

# Spatio-temporal distribution patterns and conservation of fish assemblages in a Chilean coastal river

Evelyn Habit · Mark Belk · Pedro Victoriano ·  
Edilia Jaque

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**Abstract** River environments are characterized by extreme spatial and temporal variation in the physical environment. The relationship of fish assemblages to environmental variation is poorly understood in many systems. In Chile zonation patterns of fish assemblages have been documented in several Andean river drainages. Coastal river drainages are comparatively small, but inordinately important because of their highly endemic flora and fauna and their proximity to major human populations. For conservation purposes it is important to understand what environmental factors affect assemblage structure of fishes especially in the comparatively high diversity coastal drainages. We studied patterns of fish distribution and abundance in three rivers of the coastal, Andalien drainage near Concepción, Chile. We used multi-dimensional scaling analyses to compare patterns among zones (rithron, transition and potamon) and high and low flow seasons. Species assemblages differed by zone, but not with season. Assemblages consisted of nested subsets of species characterized by their range of distribution among zones. One species group was composed of widespread species that occurred in all three zones, another species group consisted of species found only in transitional and potamal zones, and a final group was comprised of species found only in the potamal zone. The potamal zone contained the most diverse and abundant fish assemblage. Fish assemblages were related to both water quality and habitat

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E. Habit (✉)  
Aquatic System Unit, Environmental Science EULA-Chile Center, Universidad de Concepción,  
Casilla 160-C, Concepcion, Chile  
e-mail: ehabit@udec.cl

M. Belk  
Department of Integrative Biology, Brigham Young University, Provo, UT 84602, USA

P. Victoriano  
Depto. Zoología, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción,  
Concepcion, Chile

E. Jaque  
Depto. Geografía, Facultad de Arquitectura, Universidad de Concepción, Concepcion, Chile

structure variables. This study suggests that the key to conserving the diversity of native fish communities in coastal Chilean rivers is in the conservation of potamal regions. Unfortunately, most protected areas in Chile are in the depauperate headwaters of drainages. Protection of only headwaters is clearly inadequate and will not contribute to the conservation of this unique freshwater fish fauna.

**Keywords** Zonation · Habitat structure · Water quality · Coastal drainage · Chile

## Introduction

Longitudinal zonation is one of the most frequently described distribution patterns for freshwater fish faunas in river systems (Schlosser 1982; Campos 1985; Oberdorff et al. 1993; Ostrand and Wilde 2002). This pattern consists of changes in species richness, abundance, diversity, and assemblage composition associated with changes in environmental gradients spanning from the headwaters (rithron) to the river mouth (potamon; Illies and Botasaneanu 1963; Welcomme 1985; Granado 2000).

Environmental variables such as elevational gradient, river order (Hawkes 1975; Welcomme 1985), and habitat structure and complexity (Gorman and Karr 1978; Schlosser 1982; Arunachalam 2000) have been correlated with patterns of zonation. However, fluvial systems are dynamic and how patterns of fish distribution relate to temporal variation in the environment is not well known. Some environmental variables such as water chemistry variables (e.g., conductivity, pH, total dissolved solids, etc.) may be temporally variable whereas habitat structure (e.g., gradient, dominant substrate, order) may be more constant through time (Callow and Petts 1994). Fluvial systems are seasonally variable, and many rivers exhibit broad shifts in physical conditions as a result of seasonal fluctuations in flow (Poff et al. 1997). Mean velocity and flow increase dramatically during high flow periods along the entire river, and consequently the variance in some physical conditions (e.g., temperature, pH, conductivity, etc.) decreases among river segments (Callow and Petts 1994). Homogenization of some physical gradients may change fish assemblages and zonation patterns. In contrast to water chemistry variables, habitat structure may remain relatively unchanged across different flows. Habitat structure is determined by geomorphology, and substrate, factors that are not likely to change with seasonal variation in flow.

One area where strong zonation patterns have been documented is in the rivers of Andean origin in central and southern Chile (Campos 1985; Campos et al. 1993a, b). Zonation in these rivers is thought to be influenced by the contrast between the high gradient, torrential character of upstream segments (rithron) resulting from the height and nearness of the Andes mountain range, and the broad, slow-flowing character of downstream segments (potamon) near the ocean. In Andean rivers, native fish species richness varies from 2–3 species at upper elevations to 8–10 species at lower elevations, and dominant taxa include catfishes, and galaxiids (Habit et al. 2006).

In contrast to the rivers of Andean origin, coastal rivers in Chile originate in the coastal mountain range and are thus shorter and have a different pattern of flow compared to Andean rivers. Because of their shorter length they exhibit a rapid transition from rithral (high velocity, upland zone) to potamal (low velocity, lowland zone) characteristics (Habit and Victoriano 2005). Andean rivers typically exhibit two annual peaks in water flow—one during the winter rainy season and the other from snow melt in the high Andes in the spring (Parra et al. 2004). Coastal rivers experience only one annual peak in flow during the winter rainy season. Zonation patterns of fishes have been documented in coastal rivers

(Ruiz 1993), but it is not known how fish assemblages respond to seasonal variation and what environmental variables are the best predictors of fish distribution and abundance in coastal rivers.

Chilean coastal drainages are comparatively small, but inordinately important because of their highly endemic flora and fauna (Smith-Ramirez 2004) and their proximity to major human populations. Coastal drainages were important refugia for freshwater organisms during the Pleistocene glacial periods (Villagrán 2001; Smith-Ramirez 2004; Smith-Ramirez et al. 2005). Currently, some coastal rivers appear to be important refuges for native fishes because they maintain a relatively large number of native species compared to the larger Andean river systems (Soto et al. 2006). Thus it is important to understand what environmental factors affect assemblage structure of fishes especially in the comparatively high diversity coastal drainages.

Introduced fish species are widespread in Chile. Over the past century 22 species of freshwater fishes have been introduced to Chile. Twenty of the 22 are in families not native to the country, and salmonids are the most widely distributed and are dominant species in many systems (Dyer 2000). Most species were introduced for recreational or aquacultural purposes (Welcomme 1988), but they now have large self-sustaining, wild populations. In Andean systems introduced salmonids occur primarily in areas removed from the highest diversity of native species. However, in coastal rivers they can occur in all zones of the river. Understanding how distribution of nonnative fishes relates to distributional patterns of native species is important for conservation and management efforts.

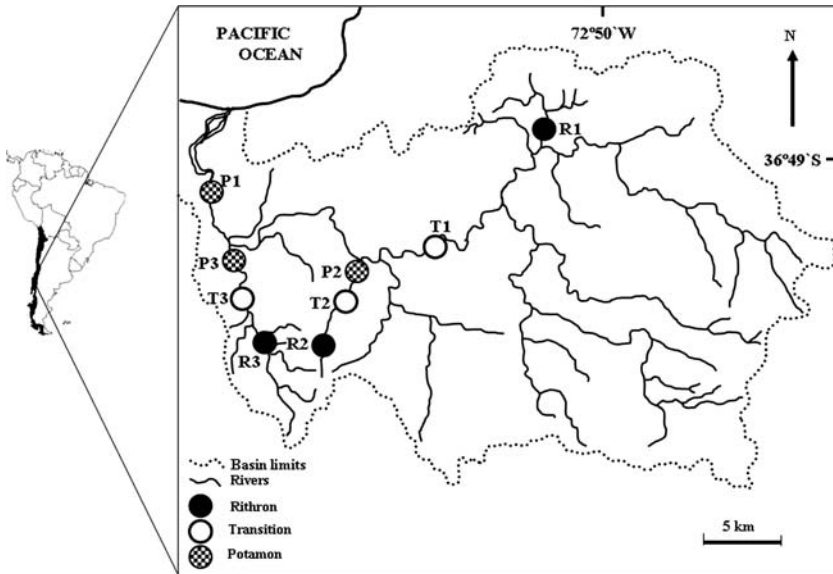
The Andalien River basin is a coastal drainage system, located in the South-Central area of endemism of the Chilean Province (Dyer 2000), which contains a high diversity of native fishes (Ruiz 1993). In addition, the Andalien drainage supports significant populations of introduced species, particularly salmonids (rainbow trout, *Onchorhynchus mykiss*, and brown trout, *Salmo trutta*). In its headwaters this basin maintains a well-preserved native forest and high water quality. It supplies drinking water for more than 200,000 inhabitants. In contrast, potamal segments of the Andalién basin flow through urban areas with high density of human use (Concepcion city has greater than 1 million inhabitants; Jaque 1994). Water quality in the lower segments is strongly influenced by human use and declines dramatically compared to headwater areas. The strong contrast in environmental conditions and the high diversity of native and introduced fishes in this coastal drainage provides a system for answering questions about the relationship between water chemistry and habitat structure and native and non-native fish distribution and abundance (i.e., zonation patterns).

To characterize zonation patterns and the relationship between fish distribution and abundance and seasonal environmental variation, we studied fish assemblage structure of native and introduced fish in three rivers in the Andalién basin during high and low flow seasons. We characterized the spatial and temporal distribution and abundance patterns of native and non-native fishes and assessed the relationship to physical factors in determining patterns of zonation, distribution, and composition of fish communities during high and low flows.

## Material and methods

### Study area

We conducted this study in the mainstem of the Andalién River and its two major tributaries the Queule and Nonguén rivers (36°42′–36°56′ S; Fig. 1). To analyze the longitudinal



**Fig. 1** Map of the study area in a coastal drainage of central Chile. Andalién river stations are represented by R1, T1, and P1, and similarly, Queule river stations are R2, T2, and P2, and Nonguén river stations are designated as R3, T3, and P3. R: rithral zone; T: transitional zone; P: potamal zone

distribution of the fish fauna, in each tributary we characterized the fish assemblage in each of three physical zones (sensu Welcomme 1985; Maddock 1999): (a) rithron, or headwaters characterized by cold water temperature ( $<12^{\circ}\text{C}$  during summer), high current velocity ( $>0.3\text{ ms}^{-1}$ ) and substratum of boulders ( $>10\text{ cm}$  diameter) (b) transition between rithron and potamon, and (c) potamon, or lower areas, characterized by fine substratum (sand or mud), low velocity ( $<0.3\text{ ms}^{-1}$ ) and higher water temperature ( $>12^{\circ}\text{C}$  in summer). The three potamal areas were found in urban or partially urban zones; and rithral and transitional reaches were in rural areas with low density of human inhabitants. In each zone, we delimited one sampling station of 100 m length for each river. Sampling stations in the same zone, but located in different sub basins were considered replicates. We sampled during two consecutive periods during high flow (July and August 2003), and two periods during low flow (March and May 2004).

Physical habitat characteristics were classified in two categories: water quality and habitat structure (Table 1). To characterize water quality, we measured dissolved oxygen, chemical oxygen demand (COD), total phosphorous, total nitrogen, organic, inorganic, and total suspended solids, and fecal coliforms from water samples collected at each station before we sampled the fish assemblage. At each station we measured temperature (mercury thermometer  $0.1^{\circ}\text{C}$ ), pH (Schott Gerate Mod. Handylab 2), conductivity and total dissolved solids (Cole Parmer Mod. 19820). To characterize habitat structure, we measured mean and maximum depth (cm), width (m), and average and maximum current velocity ( $\text{m s}^{-1}$ ; Gurley flow meter) in multiple transects across each site. In addition, we estimated flow ( $\text{m}^3\text{ s}^{-1}$ ), and percent of substrate covered by boulders ( $>600\text{ mm}$  diameter) along the 100 m sampling station. Additional structural variables of altitude, river gradient, distance to river mouth, and river order (sensu Strahler 1984), were obtained using IGM 1:50,000 scale maps (official maps of the Military Geographic Institute of Chile).

**Table 1** Mean ( $\pm$ standard deviation) of the twenty environmental variables included in the spatio-temporal analyses, pooled by zone

Unit	High Flow			Low Flow		
	Rithron	Transition	Potamon	Rithron	Transition	Potamon
Water quality						
Temperature	8.5 $\pm$ 1.8	9.0 $\pm$ 1.8	10.3 $\pm$ 1.9	10.5 $\pm$ 3.1	12.0 $\pm$ 4.1	12.8 $\pm$ 4.2
PH	7.7 $\pm$ 0.3	7.5 $\pm$ 0.2	7.5 $\pm$ 0.1	7.1 $\pm$ 0.3	7.1 $\pm$ 0.3	7.0 $\pm$ 0.3
Conductivity	72.7 $\pm$ 14.1	75.8 $\pm$ 13.9	89.8 $\pm$ 23.1	96.4 $\pm$ 27.0	101.4 $\pm$ 31.3	114.8 $\pm$ 27.9
Dissolved Oxygen	10.5 $\pm$ 0.7	10.3 $\pm$ 0.5	10.0 $\pm$ 0.3	11.4 $\pm$ 0.6	10.9 $\pm$ 1.0	10.6 $\pm$ 1.0
COD	3.0 $\pm$ 2.0	4.5 $\pm$ 2.5	6.6 $\pm$ 2.9	3.8 $\pm$ 1.2	4.0 $\pm$ 1.3	4.3 $\pm$ 1.2
Total Phosphorous	0.07 $\pm$ 0.07	0.04 $\pm$ 0.01	0.1 $\pm$ 0.05	0.03 $\pm$ 0.01	0.03 $\pm$ 0.02	0.08 $\pm$ 0.04
Total Nitrogen	0.29 $\pm$ 0.17	0.32 $\pm$ 0.09	0.54 $\pm$ 0.30	0.28 $\pm$ 0.10	0.27 $\pm$ 0.05	0.49 $\pm$ 0.13
Total Dissolved Solids	33.7 $\pm$ 9.1	33.7 $\pm$ 7.4	41.0 $\pm$ 12.3	37.5 $\pm$ 9.1	43.8 $\pm$ 10.4	44.2 $\pm$ 19.1
Total Suspended Solids	11.8 $\pm$ 8.6	12.4 $\pm$ 8.6	29.1 $\pm$ 18.7	6.9 $\pm$ 5.7	6.1 $\pm$ 4.7	19.0 $\pm$ 15.3
Fecal Coliforms	228 $\pm$ 114	205 $\pm$ 352	15631 $\pm$ 11202	6283 $\pm$ 14078	332 $\pm$ 174	18440 $\pm$ 21903
Parameter	Unit	High Flow	Potamon	Low Flow	Transition	Potamon
		Rithron	Transition	Rithron	Transition	Potamon
Habitat structure						
Mean Depth	cm	26.5 $\pm$ 5.4	28.3 $\pm$ 11.1	25.5 $\pm$ 7.3	15.5 $\pm$ 4.2	29.8 $\pm$ 19.4
Maximum Depth	cm	50.0 $\pm$ 6.3	61.8 $\pm$ 27.7	55.2 $\pm$ 17.4	26.5 $\pm$ 9.4	45.8 $\pm$ 26.6
Flow	m <sup>3</sup> s <sup>-1</sup>	0.7 $\pm$ 0.6	3.3 $\pm$ 2.6	3.6 $\pm$ 2.7	0.2 $\pm$ 0.1	0.4 $\pm$ 0.5
Avg. Velocity	m s <sup>-1</sup>	0.83 $\pm$ 0.06	1.0 $\pm$ 0.24	0.59 $\pm$ 0.3	0.23 $\pm$ 0.12	0.18 $\pm$ 0.17
Boulders	%	76.7 $\pm$ 2.5	16.6 $\pm$ 25.8	0 $\pm$ 0	76.7 $\pm$ 2.5	16.6 $\pm$ 25.8
Width	m	5.8 $\pm$ 2.2	11.8 $\pm$ 6.3	19.8 $\pm$ 15.8	6.6 $\pm$ 2.8	11.7 $\pm$ 7.9
Order	o	3.3 $\pm$ 0.5	3.6 $\pm$ 0.5	4.3 $\pm$ 0.2	3.3 $\pm$ 0.5	3.6 $\pm$ 0.5
Gradient		0.4 $\pm$ 0.09	0.2 $\pm$ 0.07	0.14 $\pm$ 0.03	0.4 $\pm$ 0.09	0.2 $\pm$ 0.07
Elevation	masl	143.3 $\pm$ 27.3	62.3 $\pm$ 33.2	27.3 $\pm$ 8.8	143.3 $\pm$ 27.3	62.3 $\pm$ 33.2
Distance from mouth	Km	35.3 $\pm$ 14.4	34.1 $\pm$ 9.1	26.5 $\pm$ 6.5	35.3 $\pm$ 14.4	34.1 $\pm$ 9.1

Fish sampling was done in a uniform way at all sampling locations so that all locations and time periods could be used as replicate samples in the analysis. The fish sampling consisted of removing all fish encountered in one 100 m segment of river on each of three successive passes with a backpack electroshocker using block nets both up and downstream. We used a backpack electroshocker Elektrofishfangerat motor JLO gasoline, 50–400 volts, DC, one anode. Captured individuals were identified on site and returned to the river within the segment where they were captured to ensure that population abundance was not affected in the following sampling period (sampling induced mortality was less than 0.1%). We used the minimum number known alive (sum of all individuals captured during the three passes) as our measure of absolute abundance (Table 2), and used relative abundance (number of individuals of a given species in the sample divided by the total number of individuals of all species in the same sample) in calculations of similarity among sampling sites. Fish were captured at all sites during all sampling periods.

To determine the relationship among river zones (i.e., rithral, transitional, and potamal) during high and low flow seasons based on physical variables, we used ordination methods based on pair-wise similarity matrices. Based on scatter plots for all variable pairs (Draftsman Plot) we log ( $x + 1$ ) transformed five variables (average and maximum velocity, width, flow and coliforms) to avoid skewed trends. In addition, if variables were highly correlated, we selected one of each highly correlated group (i.e., we selected total suspended solids and deleted inorganic and organic suspended solids and we selected average velocity and deleted maximum velocity). We then normalized all selected variables to compare variables with different unit measures (Clarke et al. 2005). This process resulted in twenty environmental variables (10 water quality variables and 10 habitat structure variables, Table 1), which we used to generate similarity matrices based on Euclidean distances. We used multidimensional scaling (MDS, PRIMER v.6 Clarke and Gorley 2005) to visualize the relationship among groups in the high-dimensional space. For all MDS analysis we evaluated 2-dimensional and 3-dimensional representations. We avoided stress values

**Table 2** Mean and standard deviation of the number captured of each species and species richness by zone. Values represent the total number captured divided by twelve (four sampling periods and three locations per zone) rounded to the nearest tenth

SPECIES	Rithron	Transition	Potamon
Natives			
<i>Trichomycterus chiltoni</i> (Eigenmann, 1927)	0.1 ± 0.3		
<i>Trichomycterus areolatus</i> (Valenciennes, 1840)	6.8 ± 9.1	70.5 ± 79.1	11.1 ± 16.7
<i>Nematogenys inermis</i> (Guichenot, 1848)	3.3 ± 4.8	3.5 ± 3.5	6.7 ± 10.9
<i>Bullockia maldonadoi</i> (Eigenmann, 1928)	0.1 ± 0.3	1.2 ± 3.8	23.6 ± 54.4
<i>Percilia irwini</i> Eigenmann, 1927	0.1 ± 0.3	10.3 ± 21.1	14.2 ± 16.7
<i>Geotria australis</i> Gray, 1851		10.3 ± 14.9	1.6 ± 2.3
<i>Percichthys trucha</i> (Valenciennes, 1833)		3.0 ± 6.0	0.8 ± 2.0
<i>Percichthys melanops</i> Girard, 1855		0.2 ± 0.6	
<i>Cheirodon galusdae</i> Eigenmann, 1928		0.7 ± 1.8	49.7 ± 64.9
<i>Basilichthys australis</i> Eigenmann, 1928		0.1 ± 0.3	3.8 ± 6.7
<i>Galaxias maculatus</i> (Jenyns, 1842)			9.3 ± 16.5
Introduced			
<i>Oncorhynchus mykiss</i> Walbaum, 1892	15.5 ± 10.2	8.3 ± 8.1	3.7 ± 5.5
<i>Salmo trutta</i> Linneo, 1758	7.1 ± 11.4	5.4 ± 9.6	1.5 ± 2.2
<i>Gambusia holbrooki</i> (Agassiz, 1859)			4.0 ± 5.6
<i>Cichlasoma facetum</i> (Jenyns, 1842)			3.3 ± 0.7
<i>Carassius carassius</i> (Linneo, 1758)			0.2 ± 0.6
Species richness	3.2 ± 1.4	5.0 ± 1.9	7.3 ± 2.6

>0.15, because visual representations with higher stress values are unreliable (Clarke et al. 2005). To be consistent we presented all results in 3-dimensional views. To analyze differences in physical variables and fish distributions among zones and seasons we used a two-way crossed analysis of similarities (ANOSIM, PRIMER v.6 Clarke and Gorley 2005), with zone (rithron, transition and potamon) and season (high and low flow) as factors.

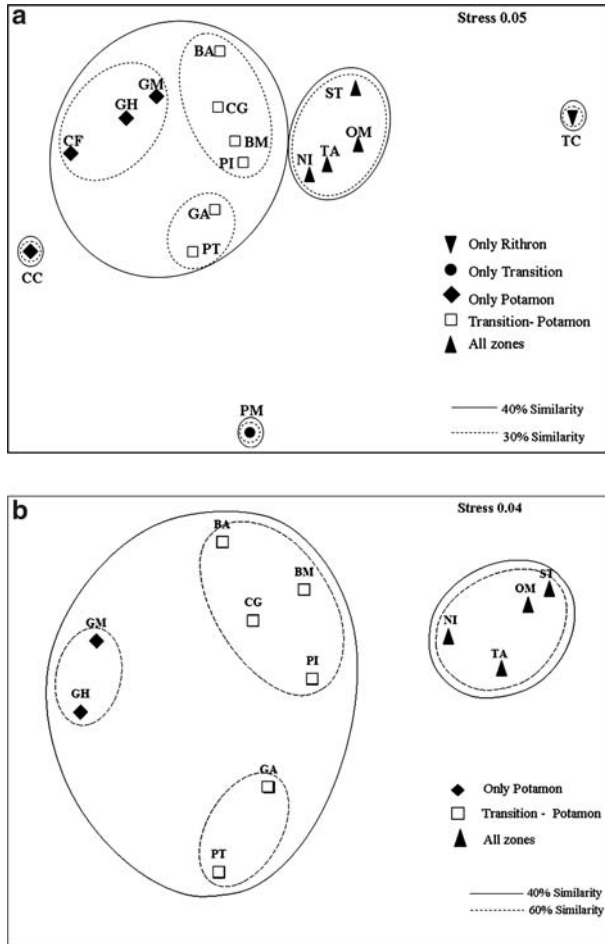
To determine the relationship among river zones based on fish distribution and abundance, we used a similar procedure as detailed above. First we standardized fish abundance to reduce sampling location biases, and then we fourth root-transformed values to down-weight the influence of abundant taxa and account for rarer taxa as well (Kreutzweiser et al. 2005). Similarity matrices based on the Bray-Curtis index were used for the MDS procedure (Matrix had 16 columns representing species and 36 rows representing samples—nine locations by four sampling periods). To determine if zones and seasons differ in fish assemblage and abundance we used a two-way crossed analysis of similarities (ANOSIM), with zone and seasons as factors. This analysis tests for differences among factors and levels using permutation and randomization methods based on the similarity matrix (Clarke et al. 2005).

Finally, to determine how environmental variables (water chemistry and habitat structure) related to patterns of fish abundance and distribution, we used a matching analysis with a permutation test to determine significance (BioEnv, PRIMER v.6 Clarke and Gorley 2005; Clarke et al. 2005). This procedure uses a multiple regression approach to determine which environmental variables best explain the multivariate relationship of the fish assemblage (Clarke et al. 2005).

## Results

### Fish distribution and abundance

Multi-dimensional scaling (MDS) of fish relative abundances revealed five distinct groups at 30% similarity (Fig. 2a). Three groups are composed of only one rare species restricted to one zone: *Trichomycterus chiltoni* to rithron, *Percichthys melanops* to transition and *Carassius carassius* to the potamon zone. The remaining groups are species assemblages not defined by zones, but rather by their breadth of distribution among zones. One group is composed of widespread species found in all zones (*S. trutta*, *O. mykiss*, *Trichomycterus areolatus*, and *Nematogenys inermis*). The other group is represented by species found in transitional and/or potamal zones, but not in rithral areas. At 40% similarity this second group is divided into three subgroups. One subgroup is represented by species found only in the potamal zone (*Galaxias maculatus*, *Gambusia holbrooki*, and *Cichlassoma facetum*), but with higher abundance than *C. carassius*. The other two subgroups are comprised of species found in both the transition and potamon zones. The subgroup of *Geotria australis* and *Percichthys trucha* is characterized by higher abundance in transitional zones. The other group is characterized by species with higher abundances in the potamon. Overall, groups differ significantly (ANOSIM, Global  $R = 0.83$ ,  $p = 0.01$ ). Specifically, the widespread species group differs from the potamal/transitional group (ANOSIM, pairwise test,  $R = 0.722$ ,  $p = 0.05$ ), and the potamal only subgroup differs from the potamal/transitional subgroups (ANOSIM, pairwise test,  $R = 0.65$ ,  $p = 0.05$ ). This result is robust even when rare species are excluded. A subset MDS with no rare species (i.e., excluding *T. chiltoni*, *P. melanops*, and *C. carassius*), shows a similar pattern with a nested group of transitional-potamal species at 40% similarity and a second group composed of the widespread species (Fig. 2b).

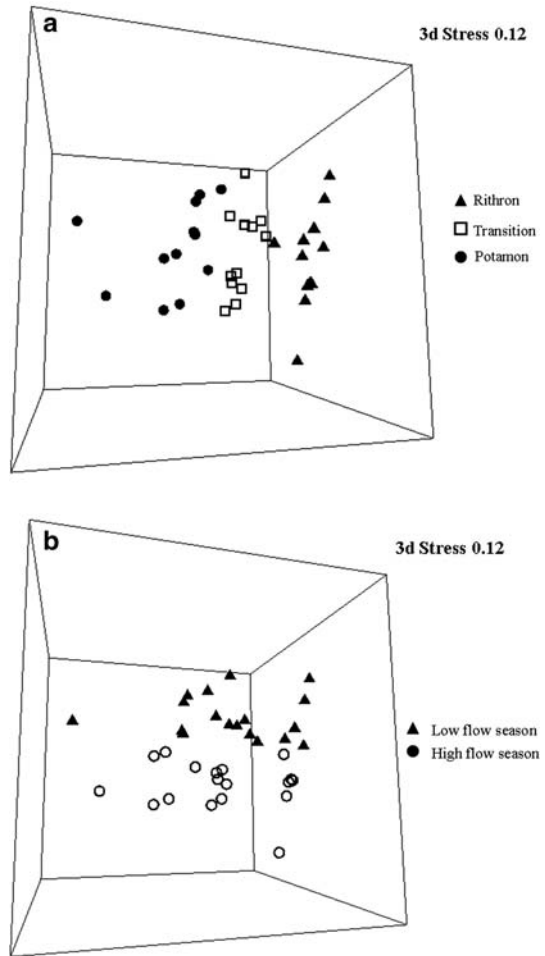


**Fig. 2** Visualization of fish assemblage cluster patterns based on multi-dimensional scaling analysis (MDS) of species relative abundance values. Groups are characterized by their breadth of distribution among river zones. (a) MDS with all species and (b) MDS excluding rare species. TC: *T. chiltoni*; ST: *S. trutta*; OM: *O. mykiss*; TA: *T. areolatus*; NI: *N. inermis*; BA: *B. australis*; CG: *C. galusdae*; BM: *B. maldonadoi*; PI: *P. irwini*; Ga: *G. australis*; PT: *P. trucha*; GM: *G. maculatus*; GH: *G. holbrooki*; CF: *C. facetum*; CC: *C. carassius*; PM: *P. melanops*

Patterns determined by physical variables

The multivariate spatio-temporal relationship of sampling locations based on environmental variables was best explained in three dimensions (three dimensions stress = 0.12; two dimensions stress = 0.19; Fig. 3). Significant differences in physical variables exist among zones (ANOSIM, Global  $R = 0.386$ ,  $p = 0.001$ ) and between seasons (ANOSIM, Global  $R = 0.263$ ,  $p = 0.05$ ). The ANOSIM pairwise test for zones, reveals significant differences among all zones: rithral and transitional zones ( $R = 0.395$ ,  $p = 0.001$ ), rithral and potamal zones ( $R = 0.631$ ,  $p = 0.001$ ), and transitional and potamal zones ( $R = 0.151$ ,  $p = 0.04$ ).

**Fig. 3** Visualization of relationship of sampling locations based on MDS analysis of environmental and habitat variables by (a) zone and (b) season



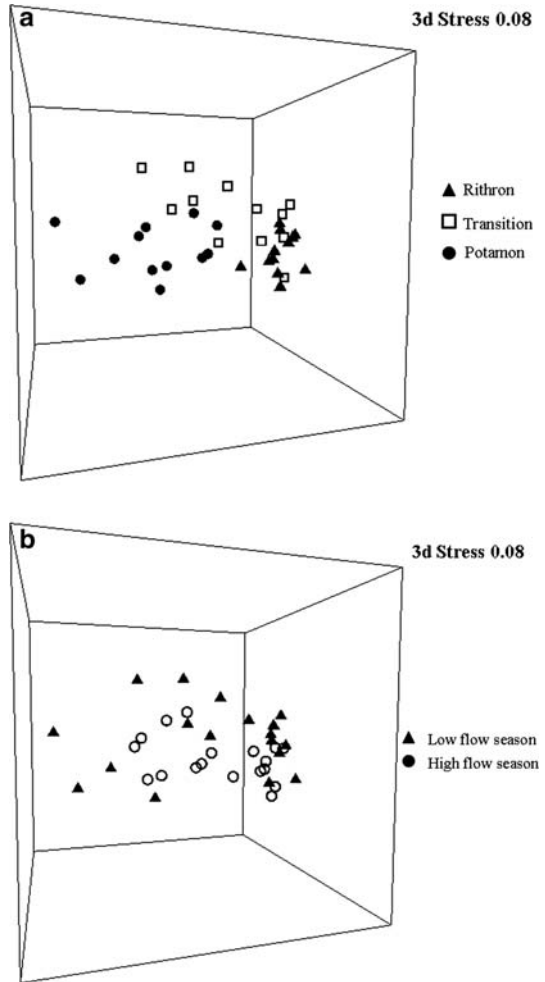
#### Patterns determined by fish assemblages

To be consistent with the visualization derived from environmental variables, we present the MDS results of fish relative abundance in three dimensions (stress value for two dimensions = 0.11, stress value for three dimensions = 0.08). Fish assemblages' structure differs among zones (ANOSIM Global  $R = 0.517$ ,  $p = 0.001$ ), but not between seasons (Global  $R = 0.190$ ,  $p = 0.08$ ; Fig. 4). There are significant differences among all zones (rithron–transition, ANOSIM pairwise test,  $R = 0.281$ ,  $p = 0.001$ ; rithron–potamon,  $R = 0.808$ ,  $p = 0.001$ ; transition–potamon,  $R = 0.460$ ,  $p = 0.001$ ).

#### Relationship between fish assemblage and environmental variables

Because environmental variables were significantly different between seasons, but not fish assemblage structure, we included season as an environmental variable in all the subsets for

**Fig. 4** Visualization of relationship of sampling locations based on MDS analysis of fish relative abundance by (a) zone and (b) season



this analysis (Clarke, personal communication). The best subset of all environmental variables to explain the multidimensional structure of the fish assemblage contained two water quality variables (total nitrogen, and concentration of fecal coliforms) and three habitat structure variables (flow, percent boulders, and elevational gradient), and resulted in a significant Spearman correlation (BioEnv,  $r = 0.692$ ,  $p = 0.01$ ). Season was not selected as a predictive variable.

## Discussion

In the Andalién River system zonation of fish assemblages does not result from replacement of species along environmental gradients, but rather from an accumulation of new species without loss of other species from upstream to down. Widespread species occupy rithral, transitional, and potamal zones (e.g., *T. areolatus*, *N. inermis* and the two introduced trout *O. mykiss* and *S. trutta*), other species occupy only transitional and potamal

zones, and some species are found exclusively in the potamal zone (e.g., native species *Cheirodon galusdae*, and *G. maculatus*, and introduced species *G. holbrooki*, *C. facetum*, and *C. carassius*). Thus, fish assemblages at transitional and rithral locations represent a nested subset of the assemblage found in the potamal zone. This pattern corresponds with that reported for other rivers, in which species richness tends to increase downstream (Schlosser 1982; Ostrand and Wilde 2002) as new species are added. In addition, this pattern of nested subsets of species resulting in longitudinal zonation of the fish assemblage observed in this coastal river coincides with that described in several Andean rivers (Maipo River, Duarte et al. 1971; Itata River, Habit 1994, 1998; Laja River, Ruiz 1996; and the Tolten, Valdivia, Bueno, and Maullin rivers, Campos 1985). There are two rare native species that are exceptions to this pattern being found only in the rithral (*T. chiltoni*) or transitional zones (*P. melanops*) in our samples. However, these species are encountered infrequently and absence in lower locations may be due to sampling error.

Most native Chilean fish species are adapted to habitats with low velocity, fine substratum and high concentrations of organic matter and nutrients, and are thereby restricted to lower zones (Campos et al. 1993a). Thus, low diversity in rithral zones results from a lack of species adapted to this high-energy environment. Campos et al. (1993a) suggested that the low fish species richness in rithral zones of Chilean rivers was a result of glacial coverage of upper parts of Andean drainages during glacial periods, and the lack of species adapted to colonize such areas when they became available at the end of the Pleistocene (Cussac et al. 2004). However, coastal drainages as well, are dominated by rithral habitats, and coastal areas at the Andalién latitude were unaffected by glacial coverage (Villagrán and Armesto 2005). Therefore, lack of species in rithral habitats cannot be entirely due to recent historical effects of glacial periods on availability of such habitats. Rather low species diversity in rithral areas appears to be due to a long-standing lack of evolutionary potential in the native fish fauna.

In Chilean rivers the low number of native species in rithral zones, and their relatively small body size may suggest that introduced stream salmonids (i.e., *O. mykiss*, and *S. trutta*) occupy a somewhat vacant niche in Coastal and Andean rivers. However, introduced salmonids cluster with the widespread species group and thus occupy all zones of the river. In rithral areas, because native species richness is low, they do occupy a somewhat vacant niche, but in other zones, native species occur with similar feeding ecology and habitat requirements (e.g., *P. trucha*), (Macchi et al. 1999). In addition, occupying a “vacant niche” does not imply that there will be no effect on co-occurring species (Soto and Arismendi 2005). On the contrary, introduced species may exert especially strong negative impacts on previously isolated, depauperate fish faunas such as Chilean river fishes (Mills et al. 2004). Further study of the interaction between trout (*O. mykiss* and *S. trutta*) and native species in Chilean rivers is needed to fully understand the effect of introduced species.

As expected, environmental variables differed between seasons. In contrast, fish assemblages did not differ between high and low flow seasons. High flows and the corresponding homogenization of some environmental conditions (e.g., conductivity, and dissolved oxygen, see Table 1) during winter in this study of the Andalién system appeared to cause little change to the pattern of longitudinal zonation of fish species. Overall, the environmental variables that best explained the pattern of fish distribution and abundance were variables that showed strong differences among zones, but changed little with seasons. This suggests that the fish abundance and distribution patterns do not respond to short-term, seasonal variation in the environment. In addition, our results indicate little effect of poor water quality on distribution of native species in the lower zones. Both species richness and abundance of many species are highest in potamal areas, which have the highest levels of

pollution (mainly organic and bacterial pollution). There are two likely reasons that pollution seems to have little noticeable effect. First, most native species appear to be adapted to relatively eutrophic conditions, and the main type of pollution in the Andalién drainage is increased organic matter rather than chemical contaminants. Second, effects of pollution, mainly due to coliform bacteria, may be somewhat localized because of the high flushing rate of the rivers in Chile. In contrast, a recent study in the adjacent Biobío River showed a strong negative effect of chemical contamination and poor water quality on fish assemblages in the middle regions of the river (Habit et al. 2006). Effects of pollution on fish assemblages depend on the specific type of pollution and the characteristics of the fish assemblage.

This study suggests that the key to conserving the diversity of native fish communities in coastal Chilean rivers is in the conservation of potamal regions. There are some notable exceptions such as *Diplomystes* sp. (in Andean rivers), but most of the rare or limited species occur in the potamon. Unfortunately, most protected areas in Chile are in the depauperate (for fish species) headwaters of drainages (the only protected area in the Andalien drainage is in the headwaters of the Nonguén river). These areas are important for water conservation, native forest preservation, terrestrial species preservation, and scenic values. However, protection of only such habitats is clearly inadequate and will not contribute to the conservation of this unique freshwater fish fauna. Managers must consider preservation of potamal regions of Andean and coastal rivers as a high priority.

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