArcView. The convenient break at 200 m a.m.s.l. was chosen because approximately half (52%) of the landmass on Banks Peninsula is below 200 m.a.s.l., and allows an unbiased comparison amongst catchments to be made unbiased by catchments size and amount of forest cover. To determine whether a catchment was categorised as upland or lowland forest-dominated, I converted the forest polygon cover to a grid of same extent and resolution as the elevation grid, and plotted cumulative percentage forest cover against the average altitude of forest and recorded the overall position of forest cover as either predominantly in the lower

(< 200 m.a.s.l.) or upper (> 200 m.a.s.l.) parts of the catchments (Figure 1b and c). The influences of proportion of forest cover in catchments, and position of forest cover in the catchments on arcsine square root-transformed proportion of sites with koaro was tested using ANCOVA in SPSS 11.0 Standard Version. I treated the position of forest in a catchment (upland or lowland) as a fixed main effect, the proportion of total catchment forest cover as a covariate and position, and also tested the interaction of forest position and total cover on koaro site occupancy. To distinguish between the effects of total forest cover, exotic forest cover (mainly pine plantations), scrub (regenerating native forest), and native forest, I ran the ANCOVA with total forest cover, exotic forest cover removed, and with exotic and scrub removed. I also performed a multivariate analysis of variance (MANOVA) followed by univariate analyses to determine if the effect of dominant forest position, total forest cover and their interaction on the proportion of sites with koaro was the same for sites with and without riparian forest. For all tests, significance was judged at alpha = 0.05.

2.4. Results

Sampled catchments ranged in size from 2.8 to 56.7 km², with total forest cover within catchments ranging from 7.8 to 66.3 % (Tables 2.1 and 2.2). Total stream length within catchments ranged from 2.8 km to 54.6 km, and stream orders of 1–4 as shown on 1:50,000 topographic maps based on Strahler’s (1957) method of stream order determination. No sample sites were located in 4th order streams. Altitudes of the highest headwater streams within catchments ranged from 266 m to 560 m (Table 2.1).

Table 2.1 Physical characteristics of catchments sampled on Banks Peninsula, South Island, New Zealand. Highest stream altitude taken from Land Information New Zealand 260 Map Series (1:50,000 scale).

Catchment characteristics	Minimum	Maximum	Mean	± S.D.
Area (km ²)	2.8	56.7	13.7	13.2
Forest cover (%)	7.8	66.3	26.7	14.7
Highest stream altitude (m a.m.s.l.)	266	560	428	14
Total stream lengths (km)	2.8	54.6	13.6	13.3
Maximum stream slope (deg)	0	60	24.1	12.6
Stream order (Strahler)	1	4		

Of the 24 sampled catchments, 13 were dominated by forest situated predominantly high in the catchments (> 200 m.a.s.l.), and 11 by forest situated predominantly low in the catchment (< 200 m.a.s.l.). Koaro were found at 75 out of 172 sites. The steepest downstream slope

gradient known to be ascended by koaro in the study streams was 60 degrees (based on 25 m resolution digital altitude model) (Table 2.3), which was also the steepest slope within the sampled catchments (Table 2.1). The highest altitude at which koaro were found was 375 m., 16.8 km from the sea (Table 2.3). Forest cover comprised over 2420 patches, with average patch size ranging from 11.9 ha for exotic forests to 8.1 ha for native forests (Table 2.3).

Predominant position of forest within a catchment had a significant effect on the distribution of koaro. Catchments with forest positioned high in the catchment had a significantly higher proportion of sites with koaro (Figure 2.2a). Similarly, at the site-scale, streams with riparian cover were more likely to contain koaro than streams lacking riparian cover (Figure 2.2b).

Table 2.2 Location of catchments sampled on Banks Peninsula. Northing and easting (New Zealand Map Grid 2000) for catchment outflows given to 100-m accuracy. Forest position was designated upland (> 200 m.a.s.l.) or lowland (< 200 m.a.s.l.) based on the location of the majority of forest within the catchment.

Catchment	Northing	Easting	Area (km ²)	% Forest	Position	Sites
Anchorage Bay	57095	25023	4.7	24.3	Lowland	5
Armstrong	57044	25106	4.5	45.2	Upland	5
Aylmer	57109	25068	4.4	24.2	Lowland	5
Barrys Bay	57162	25028	10.6	11.0	Upland	9
Flea Bay	57044	25104	4.3	52.1	Upland	6
French Farm	57143	25026	7.9	22.1	Lowland	5
Kaituna	57146	24822	46.0	24.4	Upland	10
Little River	57142	24924	57.7	23.1	Upland	9
Ohinepaka	57079	25025	2.8	31.8	Lowland	5
Okuti	57132	24931	26.2	27.1	Upland	9
Opara Stream	57238	25145	27.2	7.8	Lowland	6
Otanerito Bay	57076	25146	10.6	66.3	Upland	7
Owhetoro Stream	57272	24955	12.5	10.2	Upland	6
Pawsons	57174	25045	9.2	14.0	Lowland	5
Peraki Bay	57052	24957	16.8	47.2	Lowland	12
Pigeon Bay	57245	25016	26.3	13.9	Upland	15
Pipers Valley	57171	25053	7.0	7.8	Lowland	5
Port Levy trib.	57273	24948	3.8	16.3	Lowland	5
Prices Valley	57126	24846	16.3	25.9	Lowland	6
Robinsons Bay	57159	25070	12.0	11.5	Lowland	7
Te Kawa Stream	57272	24951	14.8	44.1	Upland	5
Te Oka Bay	57064	24927	7.8	24.9	Upland	7
Tumbledown Bay	57060	24913	4.6	22.7	Upland	9
Wainui	57102	25023	9.8	26.6	Upland	9

Table 2.3 Summary characteristics of GIS derived variables for sites with koaro on Banks Peninsula. The number of sites classified by stream order also given. The forest patches, with frequency and average size, for the entire Banks Peninsula is given as per New Zealand Landcover Database Version 2.

	Minimum	Maximum	Mean	± Std. dev.
Slope below site (deg.)	0.0	60.0	24.9	13.0
Site slope (deg.)	0.0	60.0	9.2	9.8
Site elevation (m a.s.l.)	5.0	375.0	121.0	91.0
Distance from sea (km)	0.1	16.8	3.3	3.9
Number of sites in streams (as indicated by 1:50,000 scale maps) of				
1 st order	18			
2 nd order	44			
3 rd order	13			
Forest fragments of three sub-categories		Total number	Area (ha ± S.E)	
Exotic		256	11.9 ± 2.4	
Scrub		1096	9.8 ± 0.7	
Native		868	8.1 ± 0.5	

Dominant forest position and total catchment forest cover affected the proportion of sites with koaro as indicated by the significant *p*-values in the ANCOVA with total forest cover included (Table 2.4a). There were no significant two-way interactions of dominant forest position and total catchment forest cover (Table 2.4a). Similar results were obtained when the effects of exotic forest cover was removed, with a slightly weaker relationship than with total forest cover (Table 2.4b). When the effects of both exotic forest cover and scrub were removed, only dominant forest position was related to koaro presence (Table 2.4c). No significant two-way interactions were obtained when testing exotic or bush cover by themselves using ANCOVA.

Multivariate analysis of variance to test the effects of forest position, total catchment forest cover, and their interaction for sites with and without riparian cover showed that all factors were significant (Table 2.5). Separate univariate ANOVAs showed that in sites with riparian cover, the coefficients of determination explained 65.7 % of the variance in koaro site occupancy. However, in the absence of forest cover, no catchment-scale factors were significant and only 39.4 % of the variance in koaro site occupancy was explained.

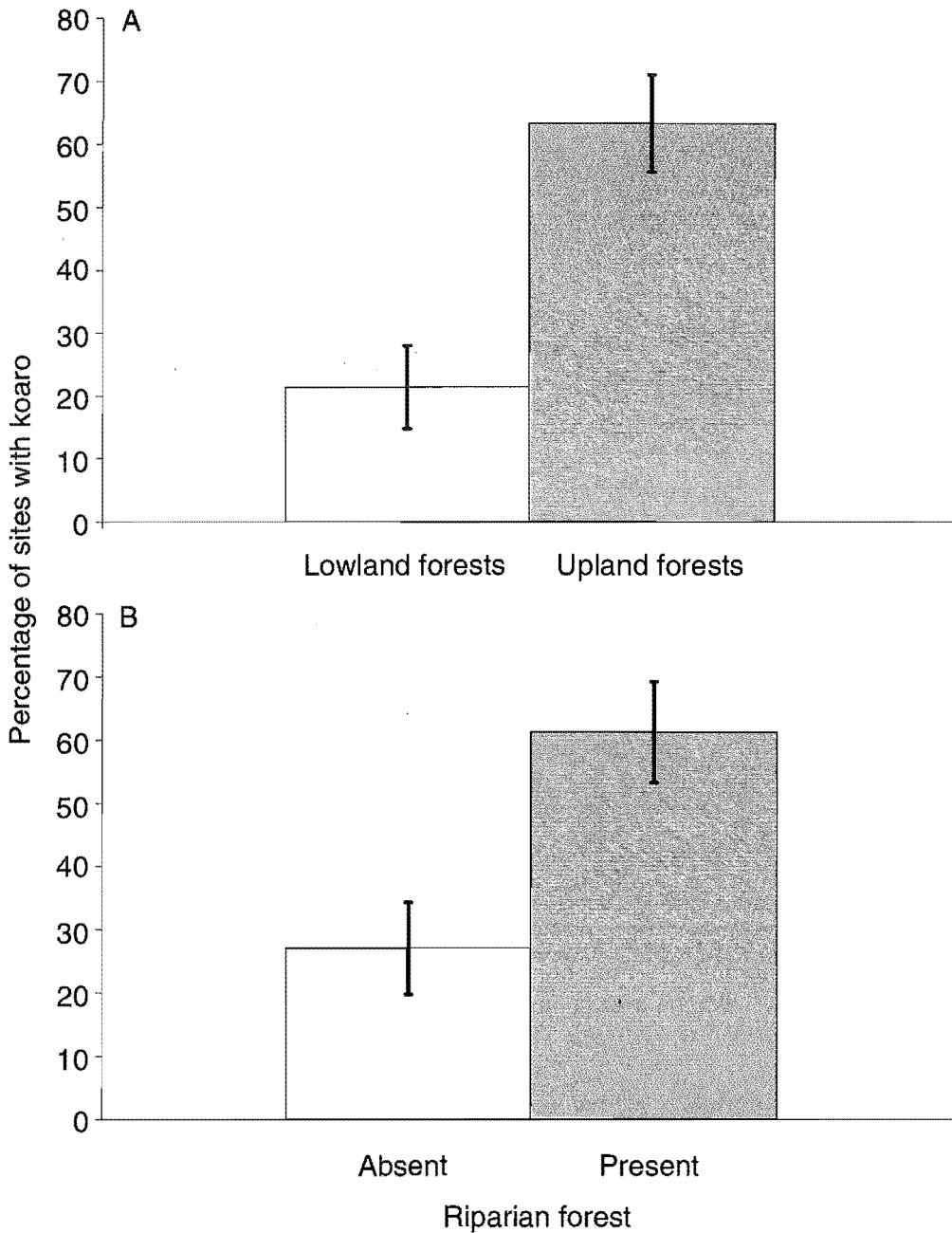


Figure 2.2 (A) Percentage of sites (\pm S.E.) with koaro in catchments with upland- and lowland positioned forests (Independent samples t -test: $t_{(2),22} = -4.066$, $P = 0.001$). (B) Percentage of sites (\pm S.E.) with koaro in stream with riparian zones forested- and non-forested (Paired sample t -test: $t_{(2),23} = -4.508$, $P < 0.001$).

Table 2.4 Results of ANCOVA testing the relationship between proportion of sites with koaro, position of forest in catchment (upland or lowland), and total catchment forest cover for (A) total forest cover, (B) with exotic forest removed, and (C) with exotic and scrub cover removed. The coefficients of determination for the models were 0.669, 0.600, and 0.570, respectively.

A. Source	d.f.	MS	F - ratio	P - value
Position	1	0.003	7.295	0.014
Catchment forest cover	1	0.005	14.430	0.001
Position * Catchment forest cover	1	< 0.001	2.667	0.118
Error	20	< 0.001		
Total	24			
B. Source	d.f.	MS	F - ratio	P - value
Position	1	0.003	7.284	0.014
Native + Scrub cover	1	0.003	8.401	0.009
Position * (Native & Scrub cover)	1	< 0.001	2.220	0.152
Error	20	< 0.001		
Total	24			
C. Source	d.f.	MS	F - ratio	P - value
Position	1	0.005	10.565	0.004
Native cover	1	0.002	3.373	0.081
Position * Native cover	1	0.002	3.327	0.083
Error	20	< 0.001		
Total	24			

Thus, the percentage of sites with koaro was positively correlated with amount of catchment forest cover (Table 2.5); however, the strength of the relationship depended on the influence of riparian forest cover (Figure 2.3). Sites with riparian cover showed a positive relationship between percent catchment forest cover and presence of koaro (Figure 2.3a and b). At sites without riparian cover, no relationships were found between the proportion of sites with koaro and catchment forest cover (Figure 2.3c and d). There were significant interactions between forest position and total forest cover for sites with riparian cover (Table 2.5). This occurred because total catchment cover had a stronger positive influence on koaro occupancy when the majority of the forest was positioned in the lowland (Figure 3a and b).

Table 2.5 Multivariate analysis of variance (MANOVA) and univariate analyses using dominant forest position (upland/lowland) as fixed effect, total catchment forest cover as covariate, and their interaction for the total proportion of sites with riparian forest and no riparian forest streams with koaro for 24 catchment.

Response variable	Source	df	M.S.	F-value	P-value
MANOVA	Constant	2, 19	0.967*	0.324	0.727
	Position	2, 19	0.643*	5.263	0.015
	Total forest cover	2, 19	0.519*	8.820	0.002
	Position * Total forest cover	2, 19	0.696*	4.157	0.032
Riparian cover	Constant	1	0.059	0.408	0.530
	Position	1	1.371	9.478	0.006
	Total forest cover	1	2.672	18.471	< 0.001
	Position * Total forest cover	1	0.745	5.149	0.034
	Error	20	0.145		
No riparian cover	Constant	1	0.024	0.113	0.740
	Position	1	0.035	0.167	0.687
	Total forest cover	1	0.147	0.693	0.415
	Position * Total forest cover	1	0.321	1.519	0.232
	Error	20	0.212		

* Wilks' Lambda

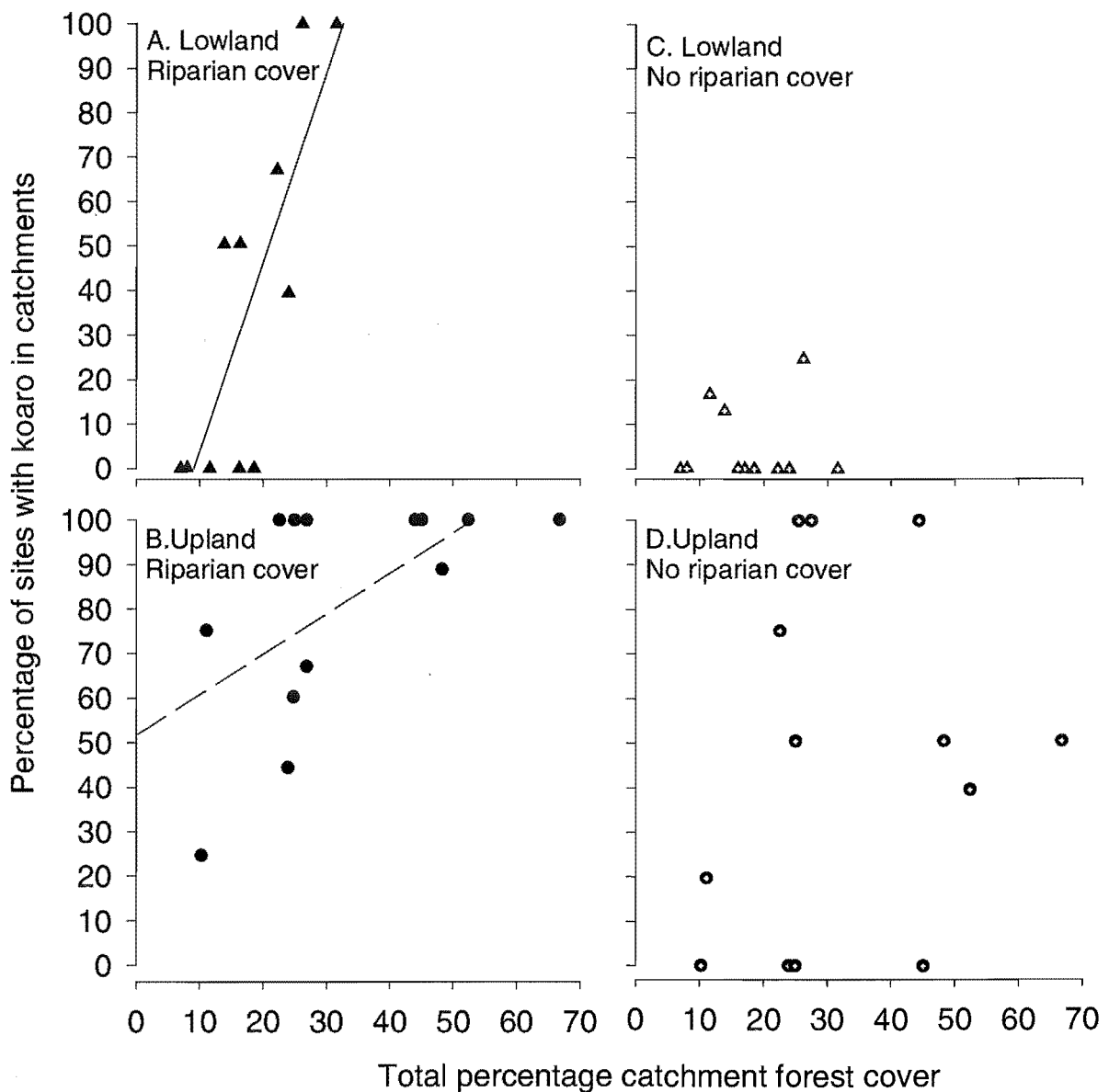


Figure 2.3 Relationship between percentage of sites with koaro and total percentage forest cover in four subgroups of catchments varying in the position of forest and two riparian cover categories: (A) Lowland with riparian cover, (B) upland with riparian cover, (C) lowland without riparian cover, and (D) upland without riparian cover. The equations for the regression lines are (A) $y = -1.53 + 4.92x$ ($r^2 = 0.646$, $P = 0.002$) and (B) $y = 0.49 + 1.28x$ ($r^2 = 0.381$, $P = 0.02$). No significant relationships were found between catchment forest cover in lowland (C) and upland forest (D) dominated catchments and percentage of sites with koaro in the absence of riparian cover. Each point in the graphs represents a catchment. Overlapping points have been dithered for visual clarity.

2.5. Discussion

The aim of this study was to determine how landscape features influenced the distribution of koaro in Banks Peninsula streams, and at what scales these factors operated. My results indicate the presence of riparian forest cover, the position of forest within catchments and the total amount of catchment forest cover, regardless of forest type, influence the overall distribution of koaro. However, the catchment-scale variables were most influential when local riparian cover was present

Wilson (1994) reported indigenous vegetation once covered 98 percent of Banks Peninsula, but most of the land above 300 m.a.s.l. is now dominated by tussock, whereas ryegrass and cocksfoot grazed by sheep and beef cattle is the dominant vegetation on many of the valley floors (Harding 2003). In my study catchments, forest cover ranged from 7.8 % to 58.3 %, and the decrease in forest cover was paralleled by an increase in fragmentation of the forests. Agricultural land use practices and deforestation have been identified as major sources of sediment and nutrient input to streams in New Zealand and elsewhere, and are considered to be important factors limiting usable fish habitat (Russell *et al.* 1998, Huryn *et al.* 2002, Quinn & Stroud 2002, Sutherland *et al.* 2002), although riparian buffer strips can reduce the inputs and help retain substrate integrity in streams (Ryan 1991). On Banks Peninsula, windblown loess may be a huge potential source of fine sediment input. Thus, it is not surprising that koaro, a fish commonly associated with high habitat quality, occurred more frequently in catchments with higher proportions of forest cover and riparian forest cover.

In the absence of riparian forest cover, catchment forest cover had little effect. When riparian forest cover was present, two patterns emerged, depending on the predominant location of forest within a catchment. In catchments with predominantly lowland forest there was a strong positive relationship between koaro occupancy and the total percentage of catchment forest cover. The positive response to the presence of lowland forest may be because it improves the quality of the most accessible habitat for koaro on Banks Peninsula. In catchments with predominantly upland forests, the slope of the relationship between koaro site occupancy and percentage forest cover and the proportion of variance explained by the regression were lower. However, when the presence or absence of riparian cover was not included, I found that streams draining catchments with forests situated in upland areas had higher proportions of sites with koaro, and all catchments with forest predominantly in upland areas contained koaro. Thus, my

results indicate that koaro are sensitive to the overall location of forest within catchments, but the strength of their response depends on the presence of forested riparian vegetation.

The presence of riparian forest cover may be important to koaro because they take a variety of terrestrial invertebrate prey, in addition to aquatic species (Main & Winterbourn 1987, McDowall 1990, Hayes 1996, McDowall 2000). A loss of, or change in, riparian cover can reduce the abundance and diversity of terrestrial invertebrates both in and outside the stream, thereby reducing food availability to fish (Cadwallader *et al.* 1980, Edwards & Huryn 1995, Edwards & Huryn 1996). Riparian forest cover may also be important for creating fish habitat. In New Zealand, removal of riparian vegetation has been associated with declines in woody debris, and has influenced the pool-riffle formation of some streams draining native forests (Baillie & Davies 2002). Not only do fallen riparian trees provide in-stream refugia, but they also ameliorate stream morphology by creating pool and riffle habitats for fish. Likewise, in-stream woody debris is likely utilised by koaro as daytime refugia (McDowall 1990). Therefore, koaro may be less likely to occupy sites without riparian cover because of a reduction in in-stream habitat.

It has been argued that upland areas often contain the last vestiges of intact stream habitats because of their poor agricultural potential, but they may become progressively isolated from their lower reaches by development lower in the catchment (Pringle 2001, March *et al.* 2002). Using this reasoning, if lowland areas were modified such that most forest was in upland areas, one might have expected a diadromous fish like koaro to have difficulty accessing upland streams because of the modified lowland reaches they must negotiate during their migration. This was not the case in my study because koaro occurred more frequently in catchments with most forest in upland areas. The relatively low altitudes, gradients, short distances from the sea, and the absence of dams and weirs in my study catchments, mean that migratory barriers were unlikely to influence the koaro distribution patterns observed. However, it is still difficult to determine why catchments with forested upland areas had higher proportions of sites with koaro than catchments with forested lowlands. It may be that streams in forested upland areas are important to koaro because they provide suitable spawning habitat. However, this cannot be the whole explanation because koaro were present in lowland forested streams and less common in non-forested upland streams.

One likely explanation for the high occurrence rate of koaro in catchments with upland forest is the influence of upland forest on habitat quality throughout the catchment. Because of

their steep slopes, upland streams are sensitive to land use changes (Gomi *et al.* 2003) and fine sediments from surface runoff are frequently transported to headwater streams and subsequently down the catchment. Sediment originating from these headwater streams may later degrade in-stream habitat throughout the catchment (Berkman & Rabeni 1987, Gregory *et al.* 1991, Montgomery & Buffington 1998). Fine sediment is likely to influence koaro by impacting aquatic invertebrates that provide food, hindering feeding (particularly at the whitebait stage) through increased turbidity and clogging of substratum interstices that provide cover for koaro (Boubee *et al.* 1997). Having forested upland areas may protect sensitive headwater streams from these impacts, thereby reducing habitat degradation throughout the catchment, resulting in higher site occupancy as I have observed, regardless of whether riparian vegetation is present. It may also be that woody debris from upland forests is transported downstream, in turn creating aquatic habitat favourable for koaro.

Although I was able to describe the distribution patterns of koaro on Banks Peninsula in detail using my methodology, the underlying mechanisms resulting in the observed distribution are still unclear. While the presence and distribution of vegetation are implicated, other factors may also be important. For example, banded kokopu (*Galaxias fasciatus* Gray), a closely related amphidromous fish, are also known to have a negative influence on the distribution of koaro (Chapter Three), and may displace it from otherwise suitable habitats in lowland reaches. However, while there is a need to understand the specific mechanisms contributing to koaro distribution patterns, such observed distribution patterns can still be used to guide management.

In the present study I assessed variables that can be quantified rapidly using a GIS without the need for extensive field sampling to evaluate the influence of land use on the distribution of a diadromous fish. My results suggest the need for stream fish management that better integrates both landscape and local processes. Without immediate protection of stream margins by riparian vegetation, larger-scale effects of catchment forest cover, such as lowland versus upland forest position, and amount of catchment forest cover, had no impact at local scales. Hence, based on my observations, the aim for koaro management should be not only to increase the overall forest cover of catchments, but also to afforest the riparian zone to increase the overall proportion of sites that potentially will support koaro. In catchments with lowland forests the primary aim should be to afforest the riparian zone, whereas in catchments with upland forests the aim should be to increase the overall proportion of catchment forest cover.

The results of my study indicate that catchment scale processes have relevance for processes at local scales, but processes at the two scales interact to affect koaro distribution. Similarly, catchment scale features interact with reach scale features including riparian vegetation to determine the distribution of non-migratory fishes, such as cyprinids, campostomids, centrarchids, and percids in the Northern Lakes and Forest Ecoregion in the north-central United States (Wang *et al.* 2003). Together, these studies reinforce the need for more landscape oriented research to better understand the distributional patterns of fishes.

Chapter 3. Spatial modelling and habitat quantification for two diadromous fish in New Zealand streams: a GIS – based approach with application for conservation management

3.1. Summary

I developed logistic regression models from data on biotic and abiotic variables for 172 sites on Banks Peninsula, New Zealand, to predict the probability of occurrence of two diadromous fish, banded kokopu and koaro. Banded kokopu occurrence was positively associated with small streams and low intensity land uses (e.g. sheep grazing or forested), while intensive land uses (e.g. mixed sheep and cattle farming) and lack of riparian forest cover impacted negatively on occurrence at sampled sites. Also, if forests were positioned predominantly in lowland areas, banded kokopu occurrence declined with increasing distance to stream mouth. Koaro occurrence was positively influenced by catchment forest cover, high stream altitudes, and areas of no farming activity or mixed land uses. Intensive land uses, distance to stream mouth, and presence of banded kokopu negatively influenced koaro occupancy of stream reaches. Banded kokopu and koaro presence was predicted in 86.0 % and 83.7 % agreement, respectively, with field observations. I used the models to quantify the amount of stream reaches that would be of good, moderate, and poor quality, based on the probability of occurrences of the fish being greater than 0.75, between 0.75 and 0.5, or less than 0.5 respectively. Hindcasting using historical data on vegetation cover undertaken for one catchment, Pigeon Bay showed they would have occupied most of the waterway prior to anthropogenic modification. I also modelled potential future scenarios to project potential fish distribution.

3.2. Introduction

An understanding of local habitat parameters such as water depth, flow velocity, and substrate characteristics underpins models used to describe fish distribution and abundance at local scales (Gore *et al.* 1991, McDowall 1993, Lammert & Allan 1999, Vilizzi 2002). Models for the assessment of fish communities have been developed in North America (Karr 1981), and predictive models for the presence/absence of native fish and invertebrates are in use in New Zealand (Broad *et al.* 2001b, Joy & Death 2001, Joy & Death 2002, Joy & Death 2004). For example the Index of Biotic Integrity (IBI) assesses the biotic integrity of impacted sites based on non-impacted reference sites nearby (Karr 1981, Fausch *et al.* 1984, Miller *et al.* 1988, Karr 1991, Hoefs & Boyle 1992). The IBI metrics include species composition, species richness, fish abundance, trophic composition, fish reproductive guilds, and fish condition (Karr 1991). Assessments must be undertaken by experienced biologists who set standards based on knowledge of the regional biota (Karr 1991), a task that may require intensive monitoring over an extensive period of time (Yoder & Smith 1996). While effective for inland streams, IBI assessments may be less useful when assessing the distribution of diadromous species, such as the predominantly diadromous fish fauna of New Zealand, where the influences of distance from the sea, altitude (McDowall 1993, McDowall 1996a, McDowall 1998a, McDowall 1998b, Joy & Death 2001, Joy & Death 2003), and anthropogenic barriers to fish migration have resulted in a breakdown of the relationship between fish occurrences and proximal habitat quality (Joy & Death 2000).

Diadromous fish by nature of their migratory behaviour exhibit continuous distributions, with species abundance tapering off with distance inland and increasing elevations (McDowall & Taylor 2000). Their spatial distributions should consequently be modelled on a species by species basis. I assert that a continuous view of rivers and streams to allow for effective research and conservation of diadromous freshwater fish, as they are sensitive to contemporary land uses and configuration of terrestrial landscape elements throughout catchments.

Diadromy can be divided into three sub-categories (Myers 1949), each of which were progressively refined by McDowall (McDowall 1997a) on the basis of feeding, growing, and reproductive biomes. In anadromous fishes, the feeding and growth biomes are at sea, while the reproductive biome is in fresh water. Catadromous fish feed and grow in fresh water, then migrate to sea as adult fish to reproduce. Amphidromous fishes migrate to sea as larvae soon

after hatching, and then migrate back to a freshwater environment as post-larval juvenile fish. With perhaps the exception of anadromous fishes that return to their natal streams, the contemporary recruitment and distribution of catadromous and amphidromous fish to streams is likely to reflect large scale contemporary land uses and environmental pressures as well as habitat features. These fish can undertake long-distance movements that cease when suitable habitat and resources are encountered; a migratory movement termed ranging behaviour (Dingle 1996). Because the presence of amphidromous fish in a reach is related to contemporary land use it should not be difficult to calculate the probability of encountering a diadromous fish provided barriers to dispersal are considered.

Both banded kokopu (*Galaxias fasciatus* Gray, 1842) and koaro (*G. brevipinnis* Günther, 1866) are amphidromous species (McDowall 1996a, McDowall 1998a, McDowall 1998b), which potentially allows them access to a variety of habitats during migration from the marine environment back to adult freshwater habitats. Both species have the ability to form land-locked populations, but on Banks Peninsula, South Island, New Zealand, the adults of these species are restricted to lotic environments. Koaro and banded kokopu are exceptional climbers, with the former found at the highest elevations of any New Zealand's native freshwater fish (McDowall 1990). Banded kokopu favours pools and backwaters in first to third order streams with extensive riparian vegetation (McDowall 1990). Koaro, while found in tussock streams at high altitudes, also favours cobble-boulder substrates in streams with extensive riparian vegetation. Both species are generalist predators feeding on a variety of terrestrial and aquatic invertebrate prey (Main & Lyon 1988, McDowall 1990). Koaro and banded kokopu contribute significantly to a recreational and commercial catch of the migrating juveniles known as "whitebait" (McDowall 1990). Koaro and banded kokopu are still common throughout New Zealand and are currently not listed as threatened (Hitchmough 2002), but their adult habitat is thought to have been greatly reduced by changes in land use from native forest to pasture (Hanchet 1990, Rowe *et al.* 1999).

Statistical methods not dependent upon continuous input variables, such as binary logistic regression models, can be used effectively to predict dichotomous outcomes where there is a linear relationship between independent and dependent variables (Hosmer & Lemeshow 2000), and have been used successfully to predict presence of longfin (*Anguilla dieffenbachii* Gray, 1842) eels in a New Zealand river (Broad *et al.* 2001b). The goal of logistic regression analysis is the same as for any other model building techniques: to establish the relationship between an

outcome variable (presence/absence of the focal species) and a set of independent variables (continuous or discrete) that are biologically reasonable, yet parsimonious (Hosmer & Lemeshow 2000). I applied binary logistic regression techniques with leave-one-out cross validation procedures to model the spatial distribution and quantify the amount of suitable habitat for two species of diadromous fish, koaro and banded kokopu, in streams on Banks Peninsula. The logistic regression approach may aid understanding the influence forested riparian zones, catchment vegetation, as well as specific land uses have on the distributions of diadromous fish, and highlight the influence of habitat/catchment modification and configuration of landscape elements on migratory fish distributions. Additionally, the approach may elucidate the influences of abiotic factors such as distance from source, altitude, and potential barriers encountered in terms of steep slopes encountered. This would illustrate that the ecological dynamics of the system may respond to the configuration of patches in the landscape, even if the relative proportion of patch-types in the system remain the same (Fausch *et al.* 2002).

3.3. Materials and Methods

3.3.1. Study Area

Banks Peninsula is an 1102 km² promontory located between latitudes 43°33'S and 43°54'S on the eastern side of South Island, New Zealand (Figure 3.1a). The Peninsula consists of a series of volcanic cones of mid-Miocene basalt (Weaver *et al.* 1985, Sewell 1988, Sewell & Weaver 1990, Wilson 1992). The Peninsula rises to 919 m a.s.l. and is dissected by more than 100 isolated, short, steep catchments (Harding 2003). The eroded slopes of the volcanoes have been mantled by wind deposited loess derived from the Southern Alps, which lie some 70 km to the West, during the interglacial periods of the past two million years (Sewell & Weaver 1990). Loess represents a potential fine sedimentary input to streams, and may degrade in-stream habitat for fish favouring cobble-boulder substrates.

Prior to human arrival, Banks Peninsula was almost completely vegetated in Podocarp/ hardwood forests on wetter Western slopes and Southern beech (*Nothofagus* spp.) in the east (Wilson 1992). However, human activity has resulted in deforestation of much of Banks Peninsula. Prior to 1850, Maori had cleared some of the forest on the peninsula (Petrie, 1963). Most of the remaining forests were felled by Europeans within a period of 50 years after the establishment of Christchurch in 1850 (Petrie 1963). Kanuka (*Kunzea ericoides* A. Rich), tussocks (*Carex* spp.), and scrub, including the invasive weed gorse (*Ulex europaeus* L.), have

spread into some of the cleared land. Isolated fragments of old growth and regenerating podocarp (*Podocarpus* spp.) forest are found in a few valleys, scenic reserves, and in the steeper headwaters of some streams (Wilson 1992).

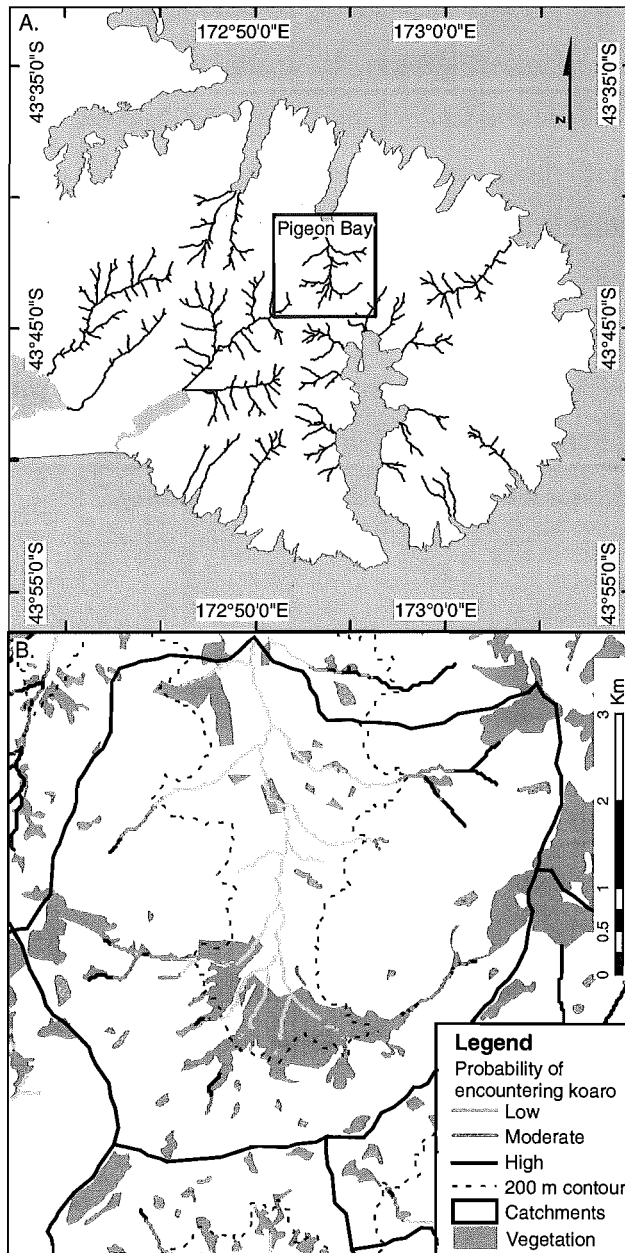


Figure 3.1 (A) Location of the 24 sampled catchments on Banks Peninsula, South Island, New Zealand, with a box (B) showing the Pigeon Bay catchment. Catchments with the majority of forest cover above the 200 m contour line are classified as being upland forested catchments. Catchments are delineated according to topographic divides. Probability of encountering koaro was derived using backward conditional logistic regression procedures, and mapped by applying the probability equation (Eq. 1) to the database associated with the digital hydrology network.

3.3.2. Fish Sampling and Habitat Assessment

I used a geographical information system (GIS: ArcView 3.2 and ArcMap 8.0) to identify stream segments associated with different vegetation cover classes, and sampled stream reaches in proportion to the overall percentage forest cover in catchments. To select the stream reaches to be sampled I randomly identified reaches with the appropriate land cover, with the restrictions that stream segments should have easy access upstream or downstream of roads, and larger catchments should have proportionally more reaches sampled. The stratified approach allowed for accurate representation of the land uses within the study area, covering a representative range of elevations, slopes, and distances from the sea for each catchment.

Records of fish occurrence for a total of 172 stream reaches in 24 catchments were included in my inventory. Of these, 37 records were sourced from the New Zealand Freshwater Fish Database (NZFFD; <http://fwdb.niwa.cri.nz>), while the rest were sampled specifically for this study. One-hundred-and-thirty-six stream reaches were sampled by single-pass qualitative electric fishing and 36 by spotlighting techniques. All newly sampled stream reaches were sampled in an upstream direction, and were 50 metres in length. Electro-fishing was conducted using a Kainga EFM 300 backpack electric fishing machine (NIWA Instrument Systems, N. Z.), producing 400–600 V pulsed DC (pulse width ~ 3 ms, 60 pulses·s⁻¹), and fish were captured in hand held stop or dip nets. Where overhanging vegetation prevented the use of electro-fishing, spotlighting was used. All available habitat types within the sampling reach (i.e., riffle, pool, backwater, and runs) were sampled at each site.

3.3.3. Digital Data Collection and Preparation

For all sampled stream reaches, data on riparian vegetation (within 5 m of water's edge), canopy-cover, presence of migratory barriers and species occurrences were collected from field observations or from information contained on the NZFFD, and ground referenced in the field using a hand-held global positioning unit (GeoExplorer 3) to assess the accuracy of the digital landcover database layers. A 25 m resolution digital elevation model (DEM) of the study area was used to create a slope grid, which in turn allowed for flow direction and flow accumulation grids to be produced. In combination, these grids allowed for automated delineation of catchments in my study area according to direction and accumulation of flow, along with topographic divides. The DEM was also used to establish upland and lowland positioning of forests by plotting the cumulative percentage of cells in the DEM with increasing elevation, and

establishing the breakpoint at 200 metres above mean sea level, as fifty percent of the landmass of Bank Peninsula was accounted for when this elevation was reached. The delineated catchments were then used to intersect digital landcover maps (New Zealand Landcover Database 1 Version 2) of the study area to allow for calculation of proportion of catchment land uses within catchments. The predominant forest position within catchments was determined by draping the landcover maps over the DEM, and if over fifty percent of the forest cover was in lowland areas, the catchment was categorised as a lowland forested catchment. A digital version of the hydrology network (Map sheet 262-13 1:50,000 Topographic Vector Data) was then cut according to the landuses, and further sliced into 25 m segments before rebuilding the T-F node topology (To and From node) that establishes the connectivity in the network. The underlying elevations and slopes of the hydrology network were then sampled from the DEM. Maximum downstream slopes, distances from sea, and length of streams flowing through various land use types were propagated up and down the stream network using the connectivity of stream segments established by the T-F topology. This propagation allowed values for the variables to be determined for any 25 m stream segment. Specific land uses with respect to farming practices were taken from AgriBase 2000, a national spatial farm database originally developed by MAF Quality Management Ltd, and contains information on the dominant farm types, farm sizes, and land parcels that make up the farm.

3.3.4. Data Analysis

Logistic regression examines the functional relationship between a categorical dependent variable and independent variables that may be either discrete or continuous in their distribution (Trexler & Travis 1993). Logistic regression works particularly well with binary data, such as presence/absence data, and can be used to generate predictive equations for the presence or absence of the focal species. In logistic regression, dichotomous and other categorical variables receive a numerical code, and in the statistical analysis one of the codings for each dichotomous variable is treated as a reference by which the regression coefficients for the rest of the categories are calculated. Subsequently all sites included in the model are classified and cross validated using leave-one-out cross validation procedures (Fielding & Bell 1997). Data on catchment sizes, reach slopes, maximum downstream slopes, stream reach altitudes, distances from stream mouth (sea or lake), and proportion catchment forest cover were derived from the GIS. Proportion catchment forest cover was arcsine transformed, whereas distance measures, such as

distance from source and amounts of stream reaches flowing through various land use types, were square root transformed to obtain normality. The dichotomous variables, such as dominant catchment forest position, riparian cover category, and specific land use were also determined using the GIS. These variables were then analysed using backward conditional binary logistic regression procedures in SPSS (Version 11.0). The resulting coefficients of determination for input variables were then used in a probability calculation using the following equation:

$$P = (e^{a + \beta X}) / (1 + e^{a + \beta_1 X_1 + \dots + \beta_i X_i}), \quad \text{(Equation 1)}$$

where P is the calculated probability of an event, e is the base of the natural logarithm, a is a constant, and β is the correlation coefficient for variable X . Given that I have only 1s and 0s for presence or absence for my dependent variables, the final equation gives a probability of presence in the range of 0 to 1. The base of the natural logarithm raised to the value of the regression coefficient is the value by which the odds of the event change when the i^{th} independent variable increases by one unit. If this value is greater than 1, the odds are increased; if the value is less than 1, the odds are decreased. A value of 1 leaves the odds unchanged.

3.3.5. Pigeon Bay Hindcasting and Forecasting Modelling

To illustrate potential uses of the spatial prediction model, I undertook hindcasting and forecasting modelling of Pigeon Bay (Figure 3.1b), a 26.3 km² catchment on the northern part of Banks Peninsula. I digitized landcover maps for three time periods, 1860, 1880, and 1950, drafted by Petrie (1963) and projected them to New Zealand Map Grid 2000, and used them as historical input for hindcasting of koaro and banded kokopu distributions with respect to land cover changes. These digitised maps allowed for estimation of amount of forest cover and derivation of the spatial configuration of forest cover within the study catchment. For forecasting scenarios, I modelled specific land use changes based on digital land use data from AgriBase, a national spatial farm database indicating the dominant farm type classification as of February, 2000. I also modelled four potential future scenarios based on potential changes in current land uses of Pigeon Bay. The hindcasting, present day and forecasting scenarios for Pigeon Bay are outlined below.

3.3.6. Pigeon Bay Scenario 1860

No specific information on the amount of forest cover of Pigeon Bay for the period prior to 1860 is available. However, estimated from Petrie's (1963) forest cover map for 1860, the amount equated to 91 % forest cover for this period. This amounted to 22.6 km of forested stream reaches, or approximately 83 % of streams located in forested areas. For this 1860 scenario, I assumed very little commercial farming activity was taking place and that the open land had been cleared for the purpose of obtaining building materials for nearby Lyttelton (Ogilvie 1992).

3.3.7. Pigeon Bay Scenario 1880

By 1880, the forest cover was reduced to 45 % of the catchment area. Taking into account the spatial configuration of forest based on the digitised maps of Petrie (1963), this equated to 4.6 km of forested stream reaches. Again, for this early time period, I made no assumptions as to particular farming activities that might have been established, although there was some indication that dairy farming was taking place in the catchment (Ogilvie 1992).

3.3.8. Pigeon Bay Scenario 1950

In 1950, only 20 % of the catchment remained forested (from Petrie 1963). Considering the spatial configuration of forest cover within the catchment, this equated to 6.8 km of forested stream reaches. For this time period, the main farming activity was intensive dairy farming, with the local cheese factory producing over 200 tonnes of cheese per annum (Ogilvie 1990, Ogilvie 1992).

3.3.9. Pigeon Bay Scenario Present

This scenario gives the present day situation of Pigeon Bay and is a part of the original distribution model developed. At present, there are 7.1 km² of dairy pastures, 3.3 km² of sheep pastures, and 12.3 km² of mixed sheep and dairy pastures when 3.6 km² of existing forested cover has been accounted for (from AgriBase 2000).

3.3.10. Pigeon Bay Scenario One

In this scenario, six parcels of mixed sheep and dairy pasture were converted to forest. This land conversion would result in a net forest gain of 3.7 km², more than doubling the present day situation with respect to forest cover. When the spatial configuration of this gain in forested

landcover is accounted for, 3.2 km of stream reaches, that at present have no forest cover along the stream margins would have the riparian zone afforested, resulting in 11.6 km of forested stream reaches within the Pigeon Bay study catchment. What would the result of this land conversion be for koaro and banded kokopu?

3.3.11. Pigeon Bay Scenario Two

Fencing of waterways to prevent animals from trampling stream banks is one way in which streams and their biota can be protected from the direct negative effects of farm animals. If one were to protect streams with a 10 m fenced off buffer on both sides of the stream that would then be allowed to afforest, what would the modelled benefit be to banded kokopu and koaro? A 10 m forested buffer around all stream reaches that at present do not have riparian forest cover would result in a net gain of 2.1 % forest cover within the Pigeon Bay catchment.

3.3.12. Pigeon Bay Scenario Three

Streams with protected forested margins may have the indirect effects, such as runoff from nearby farms, reduced. If both the direct (animals trampling stream banks) and indirect effects of land uses were eliminated, then what would the modelled benefit for the two diadromous fish species be?

3.3.13. Pigeon Bay Scenario Four

How could one potentially restore the streams of Pigeon Bay to a level equivalent of 1860 for both species of diadromous fish, and still leave enough room for present day activities? Can one establish a balance of specific land uses that would allow for this?

3.4. Results

3.4.1. General results

Variables included in the logistic regression analysis for the presence or absence of banded kokopu and koaro are given in Table 3.1. The table shows that the majority of sampled sites were in areas of no farming. However, mixed sheep and cattle grazing was the immediate land use at 33 sites, with another 15 and 5 in sheep or cattle paddocks respectively. Most sampled sites were in second (55 %) and third order (28 %) streams, although first order headwater streams (17 %) were also represented (Table 3.1).

71 sites had riparian forest cover (within 5 m of water's edge), whereas 101 were in open areas devoid of riparian vegetation other than grasses. Most of the streams drained directly into the ocean, although forty sites were only accessible to migratory fish through lakes (Table 3.1). One third of the sampled sites were in catchments with forest predominantly in lowland areas (below 200 m), and the remaining two thirds in catchments with predominantly upland forests (above 200 m) (Table 3.1). Banded kokopu was present at fifty-five sites.

Variables retained in the models and the significance values from backward conditional binary logistic regression for presence of banded kokopu and koaro are given in Table 3.2. The regression coefficients of determination for the occurrences of banded kokopu and koaro at sampled sites explain 72.9 % and 62.5 % of the variance in site occupancy by the two species, respectively. The models performed well for both species, with 86.0 % of banded kokopu and 83.7 % of koaro sites classified correctly using leave-one-out cross-validation techniques (Table 3.3). Banded kokopu were more likely to be absent from stream reaches flowing through areas of cattle farming, mixed sheep and cattle farming, or having no riparian forest cover along the stream margins (Table 3.2).

Additionally, if the majority of forest cover within catchments is predominantly in the lower parts of catchments banded kokopu are more likely to be absent. There was also a negative influence of distance from stream mouth (to sea or lake) on occurrence of banded kokopu at sites. Banded kokopu were more likely to be present in small streams flowing through sheep pastures than cattle pastures.

For koaro, there were positive influences on occurrence at sampled sites with increases in proportion of catchment forest cover, higher stream reach altitudes, and mixed sheep and cattle farming (Table 3.2). Koaro site occupancy was also negatively associated with distance from source of juveniles, cattle farming, and furthermore by sheep farming. Of particular interest was a strong negative interaction between the presence of banded kokopu and presence of koaro, where koaro were more likely to be absent when banded kokopu were present.

Table 3.1 Backward conditional binary logistic regression procedures for both discrete and continuous variables. Within categories, site records were assigned a numerical code according to the specific sub-category of the variable. Most continuous variables for all sites in my inventory were transformed to obtain normality.

Discrete variables		Frequency	Numerical code
Farming activity (Agribase 2000)	No	119	0
	Sheep	15	1
	Cattle	5	2
	Sheep and cattle	33	3
Strahler's stream order (1:50,000)	First order	29	1
	Second order	94	2
	Third order	49	0
Riparian zone	Forested	71	0
	Non-forested	101	1
Stream mouth	Lake	40	0
	Sea	132	1
Predominant forest position	Lowland (below 200 m)	58	1
	Upland (above 200 m)	114	0
Banded kokopu	Absent	117	1
	Present	55	0
Continuous variables		Transformation	
Proportion catchment forest cover		Arcsine square root	
Maximum slope downstream of sampled site (deg)		None	
Mean stream slope at location of sampled site (deg)		None	
Length of stream downstream of sampled site (m)		Square root	
Mean stream reach altitude at sampled site (m)		None	
Sheep farming upstream of sampled site (m)		Square root	
Sheep farming downstream of sampled site (m)		Square root	
Dairy farming upstream of sampled site (m)		Square root	
Dairy farming downstream of sampled site (m)		Square root	
Mixed sheep and dairy upstream of sampled site (m)		Square root	
Mixed sheep and dairy downstream of sampled site (m)		Square root	

Table 3.2 Backward conditional binary logistic regression results for presence of banded kokopu and koaro at a site. β represent the estimated regression coefficients for the predictor variables, with the standard errors, S.E., given. The Wald statistic is the ratio of the β to S.E. of the regression coefficient squared. Reference conditions have more degrees of freedom as they are used as reference for the estimation of coefficients for the non-reference conditions. The significance of each variable is given by the p -value. The $\text{Exp}(\beta)$ is the predicted change in odds for a unit increase in the predictor variable.

Banded kokopu	β	S.E.	Wald	df	p -value	$\text{Exp}(\beta)$
Stream order (1:50,000)						
First order	2.998	1.163	6.601	1	0.010	19.837
Second order	3.191	1.091	8.553	1	0.003	24.319
Third order [†]			8.554	2	0.014	
Commercial land use activity						
None [†]			11.133	3	0.011	
Sheep farming	1.602	0.784	4.175	1	0.041	4.961
Cattle farming	-0.661	1.367	0.234	1	0.629	0.516
Sheep and cattle	-2.558	1.103	5.379	1	0.020	0.077
Riparian zone non-forested	-1.939	0.552	12.319	1	< 0.001	0.144
Lowland forest position	-1.031	0.518	3.965	1	0.046	0.357
Downstream length	-0.041	0.009	23.290	1	< 0.001	0.959
Koaro	β	S.E.	Wald	df	p -value	$\text{Exp}(\beta)$
Commercial land use activity						
None [†]			14.611	3	0.002	
Sheep farming	-2.568	0.839	9.359	1	0.002	0.077
Cattle farming	-3.163	2.082	2.308	1	0.129	0.042
Sheep and cattle	1.298	0.630	4.248	1	0.039	3.660
Banded kokopu present	-3.370	0.640	27.580	1	< 0.001	0.030
Reach altitude	0.016	0.005	12.444	1	< 0.001	1.016
Downstream length	-0.028	0.012	5.524	1	0.019	0.973
Proportion forest cover	7.096	1.641	18.704	1	< 0.001	1207.358
Reference condition [†]						

Table 3.3 This classification table assessed the performance of my model by cross-tabulating the observed presence/absence of banded kokopu and koaro categories with the predicted presence/absence of the two species from logistic regression procedures. For each case, the predicted response was the category treated as 1, if that category's predicted probability was greater than specified probability cut-off of 0.5. Cells on the diagonal from top-left to right-bottom were correct predictions. Cells on the opposite diagonal, from bottom-left to top-right, were incorrect predictions.

Observed in the field		Predicted by logistic regression		Percentage Correct
		Banded kokopu Absent	Banded kokopu Present	
Banded kokopu	Absent	104	13	88.9
	Present	11	44	80.0
Overall percentage				86.0

Observed in the field		Predicted by logistic regression		Percentage Correct
		Koaro Absent	Koaro Present	
Koaro	Absent	85	12	87.6
	Present	16	59	78.8
Overall percentage				83.7

The location of streams flowing through the four primary land uses differed both with mean distance from stream mouth and altitude above mean sea level (Figure 3.2). Streams with no commercial land use activity were generally located further inland and at higher altitudes than streams with commercial farming activities. Streams flowing through sheep paddocks were generally located at lower altitudes than any other commercial farming activity, and approximately equidistant from stream mouths compared to cattle paddocks (Figure 3.2). Mixed sheep and cattle areas were closest to stream mouths, but at higher altitudes compared to pure sheep or cattle paddocks (Figure 3.2). Koaro penetrated significantly further inland than banded kokopu, but no significant differences with respect to elevations or maximum slope encountered during migration were found, and both species occupied stream reaches of similar slopes (Table 3.4).

Results of backward conditional binary logistic regression analysis were applied to the digital hydrology network by inserting the probability equation (Equation 1) into its associated database and calculating the probability of occurrences for the two species under the various case scenarios. This allowed for visualisation (Figure 3.1b) and quantification (Figure 3.3) of suitable

stream reaches, based on probability of occurrence in a stream reaches, for the two species. The amount of stream reaches modelled as good ($P > 0.75$), moderate ($0.75 < P > 0.50$), and poor ($P < 0.50$) was predicted to be similar for each species (Figure 3.3), but the spatial distribution of the two species differed considerably, although there was considerable spatial overlap in the streams classified as poor for both species (Figure 3.3 and 3.4). Streams modelled as moderate and good for banded kokopu occurred further inland than streams classified similarly for koaro, whereas poor banded kokopu streams occurred closer to sea (Figure 3.4). Mean altitude for good koaro streams was higher than similarly modelled banded kokopu streams, but streams classified as moderate or poor for koaro were at lower altitudes than similar streams for banded kokopu (Figure 3.4). Mean distance from source for good, moderate, and poor stream classifications for both species occurred at 3.4, 4.2, and 3.3 kilometres from the source of juveniles respectively. Mean altitudes for the same overlapping stream reaches occurred at 299, 238, and 70 metres above mean sea level.

Table 3.4 Descriptive statistics for sites with banded kokopu ($n = 55$) and koaro ($n = 75$) sampled sites.

Variables for banded kokopu sites	Min	Max	Mean	S.E.
Reach slope at sites (deg)	0	59	9.7	1.4
Slope downstream of sites (deg)	8	59	26.2	1.5
Altitudes of sites (m)	102	278	100	8.1
Length downstream of sites (m)	103	6477	1908	165
Variables for koaro sites	Min	Max	Mean	S.E.
Reach slope at sites (deg)	0	59.5	9.4	1.1
Slope downstream of sites (deg)	1	59.5	25.3	1.4
Altitudes of sites (m)	9	374.6	123	10.4
Length downstream of sites (m)	24	16833	3313	448
T-test independent samples between banded kokopu and koaro sites	t-value	df	p-value	
Reach slope at sites (deg)	-0.224	128	0.822	
Slope downstream of sites (deg)	-0.428	128	0.669	
Altitudes of sites (m)	1.647	128	0.102	
Length downstream of sites (m)	2.589	128	0.011	

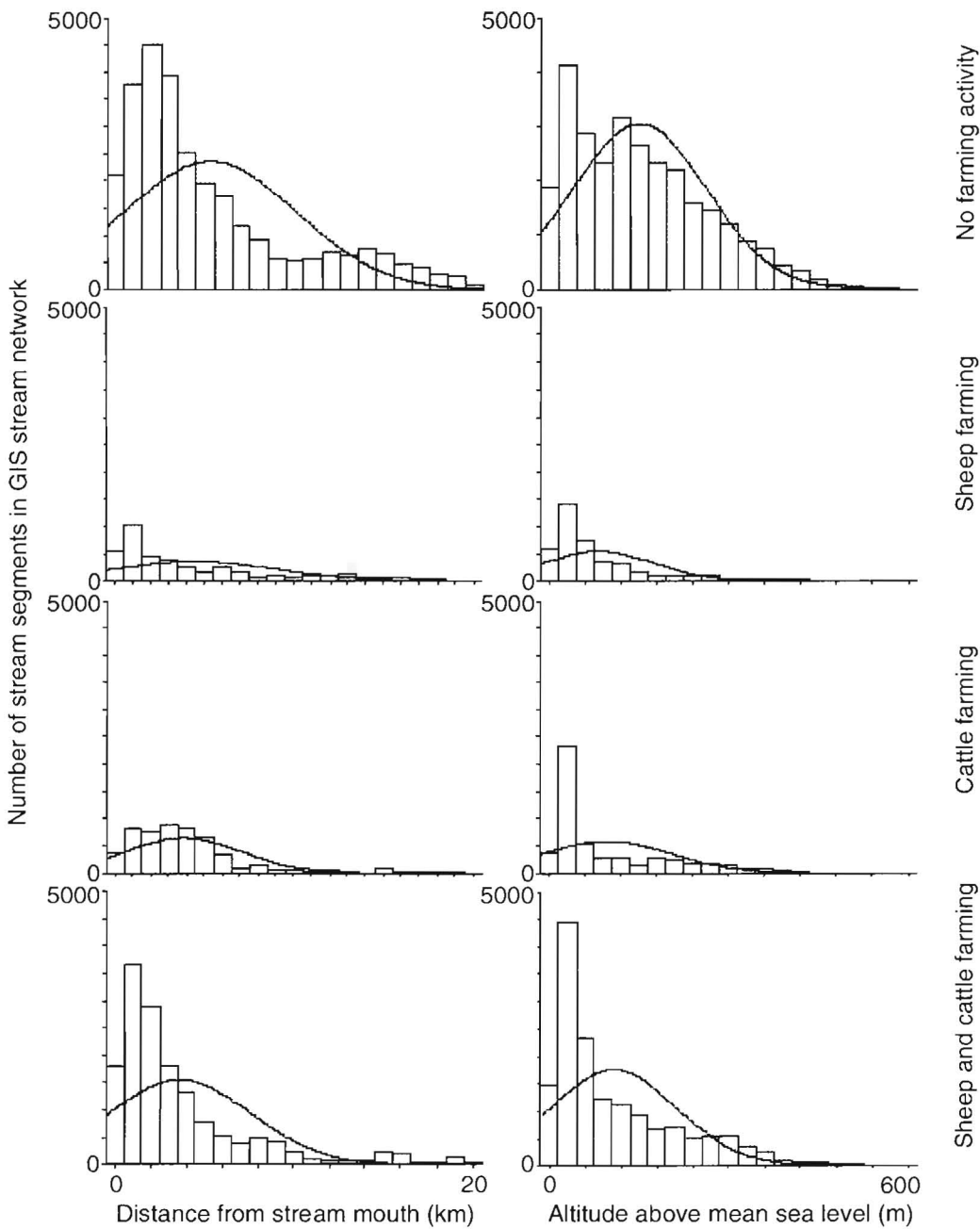


Figure 3.2 Location of stream segments in the GIS hydrology network for Banks Peninsula relative to stream mouth (distance to stream mouth) and elevation above mean sea level (altitude) for four categories of landuses. From top to bottom, stream reaches flowing through areas of no farming, sheep, cattle, and mixed sheep and cattle farming are given. Normal distribution curves are represented by the solid black lines.

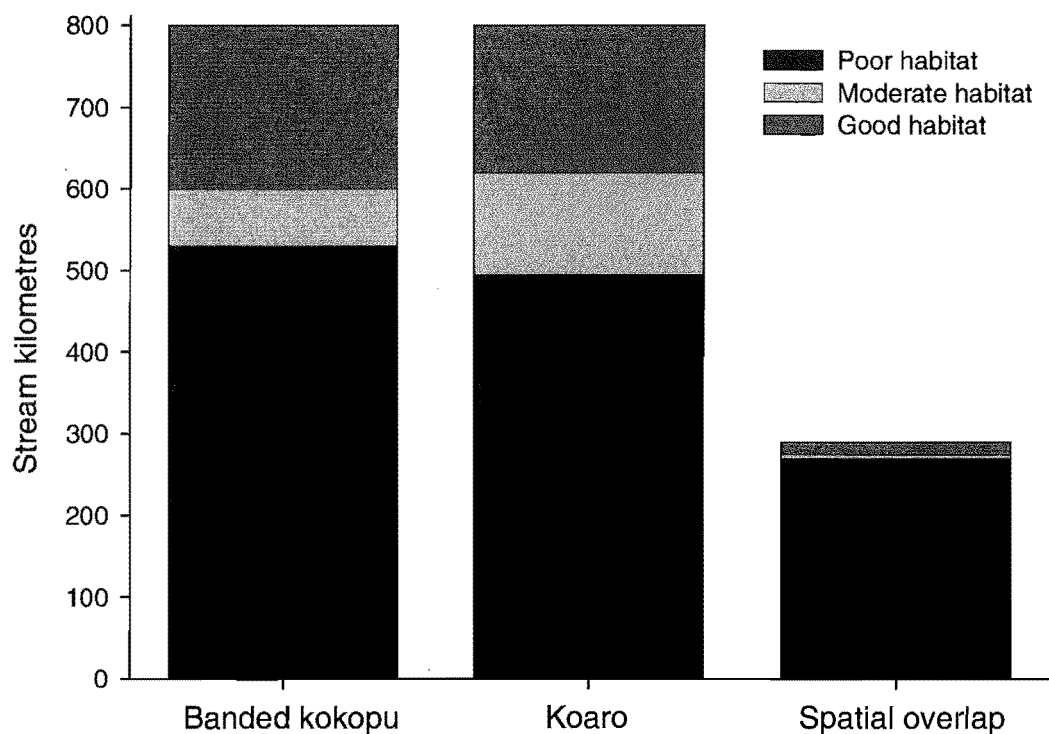


Figure 3.3 Stream reaches were classified as good ($P > 0.75$), moderate ($0.75 < P > 0.50$), and poor ($P < 0.50$) for banded kokopu and koaro according to the calculated probability of encountering the species from the logistic regression procedures. This figure shows the amount of stream kilometres on Banks Peninsula that comprise these categories for the two species. Also shown is the amount of spatial overlap of stream reaches for the three classification categories in kilometres for Banks Peninsula. Note that there is considerable overlap in stream reaches classified as poor for both species, whereas moderately good and good habitat had less overlap.

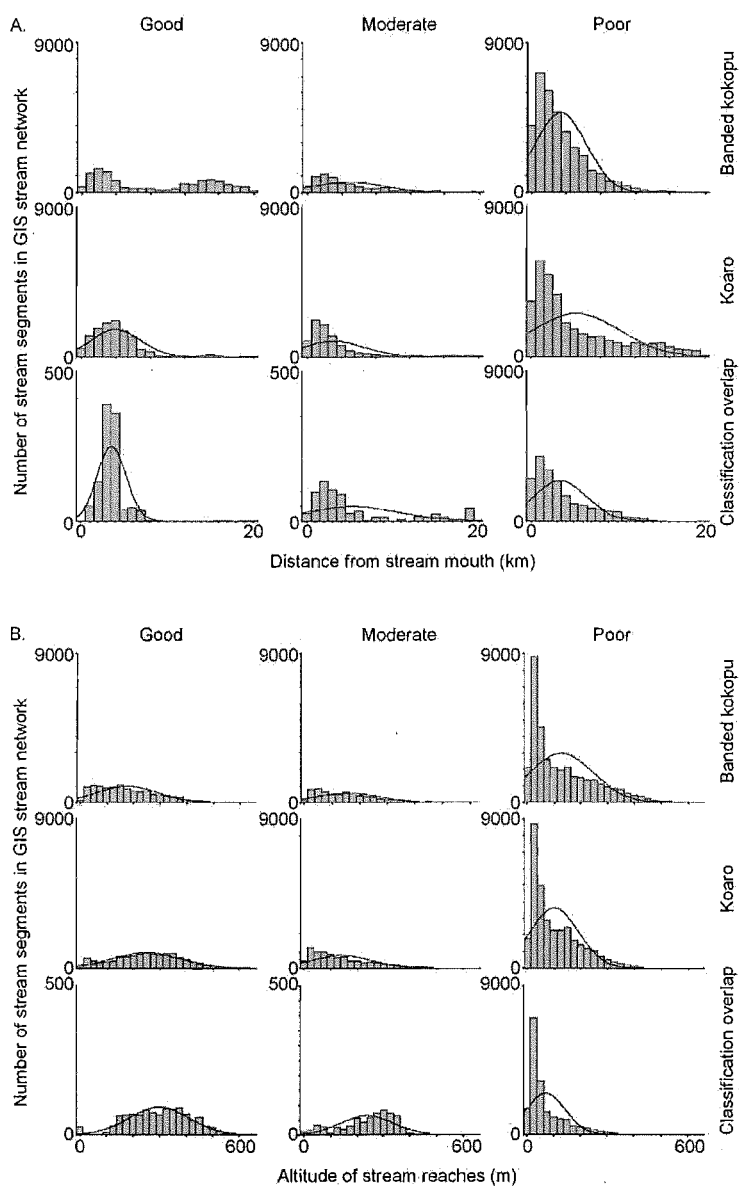


Figure 3.4 (A) The y-axis represents the number of stream segments in the digital hydrology network for Banks Peninsula, all of which are less than 25 metres in length. The x-axis represents categories of distance to stream mouth, either to a lake, or to the sea, giving an indication of the spatial location and the amount of stream segments at given distances from the stream mouth. Normal curves for the distributions are given by solid black lines. From left to right, graphs represent stream reaches classified as good, moderate, and poor for the focal species. From top to bottom, the graphs represent banded kokopu (top), koaro (middle), and the degree of spatial overlap (bottom) of the stream segments for the two species and three

categories. Note that there is little overlap in stream reaches classified as good for the two species, and that the overlap occurs at locations proximal to the stream mouth. The distribution of overlap of moderately good stream reaches occur across the range of distances from the stream mouth, whereas poor stream reaches overlap occur close to stream mouths as well. (B) Again, the y-axis represents the number of stream segments in the digital hydrology network for Banks Peninsula, all of which are less than 25 metres in length. This time, the x-axis represents categories of stream reach elevations above mean sea level. The graphs, from left to right, and top to bottom, are in the same order as in A above. Note that overlap of stream reaches classified as good occur at most elevations, but more so at medium elevations. Similar trends were found for reaches classified as moderately good for the two species. Overlap of poor stream reaches for the two species occurred mostly at low elevations.

3.4.2. Pigeon Bay Hindcasting Results

My modelled case scenarios of koaro and banded kokopu distribution in Pigeon Bay reveal different responses, by both species, to changes in land uses of the catchment (Figure 3.5). In 1860, my model predicts koaro would have been present throughout the catchment, whereas banded kokopu would have occupied a few kilometres less (24.2 km). By 1880, the effects of forest removal probably reduced the amount of good habitat for koaro (18.7 km) more so than for banded kokopu (22.4 km), a species which is more sensitive to the removal of riparian forest cover. However, by 1950, with both forest removal and changes in specific land uses from barren land to cattle pastures affecting both species, the amount of good habitat would have been about equal for both species (4.2 km for banded kokopu and 4.5 km for koaro). The present day distribution further reflects changes in specific land use from cattle farming to other land use types, such as sheep pastures and mixed sheep and cattle pastures, with less negative influence on the distribution of koaro. As a result of these land use changes, suitable stream reaches for koaro (16.4 km) are currently nine times that of banded kokopu (1.8 km) (Figure 3.5).

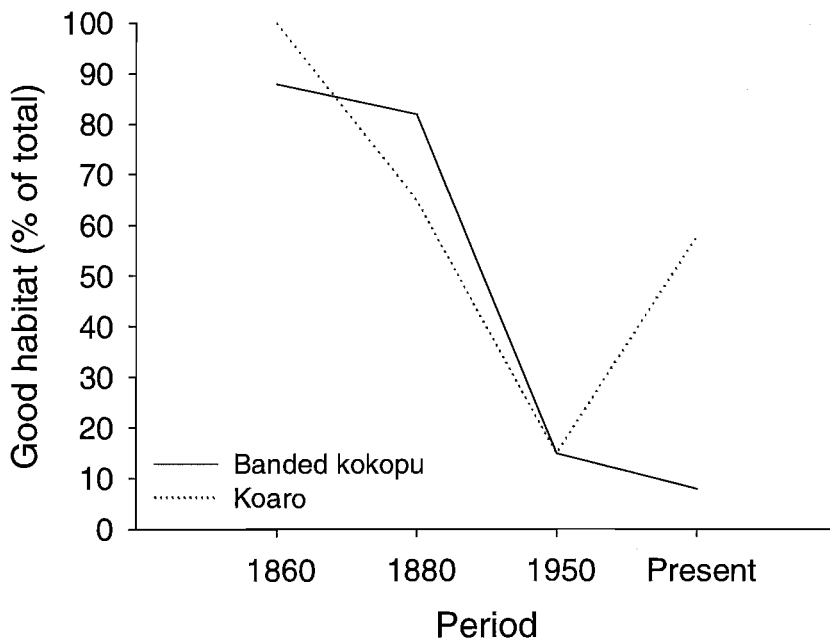


Figure 3.5 Hindcast modelling of banded kokopu (solid line) and koaro (dashed line) distributions at Pigeon Bay, Banks Peninsula, over four dates from 1860 till present. The percentage of stream length in the catchment predicted, by applying probability equation (1) with the predictor variables from logistic regression procedures, to be good habitat (i.e. $P > 0.75$ chance of banded kokopu/koaro to be present) is indicated. Figures for 1860, 1880 and 1950 were calculated using historical information on forest cover and a logistic regression model of contemporary distribution of the two species.

3.4.3. Forecasting Results

The model indicated that banded kokopu required forest cover along stream margins, while the presence of koaro was positively correlated with catchment forest cover, but not with riparian forest cover. Given the strong negative interaction between koaro and banded kokopu, and their different interaction with landscape features, land use could be selectively manipulated to benefit one or both species.

In 1984 New Zealand's Labour government took the step of ending all farm subsidies. Subsequently, marginal grazing land would be expensive to maintain, and a change in land use from mixed sheep and cattle pastures to plantation forestry would not be an unlikely scenario.

With the conversion of six parcels (3.7 km²) of mixed sheep and cattle land uses to forests, the amount of 'good' banded kokopu habitat is predicted to increase by 0.75 km due to the increase in stream length with the riparian forest, and by almost two km for koaro due to the doubling of the proportion of forest cover within the catchment (Figure 3.6; Scenario 1).

With riparian fencing and subsequent reestablishment of forested stream margins, the effect of removing the direct negative (trampling of stream banks) influences of specific farming activities is more pronounced. I predict banded kokopu would benefit more from this scenario, with the amount of good habitat increasing to about 8.5 km. This increase in good banded kokopu habitat would in turn influence koaro distribution negatively. Furthermore, the increase in catchment forest cover would not be sufficient to offset the negative effects of banded kokopu presence, and good koaro habitat would subsequently be reduced to 15.8 km (Figure 3.6; Scenario 2).

If forested riparian corridors were to completely eliminate potential negative effects of surrounding land uses, the amount of good habitat for banded kokopu would return to levels similar to 1860 conditions, with over 24 km of good habitat. However, with very little gain in proportion catchment forest cover and such a dramatic increase in good banded kokopu habitat, koaro habitat would be reduced to an all-time low of 2.5 km (Figure 3.6; Scenario 3).

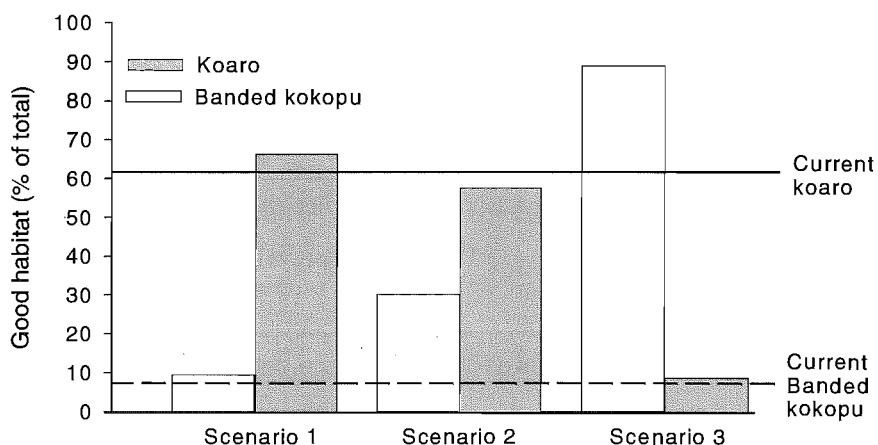


Figure 3.6 Forecast modelling of three scenarios of the amount of stream length at Pigeon Bay, Banks Peninsula, predicted to become good, by using a logistic regression model of contemporary distribution of banded kokopu and koaro under three possible future scenarios for the catchments: 1) conversion of six parcels of mixed sheep and cattle pastures to plantation forestry, 2) afforestation and fencing of the riparian margins with direct effects of livestock removed, and 3) both direct effects of livestock having access to the stream and indirect effects of adjacent land use types removed. Solid black line represents present day status for koaro. Dotted line represents present day status for banded kokopu.

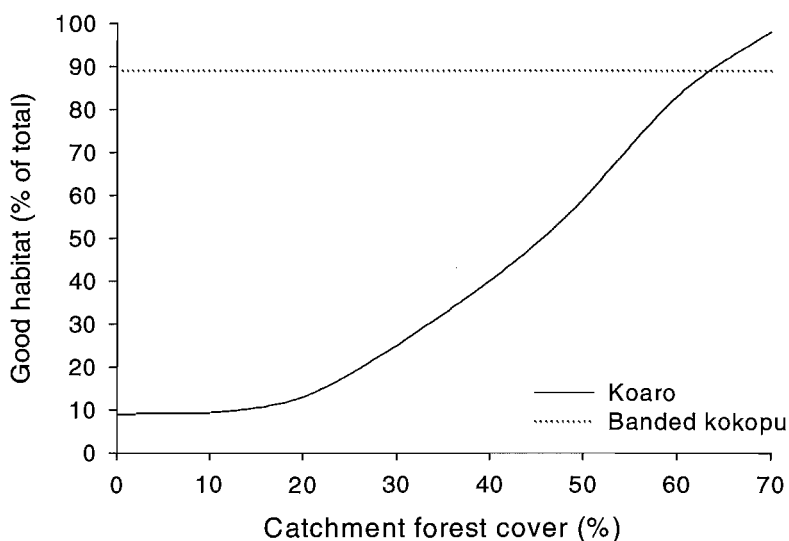


Figure 3.7 If all stream reaches were fenced off and afforested, with no direct effects of land use immediately beyond the riparian corridor, the distribution of banded kokopu is predicted by the logistic regression model to remain constant at around 90 % of the available watercourse of Pigeon Bay (Scenario 3). Koaro, however, responds strongly to the overall amount of forested cover within the catchment as a whole. This graph illustrates how much of the catchment would have to be afforested to offset the negative influence of the presence of banded kokopu on koaro distribution. Solid line show projected response of koaro to increase in catchment forest cover, whereas the dotted line show projected response of banded kokopu.

If the management goal was to achieve equal amount of habitat classified as good for both banded kokopu and koaro, having afforested the waterway margins, it could be accomplished by further planting forests within the catchment, with koaro reaching similar levels to banded kokopu at about 64 % catchment forest cover (Figure 3.7).

3.5. Discussion

3.5.1. Modelling

Typically studies of fish populations have been undertaken at small spatial scales (Minns 1990), following a logical statistical design (e.g. stratified random) that allows the researcher to draw inferences from their sample to the larger population of such sites about relationships between stream fish and their habitat, in turn providing information to managers in hopes of enhancing the focal populations (Fausch *et al.* 2002). In many cases it is not feasible to take measurements and field sample on a case-by-case basis. Consequently models based on sound pre-existing data provide a reasonable and quick alternative for field sampling, provided that the models used accurately predict the distribution of the focal species.

Koaro and banded kokopu, use the entire waterway throughout their life history, from the spawning sites in the headwaters, drifting to the sea as larvae, returning to a freshwater environment as juvenile whitebait, and eventually reaching the headwaters again as mature fish (McDowall 1990). Banded kokopu and koaro distributions on Banks Peninsula are fragmented by anthropogenic habitat degradation, and as with many other species in other parts of the world, the critical habitats required are often created through interactions with intact landscapes (Boutin & Hebert 2002).

In New Zealand, pastoral and production land uses are perceived to be the main causes of degradation of inland waters (Smith 1993, Scarsbrook & Halliday 1999), and similarly, streams on Banks Peninsula are no exception. Agriculture and deforestation alter the physical structure of small streams, either by reducing the amount of woody debris entering the streams and hence altering the depth, substrate composition, and current diversity, or by removing spatial complexity by channelisation (Schlosser 1991). In my study I found that koaro and banded kokopu responded differently to different types of land uses, resulting in distinct, yet not entirely exclusive, stream reaches classified as good, moderate, and poor for the two species based on the calculated probability of encountering the species within a given stream reach. Both species were

negatively influenced by cattle farming. It may be that cattle, by trampling the stream banks and disturbing substrates exert an intense direct negative effect on both species, as well as less intense indirect effects through contamination of streams by faecal material. Responses to sheep farming differed for the two species, with banded kokopu responding positively to sheep farming, whereas koaro was negatively influenced. It is likely that koaro, positively influenced by reach altitudes and less affected by distance from source, is absent from stream reaches with sheep farming because its migratory drive has taken it beyond the areas with this particular land use type, whereas banded kokopu still occupies these lowland reaches. Mixed sheep and cattle farming had the opposite effects of sheep farming on both species. This particular land use type on Banks Peninsula tends to occur at higher altitudes compared to either cattle or sheep farming alone. Thus, it may be that koaro is positively correlated by mixed sheep and cattle farming as a result of its spatial distribution in the landscape, rather than any direct benefit of the land use *per se*, and that banded kokopu is negatively correlated by this land use as it is generally absent from areas where banded kokopu are found.

In view of the many functions of riparian forest cover, it is not surprising that banded kokopu is negatively influenced by the absence of forested riparian margins. It is also possible that riparian cover not only provides for better microhabitat, but also improves the connectivity between suitable upland and lowland habitats. My observations are consistent with the findings of Hopkins (1979), Rowe (1981), and Hanchet (1990) who found banded kokopu and koaro to be common in streams flowing through indigenous forest, but often absent or rare in pasture streams (Hayes *et al.* 1989). It is possible that riparian cover not only provides for better microhabitat for the fish, but also improves the connectivity between suitable upland and lowland habitats.

Koaro is strongly influenced by the overall amount of forest cover within catchments, whereas banded kokopu responded to the proximal presence of forested riparian margins. At the catchment scale, conversion of native forest to plantation forest or pasture alters hydrologic patterns, and may also cause a loss of physical habitat and deterioration of water quality and substrate composition (Smith 1993). Subsequently channel morphology adjusts to these altered conditions, often expressed as a simplification of stream structure, and increased load of fine suspended and deposited sediments (Alabaster 1972, Kauffman *et al.* 1997, Jowett & Boustead 2001). It may actually be that the local presence of forested riparian cover along with catchment-scale forest cover acts to provide suitable habitat for both species, as the negative influence of banded kokopu on koaro presence in stream reaches is balanced by high proportions of forest

cover within catchments. This further emphasises the need for more landscape oriented research with respect to migratory fish distributions.

3.5.2. Hindcasting Results

The spatial distribution and amount of good quality stream habitat (classified as having a greater than 0.75 probability of encountering the focal species) for both koaro and banded kokopu in Pigeon Bay was predicted to be quite different in 1860 compared to present day. My model predicted both species to have been present throughout most of the Pigeon Bay catchment in 1860. However, possible interactions with closely related species no longer present on Banks Peninsula, such as giant kokopu (*G. argenteus* Gmelin, 1789), which was reported to be present on Banks Peninsula in the past (Stokell 1949), and shortjaw kokopu (*G. postvectis* Clarke, 1899) cannot be discounted. Giant kokopu and shortjaw kokopu are the two largest galaxiid fish species in New Zealand, and it is likely that these species would have competed or preyed on koaro, and perhaps also on banded kokopu. The immediate effects of forest removal between 1860 and 1880 on koaro and banded kokopu distributions are likely to have been dramatic, more so for koaro than banded kokopu. In my models, koaro distribution was more closely related to proportion of forest cover at the catchment scale, whereas banded kokopu distribution was related to proximate forest cover at reach scale. Riparian forest cover in Pigeon Bay was still relatively intact between 1860 and 1880, so banded kokopu were still likely to have been widespread, whereas koaro would have likely been restricted to areas without banded kokopu. By 1950, with further deforestation and land use change to more intensive cattle farming, both koaro and banded kokopu would likely have had severely restricted distributions, with the majority of the stream reaches within the catchment offering poor quality habitat for both species. The present day distribution of koaro in Pigeon Bay reflects a diversification of land use types from cattle farming, to less intensive mixed sheep and cattle and pure sheep farming, with some increase in the overall proportion of forest cover within the catchment. This diversification and conversion of land use has increased the amount of good quality habitat for koaro compared to 1950. However, the situation for banded kokopu is likely to have worsened because of further removal of riparian forest cover, but also due to the different response of banded kokopu to mixed sheep and cattle farming, a land use that affects the species more negatively than cattle farming.

3.5.3. Forecasting Results

The outcome of my conversion of six parcels of mixed sheep and cattle land use in the upper reaches of Pigeon Bay would benefit both koaro and banded kokopu. The immediate afforestation of the streams flowing through this new land use type would produce good quality habitat for banded kokopu, but with the doubling of the amount of forest cover within Pigeon Bay catchment, the benefits for koaro would be even more so than for banded kokopu. This scenario illustrates the interactions between catchment-scale and reach-scale variables, as banded kokopu responds to the reach scale presence of riparian forest cover, and koaro responding to the catchment scale proportion forest cover increase. There are encouraging signs that some New Zealand farmers are conscious of the negative influences that farming activities have on unprotected streams and their biota, and many are taking measures to prevent these negative effects (Graeme 2002). A first measure in stream protection is to fence the stream edges to prevent stock from entering the stream, thus removing the direct negative influences of the specific land use type. To assess possible outcomes of farmers' decisions to protect streams on their lands, I modelled two possible scenarios where the stream margins were protected and allowed to afforest with little gain in proportion catchment forest cover; one with the direct negative effects of stock access to the stream eliminated by fencing off streams as well as stream-side afforestation, and another with both the direct and indirect effects of adjacent land uses removed. My results indicate that in removing both direct and indirect effects of adjacent land uses, banded kokopu stands to gain the most, with good quality stream habitat increasing from < 10 % at present, to > 30 % with direct effects removed, and good stream habitat similar to 1860 conditions if both direct and indirect effects were removed. With very little gain in overall proportion catchment forest cover for these two scenarios, and given the negative interactions between presence of banded kokopu and koaro, the amount of suitable koaro habitat would be greatly reduced in both cases.

Goals for environmental management are often multifaceted, and a management outcome that only benefits one out of two species of significance rarely comprises a warranted management output. The two scenarios above beg the question: How can an acceptable management level be achieved for both species? Clearly, by protecting stream margins from the direct negative effects of production farm types by planting along riparian margins, banded kokopu would benefit greatly. To achieve the same level of benefit for koaro would require afforestation in the catchment to approximately 62 % to achieve the same level of distribution as

banded kokopu. This would offset the direct negative effects of banded kokopu presence on koaro, as the strong positive effect of forest cover on koaro distribution would prevail over the negative influence of the presence of banded kokopu.

Restoration of stream ecosystems is ultimately complicated by the fact that the status quo is often far removed from prior scenarios, and a return to any state resembling past species distributions is difficult, or perhaps impossible, especially given the reservations as to what species were actually present within the system in the past. In my case, it may be that other species, such as shortjaw kokopu and giant kokopu, with similar habitat requirements compared to my focal species might have been present within the study area, and the potential effects of their presence can only be guessed upon. If interactions with other species of similar habitat requirements were negligible for banded kokopu and koaro, I could accurately model the extent of the distribution of both species. Additionally, not all types of stream habitat degradation may be reversible (e.g. fine sediments may stay in the stream for a long time).

3.5.4. Implications for Management

The combination of site-scale and landscape scale approaches could be particularly important for the management of the large-bodied diadromous galaxiids because human alteration of the landscape occurs at multiple scales, and accordingly the ecological consequences must also be identified and managed at multiple scales. Diadromous fish, such as koaro and banded kokopu, are good habitat quality indicators because their distributions are clearly linked to contemporary land uses. By using GIS-models, which allow for continuous update to account for modifications of the landscape, and having the data output in a convenient map-format that the public at large can easily comprehend, a more effective management can be achieved. Fausch and others (2002) emphasised that a continuous view of rivers is essential for effective research and conservation of fishes and other aquatic biota in Montana, U.S.A., allowing for a view of the entire heterogeneous scene of the river environment unfolding through time. Also, a multi-scale GIS assisted approach to riverine fisheries management may greatly improve current conservation efforts, and may encourage managers to expand the scale at which solutions are sought (Boutin & Hebert 2002).

Chapter 4. Connections between terrestrial habitat fragmentation and stream inhabitants: edge effects on a fish that occupies forested streams in New Zealand

4.1. Summary

Edge effects on riverine fish have received little attention, but their influence could have important implications for stream fish populations and their management. I examined the effect of forest fragmentation on banded kokopu (*Galaxias fasciatus*), in streams on the West Coast of South Island, New Zealand. The habitat preferences for the species are well established, and they prefer small, well-shaded streams with bouldery substrates and large amounts of in-stream cover. I hypothesized that densities of banded kokopu would be higher in forested compared to open field streams, and that densities would be lower around forest margins. I sampled pools in three streams, all flowing from dense native mixed podocarp-beech forests into open field areas, using Gee–Minnow traps baited with yeast extract, on three consecutive days for each stream. Pools were sampled longitudinally on each stream from > 50 m into the forest to > 50 m downstream from the forest margin in open grassland. I found that banded kokopu densities were significantly higher in forest interior habitat ≥ 50 m into forests than in open field downstream of the forest margin. Furthermore, fish caught in open stream pools were significantly smaller than fish caught in forested pools. Predatory longfin eels were caught in all three streams, but numbers and sizes were similar in forested and open field streams. Thus, the abundance of this predator was not likely to drive the patterns observed for banded kokopu. My results indicate that terrestrial habitat fragmentation can impact stream fish populations by decreasing their occupancy of aquatic habitats in the vicinity of the boundary between terrestrial habitats.

4.2. Introduction

Habitat fragmentation, the replacement of large areas of original habitat by other habitat types, leaving isolated, disjunct habitat patches of varying sizes, can have deleterious effects on native biota (Murcia 1995). Habitat fragmentation reduces the total area of original habitat and exposes the species that remain within the habitat fragment to the conditions of a different surrounding ecosystem, and consequently, to what have been termed 'edge effects'. The interactions of the two juxtaposed ecosystems, separated by an often abrupt transition, or edge, can affect inhabitants of both systems. The effect of fragmentation on the remnant habitat patches and their biota is often of conservation concern. Typically, the emphasis of edge studies has been on patterns of species richness, particularly of birds and insects, at habitat edges and the vegetational transition near habitat edges (Didham *et al.* 1998a, Didham *et al.* 1998b, Trzcinski *et al.* 1999, Ford *et al.* 2001, Lee *et al.* 2002, Davies *et al.* 2003, Kurosawa & Askins 2003, Vance *et al.* 2003). The net effect of fragmentation is nearly always a local loss of species within fragmented patches (Turner 1996, Turner & Corlett 1996). However, edge-mediated effects may also be evident in other organisms that do not necessarily use the fragmented terrestrial landscape *per se*, such as forest dwelling stream fish. The notion that some species of fish have an affinity for elements of the terrestrial landscape, such as forests, is well known (Barton *et al.* 1985, McDowall 1990, McDowall *et al.* 1996, McDowall 1997b, Naiman & Decamps 1997, Hauer *et al.* 1999), but studies of terrestrial habitat fragmentation and associated edge effects in stream fish populations are rare. However, the consequences of reductions in fragment size and connectivity of fragments could be more severe, as dispersal of fish between fragments is restricted to existing, constrained watercourses (Fagan 2002).

Stream biota constrained to stream channels, may be affected by edges in terrestrial systems in two ways depending on how the edge habitat interacts with the stream. If the entire stream residing within forest edge habitat is being affected, sinuous streams would be affected more than relatively straight channelled streams. Alternatively, it could be that straight channelled and sinuous streams are affected in similar ways, if it is the stream distance to the edge, rather than the spatial proximity to the juxtaposed ecosystem, that is important.

To test whether edge effects could be detected in biota inhabiting streams, I located three streams flowing from dense native forests into open field pastures, all in similar settings with respect to underlying geomorphology and migratory distances (ease of access), known to contain

populations of a native New Zealand fish, the banded kokopu (*Galaxias fasciatus*), typically associated with forested streams. The banded kokopu is an amphidromous galaxiid fish endemic to New Zealand (McDowall 1990). Amphidromous fishes, such as banded kokopu, migrate to sea as larvae soon after hatching, and then migrate back to a freshwater environment as post-larval juvenile fish. Adults are still common in forested streams at low altitudes and within 150 km of the sea throughout New Zealand, although banded kokopu habitat has been greatly reduced by changes in land use from native forest to pasture. The reduction in forest has been shown to severely limit the distribution of some native fish by reducing the availability of high quality habitat (Rowe *et al.* 1999). Banded kokopu juveniles contribute to the “whitebait” fishery at river mouths as they re-enter a freshwater environment from the sea, although their contemporary contribution to this fishery is probably minor compared to what it once was (Rowe *et al.* 1999).

Adult banded kokopu are often found in pools of small streams that have large cobble-bouldery substrates beneath a closed forest canopy (McDowall 1990, Jowett *et al.* 1996, Rowe *et al.* 2000, Rowe & Smith 2003), although in catchments where introduced salmonid fish are absent, they may appear in backwater pools of larger streams (Chadderton & Allibone 2000). Where factors such as insurmountable barriers to migratory movement and turbid water do not reduce, or preclude recruitment, the presence of banded kokopu in forested streams is likely to be related to microhabitat features (Rowe *et al.* 2000, Richardson *et al.* 2001, Rowe & Smith 2003), in particular cover in pools provided by woody debris and large boulders (Rowe *et al.* 2000). Jowett, Richardson and McDowall (1996), in a study on the relative effects of land use and in-stream habitat on native fish distributions, found that all banded kokopu caught in their study were associated with undercut banks or in-stream debris, although stream shading in itself was discounted as influencing their distribution. Thus, they concluded that banded kokopu are associated with streams that provide large amounts of in-stream cover. Banded kokopu also prefer low water velocities and water depths of 20–50 cm, so are common in small stream pool habitats (Main 1988, Rowe *et al.* 2000, Rowe & Smith 2003).

The majority of New Zealand’s freshwater fish are insectivorous, feeding mainly on stream benthos. However, some terrestrial insects are consumed by almost all native fish (McIntosh 2000) and sometimes form a major constituent of banded kokopu diet (Phillips 1926, Main & Lyon 1988). Main and Lyon (1988) showed that over 90 % by weight of the diet of banded kokopu was of terrestrial origin, comprising primarily beetles. Thus, terrestrial land use, and in particular presence of riparian forest cover, may influence the availability of suitable prey

(Jowett *et al.* 1996). McDowall (1990) concluded that removal of indigenous forest cover had reduced the abundance of banded kokopu and other related species because they are rarely caught in pastoral areas. Since reciprocal subsidies between stream and terrestrial ecosystems can be important (Nakano & Murakami 2001), fragmentation of terrestrial habitats that disrupt the resource subsidies to streams could be particularly important.

Although the distribution and habitat preferences of stream fish like banded kokopu are often well documented (Rowe *et al.* 1999, Rowe & Smith 2003), little is known about how the configuration of terrestrial habitats affect stream biota like fish (Barton *et al.* 1985). I investigated whether edge-mediated effects could be observed in banded kokopu populations.

4.3. Methods

4.3.1. Study area

I chose three streams, two of them tributaries to Kennedy Creek, the third a tributary to Waimea Creek, located on the West Coast of South Island, New Zealand (Figure 4.1). All were devoid of anthropogenic barriers to fish migrations such as weirs and dams, and all drained from dense native mixed podocarp-beech forest canopy shelter into open grassland areas. The streams supported dense populations of banded kokopu, shortjaw kokopu (*G. postvectis*), and the occasional koaro (*G. brevipinnis*) and inanga (*G. maculatus*). Native redfin (*Gobiomorphus huttoni*) and common bullies (*G. cotidianus*), were also common in these streams. Potential predatory fish in the study streams were limited to longfin eels (*Anguilla dieffenbachii*) and giant kokopu (*G. argenteus*), although introduced brown trout (*Salmo trutta*) were present in the main stem of the sampled stream well downstream of the study areas.

Pools both upstream and downstream of the forest–open interface, or edge, were sampled on three consecutive days by Gee–Minnow traps baited with “Marmite”, a brewer’s yeast (*Saccharomyces cerevisiae*) extract that is effective at attracting galaxiid fishes to traps (Chadderton & Allibone 2000). The traps were placed in pools just before dark (20:30 h New Zealand Daylight Savings Time (NZDST)),

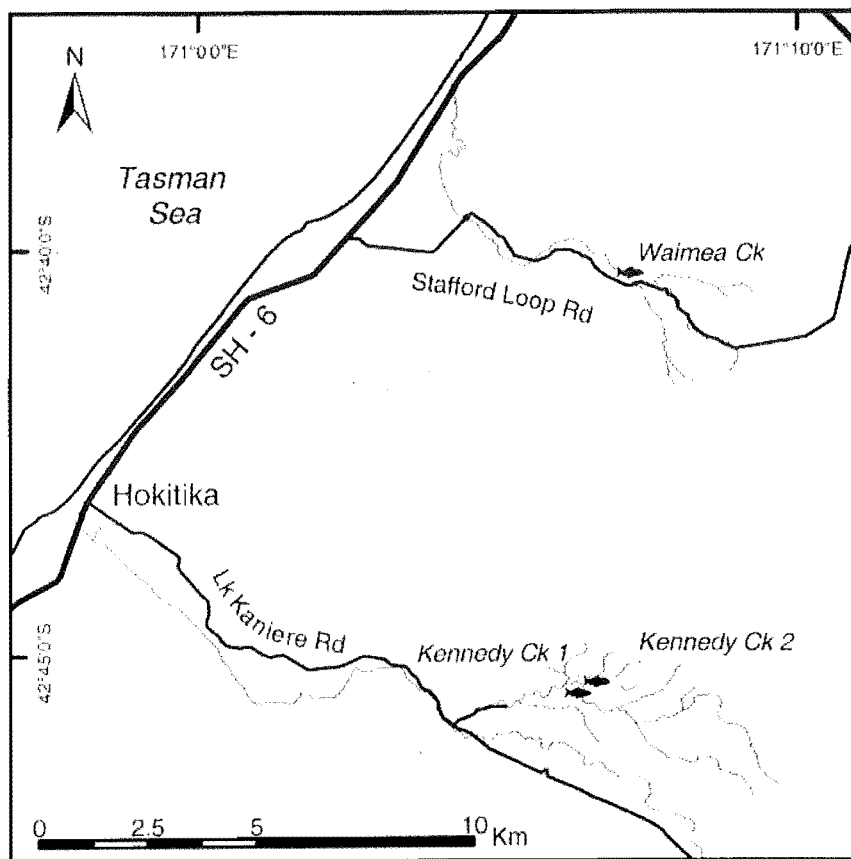


Figure 4.1 Location of study streams on the West Coast of South Island, New Zealand.

and checked for fish immediately after sunrise (06:30 h NZDST). The distance of each trap from the interface of forest covered and open area stream was measured. The number and fork lengths ($FL \pm 1$ mm) of banded kokopu and longfin eels caught over three days were recorded to get a measure of the density of fish per pool.

Substrate composition of each sampled pool was measured from the longest axis of 30 rocks randomly selected using the Wolman Walk method (Wolman 1954). The substrata for each pool were subsequently categorized as the percentage of mud (< 1 mm in size), sand (1–2 mm), fine gravel (2–20 mm), coarse gravel (20–60 mm), cobble (60–260 mm), boulder (> 260 mm), or bedrock (solid substrate) (Table 4.1).

The amount of woody material, such as logs or snags, present in the pools and along pools margins, was recorded, and the percentage of total stream bank covered by woody material calculated. The percentage of undercut stream bank, on both sides in all pools was also recorded, as this pool feature may provide refugia habitat for fish.

All pools were measured in multiple dimensions to establish their relative two and three-dimensional sizes. The widths at the upstream, middle, and downstream parts of pools were measured, and depths at ten randomly selected locations within each pool, as well as their maximum depths, were recorded, allowing for calculations of pool volumes.

The extent of canopy cover over pools was established by taking sky-view images with a fish-eye lens (Nikkor Auto 8mm f/2.8, picture angle 180°) perpendicular to the water surface at twenty locations spaced evenly in both directions from the forest-open interface to measure any gradient in shade and canopy cover. These images were then scanned at 300 dpi into Adobe Photoshop 7.0 and converted to black (canopy cover) and white (sky) by altering the contrast and brightness of each image. The images were then converted to binary ArcView 3.2a grids (300 dpi), with the value 1 for canopy cover, and 0 for sky, and the percentage canopy forest cover calculated for each location.

Table 4.1 Physical characteristics of pools in each stream (\pm SE). Significant differences in physical characteristics between study streams were determined by ANOVA. The *F* and *P* values for these analyses are presented.

Variables	Waimea Creek		Kennedy Creek 1		Kennedy Creek 2		ANOVA	
	Mean	SE	Mean	SE	Mean	SE	<i>F</i> -value	<i>P</i> -value
Shading (%)	55.06	6.53	57.44	6.830	67.83	7.07	1.02	0.366
Substrate (%)								
Mud	5.50	0.85	2.54	0.76	6.19	1.21	3.48	0.037
Sand	0.17	0.17	0.79	0.46	0.83	0.61	0.53	0.594
Fine gravel	14.50	0.91	12.22	1.62	14.76	1.98	0.66	0.522
Coarse gravel	19.50	2.94	12.54	1.36	14.64	1.46	3.06	0.054
Cobble	41.33	3.61	51.11	2.69	43.10	3.50	2.21	0.118
Boulder	18.50	3.62	20.79	2.06	19.64	3.21	0.12	0.885
Bedrock (Solid)	0.33	0.23	0.00	0.00	0.71	0.31	2.16	0.123
Woody debris (%)	10.84	4.53	15.87	4.63	7.18	3.59	1.13	0.330
Bank undercut (%)	19.20	4.66	17.67	4.47	6.62	2.07	3.88	0.025
Pool volumes (m ³)	10.67	2.74	5.28	2.70	1.47	0.39	5.41	0.007

4.3.2. Data analysis

The influence of the transition from forested to open terrestrial habitat on the catch-per-unit-effort (CPUE) of banded kokopu and longfin eels was determined by classifying sampled pools into four habitat groups: open habitat (OH, > 50 m from open-forest interface), open edge habitat (OE, < 50 m from open-forest interface), forest edge habitat (FE, < 50 m into forest), and forest interior habitat (FI, > 50 m into forest). The 50 m distance was chosen to define 'edge' habitats, as this is the distance frequently referred to in the literature as the extent of edge-mediated effects associated with forests boundaries (Murcia 1995). The mean differences in CPUE and fish sizes of banded kokopu and longfin eels were determined from each habitat

group. Differences in CPUE and fish sizes were examined using ANOVA followed by multiple comparisons of group means by Tukey's tests using SPSS 11.0.1.

Differences in physical habitat characteristics for pools within the four habitat groups for the three streams, with respect to undercut stream banks, in-stream woody debris, stream shading by vegetation canopy cover, mean substrate sizes, pool depth averages, and pool volumes, were also examined using ANOVA and Tukey's multiple comparisons tests. Significant differences in these variables amongst the four groups and CPUE for banded kokopu and eels were examined using ANOVA analysis, where the CPUE was the dependent variable, fixed effect the site, and the significant variables, from the analysis above, the covariates.

4.4. Results

There were some significant differences in the physical characteristics among the three sampled creeks: Kennedy Creek 1 had significantly less mud substrate than the other stream sampled, Kennedy Creek 2 had less bank undercut, and Waimea Creek had larger pools (Table 4.1). However, analysis of variance dismissed these as having influenced the CPUE for banded kokopu and eels.

The CPUE of banded kokopu was significantly higher in forest habitat > 50 m inside the forest margin than in the two edge habitats or open field habitat (Figure 4.2). For longfin eels, there were no differences in the CPUE among habitat groups, and catches were generally low for all four habitat groups. The relative sizes (FL) of banded kokopu also differed between habitat groups, with open areas supporting low numbers of small fish, and the forest edge and interior habitats both supporting larger fish of similar sizes (Figure 4.3).

Pools in open habitat had little undercutting of stream banks, whereas pools in forest core and forest edge habitat had substantial undercutting, with the forest edge habitat having intermediate amounts of undercutting (Figure 4.4a). Woody debris did not differ between groups (Figure 4.4b). As expected, stream shading differed significantly between forested and open areas, and although there were no significant differences in shading between the two forested habitat groups, there were significant differences in shading between open core and open edge habitats, with edge habitats being more shaded (Figure 4.4c). Substrate sizes, pool depths, and pool volumes did not differ significantly between habitat groups (Figures 4.4d, e, and f).

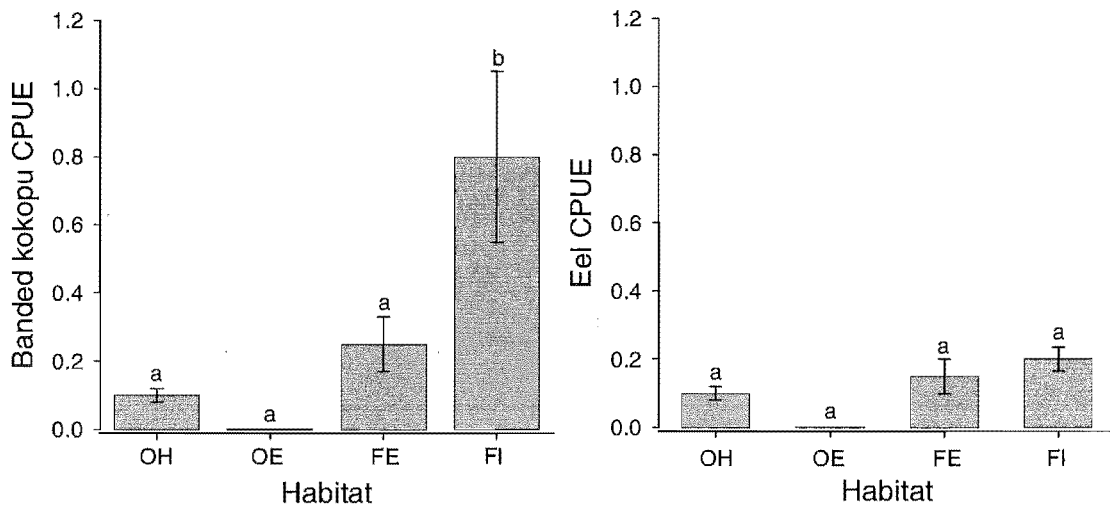


Figure 4.2 Mean (\pm S.E.) catch per unit effort (CPUE) of banded kokopu (A) and longfin eels (B) for streams in four stream habitat groupings: Open habitat (OH, > 50 m from forest interface), open edge habitat (OE, < 50 m from forest interface), forest edge habitat (FE, < 50 m into forest), and forest interior habitat (FI, > 50 m into forest). ANOVA indicated a significant difference between treatments for banded kokopu ($F_{3,65} = 10.75$, $P < 0.001$), with different letters indicating significant differences among habitat groups (Tukey's test; $P < 0.05$).

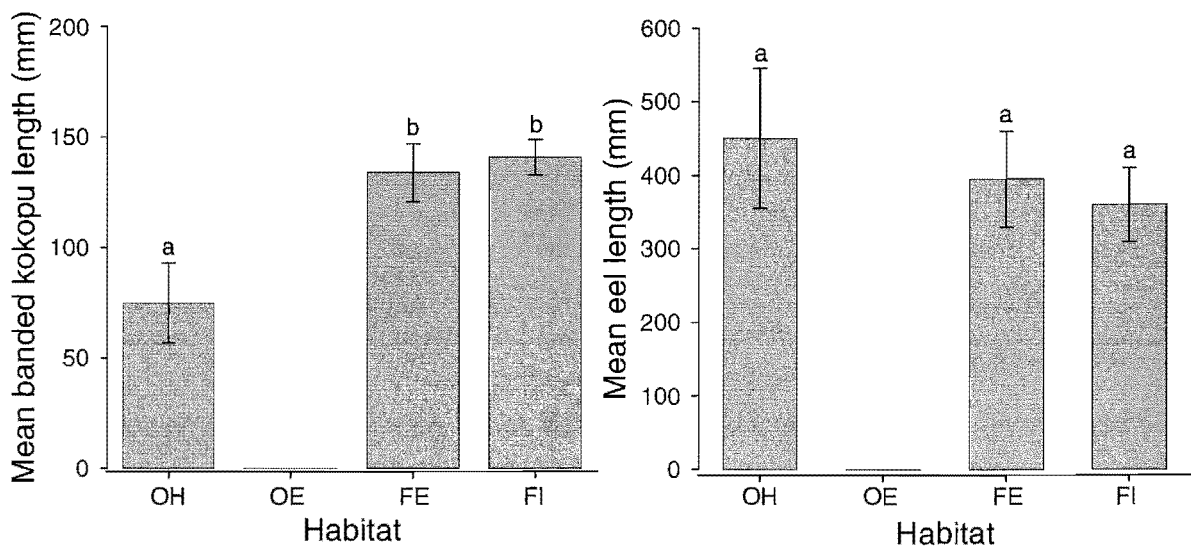


Figure 4.3 Mean (\pm S.E.) length of banded kokopu (A) and longfin eels (B) for four habitat groupings: Open habitat (OH, > 50 m from forest interface), open edge habitat (OE, < 50 m from forest interface), forest edge habitat (FE, < 50 m into forest), and forest interior habitat (FI, > 50 m into forest). ANOVA indicated a significant difference between treatments for banded kokopu ($F_{2,22} = 4.94$, $P = 0.004$), but no significant difference between treatments for eels. Different letters above error bars indicating significant differences among habitat groups (Tukey's test; $P < 0.05$).

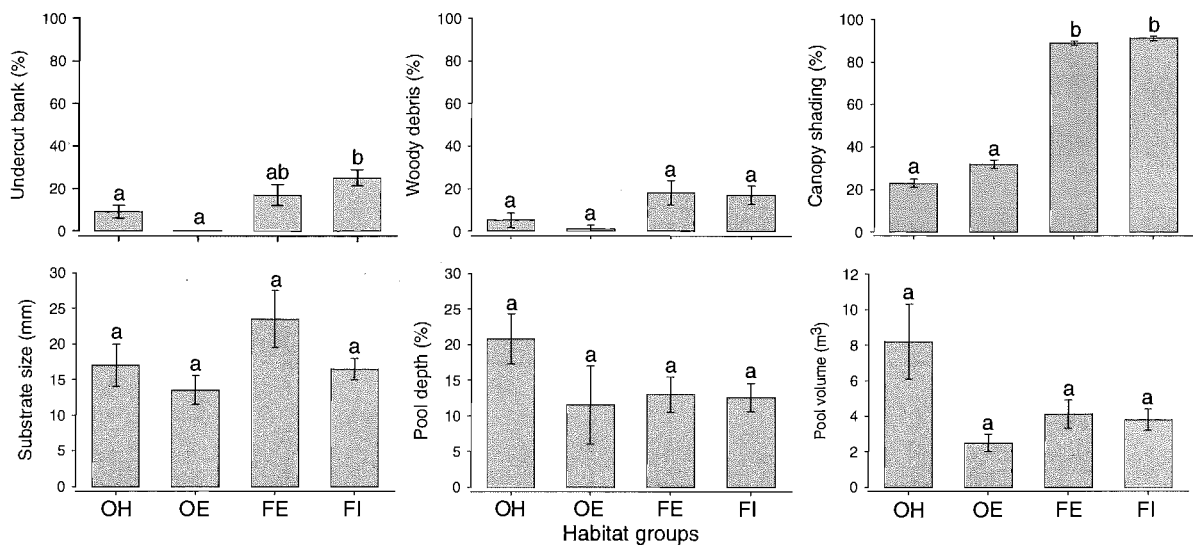


Figure 4.4 Mean (\pm S.E) stream characteristics for the four stream habitat groupings. Different letters above bars indicating significant differences among groups (Tukey's test; $P < 0.05$): (A) Degree of bank undercutting as a percentage of total stream banks of pools showing pools in forest core habitat have more bank cover than pools in other habitat groups (ANOVA: $F_{3,65} = 4.98$, $P = 0.004$). (B) Amount of stream banks of pools covered with woody debris as a percentage of total length of stream banks in pools, showing no significant difference among habitat groups (ANOVA: $F_{3,65} = 2.44$, $P = 0.072$). (C) Degree of canopy shading, showing pools in forests are more shaded than pools in open areas, and open edge pools are more shaded than open core pools (ANOVA: $F_{3,65} = 715.47$, $P < 0.001$). (D) Substrate sizes, showing no significant difference among habitat groups (ANOVA: $F_{3,65} = 1.39$, $P = 0.254$). (E) Pool depths were also similar for the four habitat groups (ANOVA: $F_{3,65} = 1.62$, $P = 0.193$). (F) Pool volumes were also similar among habitat groups (ANOVA: $F_{3,65} = 2.42$, $P = 0.074$)

4.5. Discussion

My results indicate that banded kokopu densities were significantly higher in native forest pools than in pools of open grassland, and increased with distance from the forest margin, thus exhibiting a response to edge habitat. An edge effect was also evident from the significant differences in sizes of the fish caught among habitat groups. Larger fish were caught in forested compared to open stream pools. Fish caught within the forest edge and forest core habitats were of similar sizes, but there was greater variability in sizes of fish caught in the forest edge habitat (mean fork lengths \pm SE: FE, 133 ± 9.9 mm, FI, 140 ± 6.2 mm). Fish caught in the forest core habitat were consistently large, whereas more small fish were caught in forest edge habitat. Also, the few banded kokopu caught in pools outside forested stream reaches were significantly smaller

than those caught within forests. There was no trend of decreasing densities of banded kokopu with increasing distance into open stream habitats, a clear indication that large banded kokopu have a preference for forested streams.

I observed no differences in the abundance or size of longfin eels amongst the habitats in my study. However, larger eels may not have been able to enter the Gee–Minnow traps (opening approximately 5 cm in diameter), so differences between stream habitats may have gone unnoticed. Thus, one cannot say with absolute certainty that longfin eels are not implicated in the distribution pattern observed for banded kokopu, or that they are not affected by forest fragmentation. It may be that the larger fish of any species in the interior forested streams displace smaller fish into inferior habitat downstream, as has been observed in populations of a closely related species, giant kokopu (David & Stoffels 2003).

Studies of in-stream habitat use by native fish have found banded kokopu to be positively associated with bank cover and in-stream debris (Jowett *et al.* 1996, Rowe & Smith 2003). In my study, I observed the highest abundance of fish in the stream with the least amount of bank cover, Kennedy Creek 2. Since there were no significant differences in mean substrate composition or woody debris among habitat groups, two potential refugia sources, I conclude that the presence of canopy cover is likely responsible for the observed distribution patterns of banded kokopu within my study streams. This pattern could be driven by the increased availability of terrestrial invertebrates falling into the stream from riparian forest vegetation (Edwards & Huryn 1995, Edwards & Huryn 1996, Kawaguchi & Nakano 2001), thus providing increased food subsidies to banded kokopu diet.

An implication of my results for a specialist ‘forest fish’ such as banded kokopu is that the length of stream affected by land use change like forest clearance is generally longer than the length of stream directly affected by the terrestrial land use change. Although I did not test the effects on banded kokopu of having deforested stream reaches upstream, the effects are likely to be similar, and perhaps extending further into forest patches, as impacts on stream ecosystems often manifest themselves in a downstream direction (Pringle 2003).

Another implication of edge effects on populations of banded kokopu is that the size and shape of patches are likely to play a role. Larger, wide forest patches will have more core habitat compared to long and narrow patches. However, to further elucidate the significance of size and shape, further research on edge effects, in particular with respect to increases in densities of banded kokopu in streams flowing from open areas into forests, is needed. With banded kokopu,

and perhaps also other species of native fish, being affected by edge effects, reestablishment of wide forest margins around pastoral streams may significantly improve the extent of their distribution in developed catchments.

Chapter 5. Patterns in diadromous fish distributions: testing the roles of altitude, distance, and maximum downstream slope

5.1. Summary

Understanding the factors limiting migratory behaviour is fundamental to conservation of diadromous fish. Applications of indices of habitat suitability are problematic for diadromous fish because fish presence and abundance in relation to habitat quality are confounded by barriers to fish migration. An alternative approach is to assess diadromous fish distributions in relation to distance inland and altitude above mean sea level, and subsequently generating trajectories for the various species. This approach, however, may be problematic. I show that river distance inland and elevation are only weakly correlated in my study area. Thus, in areas where steep slopes are not encountered, fish migrations to significant elevations and inland distances can be expected. In other areas, coastal cliffs and geologic fault lines provide for steep stream gradients close to the sea, and fish do not migrate far inland. To solve this issue, I developed methods for improving species trajectory approaches to explain the distribution of diadromous fish using a GIS. I adjusted distance and altitude categories so that each stratum was represented by the same number of site records, with flexible intervals for each stratum. For species capable of forming land-locked populations I manipulated input values for elevation and river distance inland to account for migrations from lakes, rather than sea. Additionally, a new GIS derived variable was introduced to better explain the distribution of diadromous fish; the maximum stream slope a fish would encounter during upstream migration. This new slope variable, independent of distance inland, is likely to be a better predictor of migratory fish occurrences than elevation above mean sea level, as the different species will have different slope-thresholds that they can overcome.

5.2. Introduction

Fish that migrate between fresh and marine waters (i.e., diadromous species) are common throughout the world, many are culturally and economically important, and some are classified as endangered (McDowall 1988, Allendorf *et al.* 1997, Drake *et al.* 2002, Dunham *et al.* 2002). On islands (e.g., New Zealand and Hawaii) diadromy is particularly common (McDowall 1990, McDowall 2003a). Many migratory species, like the salmonids of North America and Europe (Smith *et al.* 1997, Elliott *et al.* 1998, Klemetsen *et al.* 2003, Moir *et al.* 2004), migrate extended distances inland, whereas others, such as New Zealand's inanga (*Galaxias maculatus* Jenyns, 1842) and banded kokopu (*G. fasciatus* Gray, 1842), remain relatively close to the coast after re-entering the freshwater environment from the sea (McDowall 1990). The migratory behaviour of diadromous fish is fundamental to their contemporary distributions, and understanding the factors limiting migratory behaviour is critical to their conservation (Adams *et al.* 2000, Dunham *et al.* 2002).

In the absence of physical barriers to fish migration, like waterfalls or dams, inland insinuation of diadromous fish is influenced by distance from and elevation above source of migrant fish (McDowall 1998b, Joy & Death 2002). This pattern is evident in New Zealand where the proportional occurrence of fish declines with increasing elevations and river distances inland (McDowall 1993, McDowall 1996a, McDowall 1998a, McDowall 1998b, McDowall 1999, McDowall & Taylor 2000). The rate of decline, using this species trajectory approach, differs between species, and has been interpreted as a reflection of migratory capabilities and instincts, ease of access to upstream habitats, and habitat suitability (McDowall 1990, McDowall & Taylor 2000). Another methodology for assessing freshwater fish communities and quality of habitats uses indices of biotic integrity (IBIs) (Miller *et al.* 1988, Karr 1991). However, IBIs are less effective for diadromous fish because there is a breakdown of habitat suitability and abundance relationships (Joy & Death 2000, McDowall & Taylor 2000, Joy & Death 2002), likely due to lack of access by migratory fish to some suitable habitats. Thus, suitable habitat may not be occupied because it is not accessible due to migratory barriers (Gore & Hamilton 1996, Baker 2003b).

An assumption of the species trajectory approach is that migratory fish moving upstream form more or less continuous distributions, but decrease in abundance with increasing elevation and river distance inland, to the upstream limit of each species' range (McDowall 1998a, McDowall 1998b). Thus, with increasing elevation and river distance inland, species should

become rarer, and eventually absent beyond their migratory limits within rivers (McDowall & Taylor 2000). Another assumption is that with increasing elevations and river distances inland, steeper stream slopes, possibly acting as barriers to fish migrations, would be encountered. However, one predicament of this species trajectory approach, is that the distribution of sampled sites in databases of fish occurrences are rarely uniform with river distance inland and increasing elevations. For example, on the West Coast of New Zealand's South Island sampled sites have been at low elevations and not very far inland, with few sites at high elevations and extended distances from the sea. In this situation occurrences of fish at high elevations or extended distances from the sea may be inaccurate because of use of uniform elevation or distance categories. This is because when fixed categories are used there are few sites at high elevation and large distances inland, making estimates of occurrence less precise.

Some species of diadromous fish are also known to have flexible life histories. In New Zealand, landlocked populations of banded kokopu, giant kokopu (*G. argenteus*), inanga, and koaro (*G. brevipinnis*) are known from the West Coast of South Island (McDowall 1990), and the presence of shortjaw kokopu (*G. postvectis*) in areas above large lakes raises the possibility that this species may also form landlocked populations. In landlocked populations of migratory fish, the reservoir, or lake, substitutes for the ocean as a feeding biome for the fish prior to returning to lotic headwater habitats (Pollard 1974, Barriga *et al.* 2002, Olsson & Greenberg 2004). These alternative life histories should be considered when assessing the extent of migration in these species. In these cases distance and altitude from the potential source of migrant fish, rather than distance from the sea and altitude above mean sea level, need to be measured.

Distance from source and elevation above source are not always correlated. In a study in south-western France, altitude, slope, and catchment area significantly influenced local species richness of migratory fish, whereas distance from source had no impact on species richness (Santoul *et al.* 2004), indicating fish could move far inland in the absence of migratory barriers. This suggests that the slope that must be overcome to reach upstream habitats may be more important in structuring the distribution of migratory fish. Moreover, the location of steep stream slopes is frequently independent of both distance from source and elevation. Thus, both migratory distance and the slope of the terrain that must be traversed are contributing factors contributing to migratory fish distribution patterns.

In this study I developed methods for improving understanding of species occurrences by adjusting distance and altitude categories (or strata) using geographical information systems, to

ensure each stratum is represented by approximately the same number of site records, with flexible distance and elevation intervals for each stratum. Using examples from the West Coast of South Island, New Zealand, I show how more accurate distributions of diadromous galaxiids (Galaxiidae) can be obtained using a GIS. Input values for elevation and river distance inland for sites where large lakes were located lower in the catchment were also manipulated to account for migrations from lakes, rather than sea, for species with known ability to form landlocked populations. Finally, I introduce the maximum downstream slope a fish may encounter during its migration to suitable habitat to explain the distribution of diadromous fish.

5.3. Methods

5.3.1. Study area

The West Coast Conservancy of New Zealand's Department of Conservation encompasses the rivers and streams that flow from the South Island into the Tasman Sea, from Awarua Point in the south to Kahurangi Point in the north (Figure 1). The region contains extensive indigenous forests, especially at higher elevations, and the rivers and streams of the region flow through some of New Zealand's least developed landscape, although lower elevation land is frequently more developed (Wheeler *et al.* 2004).

The rivers generally drain west or northwest from the high mountains of the Southern Alps (McDowall 1998b). Steep coastal cliffs are prominent common features of the West Coast landscape, and with the proximity of the Southern Alps and multiple geological fault lines, very steep stream gradients can occur both adjacent to the coast, as well as in inland locations. Thus, the region is ideal to investigate the influences on diadromous fish distributions of non-anthropogenic factors, such as river distance inland, altitude above sources of migratory fish, and maximum stream slopes fish encounter during upstream migration.

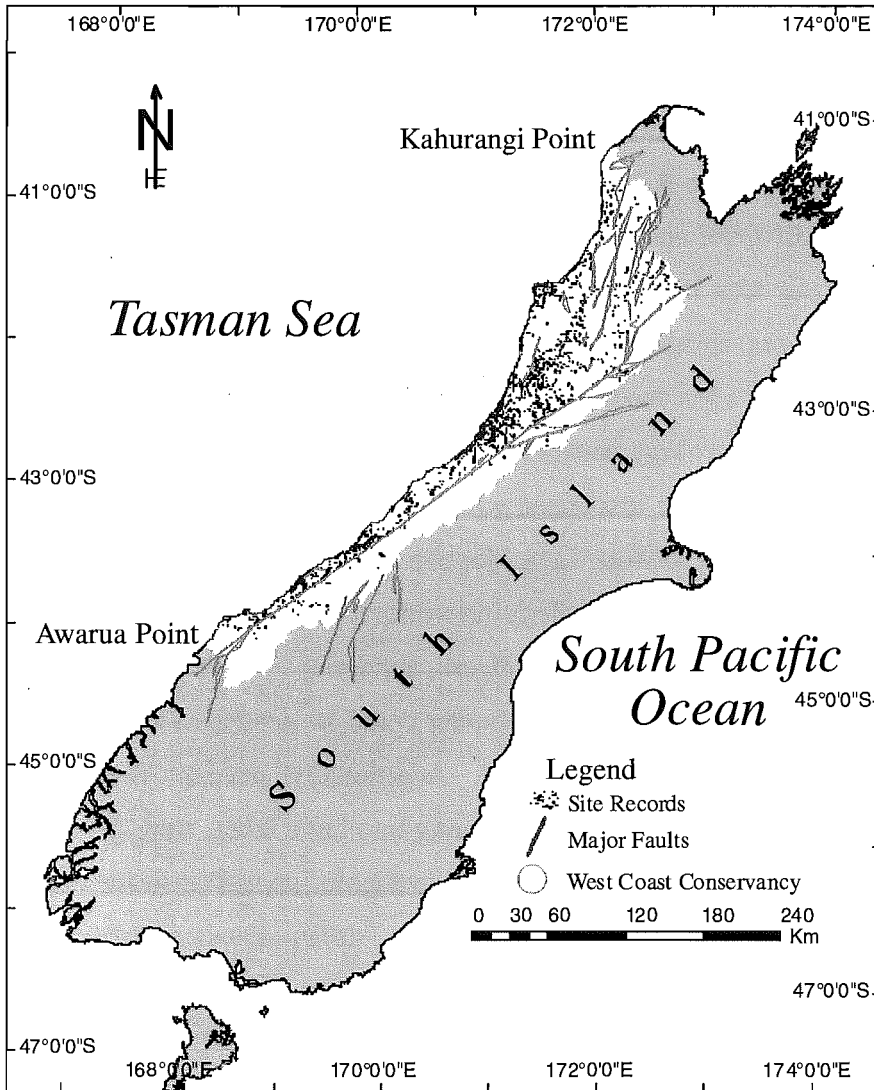


Figure 5.1 Location of records of fish occurrences within the Department of Conservation West Coast Conservancy, from Awarua Point in the South to Kahurangi Point in the North, South Island, New Zealand, from 1990 – 2004, contained in the New Zealand Freshwater Fish Database (N = 983). Note the many fault lines located along the axis of the study area (Data from Institute of Geological and Nuclear Sciences Limited, New Zealand).

5.3.2. Digital data preparation

A digital version of the 1:50,000 Topographic Vector Data (Terralink NZ Ltd.) hydrology network was used to represent the rivers and streams of my study area. A feature of digital hydrology networks is that stream reaches are represented as line segments, connected by nodes, ordered in a logical fashion by T-nodes (to-node) and F-nodes (from-node) in the associated database according to the position within the network, allowing propagation of variables up and/or down the network in a GIS. Generally, most segments vary in length, with new segments

starting where tributary segments join with other segments. However, I densified the hydrology network by using the ArcInfo (Version 8.0.2) DENSIFY command, inserting new vertices and connecting nodes at specified intervals so that no individual stream segment was longer than 50 m in length, and subsequently used the RENODE command to re-establish the arc T-and F-node topology of the network. RENODE updates the arc-node topology by renumbering the to-and-from-nodes of each arc, and identifies arcs which share the same node locations, thus restoring the connectivity in the digital stream network.

A 25 m resolution digital elevation model (DEM) for the South Island of New Zealand was used as a drape surface for the hydrology network, and the underlying slopes and altitudes were extracted and appended to the database associated with the hydrology network. This gave each individual segment of the hydrology network values for elevation and slope. The individual segment slopes were then propagated up the hydrology network, so that steeper slopes would replace less steep slopes, traversing up the stream network, rendering a network where the maximum downstream slope a migratory fish might encounter could be determined. Similarly, river distances from the sea and large lakes were derived. Additionally, altitudes, both above mean sea level and above mean lake levels for streams draining into large lakes, were generated for each segment of the hydrology network. With these new variables appended to the digital hydrology network, relationships between stream reach elevation, stream distances inland, and maximum downstream slopes were determined.

5.3.3. Records of fish occurrences

The New Zealand Freshwater Fish Database (NZFFDB) is an historic archive containing information on the distribution of New Zealand's freshwater fish. A range of individuals and institutions have provided data on the species present at particular locations. From this database, I extracted 2780 site records of fish occurrences for the West Coast Conservancy. However, because some records were not complete, or very old, records lacking information on location, or predating 1990, were filtered out, and 1323 site records were retained for further examining. These site records were further refined to represent spatial locations within the stream network, rather than individual records, by linking their spatial locations to stream reaches from the digital hydrology network using an append data by proximity function in ArcGIS. Thus, site records within 50 m of one another, with no significant stream reach slope differences between them,

were combined to represent one spatial location, or stream reach, resulting in 983 unique stream reaches with data points.

5.3.4. Data analysis

Relationships between river distance inland, site elevation, and maximum downstream slope below sites for all sites were analysed with linear regression and used to investigate the distribution of sampled sites within the drainage network. Similarly, regression analysis for all stream reach segments contained within the digital hydrology network was performed to investigate the same relationships between stream elevation, distance inland, and maximum downstream slope.

Data on fish occurrences and distance from source were stratified in three ways. Firstly, I used the traditional approach where sites were assigned to strata in 5 km wide bands of distance inland. Secondly, I considered the possibility of landlocked populations of several species within my study area, and re-established new strata based on river distances from potential sources. Thirdly, to investigate the influence of the spatial distribution of sampling sites, ten strata were established based on distances to sources of migratory fish, with approximately even numbers of site records for each stratum, and irregular strata widths. For each method of data stratification, the proportional occurrences of fish within a stratum were plotted as vertical bars, and the cumulative percent occurrence of the total was plotted as a line. To establish species trajectories, data from the third data stratification method were plotted as the cumulative percent occurrences of the different species on the y-axis, versus the mean value of river distance inland from the source of migratory fish for the ten strata.

A similar approach was used to establish strata for elevation bands. First, site records were assigned to elevation bands of regular intervals of 25 m elevation increases, with uneven numbers of sites in the various bands. I did this for elevation above mean sea level, and also for elevation above source of migratory fish where large lakes were present as potential sources. Finally, the numbers of sites per stratum were arranged into ten strata, with equal numbers of sites, but irregular elevation intervals.

For the new variable, maximum downstream slope encountered by migratory fish to reach specific upstream locations, I established ten strata with even numbers of site records. These were measured with the sea as the source for species that do not form landlocked populations, and above large lakes where these existed for species with flexible life histories. This approach

allowed new trajectories of species occurrences to be established, unbiased by river distance inland, or elevation above mean sea or lake level, by comparing the cumulative percent occurrences of fish species over the mean values of maximum downstream slope for the ten strata.

5.4. Results

Five diadromous Galaxiidae occurred in stream reaches of the West Coast Conservancy (Table 5.1). Koaro were most common, followed in order of decreasing occurrence by banded kokopu, giant kokopu, inanga, and shortjaw kokopu respectively. The latter were found at less than 10 % of the stream reaches in my inventory.

Table 5.1 Scientific and common names, migratory behaviour, and frequency of occurrence in stream reaches in the West Coast Conservancy, New Zealand, post 1990, of diadromous fish species according to the New Zealand Freshwater Fish Database. Duplicate records removed (n = 983).

Family name	Scientific name (common name)	Life history	Frequency of occurrence
Galaxiidae	<i>Galaxias maculatus</i> (inanga)	Catadromous	120
	<i>G. brevipinnis</i> (koaro)	Amphidromous	238
	<i>G. fasciatus</i> (banded kokopu)	Amphidromous	151
	<i>G. postvectis</i> (shortjaw kokopu)	Amphidromous	92
	<i>G. argenteus</i> (giant kokopu)	Amphidromous	140

The vast majority of sampled sites occurred at low elevations, not very far inland (Figure 5.2a). Low elevation sites were frequently situated above steep stream slopes close to the coast (Figures 5.2b and c), although some inland sites still had low downstream slopes. This is a result of the many coastal cliffs within my study area, as well as the multiple fault lines that parallel the Southern Alps. Regression analysis indicated a significant positive relationship between stream reach elevation and distance from sea, stream reach elevation and maximum downstream slope, and maximum downstream slope and distance from sea, although only the relationship between stream reach elevation and maximum downstream slope relationship had a large coefficient of determination (> 0.1) (Table 5.2).

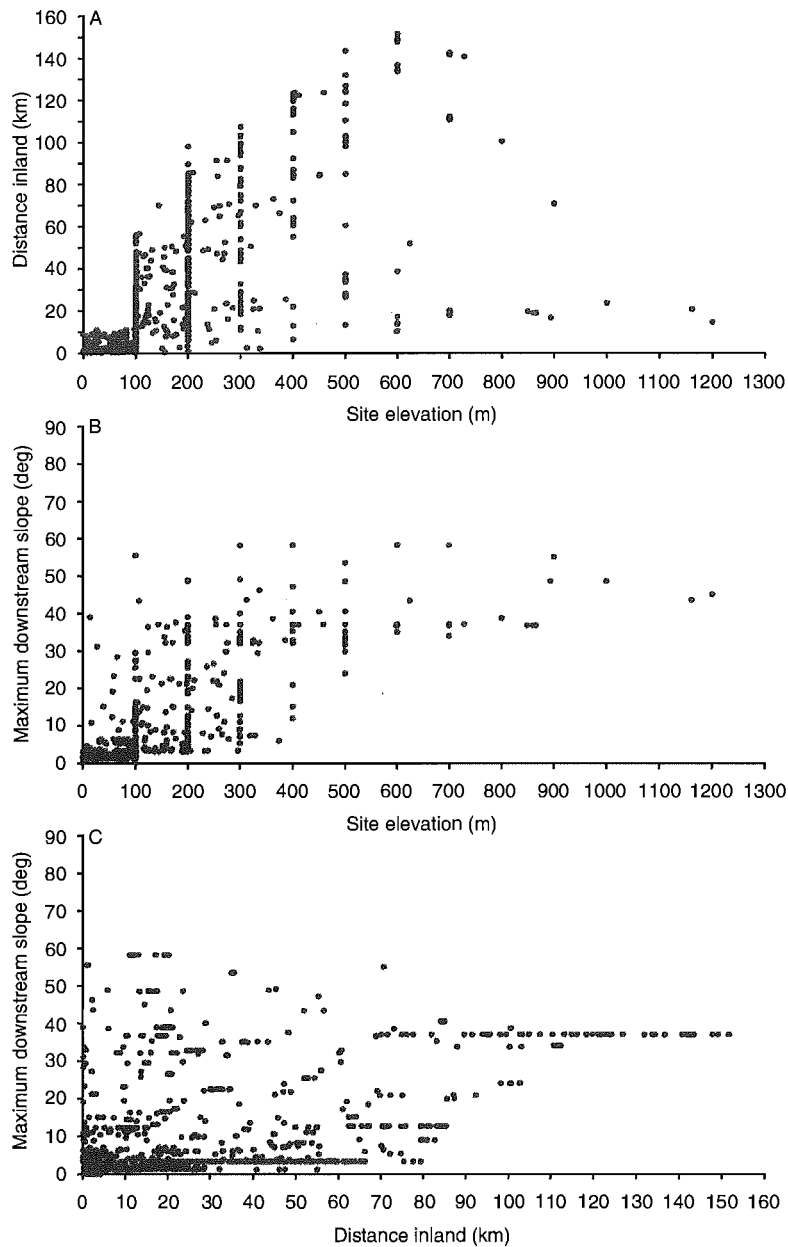


Figure 5.2 Distribution of locations sampled for fish within the West Coast Conservancy, South Island, New Zealand. (A) With respect to distance of site inland versus site elevation, (B) maximum stream slope downstream of a sampled site, as derived from 25 m resolution digital elevation model, versus site elevation, and (C) maximum stream slope downstream of a sampled site versus site distance inland. N = 983 in all cases.

Table 5.2 Linear regression results for all line segments of the hydrology network (Terralink NZ), testing the relationships between elevations, distances from the sea, and maximum downstream slopes (n = 1209963)

Dependent variables	Predictor variables	r ²	Constant	Slope	P - value
Reach elevation	Distance from sea	0.041	460.64	0.008	<0.001
Reach elevation	Downstream slope	0.580	16.61	16.125	<0.001
Downstream slope	Distance from sea	0.030	28.23	0.003	<0.001

Plotting occurrence of banded kokopu across strata (each stratum 5 km wide) of river distances inland showed that banded kokopu was mostly a coastal species, with less than 10 % of occurrences at greater than 30 km inland (Figure 5.3a). However, the remaining 10 % occur in two peaks at 45 and 90 km inland (Figure 5.3a). Banded kokopu can form landlocked populations, and when the proportion occurrences across strata of river distances inland from all sources of migratory fish, the two peaks of Figure 5.3a disappear. Thus, banded kokopu do not penetrate far inland from the source of the migrant fish (Figure 5.3b).

Plotting banded kokopu occurrence across elevations (25 m strata) shows that over 85 % of occurrences of banded kokopu are accounted for by 100 m elevation (Figure 5.3c). When landlocked populations were accounted for, the peaks at higher elevation strata were decreased, although not completely eliminated (Figure 5.3d).

When stratifying data into ten classes for each variable (Table 5.3), banded kokopu reach some locations at extended distances inland and some high elevations (Figure 5.4a and b). Banded kokopu occur in all strata, except the highest elevation stratum.

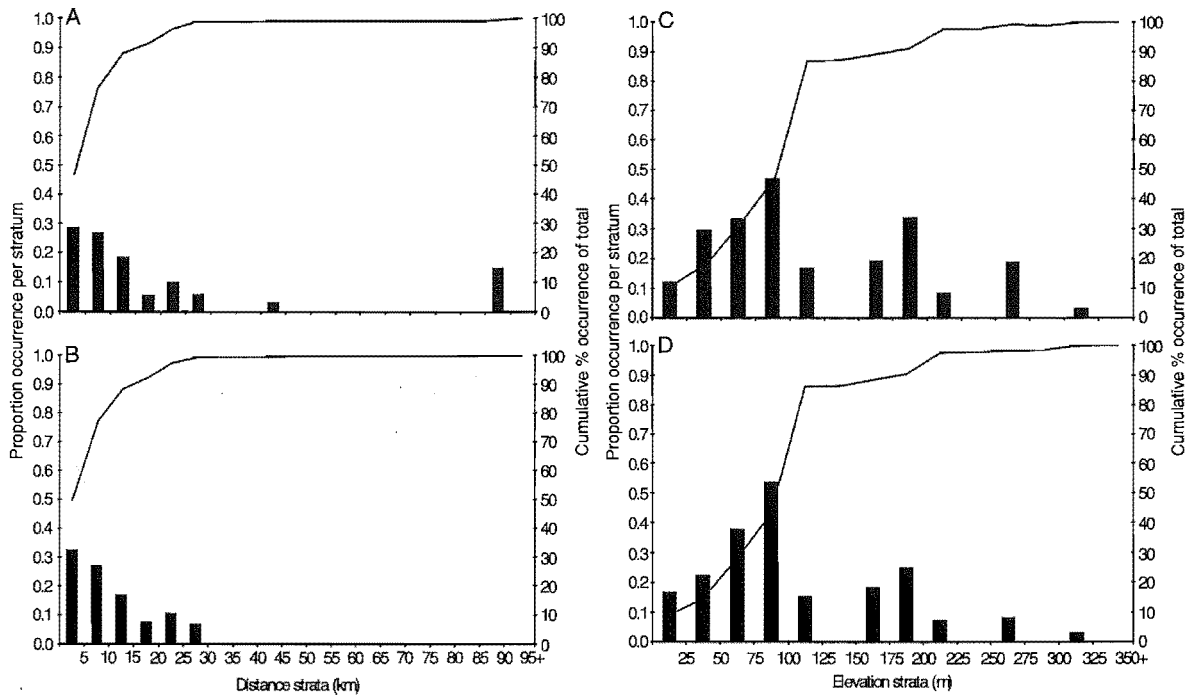


Figure 5.3 Occurrence of banded kokopu across strata (bars), each stratum 5 km wide, of extended distances inland (A and B) and across strata of increasing elevation (C and D), each stratum 25 m wide. Solid black lines show the cumulative percentage of total occurrences of banded kokopu accounted for with increasing distance from sources of migratory fish. A) Original trajectory approach used in New Zealand, in which possibility of landlocked populations not accounted for, showing two strata disconnected from the main block of strata. B) Distances calculated from potential sources of migratory fish, either the ocean or lakes, showing how accounting for possible landlocked populations improves the species trajectory for banded kokopu. C) Original trajectory approach used in New Zealand, in which possibility of landlocked populations not accounted for, showing multiple strata disconnected from the main block of strata. D) Elevations calculated from potential sources of migratory fish, above either the ocean or lakes, showing how accounting for possible landlocked populations again improves the species trajectory for banded kokopu, as evident by the decrease in size of the bars at higher elevation strata.

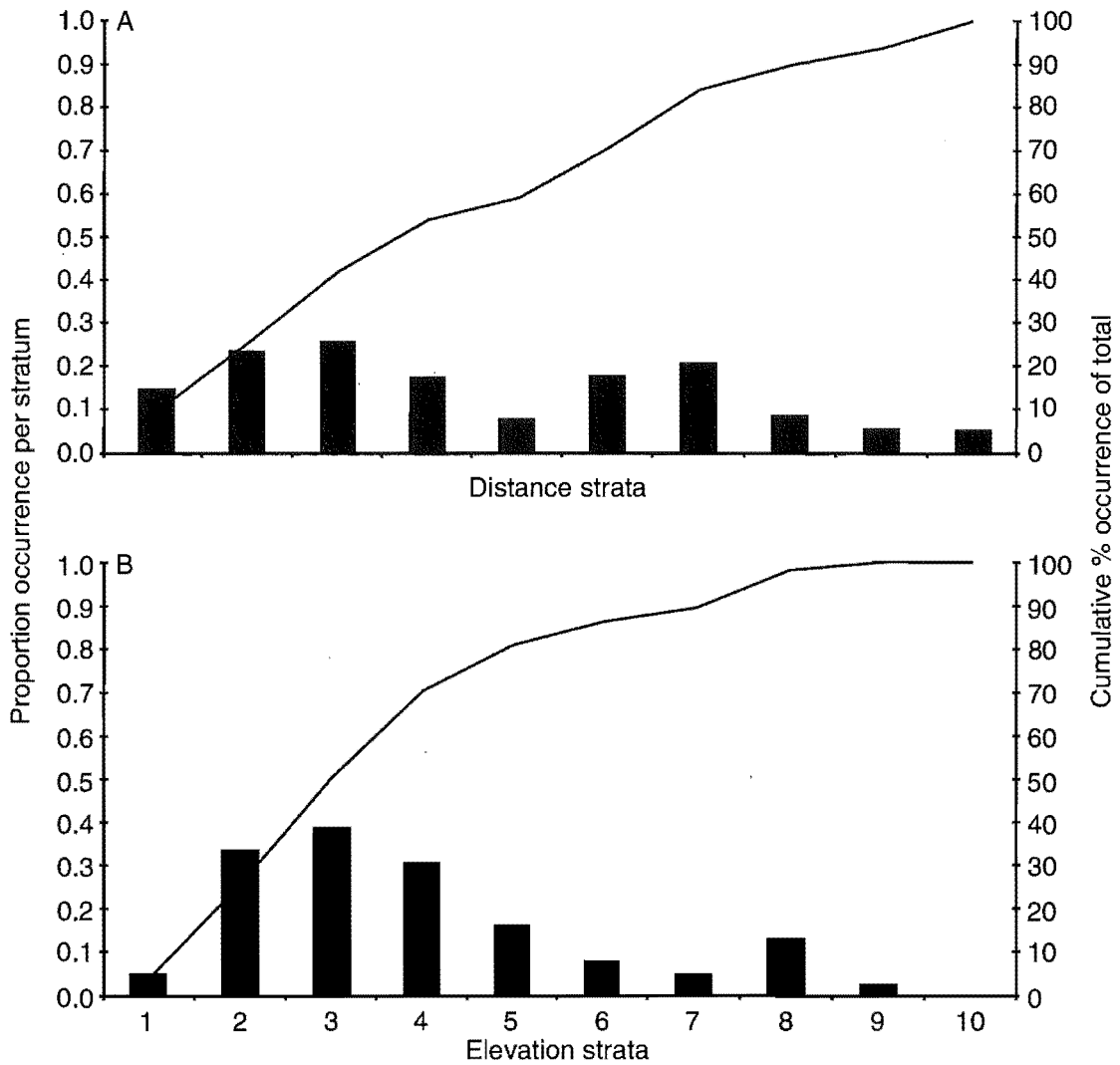


Figure 5.4 Strata corrected for the number of contributing sites, with each stratum having approximately 10 % of the total site records. A) Inland penetration from potential source of migratory fish. B) Elevation above potential source of migratory fish.

Table 5.3 Mean values of sampled sites for the 10 strata of elevation above source, distance from source, and maximum downstream slopes encountered by a diadromous fish during migration to stream reaches in the West Coast Conservancy, New Zealand. The percentage of total sites that comprise each stratum is also given.

Stratum	Elevation above source (m)	Distance from source (km)	Maximum downstream slope (deg)	Percentage of total sites (%)
1	2	0.56	0.5	9.97
2	40	2.03	1.3	9.97
3	86	4.33	1.8	9.97
4	99	7.54	2.8	9.97
5	100	10.82	3.3	9.97
6	101	15.98	3.8	9.97
7	118	21.92	6.7	9.97
8	199	31.89	13.6	9.97
9	251	52.33	29.3	9.97
10	515	96.84	42.3	10.27

To establish species trajectories, line graphs, with cumulative percentage of fish species occurrences on the y-axis versus the mean values for the individual strata on the x-axis were plotted. These trajectories show that the vast majority of the fish remain close to the source of migratory individuals (Figure 5.5a). Rankings of migration distances inland from the source, at a benchmark of 50 % cumulative occurrences accounted for (based on Figure 5.5a), show that some species migrate further than others. Inanga penetrates the least distance inland, followed by shortjaw kokopu, giant kokopu, banded kokopu, and koaro, in order of increasing inland insinuation. In terms of elevation above source of migrant fish, ranking by the 50 % cumulative occurrence benchmark, shows a slightly different result (Figure 5.5b). Inanga exhibits the same ability to cope with slopes as giant kokopu, followed by banded kokopu, whereas banded kokopu and koaro retain the same ranking as distance inland (Figure 5.5a). Another feature of Figure 5.5b is the break at 100 m elevation above source of migrant fish, whereby occurrences of all species declined sharply. With respect to stream reach slopes during upstream migration (Figure 5.5c), koaro ascend the steepest slopes. At 10 degrees slope, whereby over 80 % occurrences of the four other migratory galaxiid fish are filtered out, only about 60 % of the occurrences of koaro are accounted for (Figure 5.5c). In order of decreasing climbing ability, the fish species are: koaro, shortjaw kokopu, banded kokopu, giant kokopu and inanga

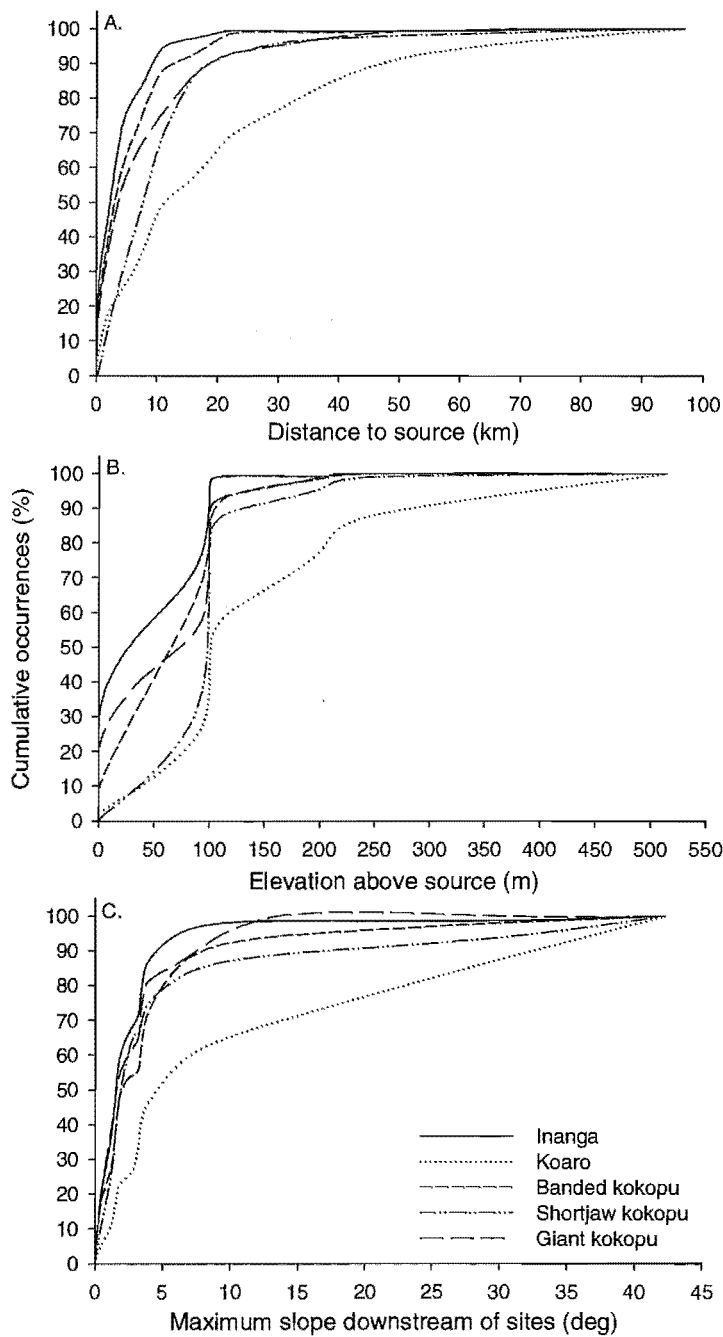


Figure 5.5 Trajectories of species occurrences for five galaxiid fish in West Coast, New Zealand, streams. A) Inland penetration from potential source of migratory fish. B) Elevation above source of migratory fish. C) Maximum downstream slope migratory fish would have encountered to reach site. Note: the trajectories for shortjaw kokopu are all with reference to the sea, as the possibility of landlocked populations for this species is at present uncertain.

5.5. Discussion

Abiotic variables such as elevation above mean sea level and river distance inland are useful in modelling and understanding the structuring of diadromous fish communities. Fish occurrence is expected to decrease gradually with an increase in either of the two variables during fish migrations (McDowall & Taylor 2000). The idea that distance inland and elevation influence diadromous fish distribution relies heavily on the notion that with increasing distance inland, steeper slopes must have been encountered, or that the migratory drive of the species has been exhausted. I have shown that river distance inland and elevation, although significantly correlated, are only weakly related in my study area. If steep slopes are not encountered, then inland migrations to significant elevations and inland distances can be expected and are indeed observed. To overcome these problems in understanding diadromous fish distributions, I used maximum downstream slope to establish migratory thresholds for the five species of diadromous fish in New Zealand.

In my study, I propagated stream reach slopes (50 m reaches), derived from a 25 m resolution DEM, up a digital river network for the West Coast of South Island, New Zealand. Maximum downstream slope was statistically weakly linked to river distances from the sea, and more strongly linked to stream reach elevation. This new slope variable, independent of distance inland or elevation, is likely to be a better predictor of migratory fish occurrences than either river distance inland or elevation above mean sea level. It could replace elevation in modelling diadromous fish distributions.

The usefulness of maximum downstream slope as a predictor of migratory fish distribution is likely due to the presence, in my study area, of extensive areas of steep coastal cliffs, as well as multiple geologic fault lines where continental tectonic plates meet, producing sudden increases in stream gradient that preclude upstream migration of most migratory fish. These geological features of the West Coast, New Zealand, landscape confound the use of river distance inland and elevation in modelling migratory fish occurrences. Maximum downstream slope overcomes this problem because it is relatively independent of distance.

As distance inland and altitude are not strongly linked to downstream slope, one could use maximum downstream slope to shed light on the importance of positioning of barriers to fish migrations in the riverscape. For galaxiids, smaller fish are more capable of coping with steep slopes, as their weight does not preclude climbing along wetted rock-faces of waterfalls. As

inland insinuation is gradual, fish become larger with increasing distance inland, and the ability to climb wetted rock-faces likely diminishes. Thus, using the maximum downstream slope variable, one should be able to shed light on the importance of positioning of barriers, such as weirs and dams, to fish migrations in the riverscape.

I also accounted for landlocked stocks of migratory fish, where large lakes allow completion of life history stages, that could potentially serve as source populations for fish below the migratory barrier, as has been demonstrated for salmonids in North America (Adams *et al.* 2000, Adams *et al.* 2001). Koaro, banded kokopu, giant kokopu and inanga are known to form landlocked populations in New Zealand (McDowall 1990), and my results show elevations and river distances inland should be considered with respect to all potential sources of migratory fish, (e.g., lakes), rather than just the ocean. The apparently disjunct distribution of banded kokopu with respect to river distances inland and elevations above mean sea level became more continuous, for example, when other potential sources of migratory juvenile fish were considered. This principle is only likely to be applicable to species with flexible life histories. For some catadromous species, like longfin and shortfin eels, the same two abiotic variables must always be considered with respect to the sea, as their life histories are more rigid and involve obligatory marine stages, and their presence above large lakes does not indicate potential self-sustaining land-locked populations.

The low cost of geographical information systems and the processing capabilities of computers (Johnson & Gage 1997), makes determining accurate values for river distances inland and elevations, both from the sea and above potential sources of migratory fish, and incorporating them into new and existing distribution models feasible. Maximum downstream slope could be used to further elucidate patterns of fish occurrences, such as species trajectory models (McDowall 1996a, McDowall 1998a, McDowall 1998b, McDowall & Taylor 2000), logistic regression models (Broad *et al.* 2001a), or any other distribution model for migratory fish species (Joy & Death 2004).

An application of my approach for conservation management is that areas above migration thresholds of migratory fish species can be readily identified, as well as the specific locations of migration barriers in the riverscape. Additionally, maximum downstream slope could aid in elucidating fragmentation patterns in diadromous fish populations where areas of suitable habitat exists, but fish are absent, possibly because of introduced species, such as brown trout, poor water quality, or over-harvesting. Furthermore, a distinction can be made between anthropogenic and natural barriers to migration, as physical migratory barriers precluding

upstream migration of fish within watersheds can be readily identified and located in the landscape (i.e. fault lines and steep gradients), providing an explanation for the apparent fragmented distribution of fish in some areas. Thus, this new downstream slope variable will allow for more targeted conservation and management measures in terms of conservation and resource consent monitoring.

Chapter 6. An assessment of the relative influence of access barriers, conditions in migratory passage, and local land uses on the distribution of diadromous fish using a hierarchical GIS analysis

6.1. Summary

Migratory fish are affected by access, conditions along the migratory path, and local land uses. Separating the relative influences of these factors is difficult, but necessary for directing management. I used data on fish occurrences extracted from a national database along with digital geospatial land use data, river network, and an elevation model in a GIS to model impacts of physical barriers, degradation of migratory passage, and site-scale landuse characteristics on diadromous fish occurrence in the Department of Conservation West Coast Conservancy, New Zealand. I used backward conditional logistic regression techniques to identify factors at these various scales affecting two galaxiid fish, banded kokopu (*Galaxias fasciatus*) and koaro (*G. brevipinnis*).

To identify accessible habitat not restricted by physical barriers, I used the migratory distance from source (sea or lakes), maximum downstream slope encountered, and their interaction, to identify accessible sites in least-impacted catchments and applied the results to all catchments within the study area. Sites modelled as accessible to banded kokopu and koaro, in forested areas without non-forest land uses upstream, were then used to model the impacts of catchment-scale deforestation and downstream land uses on the migratory passage. Sites not restricted by physical barriers or landuse-related impacts on migratory passage were then used to model the effects of local landuse. To evaluate the success of the hierarchical modelling, I used leave-one-out cross-validation of observed over expected for the final model. Additionally, I used contingency analysis on three distance and three downstream slope categories to examine occurrences of fish, and evaluated greater or lesser than expected occurrences within these categories using the standardised residuals. Physical barriers to upstream migration allowed koaro and banded kokopu to access 28000 km and 5300 km, respectively, of the ca. 40600 km of streams within the study area. Impacts on the migratory passage reduced the amount of accessible

habitats for koaro and banded kokopu by 55 % and 70 % for each species, respectively. Local land uses further reduced koaro and banded kokopu habitats to 70 % and 90 % of total accessible habitats for koaro and banded kokopu, respectively. By reducing anthropogenic impacts on migratory passages to ensure more habitats become accessible, the contemporary distribution of diadromous fish, such as koaro and banded kokopu, could be extended.

6.2. Introduction

Fish that migrate between marine and freshwater environments are particularly common on islands such as New Zealand, Hawaii, and Falkland Islands (McDowall *et al.* 2001, McDowall 2003a). Depending on their migratory drive and ability to cope with barriers to migration (Smith *et al.* 1997, Elliott *et al.* 1998, Klemetsen *et al.* 2003), diadromous fish often journey extended distances inland to considerable elevations. During their up-and-downstream journeys, fish may encounter many barriers, anthropogenic and natural, that may limit, preclude, or aid in movement (Adams *et al.* 2001, Novinger & Rahel 2003, Thorstad *et al.* 2003). Thus, the specific location of such barriers in the landscape may play important roles in the distribution patterns observed for migratory fish. Moreover, disentangling the relative roles of migratory distance, slope-related barriers, and anthropogenic impacts is important if land-use effects on diadromous fish are to be managed effectively.

Distance inland and altitude above mean sea level have long been recognised as factors limiting the distribution of migratory fish (McDowall 1988, McDowall 1993, McDowall 1998a). However, some features of New Zealand's environment, such as the presence of steep coastal cliffs and multiple geologic fault lines, provide for sudden increases in stream gradients and large waterfalls which make altitude less useful (Chapter Five). These potential barriers to fish migration would preclude upstream migration of fish that overcome barriers by jumping or burst swimming (i.e., Salmonidae) (Adams *et al.* 2000, Adams *et al.* 2001), but may pose less of an impediment to fish that use the surface tension between their ventral surface and substrate to climb the wetted surfaces along the margins of waterfalls (i.e., some Galaxiidae and Anguillidae) (Jellyman 1977, McDowall 1990, McDowall 2003b). For fish species using surface tension to adhere to wetted surfaces while climbing, smaller size is a great advantage as the surface area to weight ratio decreases with increasing size (Jellyman 1977). For longfin (*Anguilla dieffenbachii*) and shortfin (*A. australis*) eels, the elvers of both species lose their ability to climb vertical wetted surfaces when reaching twelve centimetres in length (Jellyman 1977). This loss of climbing ability could apply to all fish species that use this method to overcome obstacles to

upstream migration, such as the five diadromous New Zealand galaxiid fish that comprise the “whitebait” fishery in New Zealand; giant kokopu (*Galaxias argenteus*), koaro (*G. brevipinnis*), banded kokopu (*G. fasciatus*), shortjaw kokopu (*G. postvectis*), and inanga (*G. maculatus*). Small migrant juvenile galaxiids would have a large surface area to body weight ratio, and should be able to overcome steep stream gradients. However, because inland insinuation of migratory galaxiid fish is gradual, as fish reach locations further inland, the fish would also be larger, and eventually lose their abilities to overcome steep stream gradients. In locations close to the source of juvenile fish, where the migrating fish are small, I expected to find fish even above steep stream gradients. As one progresses further inland, and migrant fish presumably are larger, I expected that fish occurrences above steep stream gradients would decline and that only the species apt at climbing would be found above steep stream gradients far inland. Thus, I expected to observe an interaction between migratory distance and the maximum downstream slope encountered by migrating fish.

Juvenile fish of the five migratory native *Galaxias* migrate upstream into rivers from the sea during spring (McDowall 1996b). Upstream migration to adult habitat is gradual, with the abundance of fish declining with distance inland and increasing elevations, as fish either find suitable habitat or are precluded from further upstream migration by natural or anthropogenic barriers. Research has investigated fish passage facilities that assist upstream migrating fish in moving past obstructions (Mitchell 1991, Laine *et al.* 2002, Baker 2003b). However, little research has dealt with the significance of the location of natural barriers in the landscape, such as steep stream gradients, and how the location of these in the landscape may limit the distribution of native fish. It may be that natural waterfalls located close to the source of migrating fish may be surmountable, whereas similar waterfalls in inland locations preclude upstream fish migration. Furthermore, accessible habitat from a migratory viewpoint may be affected by downstream land uses and catchment-scale effects, further reducing accessible habitat (Chapter Two). Intensive land-use practices affecting the migratory passage may preclude accessible suitable upstream habitats from being occupied by migratory fish due to input of fine sediments to the streams (Boubee *et al.* 1997, Rowe & Dean 1998, Rowe *et al.* 2000, Richardson *et al.* 2001). And finally, habitat that is accessible and not impacted by downstream land uses or catchment-scale effects may be affected by local site-scale conditions, whereby local landuses, such as dairy and mixed dairy and sheep farming reduce fish (Chapter Three).

Firstly, I hypothesised that the occurrence of migratory fish using surface tension to adhere to wetted substrates to overcome barriers, above steep stream gradients, may be a function

of the location of such gradients in the landscape. It may be that the available habitat is limited by downstream stream slopes, extended distance inland, and that with extended distance inland stream slopes limit upstream fish migration.

Secondly, I hypothesised that fish are precluded from occupying some accessible (i.e., not above physical barrier) habitat by catchment-scale effects of land use (proportion forest cover remaining) and land use negatively affecting conditions on the migratory passage (proportion of stream length flowing through farm-impacted areas).

Finally, I hypothesised that given the above limiting factors on access to local habitats that fish distributions are further limited by site-scale effects of land uses and local conditions, such as the presence of riparian forest, stream size and gradient that affect local habitat quality.

To examine these hypotheses, I conducted a three-level hierarchical analysis using existing data on fish occurrences within the Department of Conservation's West Coast Conservancy, South Island, New Zealand, from the New Zealand Freshwater Fish Database (NZFFD).

6.3. Methods

6.3.1. Study area

From Awarua Point in the south to Kahurangi Point in the north, the West Coast Department of Conservation Conservancy encompasses streams flowing from the Southern Alps into the Tasman Sea (Figure 6.1). The region at large retains extensive areas of indigenous forests, especially at higher elevations, and contains some of New Zealand's least disturbed landscapes. However, some catchments are impacted by various types of farming, forestry, and mining practices. Very steep stream gradients occur both adjacent to the coast as well as far inland. Features such as coastal cliffs, multiple geologic fault lines, and the Southern Alps are prominent in the West Coast landscape. Thus, the region is ideal for investigating the influences of non-anthropogenic factors such as the location of steep stream gradients in the landscape as well as land use impacts on distributions of migratory fish.

6.3.2. Digital data preparation

I used a digital version of the 1:50,000 Topographic Vector Data (Terralink NZ Ltd.) hydrology network to represent the streams of our study area. Stream reaches in this network are represented as line segments, connected by T-nodes (to-node) and F-nodes (from-nodes) ordered

in a logical fashion, allowing propagation of variables up and down the network in a GIS. I densified this hydrology network using the DENSIFY command in ArcInfo (Version 8.0.2), inserting new vertices and connecting nodes at specified intervals, ensuring no individual line-

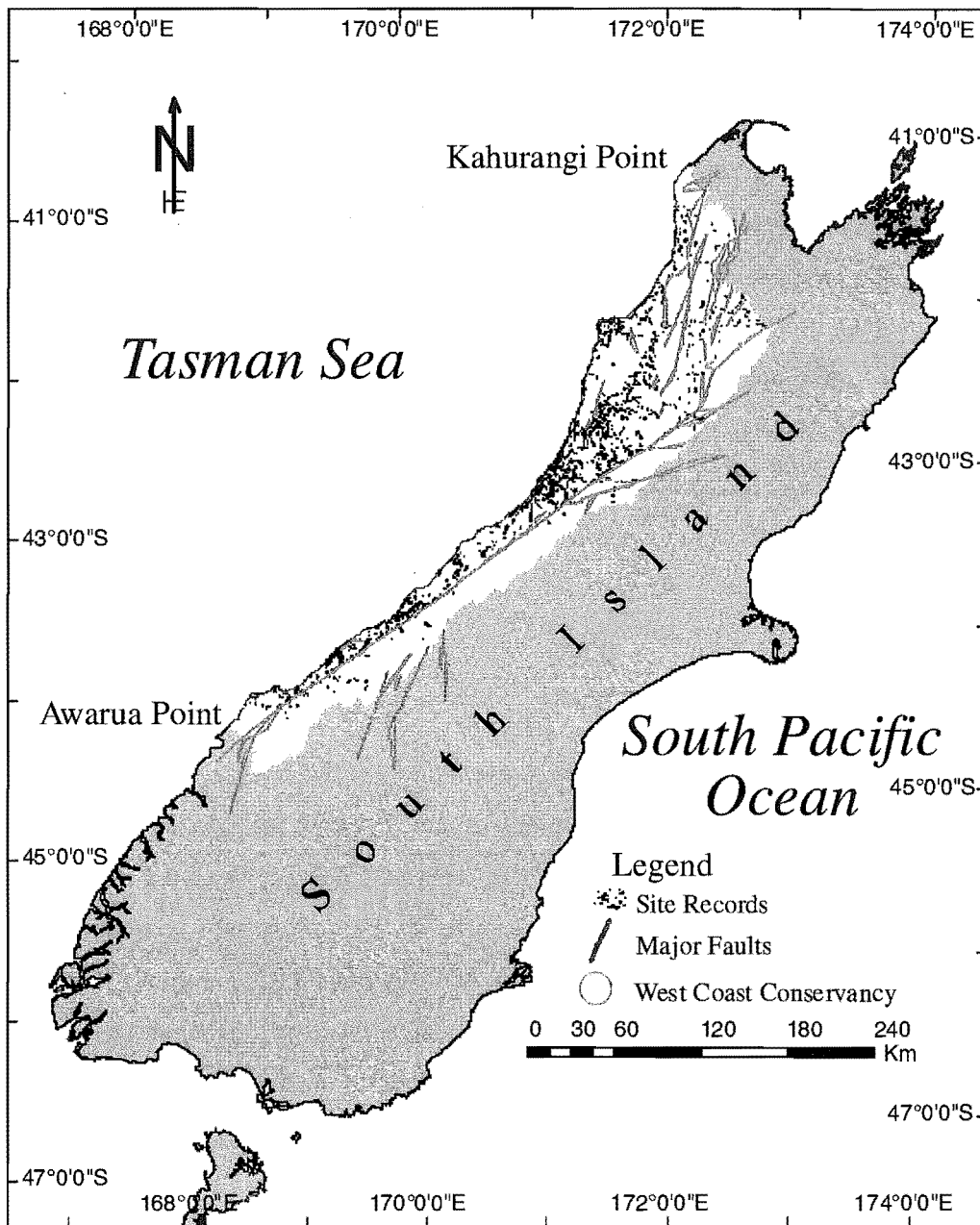


Figure 6.1 Locations of site records from the New Zealand Freshwater Fish Database within the Department of Conservation West Coast Conservancy. Major geologic fault lines responsible for sudden increases in stream gradients are also shown.

segment of the digital stream network was longer than 50 m in length. Subsequently, I used the RENODE command to re-establish the T-and F-node topology, thus restoring the digital connectivity of the stream network. Stream segments were also assigned to stream order

according to their position within the network, where two first order streams join to form a second order stream and so forth (Strahler 1957).

I derived slopes and altitudes for the individual stream segments by draping the hydrology network over a 25 m resolution digital elevation model (DEM) for the South Island of New Zealand. I then propagated stream slopes up the stream network, so that steeper slopes replaced less steep slopes, traversing up the network. This rendered a stream network where the maximum downstream slope a migratory fish would have encountered during upstream migration could be determined for any location within the network. Similarly, I derived river distances inland, both from the sea and lakes. Using the above propagated variables, I classified the stream reaches of our hydrology network with respect to downstream slopes as low (< 5 degrees), moderate (5 - 10 degrees), and steep (> 10 degrees) gradients, as well as with respect to distance inland from ocean or lakes as coastal (within 25 km of ocean or lakes), inland (between 25 and 100 km), and far inland (100 + km inland). The rationale for these categories was based on a previous study of abiotic influences on diadromous fish distributions, where declines of most species of diadromous fish occurred between these distance and slope categories (Chapter Five).

I extracted data on fish occurrences for the West Coast Conservancy for the period 1990–2004 from the NZFFD, a national historic archive on fish occurrence and habitat information. Because a range of individuals and institutions have contributed information to this database, with surveying methods varying from quantitative multiple pass electric fishing techniques, to qualitative night-time spotting, I converted abundance data to binary presence/absence data. As many of the records of fish occurrences were in close proximity to one another, I filtered the data to represent spatial locations within the stream network. Thus, site records within streams 50 m of one another were combined to represent one spatial location, resulting in 1278 unique stream reaches with sufficient data for analyses.

I appended the data from the modified digital hydrology network, containing information on stream orders, maximum downstream slopes (low, moderate, or high gradients), stream reach altitudes, river distances inland (coastal, inland, or far inland) from ocean and lakes, and land covers from the landcover database, to the records of fish occurrences.

6.3.3. Data analysis

To investigate the relative influence of distance and downstream slope, I used 3 by 3 contingency analysis to determine the relationships between nine combinations of distance and slope categories and occurrences of five galaxiid fish. I also quantified the amount of stream

habitat in these categories. From the results of these analyses I used adjusted standardised residuals of the observed over expected ratio of fish occurrences to assess greater or lesser than expected fish occurrence/non-occurrence in these habitats.

To further investigate the relative influences of anthropogenic factors on migratory fish distributions, I conducted an analysis in three levels which aimed to determine the effect on the amount of useable habitat lost due to physical access barriers, conditions along the migratory passage, and conditions at a site. I did this using a hierarchical analysis which sequentially dealt with each particular influence.

In level one, to test whether distance or maximum downstream slope encountered by migrating fish limited distribution patterns of banded kokopu and koaro, I used a least-impacted reference site approach and selected data from catchments with more than 90 percent forest cover and no non-forested land uses along the migratory passage upstream or downstream (Figure 6.2a) (Joy & Death 2000). I then used logistic regression, using distance and downstream slope variables transformed to a common scale, to examine the effects of physical barriers to banded kokopu and koaro migrations in these relatively pristine catchments. The interaction of distance from source and maximum downstream slope was included to test whether location of steep stream slopes significantly influenced fish distributions. By comparing the magnitude and sign of the coefficients of determination for the presence of the different species, I could determine whether the distributions were limited by distance, maximum downstream slope encountered, or their interaction. I then applied this model to all catchments within the study area to identify sites and quantify stream kilometres that were accessible to banded kokopu and koaro.

In level two of the analysis I used sites within areas judged to be accessible in level one and excluded sites with local or upstream land use impacts. The sites retained were in forested areas and had upstream catchments with > 90 % forest cover with no non-forest land uses along the watercourse upstream of the sites. This meant all sites used in the level two analysis had no physical access barriers and had good local habitat conditions. I then applied a second logistic regression analysis to assess the effects of proportion catchment forest cover and downstream land uses which could affect conditions on the migratory passage on banded kokopu and koaro occurrences (Figure 6.2b). This approach allowed me to differentiate between the effect of physical barriers along the migratory passage and effects of land uses at the catchment-scale that deleteriously affect migratory passage. Separating these allowed me to determine how many stream kilometres of fish habitat were lost due to catchment-scale land use effects along the migratory route, making them inaccessible.

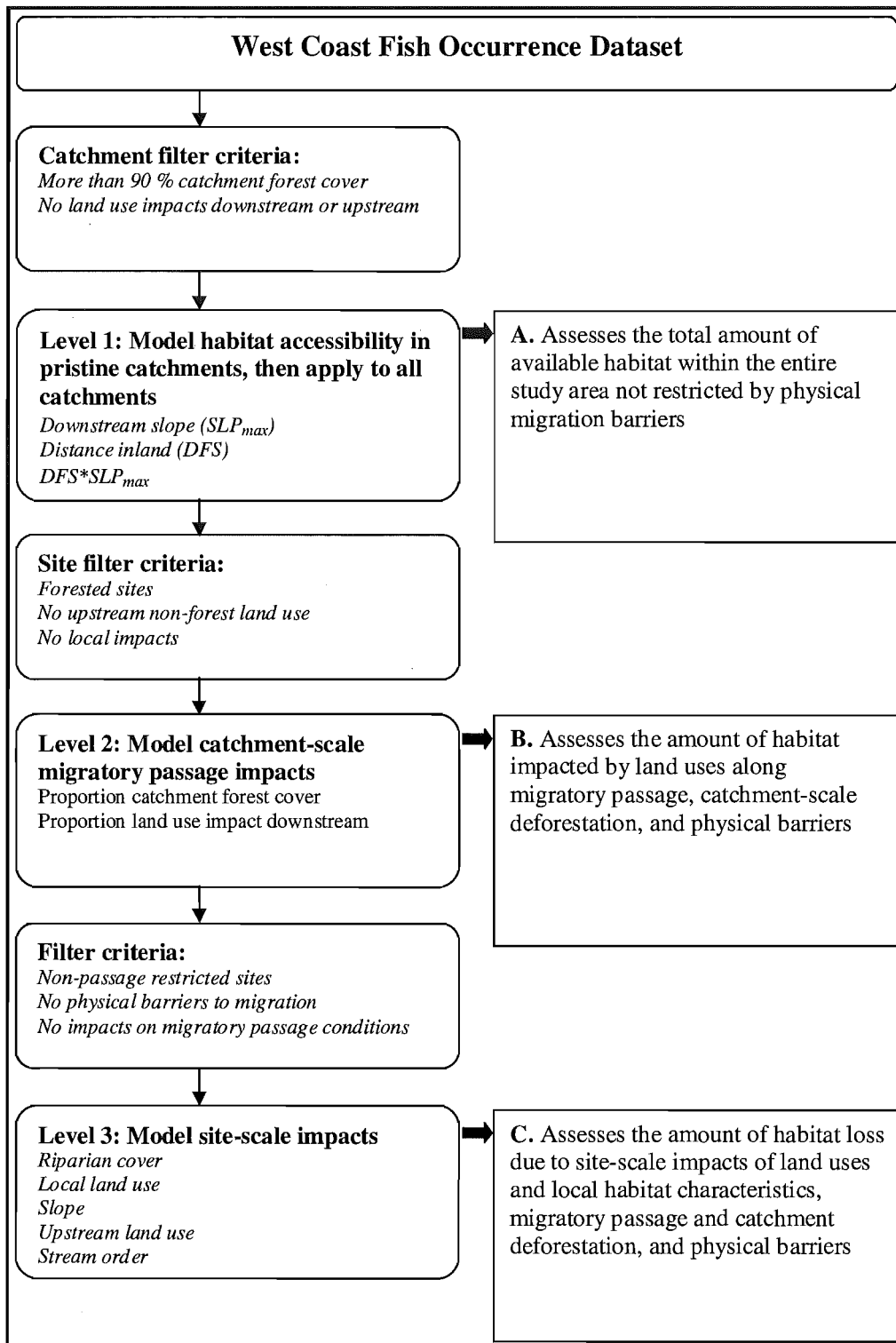


Figure 6.2 Flowchart of the three-level hierarchical data analysis approach to differentiate between physical access barriers to upstream migration, catchment-scale deforestation and intensive landuse influences on migratory passage, and local landuse and environmental variables.

Finally in the third level, I applied the level two model to accessible sites to filter out sites inaccessible due to catchment-scale land uses affecting conditions along the migratory passage. On the sites retained, I applied a third logistic regression procedure to assess the effects of local conditions and the effects of upstream land uses (Figure 6.2c). Upstream land use was assessed as the proportion of stream above sites flowing through farmed land, such as sheep, cattle, mixed sheep and cattle, and production agriculture. Local land uses were defined as no commercial farming activity, sheep, cattle, or sheep and cattle pastures. Presence of riparian forest cover, stream slope, and stream order were also included as local environmental variables in this level of the analysis. This further allowed me to differentiate between physical barriers to migratory access, effects of catchment scale land uses on fish passage, and effects of local land uses and habitat characteristics, and allowed me to quantify the amount of habitat lost due to land-use effects on local conditions. To assess the success of each model, I used leave-one-out cross-validation of observed over predicted classification for the two species.

6.4. Results

Available stream habitat is distributed evenly within coastal, inland, and far inland locations (Table 6.1). However, distribution of streams with respect to maximum downstream slopes is bimodal, with 20.0 % having low downstream gradient, 4.8 % above moderate stream gradients, and 75.2 % above steep stream gradients (Table 6.1).

Table 6.1 Percentage distribution of available stream habitat in a matrix of three distance inland and three downstream slope categories. The source is defined as the origin of migratory juvenile galaxiid fish, and can be the ocean, or lakes for species with flexible life-histories.

Category	Coastal (< 25 km to source)	Inland (25-100 km to source)	Far inland (> 100km to source)	Sum
Low gradient (< 5 deg)	13.3	4.3	2.4	20.0
Above moderate gradient (5-10 deg)	2.8	1.1	0.9	4.8
Above steep gradient (> 10 deg)	19.3	20.6	35.3	75.2
Sum	35.4	26.0	38.6	100.0

Inanga were restricted to streams proximal to the source of juvenile migrant fish, and primarily in streams of low gradients where the residuals of the observed over expected ratio indicated a far greater than expected occurrence in this habitat (Figure 6.3a). Koaro, however, were found from the sea to locations far inland and across all stream gradient categories. However, the contingency analyses showed that occurrences were far lower than expected in far inland locations above steep gradients (Figure 6.3b). I found higher than expected occurrences of koaro in coastal streams, above moderate and steep gradients (Figure 6.3b). This occurrence

pattern could be due to the migratory drive, or conditions along the migratory route and local habitat conditions.

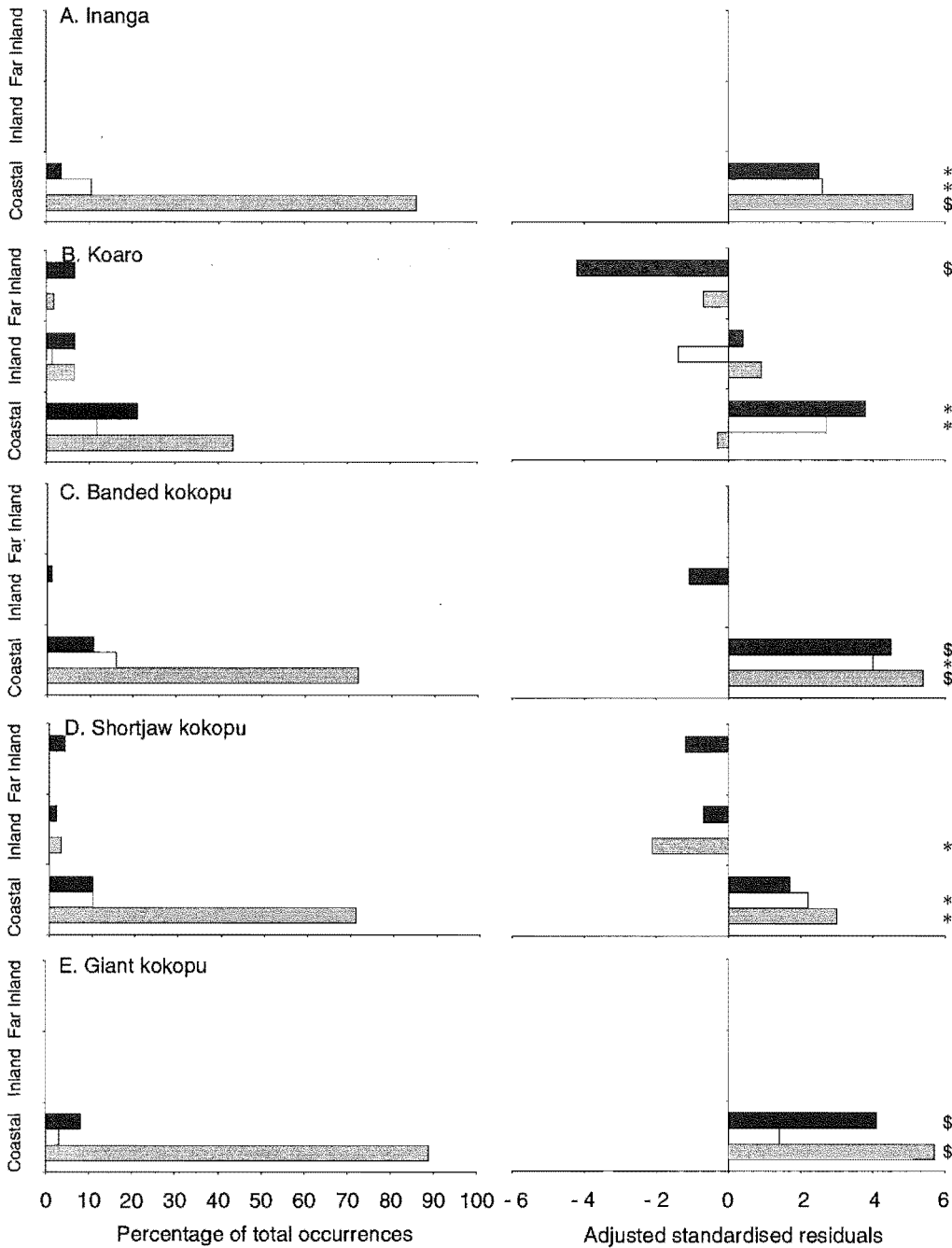


Figure 6.3 Percentage occurrences of five native galaxiid fish with respect to three distance inland from source and three stream slopes below sites categories: Coastal (< 25 km to source), inland (25-100 km), far inland (> 100 km), low (< 5 deg), moderate (5-10 deg), and steep (> 10 deg). Solid black bars represent percentage of total occurrences in streams with steep slopes downstream, un-filled bar occurrences where moderate slopes occur below sites, and grey bars for low gradient streams. Standardised adjusted residuals of observed over expected are given as a measure to assess preference/avoidance by fish of streams of the nine slope/distance combinations. *, P < 0.05; \$, P < 0.01.

Banded kokopu were absent from streams located far inland from sources of migrant fish, but did occur, although infrequently, in inland locations. Banded kokopu were most common in coastal streams of low gradients, but were not uncommon in streams above moderate to steep gradients (Figure 6.3c). Again, this may be an indication of an interaction between accessibility of habitats, conditions on the migratory passage, and local landuses. Shortjaw kokopu occurred most frequently in low gradient coastal streams, but did occur far inland above steep stream gradients (Figure 6.3d). Shortjaw kokopu occurred in more instances than expected in coastal, low and moderate gradient streams, and in fewer instances than expected in inland streams of low gradients (Figure 6.3d). Similar to inanga, giant kokopu were restricted to coastal environments, and occurred in more instances than expected in streams of low gradients, and above steep gradients (Figure 6.3e).

The level one analysis (Table 6.2) indicated that the abilities of the five migratory galaxiids to cope with long migratory distances and steep downstream slopes varied. Inanga and banded kokopu occurrences were strongly influenced by distance from source, but not by the maximum slope encountered. However, inanga and banded kokopu were subject to significant negative interactions of distance from source and maximum downstream slope. Koaro were negatively influenced by distance from source, but positively influenced by maximum downstream slope, and not influenced by the interaction of downstream slope and distance from source. Shortjaw kokopu distributions were negatively influenced by distance from source, but not by maximum downstream slope or the interaction of downstream slope and distance. Giant kokopu distributions were negatively influenced by distance from source, maximum downstream slope, and their interaction. Inanga, banded kokopu and giant kokopu show significant interactions between distance from source and maximum downstream slope, an indication that their abilities to overcome steep stream gradients decline the further inland they get.

The backward conditional binary logistic regression procedures for differentiating between habitat accessibility, impacts on migratory passage, and local impacts for banded kokopu showed that distance from source was a strong predictor of fish occurrences in non-impacted, pristine catchments (Table 6.3; Level 1).

Table 6.2 Distance inland (DFS), maximum downstream slope (SLP_{max}), and interaction of DFS and SLP_{max} coefficients of determination for the presence of five galaxiid fish and introduced salmonids. Both variables were adjusted to a common scale. Thus, the magnitude and sign of the coefficients indicates the nature of the variable and fish occurrences, and the Wald statistic indicates which is the stronger predictor variable.

Species	Variable	β	S.E.	Wald	df	<i>p</i> -value
Inanga	DFS	- 0.131	0.035	14.2	1	< 0.001
	SLP _{max}	- 0.006	0.012	0.254	1	0.615
	DFS*SLP _{max}	- 0.006	0.002	7.94	1	0.011
Banded kokopu	DFS	- 0.141	0.022	39.9	1	< 0.001
	SLP _{max}	- 0.005	0.008	0.386	1	0.535
	DFS*SLP _{max}	- 0.003	0.001	4.94	1	0.021
Koaro	DFS	- 0.010	0.008	1.57	1	0.210
	SLP _{max}	0.021	0.004	31.0	1	< 0.001
	DFS*SLP _{max}	- 0.0002	0.0001	1.45	1	0.229
Shortjaw kokopu	DFS	- 0.035	0.014	5.97	1	0.015
	SLP _{max}	- 0.009	0.007	1.67	1	0.196
	DFS*SLP _{max}	0.0003	0.0003	0.618	1	0.432
Giant kokopu	DFS	- 0.113	0.029	15.4	1	< 0.001
	SLP _{max}	- 0.051	0.020	6.17	1	0.013
	DFS*SLP _{max}	- 0.006	0.002	7.72	1	0.012

Table 6.3 Three-level hierarchical backward conditional binary logistic regression results for presence of banded kokopu at a site. β represent the estimated regression coefficients for the predictor variables, with the standard errors, S.E., given. The Wald statistic is the ratio of the β to S.E. of the regression coefficient squared. Reference conditions have more degrees of freedom as they are used as reference for the estimation of coefficients for the non-reference conditions. The significance of each variable is given by the *p*-value.

Banded kokopu	β	S.E.	Wald	df	<i>p</i> -value
Level 1. Migratory access					
DFS	- 0.141	0.022	39.9	1	< 0.001
SLP _{max}	- 0.005	0.008	0.386	1	0.535
DFS*SLP _{max}	- 0.003	0.001	4.94	1	0.021
Level 2. Landuse impacts on migratory passage					
Proportion (Pi) forest cover	2.336	0.728	10.3	1	0.001
Pi downstream land use impacted	- 0.016	0.014	1.42	1	0.233
Level 3. Local impacts					
Riparian forest present	0.754	0.204	13.6	1	< 0.001
Stream order					
First	6.595	28.377	0.054	1	0.816
Second	6.258	28.377	0.049	1	0.825
Third	5.258	28.377	0.034	1	0.853
Fourth	4.558	28.383	0.026	1	0.872
Fifth	5.796	28.381	0.042	1	0.832
Sixth and above*			34.5	5	< 0.001
Land use					
No farming*			4.20	3	0.241
Sheep	2.305	1.263	3.33	1	0.068
Cattle	- 0.176	0.301	0.342	1	0.559
Sheep and cattle	- 6.713	1.092	37.8	1	< 0.001
Pi upstream land use impacted	- 0.009	0.015	0.345	1	0.557
Stream slope (deg)	- 0.004	0.023	0.024	1	0.878

* Reference condition

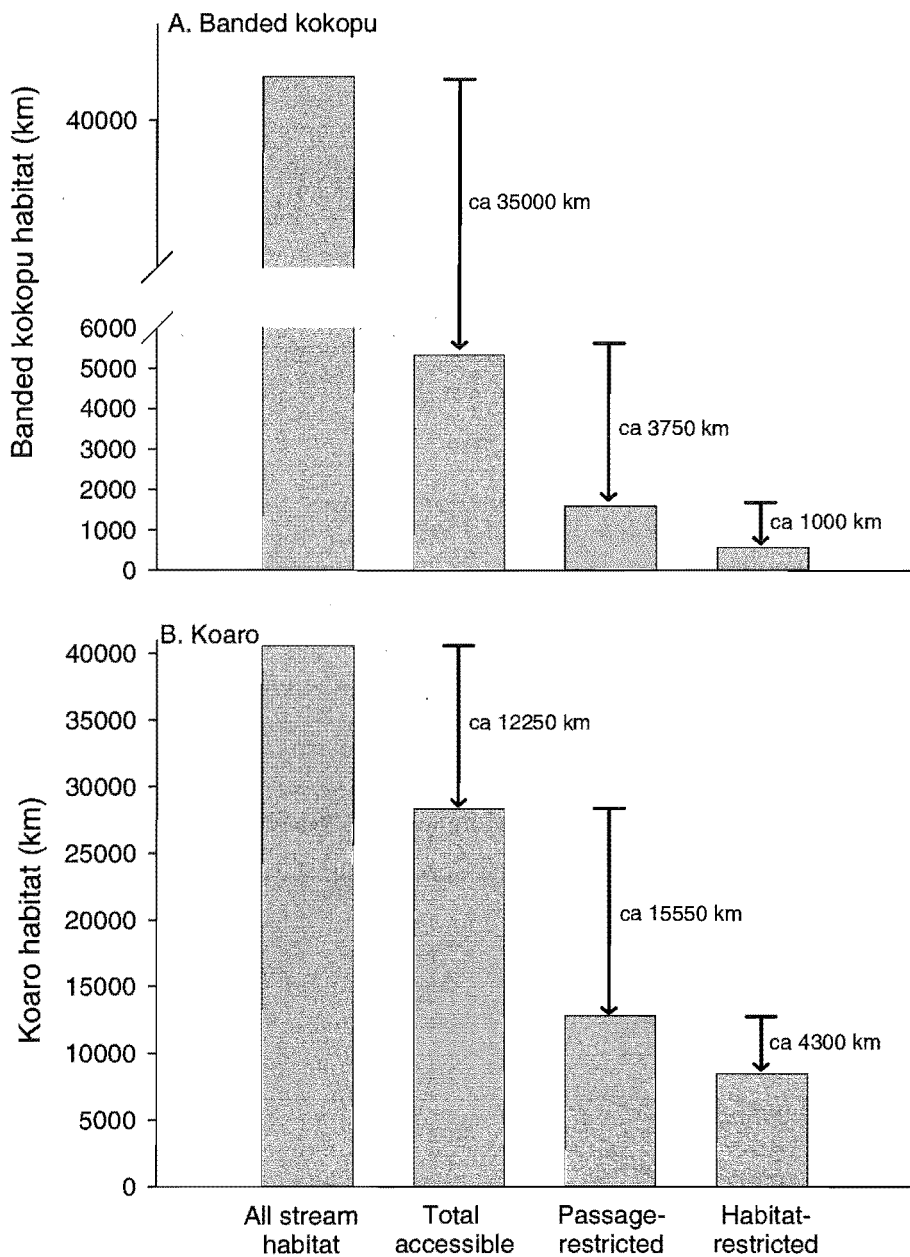


Figure 6.4 The total available stream habitat, the amount of available stream habitat based on abiotic variables of maximum downstream slope, distance, and their interaction, available habitat after accounting for access issues of land uses along waterways and catchment forest cover, and available habitat when accounting for site characteristics of land uses, slope, and riparian cover for koaro (A) and banded kokopu (B).

When applied to the hydrology network, it showed that 5300 km of streams should have been accessible to banded kokopu (Figure 6.4a). When applied to all catchments within my study area, leaving sites inaccessible due to physical barriers out, the proportion catchment forest cover

was a strong predictor of banded kokopu occurrence at the catchment scale, although the conditional logistic regression procedure retained the proportion downstream land use variable as well (Table 6.3; Level 2). Thus, the level two analysis indicates that catchment land-use effects downstream of sites which likely affect migratory passage conditions were associated with a 70 % reduction in available habitat, leaving 1600 km of accessible habitat (Figure 6.4a). At the site-scale in the level three analysis, presence of riparian cover positively influenced banded kokopu occurrence, whereas intensive land uses such as mixed sheep and cattle had a strong negative influence on banded kokopu occurrence. Other variables retained by the logistic regression procedures at level three included stream order, where smaller streams had higher positive regression coefficients, and proportion upstream land uses and stream slopes, both with negative regression coefficients (Table 6.3; Level 3). This third level of analysis indicates that site-scale factors further reduced good banded kokopu habitat to 600 km, about a 90 % reduction compared to the original accessible habitat (Figure 6.4a).

Table 6.4 Three-level hierarchical backward conditional binary logistic regression results for presence of koaro at a site. β represent the estimated regression coefficients for the predictor variables, with the standard errors, S.E., given. The Wald statistic is the ratio of the β to S.E. of the regression coefficient squared. Reference conditions have more degrees of freedom as they are used as reference for the estimation of coefficients for the non-reference conditions. The significance of each variable is given by the *p*-value.

Koaro	β	S.E.	Wald	df	<i>p</i> -value
Level 1. Migratory access					
DFS	- 0.010	0.008	1.570	1	0.210
SLP _{max}	0.021	0.004	31.0	1	< 0.001
DFS*SLP _{max}	- 0.0002	< 0.001	1.45	1	0.229
Level 2. Landuse impacts on migratory passage					
Proportion (Pi) forest cover	0.028	0.568	0.002	1	0.961
Pi downstream land use impacted	- 0.040	0.012	11.1	1	0.001
Level 3. Local impacts					
Riparian forest present	0.510	0.159	10.2	1	0.001
Stream order					
First	3.318	6.751	0.242	1	0.623
Second	3.590	6.751	0.283	1	0.595
Third	3.234	6.751	0.229	1	0.632
Fourth	3.266	6.754	0.234	1	0.629
Fifth	2.715	6.767	0.161	1	0.688
Sixth and above*			6.77	5	0.342
Land use					
No farming*			3.95	3	0.267
Sheep	1.369	1.015	1.82	1	0.177
Cattle	- 0.313	0.257	1.48	1	0.224
Sheep and cattle	- 0.455	0.666	0.467	1	0.495
Pi upstream land use impacted	- 0.010	0.013	0.684	1	0.408
Stream slope (deg)	0.020	0.014	2.24	1	0.135

* Reference condition

The same three-level backward conditional binary logistic regression analysis approach for koaro showed that at level one, koaro was positively influenced by maximum downstream slope (Table 6.4). When applied to streams in all catchments within my study area, I found that koaro could access over 28000 km of the approximately 40000 km of streams within my study area (Figure 6.4b). At level two, the proportion downstream land uses impacting on the migratory passage had a significantly negative influence on koaro occurrence (Table 6.4). This reduced the accessible habitat by 55 %, leaving less than 13000 km of streams accessible. At the site-scale, riparian forest cover had a positive influence on koaro occurrences (Table 6.4; Level 3). Stream size, specific land uses, proportion upstream land use impacts and stream slopes were not significant by themselves, but were retained by the conditional regression procedures (Table 6.4; Level 3), because taking these out would have caused the model to itself to become insignificant. When site-scale impacts were accounted for, 8500 km of streams within our study area were classified as good koaro habitat, a 70 % reduction compared to accessible habitat, or one fifth of the total available stream network (Figure 6.4b).

Table 6.5 This classification table assessed the performance of the three levels of regression models by cross-tabulating the leave-one-out cross-validated observed presence/absence of banded kokopu and koaro categories with the predicted presence/absence of the two species from logistic regression procedures. Cells on the diagonal from top-left to right-bottom were correct predictions. Cells on the opposite diagonal, from bottom-left to top-right, were incorrect predictions.

Occurrences in database		Predicted by logistic regression		Percentage correct
		Absent	Present	
Level 1				
Banded kokopu	Absent	468	48	90.7
	Present	43	118	73.3
Overall				86.6
Koaro	Absent	472	44	91.5
	Present	31	130	80.7
Overall				88.9
Level 2				
Banded kokopu	Absent	109	12	91.6
	Present	14	70	83.3
Overall				87.3
Koaro	Absent	294	41	87.7
	Present	36	203	84.9
Overall				86.6
Level 3				
Banded kokopu	Absent	569	28	95.3
	Present	67	73	52.1
Overall				87.1
Koaro	Absent	556	13	97.7
	Present	38	159	80.7
Overall				93.3

Leave-one-out cross-validation of observed over expected for the three levels of the hierarchical logistic regression procedures for banded kokopu and koaro correctly predicted presence/absence at greater than 85 % at all levels for both banded kokopu and koaro (Table 6.5).

6.5. Discussion

6.5.1. Accessible habitat

Many barriers to fish migrations, such as large waterfalls or steep stream gradients, are part of natural landscapes and exist in their respective locations due to geologic events beyond human control. My results indicate barriers affect the distribution of migratory fish differently according to their mode of movement and life history. In contrast to trout and salmon that jump to overcome waterfalls (Adams *et al.* 2000), galaxiids and anguillids use their pectoral fins to cling to the substrate while scaling waterfalls and steep stream gradients, even scaling the wetted surfaces of dams and structures intended to impede fish passage (see pectoral fins of koaro and banded kokopu in Frontispiece images) (Jellyman 1977, McDowall 1990, McDowall 2003b). Thus, the presence of natural populations of migratory fish above such barriers reflects the migratory drive and ability of these fish to surmount such obstacles.

In my study, I showed that all migratory galaxiids were capable of reaching habitats above steep stream gradients, but for inanga, banded and giant kokopu, their ability to cope with steep gradients declined with migratory distance from the source. Koaro and shortjaw kokopu, however, were not impacted by the interaction of distance inland and downstream slope, and this is reflected in their contemporary distributions. Although shortjaw kokopu are relatively uncommon, they do occur in some far inland streams above steep gradients, a reflection of their ability to climb steep slopes regardless of distance inland. However, they mostly occur in coastal locations, hence the significant effect of distance. Koaro is the most widespread native galaxiid species, and can access habitats far inland above steep stream gradients that are inaccessible to most other species. Adult koaro (Frontispiece) retain the slender, anguilliform, characteristics of its juvenile stage and does not lose the ability to climb steep stream gradients as it grows (McDowall 1990, McDowall 2003b). Banded (Frontispiece) and giant kokopu, however, change morphologically as they grow, becoming more stout as they reach adulthood (McDowall 1990). Thus, as they slowly migrate inland they lose their ability to overcome steep stream gradients.

Although my results would indicate species' ability to cope with slope barriers in the landscape declines with migratory distance inland, it may not be the only explanation for the

distribution patterns observed. Inanga is a relatively short-lived species, and because of its short life history, preference for spawning sites in coastal estuarine environments, or inability to cope with waterfalls and swift currents, this may not reach suitable habitat in inland locations (McDowall 1990, Allibone 2003). Giant kokopu, a top predator known to consume other fish (Bonnett & Lambert 2002, Whitehead *et al.* 2002), although capable of reaching habitat above steep stream gradients in coastal environments, may prefer coastal environments where available prey would be most abundant, and thus not migrate further inland. Koaro and shortjaw kokopu, both apt climbers, may colonise suitable habitat in locations inaccessible to the other species and competition for space may be less intense.

6.5.2. Migratory passage restriction

The vast majority of streams within my study area were not beyond the reach of koaro in terms of physical barriers to upstream migration. Accessible banded kokopu habitat, however, was restricted by physical barriers to upstream migration, and less than 15 % of the streams within my study area were accessible. When the effects of physical barriers to upstream migration were factored out, and the impacts of catchment-scale deforestation and land use impacts on the migratory passage were considered, banded kokopu was more impacted than koaro relative to their accessible habitats, with a 70 % reduction in available habitat. This may be because banded kokopu is more sensitive to catchment deforestation and the associated potential impacts on water quality (Rowe & Dean 1998, Rowe *et al.* 2000, Richardson *et al.* 2001), but also because its accessible habitat is in coastal, lowland areas where deleterious land uses are more common. Banded kokopu is strongly influenced by catchment-scale deforestation, and it may be that it does not reach suitable habitat in inland and far inland locations because the overall degradation of the catchments preclude them from colonising these habitats. Banded kokopu is the most sensitive of the migratory galaxiids to suspended sediments, so it is not surprising that catchment land uses preclude upstream migration into many habitats (Boubee *et al.* 1997, Rowe & Dean 1998, Rowe *et al.* 2000, Richardson *et al.* 2001). Koaro on the other hand, can access more stream reaches in areas where intensive negative land uses are less likely to occur, and was affected by conditions likely to affect migratory passage less than banded kokopu, with only 55 % reduction of accessible habitat. However, when looking at the total kilometres of accessible habitat lost, koaro habitat loss amounted to over 15000 km, primarily from the larger catchments, like the Buller and Grey Valleys, heavily impacted by intensive land uses, such as dairy farming.

6.5.3. Local land-use effects

Local impacts of land uses and lack of riparian forests further reduced the useful habitat for koaro and banded kokopu by 15 % and 20 % for the two species, respectively. Again, that banded kokopu is relatively more affected than koaro is likely a result of the location of the accessible habitat for this species, whereas koaro migrate further upstream where intensive land uses are less likely to occur, or the topography of landscape itself negates intensive land uses to be established. That neither banded kokopu nor koaro are particularly affected by upstream land uses at the local scale may be because of their preference for small streams that drain relatively intact upper catchments (Chapter Two, Chapter Three, and Chapter Four). Thus, the local land use rather than upstream land use was a stronger predictor of fish occurrence, although local effects could be much larger if conditions along the migratory passage were improved (i.e., smaller passage effect).

6.5.4. Understanding migratory fish biology and Implications for management

My results show that the effects of intensive landuses on migratory fish are large and widespread. Migratory fish are likely more affected by intensive land uses than non-migratory species because their life histories means that they are exposed to the adverse conditions along the migratory passage as well as at their local adult habitats. Moreover, their life histories mean they must pass through these locations twice. In the case of New Zealand's migratory galaxiids, they are first exposed to conditions of the migratory passage as vulnerable larval fish drifting to sea (or lakes), then again as they re-enter lotic environments as juvenile 'whitebait', also a vulnerable life-stage. For example, high turbidity has been shown to impede feeding and slow down migratory behaviour in juvenile galaxiids (Boubee *et al.* 1997, Rowe & Dean 1998, Richardson *et al.* 2001).

In New Zealand, by far the most easily accessible and used habitats by all migratory galaxiid species are low gradient streams in coastal areas. These account for more than 40 % of fish occurrences within my study area. In coastal areas, steep stream gradients did not preclude fish occupancy, and all species were capable of accessing and using this habitat. However, due to extensive areas with coastal cliffs, multiple geologic fault lines, and the proximity of the Southern Alps in my study area, a disproportionate amount of stream habitat in the West Coast

Conservancy is located above steep stream gradients in inland locations inaccessible to some of the migratory galaxiids. My analysis has enabled the detection and differentiation between the effects of access restrictions due to physical barriers, land uses along the migratory passage and local habitat characteristics on migratory fish. It shows that for maximum return on conservation efforts, restoration and protection of streams should be targeted towards land-use impacted streams that are not restricted by physical barriers to upstream migration where restoration efforts would benefit all migratory species. This could be accomplished by establishing protective forested buffer zones around streams, thus restricting access by live-stock and reducing farm run-off (Barton *et al.* 1985, Osborne & Kovacic 1993). Not only would this improve conditions along the migratory passage, but it would also improve the site-scale characteristics by providing riparian cover, important to native migratory fish.

Chapter 7. Habitat fragmentation and native New Zealand freshwater fish

7.1. Introduction

Changes in the landscape due to deforestation, grazing, farming, water abstraction, impoundments, and the introduction of exotic species have influenced New Zealand watersheds directly and indirectly following European colonisation, sometimes leading to a rapid decline of native freshwater fish stocks. Today, 59 species of freshwater fish are recognised in New Zealand, of which 21 are introduced (McIntosh & McDowall 2004). Of the native species, 18 are diadromous, spending parts of their lives at sea and parts in fresh water. These fish are highly mobile, strong swimmers, and can potentially navigate watercourses to remote inland locations to reach suitable habitat in headwater streams. Both changes in land use and the introductions of exotic species affect some native fish species, but the mechanisms involved, the generalities of the effects, and the species affected were largely unknown. Also, natural features of the landscape, such as coastal cliffs and geologic faults, may be implicated in the fragmented distributions observed for these species.

7.2. Effects of forest fragmentation

Land use changes from native forests to pasture have been implicated in the decline and disappearance of native fish in many areas (McDowall 1990, Rowe *et al.* 1999), but the influences of the spatial configuration and amount of forests in catchments on native fish were unclear. My work has shown that the overall proportion catchment forest cover, the predominant position of forests within catchments, and the local presence of forest cover along stream margins affect native diadromous fish such as koaro (Chapter Two). Stream reaches with riparian forest have higher proportion of koaro occurrences, and catchments where forests were located predominantly in upland areas, regardless of riparian forest, had higher overall proportions of sites with koaro. In forested streams, dominant forest position and extent of forest cover explained 65.7 % of the variance in koaro occurrences. Predictive logistic regression models also showed that banded kokopu and koaro were positively associated with forested streams, and that intensive land uses (e.g. mixed sheep and cattle farming) impacted negatively on occurrences at sampled sites (Chapter Three). These models predicted koaro and banded kokopu presence at 83.7 % and 86.0 % for each species respectively (Chapter Three). Banded kokopu, a forest

specialist species, is also affected by edge-mediated effects, and are found in significantly higher numbers and larger sizes in forest interior streams compared to open streams (Chapter 4).

7.3. *Effects of abiotic variables affecting migratory passage*

In large river systems, river distance inland and elevation are known to limit the distribution of migratory fish. However, features of the New Zealand landscape include the presence of steep coastal cliffs and geologic fault lines, both providing steep stream gradients in locations proximal and distal to the sea. The maximum downstream slope amphidromous New Zealand fish encounter during upstream migrations, from the sea or inland lakes, have been shown to limit their upstream distribution, with over 50 % of all occurrences of koaro and kokopu accounted for when stream gradient reaches 5 degrees (Chapter Five). This variable is likely a better predictor of fish occurrences as it is independent of river distance inland, and may explain the absence of fish in pristine habitats at low altitudes close to the source of migrant fish. Inland river insinuation by native fish is gradual. As shown by Jellyman (1977), fish using their ventral surface and pectoral fins to adhere to substrates to overcome slope barriers, the ability to climb vertical, wetted, surfaces decline with increases in fish size. This is because the weight-to-surface ratio increase and the fish subsequently lose the ability to cling to substrates while climbing. Intuitively, amphidromous fish in inland locations would be larger, and thus not cope equally well with steep stream gradients as the smaller fish in locations closer to the sea or lakes. An examination of the importance of location of slope barriers in the landscape showed that in coastal locations, all five species of amphidromous Galaxiid fish occurred above steep stream gradients. However, with increasing distance inland, occurrences of fish above steep gradients declined, and in far inland locations, only koaro and shortjaw kokopu, the most apt climbers of the native Galaxiidae, occurred above steep stream gradients (Chapter Six). Comparisons of the reduction in habitat for koaro and banded kokopu due to physical barriers to upstream migrations, catchment-scale deforestation and effects of intensive land uses on migratory passage, and local habitat and land uses showed that the species are affected differently (Chapter Six). Within the West Coast Conservancy the distributions of both species are limited by impacts on the migratory passage and local habitat characteristics and land use. However, with koaro being a much stronger and able climber, it can access habitats in inland locations inaccessible to banded kokopu, and is thus less restricted by barriers to upstream migration.

Conservation of migratory stream fish poses special conservation issues for environmental managers. Due to the life histories of diadromous native New Zealand Galaxiid

and other migratory fish, utilising the entire watercourses from the headwaters to the sea, land uses throughout catchments and along water courses impact on their distribution. Because of their migratory life histories, they are affected by the negative effects of intensive land uses more than once in their life time. First, they are affected by land uses as larval fish drifting to the sea, or lakes, then again as they re-enter lotic environments as migratory juvenile 'whitebait'. Thus, compared to non-migratory species, diadromous fish are particularly affected by the negative effects of intensive land uses along waterways. Also, because presence of native diadromous fish in a stream reach is confounded not only by land uses, but also by accessibility of fish to suitable habitat, management to improve or sustain native fisheries should be targeted. Because little can be done about natural barriers to fish migration in the landscape, management should be aimed at mitigating the negative effects of deleterious land uses, deforestation, and barriers to fish migration. This can be achieved by afforestation of headwater streams, afforestation of stream banks to improve the immediate in-stream habitat and improving the connectivity between lowland and upland stream habitats, and by ensuring anthropogenic structures placed in streams are navigable by stream fish. In particular, small streams close to the source of migrating juvenile fish should be targeted by resource managers because these are accessible to all five species of diadromous galaxiid fish. Thus, restoration of degraded streams in these areas will have a disproportionately positive effect on the overall abundance and distribution of native galaxiid migratory fish fauna, not only because restoration efforts would not be compromised by habitat not being accessible to fish, but because impacts on the migratory passage in these coastal areas affect upstream occupancy of suitable habitats.

7.4. Conclusion

By using geographical information systems as a tool in resource management, identifying the location of land uses that may be detrimental to stream fish as well as locating barriers to upstream migration is achievable and available at low cost, and should be used by resource managers to target conservation efforts efficiently towards areas where the greatest results will be achieved. My study showed that with the availability of large databases on species occurrences and environmental variables, such as the New Zealand Freshwater Fish Database, and the use of geographical information systems to derive and improve variables, robust predictive models for species occurrences could be made for extensive areas without the need for labour intensive and expensive field explorations. This GIS assisted approach to conservation management is

transferable to other species, migratory and non-migratory alike, as well as to other regions and countries.

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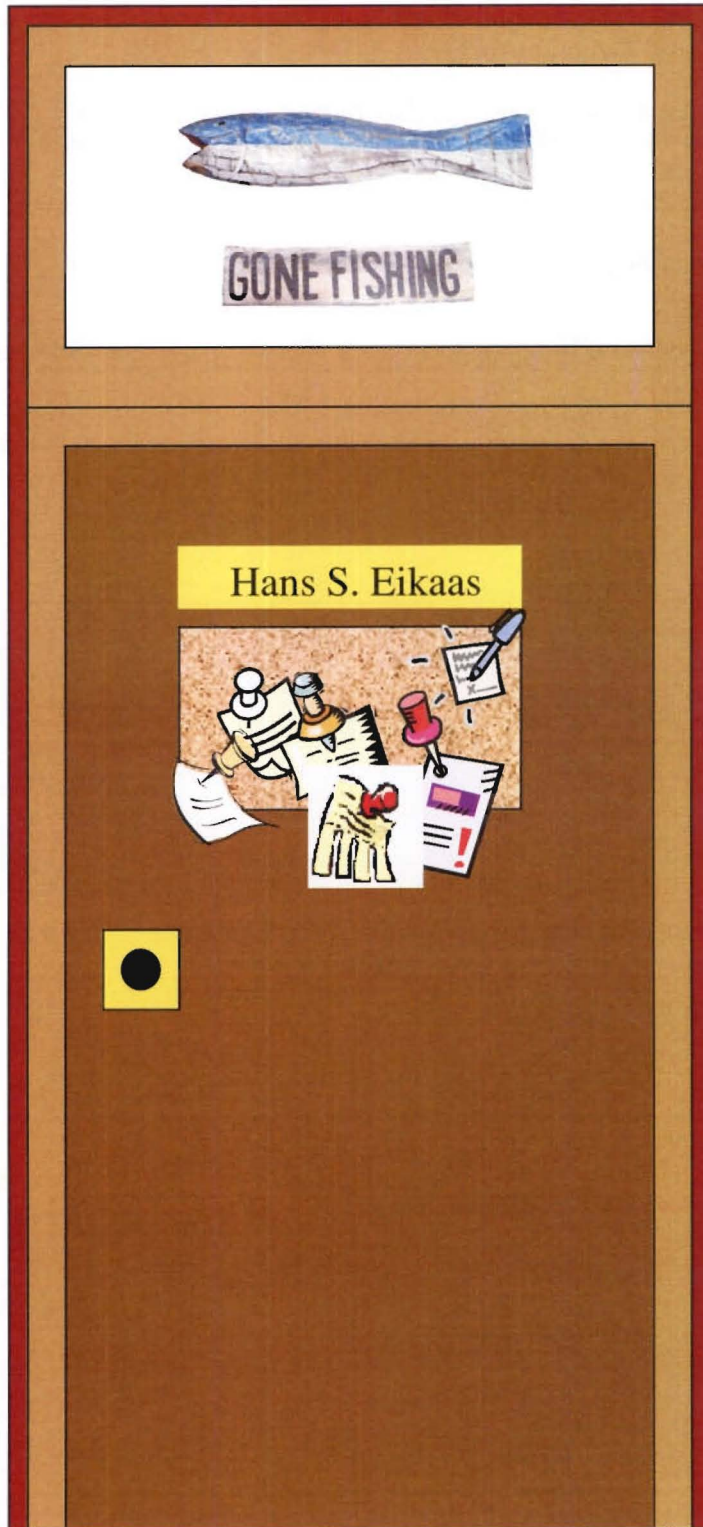
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