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Habitat preferences of giant kokopu, *Galaxias argenteus*

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Abstract The giant kokopu (*Galaxias argenteus* (Gmelin 1789)) is endemic to New Zealand, and is regarded as threatened. A perceived decline of the species has been attributed mostly to the loss and degradation of its habitat. To determine habitat requirements, information from the New Zealand Freshwater Fisheries Database, and from field surveys in the South Island were analysed. These indicated that five habitat features are important: in-stream cover, deep water, low water velocity, proximity to the sea, and overhead shade/riparian cover. These features were important in two distinct regions surveyed and for both juvenile and adult fish. The effects of different types of riparian and in-stream cover were examined, but it appeared that the presence of some form of cover was more important than its composition. The conservation and management of giant kokopu will probably continue to be based upon management of their habitat, and these processes will be enhanced by the knowledge of the species' habitat requirements.

Keywords giant kokopu; *Galaxias argenteus*; New Zealand; habitat; habitat preference; freshwater fish

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INTRODUCTION

The giant kokopu (*Galaxias argenteus* (Gmelin 1789)) is the largest of the galaxiid fishes, and is endemic to New Zealand. Some landlocked (non-migratory) populations exist, but giant kokopu are normally diadromous, and the juveniles comprise a small proportion of the annual whitebait harvest (McDowall & Eldon 1980).

The giant kokopu was widely known to early explorers and settlers (Heaphy 1842; McDowall 1980). However, it is now regarded as an uncommon and threatened species (Williams & Given 1981; Tisdall 1994) , and proposed changes to whitebait fishing regulations because of its rarity led to controversy (New Zealand House of Representatives 1994). The decline in range and numbers of the species has coincided with extensive land development, wetland drainage, and stream realignment in many parts of New Zealand. McDowall (1990) suggested that as pastoral development continues, it is likely that the decline of the species will continue.

Land-use changes, as well as introduced exotic species, have caused changes in the distribution of New Zealand's native fish species; McDowall (1984) and Minns (1990) identified that the primary conservation need of the native fish fauna is sufficient and suitable habitat. Thus, the conservation of giant kokopu depends upon a clear understanding of its habitat preferences, so that suitable areas can be identified and managed.

There are various general descriptions of the habitat of the giant kokopu, most of which include some mention of its preference for in-stream and riparian cover (Taylor & Main 1987; West 1989; McDowall 1990; Rasmussen 1990; Chadderton & Allibone 2000). The species' preference for low-elevation coastal waters has also been noted (e.g., Taylor & Main 1987); and Chadderton & Allibone (2000) reported that giant kokopu favoured water >0.75 m deep. However, none of the above studies focused on the specific habitat preferences of giant kokopu. As the conservation of giant kokopu is likely to continue to be based on the management of its habitat, there is an obvious need for a more accurate understanding of its requirements to conserve, restore, or enhance giant kokopu habitat. Thus, the objectives of this study were to quantitatively define the habitat of the species, and to identify critical or “key” features of its habitat requirements.

Both regression-based and microhabitat-based approaches are commonly used for assessing fish habitat in New Zealand and overseas. Regression-based models may be used to identify wide-scale general features (e.g., stream size or gradient) that correlate with fish abundance, (e.g., McClendon & Rabeni 1987; Minns 1990; Glova et al. 1998). The term “microhabitat” was proposed by Allee et al. (1949) to describe the exact location and conditions where an animal spends all, or a portion, of its time. The term recognises that fish may habitually occupy only a small part of the entire habitat available to them. Microhabitat-based models may be used to identify the specific habitat conditions (such as water depth or velocity) used by fish (e.g., Shirvell & Dungey 1983; Moyle & Baltz 1985; Jowett & Richardson 1995; Hicks & Barrier 1996). For this study, a microhabitat-based approach was most appropriate, as the aim was to identify specific habitat preferences.

METHODS

Two separate approaches were used to identify and describe the habitat of giant kokopu.

Analysis of records from the New Zealand Freshwater Fish Database

The New Zealand Freshwater Fish Database (NZFFD) is an historic archive of information on the distribution of New Zealand freshwater fishes and contains data from as early as 1901, but principally from the last 30–40 years (McDowall & Richardson 1983; Richardson 1989). Data have been contributed by a diverse range of individuals and organisations and although many records contain only basic data (such as date, location and map reference, and presence of fish species), some records have more detailed information on the abundance of fish species and the habitats in which they were found.

Records from the NZFFD were analysed using the SYSAT 8.0 statistical software package (Wilkinson 1988). A distribution map was constructed and giant kokopu occurrence and habitat selection was examined with respect to broad habitat features such as elevation, distance inland, and water type. Information on many of the database records also provided some measure of abundance and co-occurrence with other native and introduced fish species. Chi-square tests were used, where appropriate, to test the significance of comparisons between sites where giant kokopu were recorded and all the sites where fish occurred. For many habitat features (e.g., substrate composition) there were insufficient records to make meaningful comparisons.

Microhabitat surveys

Surveys of giant kokopu habitat were undertaken in the South Island’s west coast (“Westland”, April 1998), and parts of the southern and south-eastern coasts (“Southland”, April 1999) (Fig. 1). In each region we attempted to survey as wide a range of sites as possible, including some sites where giant kokopu had been recorded on the NZFFD. Habitat measurements and assessments were made where each giant kokopu was caught. To provide a comparative basis for determining habitat selection, measurements and assessments were repeated at adjacent, randomly selected, locations that had been surveyed but where giant kokopu were absent. In streams, electro-fishing surveys typically began at the point of access and proceeded up stream; habitat measurements and assessments were completed where giant kokopu were caught and at 10 m intervals along the stream.

Fish were captured by electro-fishing or by trapping in unbaited fyke nets set overnight. After capture, most giant kokopu were anaesthetised with 2-phenoxyethanol before being measured to the nearest millimetre, although some fish were sufficiently placid to be handled without anaesthetic. All fish were retained in fresh water until completely revived, then returned as close as possible to their place of capture.

Various habitat parameters were measured where each giant kokopu was captured. The elevation and distance inland of each site were calculated from topographical maps. Water velocity and depth were measured using an electromagnetic velocity meter on a wading rod, and channel width was measured to the nearest 0.1 m with a tape measure. Substrate composition was measured using the Wolman walk method (Mosley 1982), with a minimum of 50 stones measured at each site. Substrate size was expressed as the mean size (in mm) of the particles measured.

Bank characteristics, riparian cover, and in-stream cover were estimated visually, and expressed as percentages. Water depth and velocity measurements

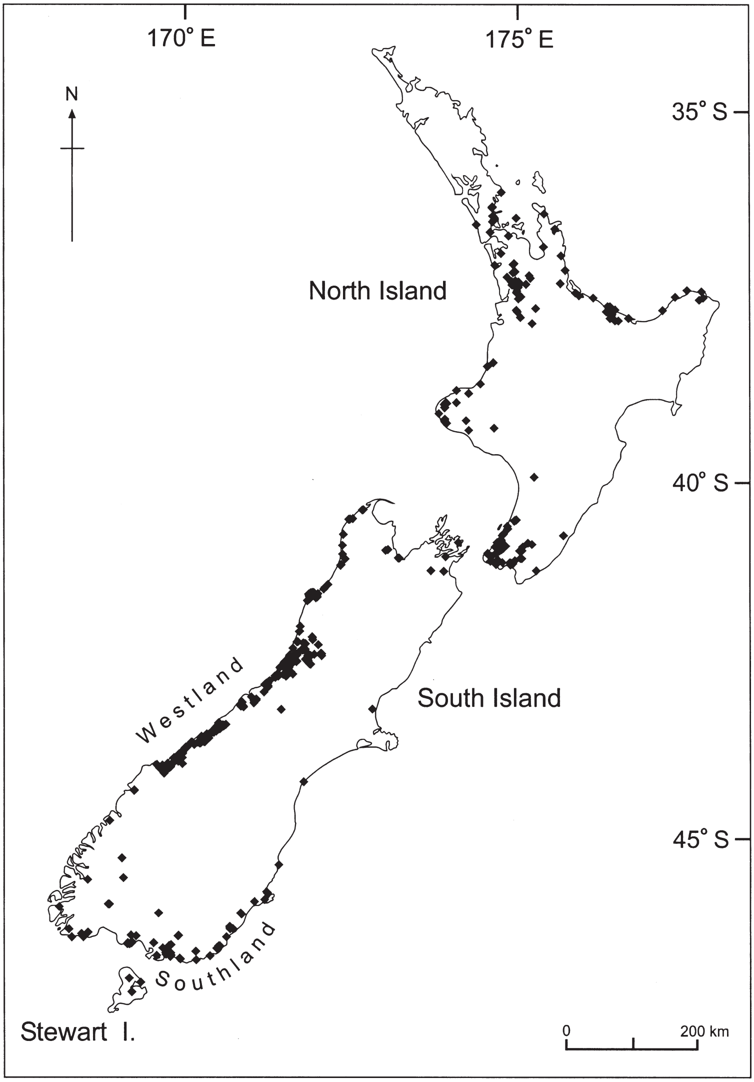

Fig. 1 Distribution of giant kokopu (*Galaxias argenteus*) (filled diamond symbols) on the three main islands of New Zealand, and place names mentioned in the text (Chatham Islands not shown).

were made within a few centimetres of where each fish was first seen or caught, whereas measurements of features such as substrate size, and assessments of habitat features such as cover, were made from an area c. 1 m in radius from the capture point.

The precise location of individual fish could not be determined accurately using fyke nets, and measurements of features such as substrate composition and proportion of in-stream cover could not be readily determined when nets were set in deep and turbid water. Thus, electro-fishing was the most accurate method of ascertaining giant kokopu habitat, although it could only be used where the water was of wadeable depth for the operator (c. <1 m), sufficiently clear to see the bottom, and of a conductivity range suitable for electro-fishing (c. 20–400 µS cm^{-1}). Consequently, surveys of giant kokopu habitat were concentrated in streams, drains, and shallow rivers.

Habitat preference curves for water depth, water velocity, and substrate size were derived by dividing the frequency of use by the frequency of available habitat (Bovee 1986) using kernel smoothed density distributions as described by Hayes & Jowett (1994). Preference curves were scaled to a maximum preference value of 1.

Data from the field surveys were also used in a series of discriminant function analyses (Hair et al. 1995) on a personal computer using SYSAT 8.0. Separate analyses were performed on eight groupings of the data (data sets), based on geographical location (Westland or Southland), fish size (juvenile ≤120 mm, or adult >120 mm), for lotic sites only (there were insufficient data for a separate analysis of lentic sites), and for all data sets combined.

Discriminant function analyses were used to find the combination of habitat variables that best classified (or discriminated between) sites with and without giant kokopu. Analyses were carried out in a backward stepwise manner so that initially all the variables were used in the model, then variables that had the least influence on the presence of giant kokopu were successively removed. Separate *F*-statistic values are listed for the variables (habitat features) that remained in the model after backward stepping. Jack-knifed classification matrix values were also calculated; these were measures of the success of self-testing in the model. For each site, using data from all other sites, the model predicted presence or absence of giant kokopu, and the jack-knifed values correspond to the percent correctly predicted.

Discriminant function analyses were repeated for all data sets using a set of combined habitat variables, as not all the habitat variables measured in the field were pertinent for both the regions surveyed. For instance, in-stream log cover was extremely rare in the Southland streams surveyed so it was not logical to relate this variable to the occurrence of giant kokopu in Southland. Thus, for the second series of analyses, categories describing in-stream cover (% logs, % vegetation, etc.) were condensed into a single variable (% in-stream cover—the proportion of in-stream cover over the streambed). Similarly, various categories of riparian cover (% native forest cover, % exotic forest cover, etc.) were combined into one variable (% riparian cover) and categories of bank composition (% sloped, % vertical, % slumped, etc.) were combined into a single variable, % bank sloped.

RESULTS

Records from the New Zealand Freshwater Fish Database

The analyses were conducted in June 1999, when there were 14 343 records in the NZFFD, with each record representing information from one site. Of these, 665 were "null" records (i.e., records from locations where no fish were caught) and 561 (4%) were records of sites containing giant kokopu. All the records are from 1949 onwards and were from 154 distinct catchments as defined in "Catchments of New Zealand" (Soil Conservation and Rivers Control Council 1956). The map references of 61 giant kokopu records matched those of previous records, but there was no way to determine how many of these sites were actually "repeats" or from localities in very close proximity, as sites >50 m apart may have been assigned identical map references. Thus, comparisons made in this study were based on the assumption that site duplication was unlikely to seriously distort the analyses.

Giant kokopu are widespread around New Zealand, but have been encountered most frequently along the western and southern coasts of the South Island (Fig. 1). Of the 561 records, 379 (68%) were from these regions. These fish have been found in a wide range of water types, including estuaries, lagoons, swamps, streams, drains, rivers, ponds, and lakes. Although 483 records (86%) came from lotic habitats, this may not be significant, as 91% of all records on the NZFFD are from lotic sites. Of the

Table 1 Chi-square values, degrees of freedom (d.f.) and probability from tests of independence between habitat variables in sites containing giant kokopu (*Galaxias argenteus*) and all sites containing fish on the New Zealand Freshwater Fisheries Database.

Habitat variable	χ^2	d.f.	*P*
Stream size	0.136	36	1
Inland penetration	83.456	7	<0.001
Elevation	9.665	12	<0.001
Species richness	25.625	10	0.004
Water temperature	19.626	29	0.989
pH	142.316	16	<0.001

Table 2 Mean, median (in parentheses), and range of values of habitat features measured or assessed in Westland and Southland sites of New Zealand.

	Westland		Southland			
	Absent	Present	Absent	Present	Min.	Max.
Site location						
Inland penetration (km)	7.53 (2.12)	3.61 (2.01)	14.4 (8.0)	9.8 (6.0)	0.05	58
Elevation a.s.l. (m)	21.5 (11.5)	17.1 (10.5)	7.9 (5.0)	5.6 (5.0)	0	140
Physical features						
Water depth (m)	0.43 (0.24)	0.63 (0.40)	0.33 (0.20)	0.32 (0.30)	0.06	1.5
Water velocity (m s^{-1})	0.10 (0.05)	0.03 (0.02)	0.17 (0.15)	0.07 (0.06)	0	0.54
Channel width (m)	3.66 (3.45)	3.9 (3.60)	2.01 (2.0)	1.81 (1.30)	0.7	100
Mean substrate size (mm)	30.6 (30.6)	30.3 (28.6)	28.5 (0.1)	1.05 (0.01)	0	341.3
Bank composition						
% flat (bank slope <c. 10°)	15 (0)	13 (0)	0 (0)	0 (0)	0	90
% sloped (bank slope c. 10–80°)	56 (50)	49 (50)	85 (100)	89 (100)	0	100
% vertical (bank slope >c. 80°)	17 (5)	16 (0)	11 (0)	5 (0)	0	100
% undercut (water extending under bank)	9 (0)	21 (0)	0 (0)	0 (0)	0	100
% slumped (bank collapsed)	3 (0)	1 (0)	4 (0)	6 (0)	0	50
Riparian cover						
% native vegetation (native forest or bush)	43 (10)	55 (90)	0 (0)	0 (0)	0	100
% exotic vegetation (exotic forest)	2 (0)	0 (0)	0 (0)	0 (0)	0	40
% scrub (mainly gorse or broom)	15 (10)	10 (0)	39 (30)	40 (30)	0	100
% raupo/flax (raupo or flax)	0 (0)	20 (0)	4 (0)	13 (0)	0	80
% open (no vegetation)	14 (0)	2 (0)	8 (0)	0 (0)	0	95
% grass (various pasture grasses)	26 (0)	13 (0)	49 (60)	47 (30)	0	100
% overhead shade (water surface shaded)	34 (15)	49 (60)	20 (10)	17 (10)	0	100
In-stream cover						
% filamentous (filamentous algae)	0 (0)	2 (0)	0 (0)	0 (0)	0	50
% substrate (substrates >c. 200 mm)	3 (0)	6 (0)	0 (0)	0 (0)	0	30
% debris (small plant material)	4 (1)	16 (10)	19 (10)	18 (10)	0	80
% logs (tree branches and logs)	3 (0)	14 (10)	0 (0)	2 (0)	0	45
% vegetation (macrophyte and emergent aquatic)	7 (0)	6 (0)	17 (5)	35 (50)	0	80
% culvert/bridge cover (bed covered by a structure)	0 (0)	0 (0)	0 (0)	1 (0)	0	10

giant kokopu recorded in flowing water, 250 (52%) were from small (<10 m wide) streams.

Table 1 summarises the results of chi square tests of independence for five habitat variables recorded on the NZFFD; these tests compared the variables in sites containing giant kokopu with those in all sites containing fish.

The records indicate that giant kokopu do not penetrate far inland or to great elevation; 331 (59%) of records were from 10 km inland or less, and 314 (56%) were from elevations of 10 m or less. Giant kokopu sites had high species richness, and this species co-occurred with a total of 33 other native and exotic fish species. It appears that giant kokopu occur more frequently in habitat where brown trout (*Salmo trutta*) are absent, as brown trout occur in 16.8% of all giant kokopu sites, whereas they occur in 31.4% of all NZFFD sites containing fish.

Water temperature and pH were recorded in 146 (26%) and 107 (19%) of giant kokopu sites respectively. The distribution of water temperature frequencies was not significantly different from those at all NZFFD sites. Of the pH records, 80 (75%) were from sites where pH was <7, and the distribution of pH in giant kokopu sites was significantly different from all NZFFD sites.

Habitat surveys

Habitat measurements were recorded at 128 sites, the majority (85%) of which were lotic. A total of 56 (44%) sites contained giant kokopu, and Table 2 compares the mean values of measured habitat features in all lotic sites from Westland and Southland. The species' preferences with respect to water depth, water velocity, and substrate size are presented as habitat preference curves in Fig. 2.

Results of the discriminate function analyses with all variables, and the repeated analyses using a condensed range of variables, are presented in Tables 3 and 4, respectively. The *F*-values in the analyses do not necessarily correlate positively to giant kokopu occurrence; e.g., the presence of giant kokopu was negatively associated with water velocity, as mean water velocity was lower in giant kokopu sites (Table 2).

The following five critical habitat features were identified: (1) In-stream cover was the habitat feature most consistently associated with the occurrence of giant kokopu. It appeared that the composition of in-stream cover might have been less important than its presence; in Westland, logs in the water were the cover that seemed most important, whereas in Southland giant kokopu were consistently associated

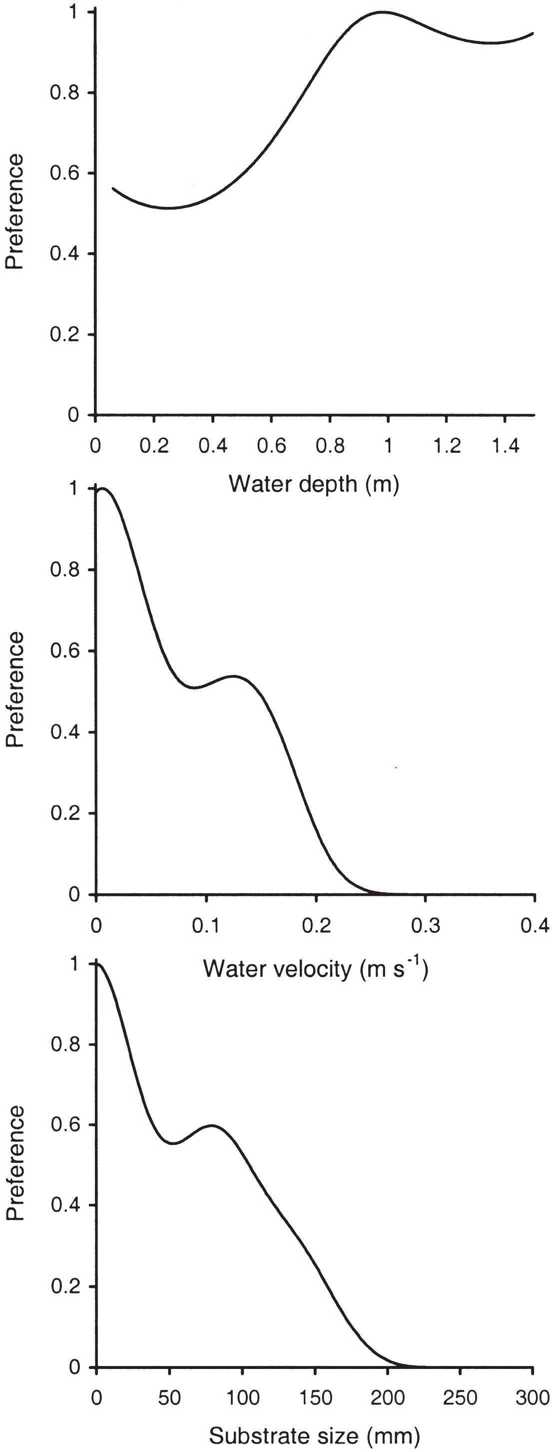

Fig. 2 Water depth, water velocity, and mean substrate size preferences of giant kokopu (*Galaxias argenteus*).

Table 3 *F*-values of habitat variables remaining in the model after backwards stepping during discriminant functions analysis. Variables were measured during surveys of habitat in Westland and Southland, New Zealand. Jack-knifed predictions are measures of the success of self-testing in each model.

Region:		Westland			Southland			All
Water type:	Lotic only	All	All	All	All	All	All	All
Fish size:	All	≥120 mm	<120 mm	All	≥120 mm	<120 mm	All	All
Habitat feature								
Inland penetration (km)				4.5	57.7	83.3	82.9	12.8
Elevation (m)	2.2			4.3	66.1	97.7	86.9	
Water depth (m)								5.7
Water velocity (m s^{-1})	4.9	8.5		4.3				5.9
Channel width (m)	2.4	7.5		6.9	2.7	4.6	2.8	2.5
Mean substrate size (mm)						5.8	3.8	4.1
% bank flat	3.1	5.5	10.8	5.1				
% bank sloped				3.4	25.9	71.2	58.6	
% bank vertical				2.8	25.1	81.2	60.8	3.4
% bank undercut	3.5		16.6	4.7				2.4
% bank slumped								
% native riparian cover	2.8	3.7	21.4	7.2				
% scrub riparian cover				3.2	38.6	76.6	62	
% exotic riparian cover								
% flax/raupo riparian cover		38.8		14.2				43.8
% grass riparian cover					68.3	121.9	100.3	
% open (no riparian cover)			4.7	2.4	48.3	103	71.8	
% water shaded overhead	7.31	9.7	15.2	7.3		6.7		5.7
% bed covered by filamentous alage		3.5	2.2	3.7				
% bed covered by substrates >200 mm	19.4	23.2	30.9	24.7				21.3
% bed covered by debris					26	29.6	31.9	5.5
% bed covered by logs	47.8	62.7	54.5	49	17.2		23.2	41.5
% bed with in-stream vegetation					95.4	318.8	248.1	65.3
% bed covered by culvert/bridge					28		32.6	6.7
No. sites fish present	21	29	2	31	14	11	25	56
No. sites fish absent	40	32	59	30	58	61	42	72
Jack-knifed predictions								
% correct absent	100	97	100	97	100	100	100	94
% correct present	90	90	0	87	93	100	96	79
% overall correct	96	93	94	92	98	100	99	88

Table 4 *F*-values of condensed habitat variables remaining in the model after backwards stepping during discriminant functions analysis. Variables were measured during surveys of habitat in Westland and Southland. Jack-knifed predictions are measures of the success of self-testing in each model.

Region:		Westland			Southland			All
Water type:	Lotic only	All	All	All	All	All	All	All
Fish size:	All	≥120 mm	<120 mm	All	≥120 mm	<120 mm	All	All
Habitat feature								
Inland penetration (km)						18.5		15.5
Elevation (m)					6.57		13.9	
Water depth (m)		12.1		11.5	4.5			7.42
Water velocity (m s^{-1})	8.9	9.6		9.4	8.8	14.9	20.2	20.3
Channel width (m)		2.4		2.5				
Mean substrate size (mm)								
% bank sloped		2.6		3				
% riparian cover							4.2	
% water shaded overhead	36.42	27.5		29.6			3.7	11.52
% bed with in-stream cover	46.49	39.5	8.67	41.5	9.35	22	5.5	50.5
No. sites fish present	21	29	2	31	14	11	25	56
No. sites fish absent	40	32	59	30	58	61	42	72
Jack-knifed predictions								
% correct absent	90	90	90	90	83	88	83	86
% correct present	90	93	0	90	57	82	88	77
% overall correct	90	92	84	90	77	87	85	82

with in-stream vegetation, plant debris, and bridge/culvert structures. (2) Low water velocity was also strongly and consistently associated with giant kokopu presence, and fish were rarely found at water velocity >0.1 m s^{-1}. (3) Shade was also often associated with the presence of giant kokopu, and appeared to be a good predictor of giant kokopu presence in Westland. It is logical to regard shade and riparian cover together as a single habitat feature, because areas with dense riparian cover would normally be shaded, and vice versa. It seems that the presence of some form of riparian cover is more important than its composition, as different types of riparian cover were often, but not consistently, associated with giant kokopu presence, whereas a lack of riparian cover (% open) was associated with fish absence in both Southland and Westland. (4) Inland penetration—giant kokopu were found mainly at low elevation and close to the sea, confirming that this is predominantly a "coastal" species. (5) Water depth was also an important feature, although it was probably the least consistent of the group that showed strong association with the presence of giant kokopu. Unfortunately, only a restricted range of depths could be sampled effectively during field surveys, and so discriminative power of this variable may have been limited.

DISCUSSION

Giant kokopu are widely distributed throughout much of New Zealand and are known to occur on the three main islands, on Great and Little Barrier Islands, and in the Chatham Islands (Skrzynski 1967; Rutledge 1992). However, they are far from being evenly distributed and most of the records on the NZFFD originated from the western and southern regions of the South Island, with relatively few records from the eastern coasts of the North and South Islands in the last 30 years. The sparseness of giant kokopu in eastern areas parallels that of three other diadromous galaxiid species—banded kokopu, shortjawed kokopu (*G. postvectis*), and koaro (*G. brevipinnis*). Of all the whitebait species, only inanga (*G. maculatus*) comes close to being uniformly distributed around the country (McDowall 1990).

In some parts of New Zealand the giant kokopu is now very infrequently encountered. In South Canterbury, for example, the species has been recorded on the NZFFD only once since 1940, despite being well known during the mid 1800s (Studholme 1940), and common enough to be considered as a food source by early settlers (Anderson 1916). The decline in giant kokopu numbers and distribution in developed areas of New Zealand has been attributed largely to loss of habitat following agricultural and urban development (McDowall 1984).

The NZFFD records revealed that giant kokopu occur in a variety of water types, including estuaries, swamps, rivers, streams, drains, lakes, and ponds, and some landlocked water bodies where the populations are non-diadromous. They also occur in various forested and pastoral habitats, from forested streams to pastoral drains. These features are in strong contrast to shortjawed kokopu, which occurs almost exclusively in streams flowing through podocarp/hardwood forests (McDowall et al. 1996), and banded kokopu, which are rarely found in streams lacking a forest canopy (McDowall 1990) or where the bush has been removed (Phillips 1926).

Analysis of NZFFD records also indicated that giant kokopu prefer low pH (acidic) water. This certainly fits with the perception that giant kokopu are associated with tannin-stained and acidic waters (Taylor & Main 1987; Main 1988), but it should be noted that pH was measured at only a small proportion (19%) of the NZFFD sites. The proportion of giant kokopu records from acidic waters may simply reflect the relative abundance of the species along the southern and western coasts of the South Island, where waters are frequently acidic and tannin-stained (Collier & Winterbourn 1987; Winterbourn & Collier 1987).

Overall, statistical analysis of NZFFD records must be viewed with caution, as the records may be incomplete and biased; some species have vastly different probabilities of capture (Chadderton & Allibone 2000) and may be misrepresented on the database. Moreover, the database is dominated by records from accessible sites, which may present a skewed picture of fish abundance and distribution.

Giant kokopu co-occur with over 30 other freshwater fish species and in many of the NZFFD sites where this species was recorded species richness was high. Brown trout is the species thought most likely to be incompatible with giant kokopu (McDowall 1990). Taylor & Main (1987) captured few giant kokopu, banded kokopu, or koaro from habitats containing adult brown trout in South Westland, and Allibone (1997) observed a lack of sympatry between kokopu and salmonids in coastal Otago. Chadderton & Allibone (2000) attributed the extensive distribution and wide habitat use of large galaxiids (including giant kokopu) in a Stewart

Island stream to intact catchment vegetation, unmodified stream channel, and the absence of introduced salmonids.

Trout and galaxiids have frequently been reported as being spatially segregated within some catchments (Frankenberg 1966; Hopkins 1971; Tilzey 1976; Cadwallader 1979; Jackson 1981; Minns 1990; Townsend & Crowl 1991). Although a comparison of records in the NZFFD indicates that giant kokopu and brown trout are not mutually exclusive, they are less frequently found together than might be expected given that both species are widespread and occur in a broad range of water types throughout the country.

The habitat preference curves generated from microhabitat surveys indicated that giant kokopu favoured deep (>0.5 m), and slow moving or still water (<0.1 m s^{-1}). The giant kokopu curves were similar to those presented for shortjawed kokopu (McDowall et al. 1996), but dissimilar to those presented by Jowett & Richardson (1995) for eight common riverine species of New Zealand native fish, particularly with respect to water depth, as most of the latter preferred relatively shallow (<0.4 m) water. Knowledge of giant kokopu habitat preferences (including habitat preference curves) seems a fundamental prerequisite for their conservation and management; Chadderton & Allibone (2000) questioned the assumption that satisfying the requirements of riffle and run species will provide adequately for other species, particularly large galaxiids.

It is apparent from this study, particularly from discriminant functions analyses, that the presence of in-stream cover, riparian cover/shade, low water velocity, and deep water in coastal streams is critical for the occurrence of giant kokopu. Some of these features were important for both adult and juvenile fish and for fish in the natural bush streams of Westland as well as the modified pastoral drains in Southland. Consequently, general descriptions of giant kokopu as a coastal, cover-loving fish that prefers deep slow moving or still waters (e. g., Taylor & Main 1987; Main 1988; McDowall 1990) are correct.

Analyses further indicated that the presence of some form of cover might be more important than its composition. A variety of cover features were identified from the initial analyses, although not consistently so for the two regions surveyed. We interpreted this as meaning that, in each region, giant kokopu utilised whatever cover was available, for instance in-stream logs in Westland bush streams, and in-stream vegetation in pastoral Southland drains.

The importance of terrestrial items in the diet of giant kokopu (Jellyman 1979; Main 1988; West 1989; Rasmussen 1990) may be linked to their association with overhead shade and riparian vegetation. Their body shape and fin arrangement may also provide them with the capability of sudden "bursts" of acceleration necessary to ambush prey in the water (Eldon 1969; Jellyman 1979) and their bilateral accessory lateral line presumably assists them in locating foods near the water surface (McDowall 1997). Thus, riparian vegetation may supply a source of food, and slow moving, relatively deep water with in-stream cover may provide conditions suitable for giant kokopu to ambush their prey. Riparian and in-stream cover may also provide protection from predation, e.g., by birds such as the harrier (*Circus approximans*) which has been observed capturing migrating ripe male giant kokopu in shallow water (McDowall 1990).

Some giant kokopu travel considerable distances upstream and attain significant elevations (McDowall 1990), and juveniles are capable of ascending substantial waterfalls (Hanchet 1990). However, from this study it appears that giant kokopu mostly do not penetrate far inland, and are mostly associated with coastal, low elevation habitats. Landlocked (non-diadromous) populations of giant kokopu occur in coastal areas and at considerable elevation and distance from the sea (McDowall 1990). Overall, however, the description "coastal species" is quite fitting, and the probability of encountering giant kokopu appears to decrease with distance from the sea. It may be that they are coastal only because the type of habitat they prefer is found at low elevations, not because of an inability to penetrate inland.

This investigation has shown that giant kokopu, despite being widespread, have distinct habitat requirements. Although these are apparently satisfied in a wide variety of situations, the decline in the distribution and abundance of giant kokopu probably reflects both an overall loss of habitat as well as significant changes in the quality of habitat in many areas of New Zealand. Habitats from which the riparian and in-stream cover have been lost are unlikely to provide suitable conditions for giant kokopu, particularly in low elevation coastal streams.

Because there are serious concerns about the conservation status of giant kokopu, ways of ensuring its long-term protection are being sought.

Without knowledge of its habitat requirements, it would be difficult to protect the species and make rational decisions about impending land-use changes or the establishment of reserves. One of the most effective contributions to ensuring its protection is to obtain an understanding of the critical features of habitats favoured by the species. The information from this study can form a basis for the development and application of viable strategies for managing populations and habitats, and for ensuring the protection of the species.

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