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Response of the riverine fish community to the construction and operation of a diversion hydropower plant in central Chile

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ABSTRACT

1. Chilean rivers have a large potential for hydropower development, and they also contain a unique native fish fauna with a high level of endemism. Several diversion hydropower plants have recently been constructed in Chile; however, the response of fish communities to these new hydropower plant designs is not well known.

2. Responses of native and non-native fish to the construction and operation of a new hydropower plant that diverts water from two rivers were quantified. The Laja River is highly regulated and manipulated with three older (40 yr) dam-based hydropower plants and irrigation diversions located upstream from the new facility. In contrast, the Rucúe River has no other hydropower facilities and is comparatively undisturbed.

3. Prior to construction, the Laja River had a fish community with lower species richness compared with the Rucúe River. The fish community structure in the Laja River was dramatically altered after the new hydropower facility began operation. On the other hand, in the Rucúe River, even though abundance of fish declined, there was less of a change in the total fish community structure. The fish community in the Rucúe River exhibited greater resistance to change compared with the Laja River.

4. The species most affected were the introduced salmonids and an endangered native species *Percilia irwini*.

5. Although diversion hydropower designs may have less impact than traditional dam-based hydropower facilities, results of this study indicate that diversion hydropower structures can cause large changes in the fish community.

KEY WORDS: diversion hydropower; fish community; native species; Laja River; Chile

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INTRODUCTION

The decline of wetlands and riverine fish habitat resulting from water resource development is a global problem (Allan and Flecker, 1993; Nunes-Godinho and Ferreira, 2000). Among the most damaging factors for fish populations are habitat alterations (e.g. pollution, damming, water diversion, changes in land use) and introduction of exotic species (Kingsford, 2000; Nunes-Godinho and Ferreira, 2000; Richter *et al.*, 2003). Use of water for hydropower generation is widespread in many river systems and is the most important renewable electricity source worldwide (Bratrich *et al.*, 2004). Negative effects of large dams associated with traditional hydropower facilities, such as habitat fragmentation, changes in fish reproductive environments and blocking of migration routes, are well known and have resulted in large-scale population and species decline (Pringle *et al.*, 2000; Morita and Yamamoto, 2002; Richter *et al.*, 2003; Young-Seuk *et al.*, 2003; Phillips and Johnston, 2004). Less well known are the effects of low-head dams and water diversions (e.g. diversion hydropower designs) on diversity and abundance of fish in rivers and streams (Benstead *et al.*, 1999; Kingsford, 2000). Diversion hydropower plants divert portions of the river flow — usually all the water up to the turbine capacity except for some instream flow — through canals or pipelines, with the use of a low or, in very rare cases, partial dam (DOE, 2004). Diversion-type hydropower plants have been considered ideal for ecologically fragile areas, if ecologically meaningful instream flows remain in the diverted river reach and fish migration across the dam is possible. Because they have no storage reservoir they are thought to cause a lower disturbance and impact to stream flow (*sensu* Bratrich *et al.*, 2004).

Most of the rivers in Chile have a large potential for hydropower development because of their high-gradient, torrential character resulting from the height and nearness of the Andes mountain range. At the same time, Chilean rivers are home to a unique freshwater biota. The fish fauna in particular exhibits a high degree of endemism, multiple species with primitive characters, many species with reduced populations and ranges, and deficient biological information (Vila *et al.*, 1999; Dyer, 2000). New hydropower plants in Chile have been constructed with some environmental considerations, such as requirements of minimum flow (mostly based only on hydrological information) or requirements for reintroduction of native fish (EWI, 1996; EWE, 2001; Habit *et al.*, 2002), but little information is available on the response of fish communities to the construction and operation of diversion hydropower facilities. Knowledge of the response of fish communities to this type of hydropower plant is essential as a foundation for conservation and management efforts in these unique river ecosystems.

Construction and operation of a new diversion hydropower plant involving two rivers in central Chile provided an opportunity to compare the fish community responses to construction and operation of the facility. Two approaches were used to assess spatial and temporal variation in the fish community in response to construction and operation of the hydropower facility. First, a comparison was made of fish abundance and community structure prior to construction to that observed during construction and operation of the hydropower plant in both rivers. Second, species-specific changes in abundance were analysed to understand differences among native and non-native species' responses.

Chilean fish fauna

The geomorphology and geological history of Chile have contributed to the development of a unique ichthyofauna, which is characterized by a high degree of endemism (Campos *et al.*, 1993; Vila *et al.*, 1999; Dyer 2000). The Andean range in the west, the Pacific Ocean in the east, and the Atacama Desert in the north of the country biogeographically isolate Chile, resulting in a species-poor, relict fish fauna, with many species characterized by primitive features and small body size. The native freshwater ichthyofauna of Chile is composed of 11 families, 17 genera and about 43 species. In the Chilean biogeographic province (*sensu* Dyer, 2000) 81% of the species are endemic, 40% of which are classified as endangered. The most abundant and species-rich groups are the siluriforms (eleven species), osmeriforms (nine species) and atheriniforms (seven species). Other groups represented in Chile are cyclostomous Petromyzontiformes (two species), teleostean characiforms (four species), cyprinodontiforms (five species), and perciforms (four species). The South Central biogeographic area of the Chilean Province has the highest species richness, and richness declines both to the north and the south of this area. The freshwater fish fauna of Chile has a high biogeographic, ecological and conservation value because of the high rate of endemism and isolation.

METHODS

Study area

In central Chile, the Biobío River drainage system supplies more than 30% (2291 MW) of the electricity used by the entire country (Parra *et al.*, 2004). Approximately half of that energy is generated in three hydropower stations in the headwaters of the Laja River, the principal tributary of the Biobío River (Figure 1). As a result of these large hydropower facilities and extensive diversion for irrigation purposes, the Laja River has experienced heavily regulated flows and high levels of disturbance for the past 40 years (Parra *et al.*, 2004). The main disturbance to the natural flow regime in the Laja River is the reduction of peak flows by the hydropower facilities and fluctuations in flow caused by irrigation diversions (*ca* $100\,m^3\,s^{-1}$) located upstream of the new hydropower plant. In contrast, the Rucúe River, a principal tributary of the Laja River, was unregulated and in near pristine condition. In September 1997, construction began on a new diversion hydropower plant in the upper-middle section of the Laja River. Operation of this plant began in October 1998. This new hydropower plant diverts water from low dams in both the Laja River ($120\,m^3\,s^{-1}$) and the Rucúe River ($10\,m^3\,s^{-1}$) into canals that feed a power-generating turbine. Both the Laja and Rucúe diversion canals connect together and cross over the Rucúe River by means of a siphon, and the diverted water reenters the system in the lowest segment of the Rucúe River ($130\,m^3\,s^{-1}$). River reaches below the diversion dams are supposed to maintain minimum flows of 4.6 and $0.46\,m^3\,s^{-1}$ for 18 and 10 km in the Laja River and Rucúe River, respectively, where they are rejoined by the outflow of the power station. However, owing to the volcanic origin of the basin, the existence of a large aquifer and unexpectedly high groundwater infiltration, actual flow was higher than the minimum during the entire sampling period, except directly downstream of both diversion structures. Mean flow during the low flow operation periods was $47.17\,m^3\,s^{-1}$ and $4.42\,m^3\,s^{-1}$ upstream of the Laja and Rucúe barriers, respectively (station 1 and station 4), and $35.17\,m^3\,s^{-1}$ and $2.82\,m^3\,s^{-1}$ below the barriers (station 3 and 6, respectively; all flows were measured at permanent gauging stations). In the study sections, both rivers have rhithral characteristics, but the Rucúe River has higher coverage of native riparian vegetation compared with the Laja River.

The main effects of construction involved direct modification of the river bed, cutting of riparian vegetation and temporary diversion of the river channel. Direct habitat alteration occurred in one reach of the Laja River at the diversion dam and in two reaches of the Rucúe River (diversion dam and siphon). Although the siphon is located above the river, during construction the river bed was completely diverted to build the foundations for the pipeline. The main effects of operating the hydropower facility are reductions in flow downstream of both diversion dams and increased flow in the tailwater reach in the Rucúe River. The river bed of the inflow area was not previously prepared for increased flows (e.g. widened).

Fish sampling and data analysis

Sampling was conducted at seven locations (three in the Laja River and four in the Rucúe River; Figure 1) on nine occasions as follows: (1) preconstruction period: July 1997; (2) construction period: September and November 1997, February and August 1998; (3) operation period: November 1998, 1999, 2000 and 2001.

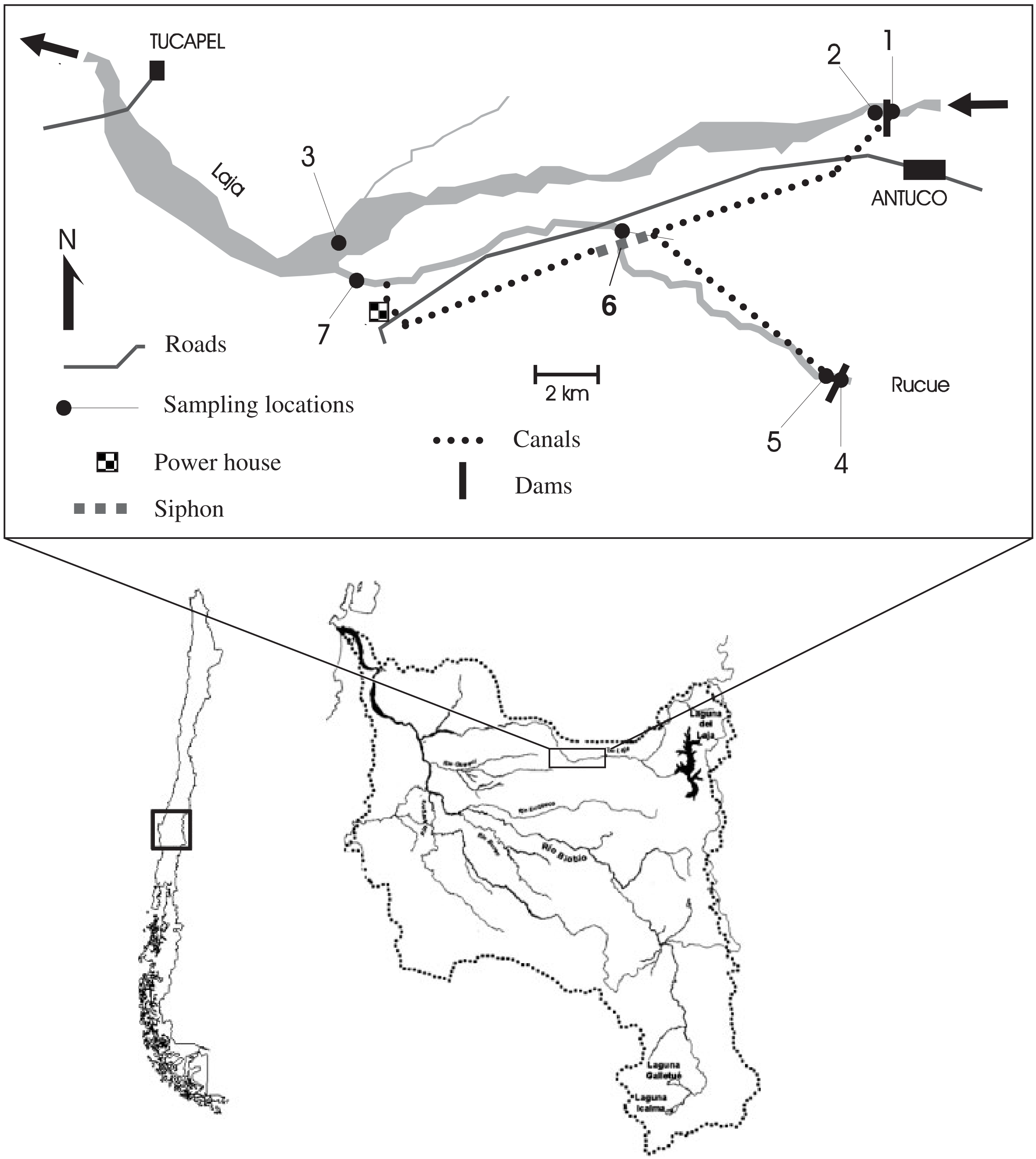

Figure 1. Map of study area in the Biobío basin of central Chile. The Laja River barrier is located between sampling stations 1 and 2. The Rucúe River barrier is located between sampling stations 4 and 5. The siphon crosses the Rucúe River in sampling station 6. Reentry of water occurs directly upstream of sampling station 7.

All sampling, except February 1998, corresponded to the high flow season. Sampling locations included areas above and below the diversion dams in both rivers and the area downstream of the point of reentry of the water in the Rucúe River.

Fish sampling consisted of removing all fish encountered in a 50-m segment of river using a backpack electroshocker. All fish were identified to species, counted, and returned to the river within the segment where they were captured to ensure that population abundance was not affected by sampling. Species richness (*S*), and abundance estimated as catch per unit effort (CPUE; standardized per 50 m^2 for 20 min of electrofishing) were calculated for each sample. Differences in sampling efficiency of gears may arise in different habitats and could confound estimates of abundance. However, three-pass depletion electrofishing in the same types of habitats in another river basin next to the Laja River yielded similar sampling efficiency among all habitats (Andalien River, Habit and Belk, unpublished data). High flows can decrease sampling efficiency; however, in this study higher abundances were found in areas and times of greater flow (e.g. preconstruction). If increased flows led to lower sampling efficiency, then the true differences in abundance would be even greater than reported. It appears unlikely that variation in sampling efficiency could account for the pattern of species composition and abundance observed in this study.

To determine the response of the fish community to construction and operation of the hydropower facility, sampling periods and sampling localities were classified as follows. Sampling periods were grouped based on timing of the sample relative to construction and operation of the diversion hydropower plant as preconstruction, construction, and operation (see above); sampling localities were grouped based on the type of alteration as (a) direct alteration — habitat structure changes, including alterations to substrate, depth, width, riparian vegetation and flow — and (b) indirect alteration — indirect downstream effects due to construction and flow changes during operation. Localities with direct alterations corresponded to stations 1 and 2 in the Laja River and stations 4, 5 and 6 in the Rucúe River. Localities with indirect alterations corresponded to station 3 in the Laja River and station 7 in the Rucúe River (see Figure 1).

Analysis of variance (ANOVA) was used to test for differences in total CPUE (data were $\log x + 1$ transformed to meet assumptions of normality) between the two rivers (Laja and Rucúe), among sampling periods (preconstruction, construction, and operation), and between direct and indirect impact locations. Significant differences were contrasted *a posteriori* with LSD test comparisons (Zar, 1999). To compare differences in species richness (*S*) between the two rivers and among sampling periods, a Kruskal–Wallis nonparametric ANOVA (Ramsey and Schafer, 2002) was used because values of *S* were small and discrete (i.e. integers).

Ordination methods based on pairwise similarity matrices were used to visualize spatial patterns and to quantify temporal shifts in fish distribution and abundance among locations and time periods. Relative abundance based on the CPUE estimates was used for this analysis, and relative abundance was fourth-root transformed to moderate the influence of extremes in species abundances (Pegg and McClelland, 2004). Similarity matrices were based on a Bray–Curtis similarity index (Bray and Curtis, 1957). To visualize the relationship of locations through time, nonparametric multidimensional scaling (NMDS) was used to produce two-dimensional plots of relationships among locations. Boundaries among groups were defined at 50% similarity based on the Bray–Curtis index. The Similarity Percentage procedure (SIMPER) on standardized variables (PRIMER v.5, Clarke and Gorley, 2001) was used to determine which species were most important in generating the resulting pattern.

The comparative index of multivariate dispersion (IMD) from the Bray–Curtis pairwise similarities (Warwick and Clarke, 1993) was used to assess the variability of the fish community structure in each river between preconstruction and construction–operation periods. This index contrasted the ranked similarities between the preconstruction phase (reference) and construction and operation periods (Clarke and Warwick, 1994). Values of IMD range from -1 to $+1$. Values near 0 imply no differences in variability between groups, whereas values near the extremes imply that variability in multivariate structures differs between groups (Clarke and Warwick, 1994).

Measured distances between means sequentially from one sampling period to the next within NMDS plots was used to estimate temporal variability within each locality and resistance of fish communities to construction and operation disturbances. All plots were drawn to the same relative x–y grid size, distances were standardized to time, and total distance (in centimetres) and percentage of variation between each period (grouped by preconstruction, construction, and operation periods) for each group of localities by river (based on type of disturbance) was measured. This approach, based on the 2-D approximation space rather than the real high-dimensional space, provides a relative measure of variability and is useful in giving insight into temporal stability in relation to changes in fluvial ecosystem conditions (Pegg and McClelland, 2004), when 2-D stress values are low.

Finally, differences among time periods and localities were analysed for species-specific CPUEs ($\log(x+1)$ transformed) to compare the response of native and introduced fishes. Comparisons were made using ANOVA with river (Laja and Rucúe) and sampling period (pre-construction, construction, and operation) as main effects (location types were not included as main effects because they were generally not significant in the analysis of total CPUE). Significant differences were contrasted *a posteriori* with LSD test comparisons (Zar, 1999). *Cheirodon galusdae* Eigenmann 1928, was not included in the individual species analyses because it was uncommon in the study area, and data were not sufficient for statistical analysis.

RESULTS

Species richness was higher in the Rucúe River than in the Laja River throughout the study ($H_{(1)} = 20.28$, $p = 0.000$) but did not vary among sampling periods ($H_{(2)} = 2.14$, $p = 0.342$; Table 1). The dominant species in both rivers in the preconstruction period were introduced rainbow trout, *Oncorhynchus mykiss* Walbaum, 1892, and brown trout, *Salmo trutta* Linnaeus, 1758. Native species observed were *Diplomystes nahuelbutaensis* Arratia 1987, *Trichomycterus areolatus* (Valenciennes, 1840), *Percilia irwin*i Eigenmann 1927 and *C. galusdae*.

Total fish abundance (CPUE) differed between rivers and among sampling periods but not between locations with direct and indirect impacts (Table 2). Total fish abundance was higher in the Rucúe River compared with the Laja River and higher during the preconstruction period compared with construction and operation periods (Table 1). The sampling period by location (direct or indirect) interaction was significant, but no other interactions were (Table 2). Total fish abundance declined more abruptly during construction in direct alteration locations compared with indirect alteration locations; however, by the time operation began, total fish abundance was equally low in both direct and indirect alteration locations.

Analysis of pairwise similarities of relative abundance of fish and the subsequent NMDS plot revealed three groups at 50% similarity for the Laja River (Figure 2). Group 1 corresponds to all Laja River localities during the preconstruction period, together with station 3 (with indirect alteration) in the first sampling period of the construction stage. Group 2 is formed by locations with direct alterations (stations 1

Table 1. Mean (± standard deviation) species richness and abundance (CPUE) in the Laja and Rucúe Rivers during preconstruction, construction and operation periods

	River	Period		
		Preconstruction	Construction	Operation
Species richness	Laja	2.3 ± 0.4	1.9 ± 1.6	2.1 ± 0.2
	Rucúe	4.5 ± 1.0	4.1 ± 0.1	3.2 ± 1.3
Abundance (CPUE)	Laja	2.7 ± 3.8	0.5 ± 1.3	0.5 ± 1.2
	Rucúe	7.6 ± 16.7	1.7 ± 2.9	1.1 ± 2.1

Table 2. Analysis of variance table for total abundance (CPUE). Significant effects are shown in bold

Source	df (num, den)	*F*	*P*
Period	2, 366	15.98	**0.000**
Location	1, 366	1.16	0.280
River	1, 366	12.66	**0.000**
Period*Location	2, 366	3.85	**0.022**
Period*River	2, 366	1.30	0.272
Location*River	1, 366	1.16	0.280
Period*Location*River	2, 366	0.35	0.699

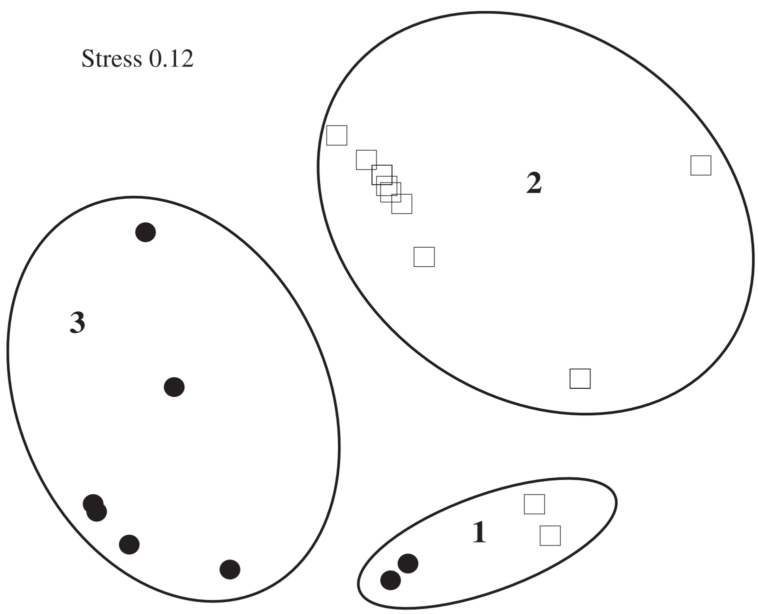

Figure 2. Nonparametric multidimensional scaling for the Laja River fish community data. Boundaries are identified at 50% Bray–Curtis similarity. Open squares represent locations with direct alterations (stations 1 and 2) and solid circles locations with indirect alterations (station 3).

and 2) during construction and operation stages. Group 3 is formed exclusively by station 3 during later construction and operation periods. Mean similarity for group 1 was 82.1% and was determined entirely by abundance of *O. mykiss* (51.1%) and *S. trutta* (43.1%). Mean similarity of group 2 was 72.6% and was determined by abundance of *O. mykiss* (57.8%) and *T. areolatus* (41.5%). Mean similarity of group 3 was 72.6% and was mostly determined by two native species, *P. irwini* (32.7%) and *D. nahuelbutaensis* (28.5%), and *O. mykiss* (30.1%).

The Rucúe River reveals a different spatio-temporal pattern, with two groups at 50% similarity (Figure 3). Group 1 is composed of all localities and sampling periods, except station 7 during operation (November 1999 and 2001, which comprise group 2). Station 7 is located at the water reentry point from the diversion canals. During November 2000, station 7 had no fish; consequently, it was not included in this analysis. Subset NMDS of group 1 shows no differences in the pattern from the full analysis. Mean similarity of group 1 was 76.7% and was determined by abundance of *T. areolatus* (29.8%), *P. irwini*

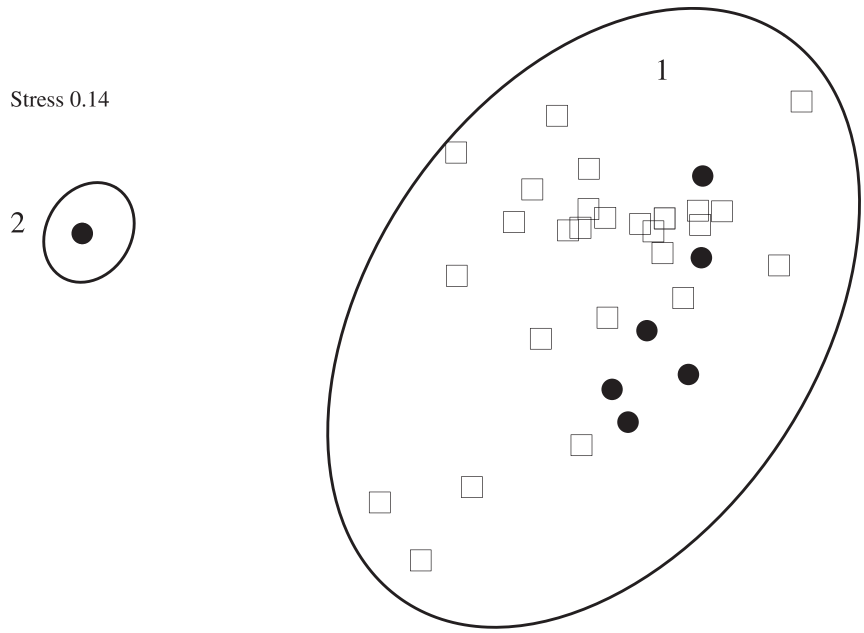

Figure 3. Nonparametric multidimensional scaling for the Rucúe River fish community data. Boundaries are identified at 50% Bray–Curtis similarity. Open squares represent locations with direct alterations (stations 4, 5 and 6) and solid circles locations with indirect alterations (station 7).

(28.6%), *O. mykiss* (24.2%), and *S. trutta* (15.6%). Mean similarity of group 2 was 99.9% and was entirely determined by *T. areolatus* (100%). This single species appears to tolerate the greatly increased flows at the water reentry point from the canals that supply the hydropower facility (station 7).

During preconstruction and construction periods, the Laja River exhibits higher relative measures of dispersion than the Rucúe River; but during the operation period, the opposite occurs (Table 3). Additionally, the Laja River shows higher variability than the Rucúe River in multivariate fish community structure between preconstruction and construction periods. On the other hand, the comparison between preconstruction and operation periods reveals higher variability in multivariate fish community structure among samples in the Rucúe River compared with the Laja River (Table 3). For both rivers, the IMD between construction and operation was near 0, indicating little change from construction to operation periods in the fish community structure.

Total temporal shifts in community structure were greater in the Laja River and in localities with direct alterations compared with the Rucúe River and localities with indirect alterations (Table 4). In all cases, percentages of variation in community structure increased from preconstruction to construction periods. However, localities with indirect alterations had lower differences of the percentages of variation between preconstruction and construction periods and between construction and operation periods than localities with direct impacts (Table 4).

Abundance was significantly lower after construction began and during operation for both introduced salmonid species (*O. mykiss* and *S. trutta*), but abundances did not differ between rivers (Table 5, Figure 4). Abundance of *P. irwini* was greater in the Rucúe River compared with the Laja River, and the river-by-period interaction was significant (Table 5). *Percilia irwini* was abundant during preconstruction in the Rucúe River and declined coincident with the construction and operation. This species was rare in the Laja River during the entire study (Figure 4). Abundances of *T. areolatus* differed by river but not by period, and abundances of *D. nahuelbutaensis* did not differ by river or sampling period (Table 5, Figure 4).

Table 3. Results of index of multivariate dispersion (IMD) comparing the relative variability of the fish community among the preconstruction (P) construction (C) and operation (O) periods of the hydropower plant

Comparison		Laja River	Rucúe River
P *vs*. C	Relative dispersion	0.494 *vs*. 1.133	0.378 *vs*. 0.869
	IMD value	−0.952	−0.606
P *vs*. O	Relative dispersion	0.494 *vs*. 0.951	0.378 *vs*. 1.186
	IMD value	−0.274	−0.683
C *vs*. O	Relative dispersion	1.133 *vs*. 0.951	0.869 *vs*. 1.186
	IMD value	0.163	−0.325

Table 4. Temporal community changes based on the distances (cm) in the NMDS plots (standardized by time) from the preconstruction to the operation stage in localities with direct and indirect alteration of the habitat

		Laja River		Rucúe River	
		Direct alteration	Indirect alteration	Direct alteration	Indirect alteration
Total change	Preconstruction–operation	9.2	5.4	7.3	1.5
% variation	Preconstruction–construction	87.1	76.5	71.9	58.4
	Construction–operation	12.9	23.6	28.1	41.2

DISCUSSION

Rivers in temperate regions of North and South America have experienced massive hydrological alterations over the past several decades (Pringle *et al*., 2000). Alterations of the natural flow regime can generate a cascade of reactions that cause the river ecosystem to simplify over time, resulting in lower native species richness and modified abundance and distribution of species (Richter *et al*., 2003). In addition, changes in flow regime can lead to a change in species assemblages from species tolerant of a variable flooding regime to those that can withstand permanent flooding (Kingsford, 2000) or no flooding.

In this study, there was a difference in response of the fish community between the two rivers depending on the history of alterations to the river. In the Laja River, the operation of three hydropower plants in its headwaters and irrigation obstructions has created a long-term perturbation to the natural flow regime. Results suggest that this change in flow regime might be the cause of the lower species richness in the Laja River and, apparently, in a fish community that is less resistant to new alterations. The assemblage of species and patterns of abundances found in the preconstruction stage in the Laja River were completely changed by the disturbance associated with construction and operation of the new hydropower facility. In particular, the abundance of introduced salmonids dramatically decreased. This decrease suggests that the Laja River ecosystem may be less resilient to disturbances because of previous human actions that have altered the magnitude, frequency and duration of disturbance regimes to which the biota is adapted (Folke *et al*., 2004).

On the other hand, the fish community of the Rucúe River exhibited a higher resistance to change, even though the degree of disturbance and the reduction of fish abundance in both rivers were of similar magnitude. Although trout were the dominant species in both rivers, the presence of up to four additional native species in the Rucúe River appeared to result in more resistance to a change in community structure compared with the Laja River. The Rucúe River fish community exhibited higher resilience in the sense that the structure of the fish community showed little overall change in response to the disturbance (Folke *et al*., 2004).

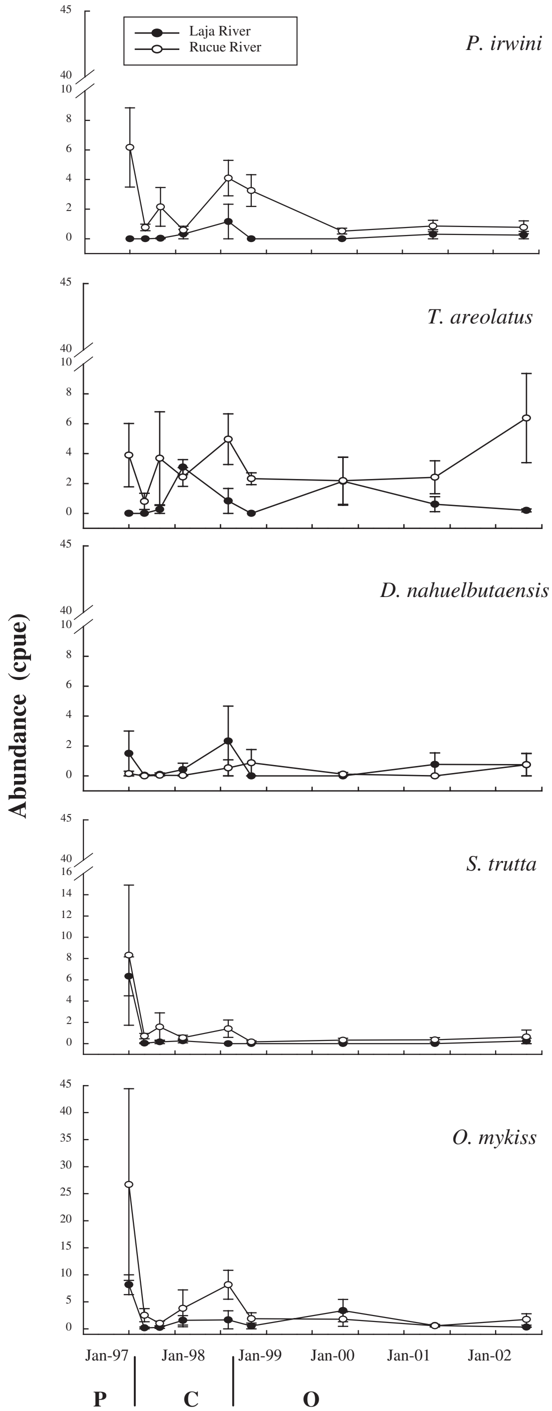

Figure 4. Mean abundance (CPUE) of common native and introduced fish species by river at each sampling time during preconstruction (P), construction (C) and operation (O) periods. Error bars indicate 1 standard error about the mean.

Table 5. Analysis of variance table for abundance (CPUE) of the five common fish species. Significant results are shown in bold

Species	Source	df (num, den)	*F* value	*P*
P. irwini	Period	2, 57	2.34	0.105
	River	1, 57	39.19	**0.000**
	Period*River	2, 57	3.59	**0.033**
T. areolatus	Period	2, 57	0.08	0.916
	River	1, 57	17.23	**0.000**
	Period*River	2, 57	0.82	0.443
D. nahuelbutaensis	Period	2, 57	0.21	0.805
	River	1, 57	1.35	0.249
	Period*River	2, 57	0.62	0.539
S. trutta	Period	2, 57	31.14	**0.000**
	River	1, 57	0.31	0.575
	Period*River	2, 57	2.16	0.123
O. mykiss	Period	2, 57	14.14	**0.000**
	River	1, 57	2.89	0.094
	Period*River	2, 57	1.06	0.350

This greater resilience in the Rucúe River may be a consequence of a history of natural flows and corresponding lack of disturbance to instream and riparian habitats.

Aquatic habitats with high spatial heterogeneity favour the structuring of communities with high diversity because it allows different organisms, in functional and morphological terms, to successfully exploit available niches (Freitas *et al*., 2005). Regulated flows cause decreased velocity and depth, causing immediate loss of some habitats (Brasher, 2003), and the loss of habitat heterogeneity as a result of long-term changes in river morphometry and associated riparian forests (Smith *et al*., 2000).

The abundance trends of each species suggest a new community structure in the Laja River and in the area of water reentry in the Rucúe River. In this new community, introduced trout are a minor constituent, and the endangered *P. irwini* (Campos *et al*., 1998), an important constituent of the community in unmanipulated areas of the river, appear to have become locally extinct. Native catfishes, particularly *T. areolatus*, are now the dominant species. *T. areolatus* is a widespread species in Chile, with a high capacity for colonization after disturbance, such as in irrigation canals (Habit and Parra, 2001) and streams polluted by domestic effluents (Habit *et al*., 2005). Although a native species dominates in the area disturbed by the construction and operation of the hydropower facility, the new community is less diverse than a typical native species community in Chilean rivers, which would usually include at least three species in this type of habitat.

One of the most damaging consequences of hydropower plants with reservoirs and associated dams is the loss of habitat connectivity for river-adapted species (e.g. Morita and Yamamoto, 2002). Diversion-type hydropower systems with low diversion dams are considered to be less damaging to river systems compared with hydropower systems with large dams and storage reservoirs, because they do not lead to fragmentation of riverine habitat as long as they have sufficient instream flows. The diversion low dam consists of a fixed, uncontrolled rock weir, sided by a concrete raceway controlled by radial gates. Thus, it may not act as a complete barrier to fish movement during the approximately 40 to 100 days per year when flows exceed the turbine capacity, thereby requiring water to be spilled over the weir or under the gates. Benstead *et al*. (1999) found that low-head dams did not act as a complete barrier to the upstream migration of juvenile shrimp, but they did create a temporary obstacle, particularly when the water flow over the dam was low or nonexistent. In the Laja system, large-bodied fish, such as rainbow trout and brown trout, are likely to move upstream over the barrier but only during high flow. However, native species are small (Vila *et al.*, 1999), and it seems unlikely that they are able to move upstream past even low barriers (Morita and Yamamoto, 2002).

Effects of construction and operation on species-specific abundances follow an interesting pattern. The three species (*S. trutta*, *O. mykiss* and *P. irwini*) that occupy the midwater column (Behnke, 2002; Ruiz, 1993) showed dramatic declines in abundance in response to construction and operation of the hydropower facility. In contrast, the two native catfishes (*T. aerolatus* and *D. nahuelbutaensis*) that are benthic-oriented (Arratia, 1983) showed no significant response in abundance. It appears that flow and habitat alterations associated with construction and operation of this facility are more detrimental to species that occupy midwater habitats compared with benthic habitats.

In comparison with traditional reservoir-based hydropower generation facilities, low-head, diversion hydropower designs are certainly less disturbing to the fish community because they do not affect flow or river structure beyond the region of river between the diversion structure and the outflow. Because of this advantage the use of diversion hydropower facilities is likely to increase in areas where reservoir-based facilities are not feasible or desired.

How can effects of diversion hydropower facilities on fish community structure and abundance be avoided or mitigated? Two main effects identified in this study are (1) possible effects of barriers on movement and connectivity of populations of small or benthic-oriented species, and (2) effects on midwater species from reduced flow. The small size of the barriers involved suggests that fishways would be an inexpensive but probably effective method of reducing the effects of barriers. Many species have been shown to use fishways around low barriers, even small benthic species that are normally not considered highly mobile (e.g. Bunt *et al.*, 2001). To ameliorate the loss of habitat complexity that typically accompanies greatly reduced flows below diversion facilities, managers should consider the creation of a channel of reduced size and increased complexity in the area of reduced flow. Especially in large rivers with braided channel morphology, reduced flow results in broad, shallow riffles and loss of deep pools and runs. An artificially reduced channel size with built-in pool–riffle structure should provide sufficient habitat for midwater species to persist. Finally, because of the immediate and direct impacts of construction, populations may have to be augmented or reintroduced once habitat alterations are completed (e.g. Habit *et al.*, 2002).

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