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Rising from the ashes: Changes in salmonid fish assemblages after 30 months of the Puyehue–Cordon Caulle volcanic eruption

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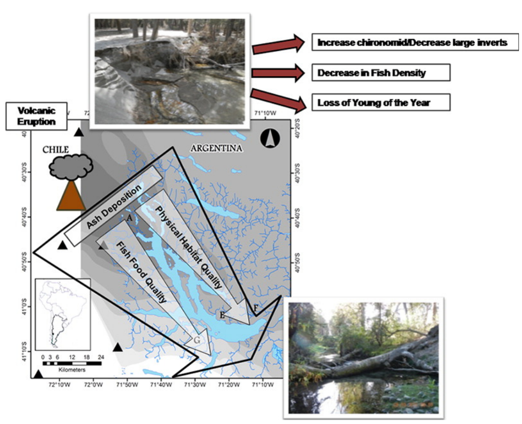
HIGHLIGHTS

- Ash accumulation modified habitat and biota composition nearest to volcano.
- Ash remobilization increased habitat instability in closest streams.
- Fish assemblages were negatively influenced by both habitat and benthic changes.
- Fish assemblages varied in species composition, abundances and recruitment.
- Changes in habitat quality and biotic community still occurring in closest streams.

GRAPHICAL ABSTRACT



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ABSTRACT

Events such as volcanic eruptions may act as disturbance agents modifying the landscape spatial diversity and increasing environmental instability. On June 4, 2011 the Puyehue–Cordon Caulle volcanic complex located on Chile (2236 m.a.s.l., 40° 02′ 24″ S- 70° 14′ 26″ W) experience a rift zone eruption ejecting during the first day 950 million metric tons into the atmosphere. Due to the westerly winds predominance, ash fell differentially upon 24 million ha of Patagonia Argentinean, been thicker deposits accumulated towards the West. In order to analyze changes on stream fish assemblages we studied seven streams 8, 19 and 30 months after the eruption along the ash deposition gradient, and compare those data to pre eruption ones. Habitat features and structure of the benthic macroinvertebrate food base of fish was studied. After the eruption, substantial environmental changes were observed in association with the large amount of ash fallout. In western sites, habitat loss due to

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Disturbance
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ash accumulation, changes in the riparian zone and morphology of the main channels were observed. Turbidity was the water quality variable which reflected the most changes throughout time, with NTU values decreasing sharply from West to East sites. In west sites, increased Chironomid densities were recorded 8 months after the initial eruption as well as low EPT index values. These relationships were reversed in the less affected streams farther away from the volcano. Fish assemblages were greatly influenced both by habitat and macroinvertebrate changes. The eruption brought about an initial sharp decline in fish densities and the almost total loss of young of the year in the most western streams affecting recruitment. This effect diminished rapidly with distance from the emission center. Thirty months after the eruption, environmental changes are still occurring as a consequence of basin wide ash remobilization and transport.

1. Introduction

Disturbances are an important structuring force in the spatial and temporal heterogeneity of populations, communities and ecological processes (Sousa, 1984; White and Pickett, 1985). Events such as fires, storms, volcanic eruptions, floods, among others, may act as disturbance agents modifying landscape diversity. In particular, volcanic impacts may include immediate devastation to surrounding ecosystems as well as from ash fall over broader geographic areas, whose persistent or long-term effects may not be as readily apparent (Ruggieri et al., 2012). Volcanic eruptions are also characterized by having varying effects at different spatial scales (both on biota and habitat) depending on the composition of ejected material, particle size, duration of the event, and intensity (Annen and Wagner, 2003; Martin et al., 2009).

In aquatic systems, instability following volcanic events is often attributed to sedimentation processes, increased sediment loads, turbidity, and channel obliteration or modification, which in turn, alters drainage patterns and water flow (Jowett and Duncan, 1990; Fausch and Bramblett, 1991). Changes due to instability were evident after the 1980 eruption of Mount Saint Helens, through changes in water turbidity, flow, substrate composition and uprooting of aquatic vegetation (Dorava and Milner, 1999; Antos and Zobel, 2005; Bisson et al., 2005). Direct and indirect impacts due to volcanic eruptions may also include changes in both the duration and magnitude of peak flows, water chemistry, and alteration of the availability of both food and cover (Naiman and Bilby, 1998) that may extend through time due to long term sediment delivery processes (Bisson et al., 2005).

Impacted habitats display a wide range of new environmental conditions following eruptions, as well as a broad spectrum of biotic responses at different scales (Turner et al., 1997). Effects on aquatic insects include abrasion of cuticles (Miserendino et al., 2012), mechanical damage (Dorava and Milner, 1999), physiological (Newcomb and Flagg, 1983; Redding et al., 1987) and behavioral changes (Whitman et al., 1982). With respect to freshwater fishes, changes in food availability (Collier, 2002) and macrozoobenthos dynamics had been recorded at the community scale (Dorava and Milner, 1999; Edwards and Sugg, 2005; Miserendino et al., 2012). Increased environmental instability as well as enhanced mortality from decreased resources and altered trophic webs may also impede recolonization in terrestrial and aquatic environments (Del Moral, 1981; Arendt et al., 1999; Del Moral and Grishin, 1999; Miserendino et al., 2012).

In the Andean range of Patagonia (36°–44° S 72° W) glacial processes and more than 50 active volcanoes have had a major role structuring landscape and resident biota (Ruzzante and Rabassa, 2011). Recent eruptions of Hudson (1991) and Chaiten (2008) enabled the first regional studies of responses to volcanic disturbances. Inbar et al. (1995) described the chemical and physical characteristics of Hudson ash fall and its effects on the terrain in the region. Geological, physicochemical characteristics and environmental consequence of the Chaiten eruption were studied by Romero (2011), Durant et al. (2012) and Pallister et al. (2010), respectively. Miserendino et al. (2012) and Brand and Miserendino (2014) reported changes to aquatic macroinvertebrate communities following this eruption. Effects on both terrestrial and aquatic environments have also been studied in relation to the Caviahue and Copahue volcanoes in the region (Geller et al., 2006; Pedrozo et al., 2008; Varekamp et al., 2009).

On June 4th, 2011, the Puyehue–Cordon Caulle volcanic complex located in Chile (2236 m.a.s.l., 40° 02′ 24″ S–70° 14′ 26″ W) experienced a rift zone eruption that remained active until July 2012. The first day produced 950 million metric tons of ejecta and deposited approximately 65 tons per hectare of volcanic materials. Due to prevailing westerly winds, the lighter ash fraction fell differentially over 24 million hectares of Argentine Patagonia (Cremona et al., 2011; Gaitán et al., 2011). Thicker deposits (both in volume and granulometry) accumulated towards the western side of Patagonia and lighter ash fractions deposited on the Patagonian steppe. The fallout affected both terrestrial (Buteler et al., 2011; Masciocchi et al., 2013) and freshwater communities (Modenutti et al., 2013; Wolinski et al., 2013; Lallement et al., 2014). Most related studies have focused on terrestrial steppe environments (Buteler et al., 2011; Elizalde, 2014; Morales et al., 2014; Pirk, 2014), where varying spatial and temporal effects for populations (Cabezas-Cartes et al., 2014), communities (Chaneton et al., 2014) and trophic food webs (Martinez et al., 2013) have been documented. Research on effects of the Puyehue–Cordón–Caulle eruption upon water bodies have thus far been restricted to changes in bacterial and zooplanktonic communities of deep oligotrophic lakes (Modenutti et al., 2013; Wolinski et al., 2013) and benthic organism of mountain streams (Lallement et al., 2014).

Several authors have pointed out the potential importance of geomorphological process, climate changes, species introductions and anthropic impacts may have had in structuring Patagonian fish assemblages (Pascual et al., 2007; Aigo et al., 2008). However, none have investigated the role of eruptions in shaping fish assemblages. In this paper our approach was to analyze habitat modifications and benthic community to establish the pattern of changes in response to the eruption of Puyehue–Cordon–Caulle complex, as context for interpreting the response of fish assemblages in streams surrounding Nahuel Huapi Lake. In addition, we described changes 8, 19 and 30 months after the eruption along the ash deposition gradient, hoping to find a gradient of impacts related to both the distance to the volcano and throughout time.

2. Methodology

2.1. Study area

The Puyehue Cordon–Caulle volcanic complex is located in a region were at least 10 active volcanoes have shown episodic activity throughout historical times (Vigliano et al., 2011) (Fig. 1), which generated ash fallouts affecting the watersheds in the area (Villarosa et al., 2006). In the last century, eruptions were recorded during the years: 1914, 1919, 1921–1922, 1929, 1934, 1960, and 1990 (Lara et al., 2006), and 2011 (Gaitán et al., 2011). Ash fallout from this last eruption affected the Limay watershed located within the Nahuel Huapi National park.

Due to the watershed's size (6980 km^2) and predominant westerly winds, most of the stream basins within the watershed were slightly or not affected by the ash fallout. Nevertheless, the northern sector of the watershed showed an ash deposition gradient, where by a small

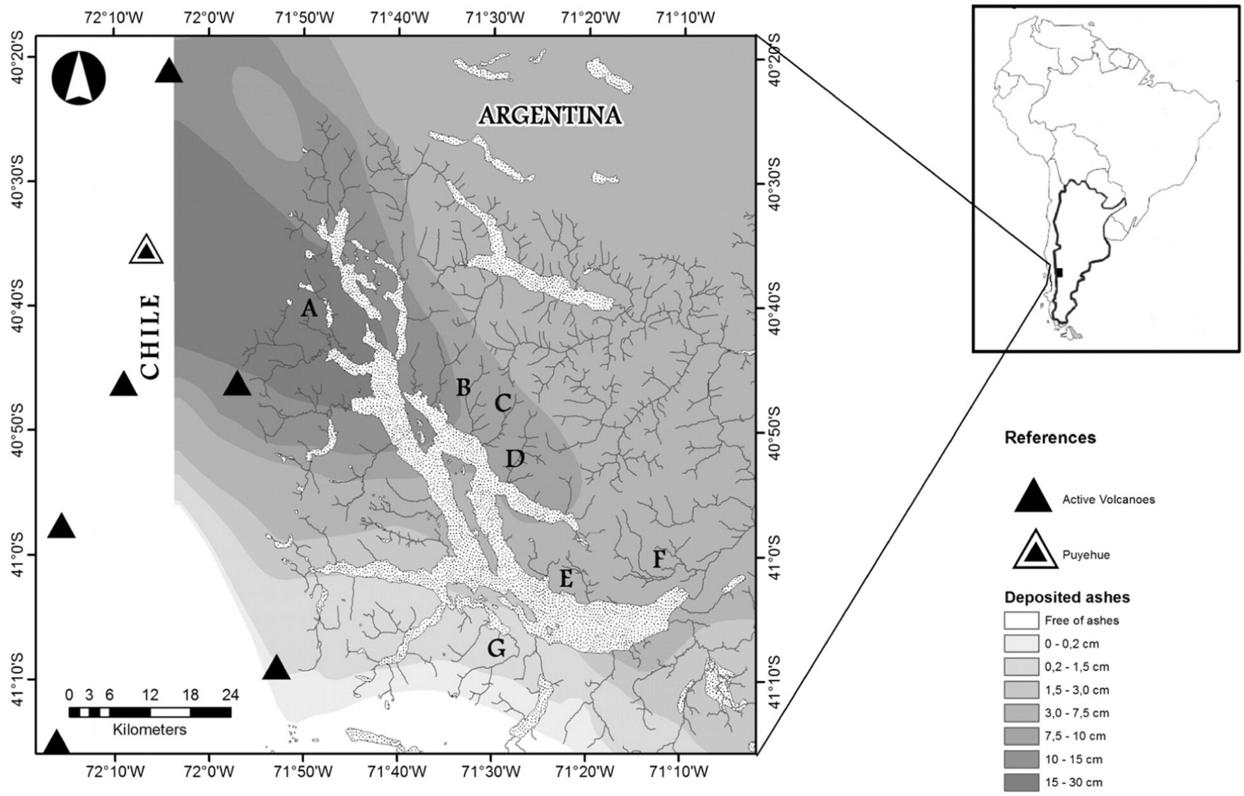

Fig. 1. Sampled streams distribution; A. Acantuco, B. Estacada, C. Ragintuco, D. Huemul, E. Castilla, F. Chacabuco, G. Casa de Piedra, and height of fallen ash (cm) along the west–east gradient (Gaitán et al., 2011).

number of stream basins in the West were heavily affected by a thick ash fallout layer diminishing towards the East. Northwestern streams basins are small in area (average area = 55.04 km^2) with higher slopes (0.13) draining through narrow heavily wooded valleys. Basins to the South and East are bigger (average area = 282.95 km^2) and of lesser slope (0.04) draining wider valleys with mixed woods in the head waters and steppe shrubs on the valley floors lower in the drainage (our data). Water chemistry correspond to very diluted waters, with calcium, bicarbonates and silicates as the major ions present due to the igneous nature of the parent rock (Pedrozo et al., 1993).

Due to the shadow effect of the Andes the area also experiences a strong climatic gradient of autumn and winter precipitation which is heavier in the West (3000 annual mm) diminishing quickly within 60 km to the East (600 annual mm) (Paruelo et al., 1998). This climatic gradient results in mixed *Nothofagus* spp. and "Cypress" (*Austrocedrus chilensis*) forest in the West and the characteristic shrub lands of the Patagonian steppe towards the East.

The watershed is also characterized by a series of large interconnected deep oligotrophic lakes of varying size, to which all streams basins and myriad of small lakes, ponds and wetlands drain (Fig. 1). This accounts for a complex hydrologic network and high connectivity between water bodies. Nahuel Huapi Lake, with an area of 529 km^2 and a maximum depth of 464 m, is the main water collector that serves as the headwater to the Limay River's Atlantic drainage. Six native species and four introduced salmonid species coexist within the watershed (Macchi et al., 1999). Nine of these are found in the major lakes, and have been intensively studied in the past years (Cussac et al., 2012). However, little is known about fish assemblages in rivers and streams. Most of the major research related to rivers in Patagonia refers to landscape or habitat scale distribution of species (Aigo et al., 2008; Pascual et al., 2002, 2007; Barriga et al., 2013). Studies at the level of streams are preliminary, and for the Limay catchment, suggests that fish assemblage composition varies among tributary catchments (Juarez et al., 2014).

2.2. Pre and post- eruption stream selection and characterization

Volcanic eruption disturbances affect abiotic variables and habitat availability (both for fishes and their benthic food resources). In order to evaluate the eruption's impact and changes on abiotic and biotic variables throughout time, availability of pre-eruption data on streams tributaries to the Nahuel Huapi Lake was examined (Fig. 1). Seven streams were chosen because of their location along the ash fallout gradient. Pre-eruption data for the Acantuco, Estacada, Ragintuco, Casa de Piedra and Castilla streams came from exploratory samplings conducted in 2007; those of the Chacabuco stream were obtained from Lippolt (2004). A seventh stream for which no previous data existed, the Huemul, was included in order to better represent the ash fallout gradient. Watershed and reach attributes used to characterize fish sampling sites prior to the eruption were obtained at the time of sampling or generated from 100 m digital elevation models from the NASA Shuttle Radar Topography Mission (SRTM) for topography (Table 1).

Post eruption abiotic and biotic samplings took place 8, 19 and 30 months after the eruption. Sampled reaches, all within the response segments of each stream *sensu* Montgomery and Buffington (1998), were the same ones of 2007 for the first five streams as well as for the Chacabuco in 2004. For the Huemul stream a sampling segment was selected following the same response segment criteria. In all cases for each stream a 100 m reach located in the response segment and at least 200 m away from the stream outlet was chosen to avoid lake influence. In all cases the sampled reach included a succession of pools and riffles, with stable banks and no impacts from human activity.

Table 1
Stream watershed characterization variables of the studied streams along the ash fallout gradient.

Stream	Acantuco	Estacada	Ragintuco	Huemul	Castilla	Chacabuco	Casa de Piedra
Distance to volcano (km)	30.00	56.16	58.94	64.02	83.82	95.43	79.98
Basin area km^2	18.25	48.35	39.74	50.39	25.21	134.93	56.01
Slope of the main channel	42	62	46	42	9	24	41
Stream order	2	3	2	3	3	3	3
Flow rate (m/s)	0.250	0.332	0.405	0.345	0.14	0.22	0.21
Annual mean precipitation (mm)	2733.68	1858.47	1995.03	1959	1572.76	1400	2058.93
Watershed orientation	W–E	N–S	N–S	N–S	N–S	W–E	S–W
Ash initially accumulated (cm)	15–30	7.5–10	7.5–10	7.5–10	3.0–5.0	3.0–5.0	0.5–1.5

For each sampling date and location we measured and recorded water Nephelometric Turbidity Units (NTU), temperature (°C), conductivity (μS/cm) adjusted by temperature, total dissolved solids (TDS, mg/l) and pH. These data were later compared to the available pre-eruption data (2007 unpublished data and Lippolt, 2004) for six of the seven streams sampled. For each reach, we also estimated the percent coverage of ash particles (<2 mm) in a 2 m wide transect oriented perpendicular to stream flow based on visual assessment of substrate particle size in the same riffle where macroinvertebrate fauna were later sampled.

2.3. Macroinvertebrates characterization

Benthic macroinvertebrates are considered, both in the short and long term, good indicators of local or landscape scale environmental changes (Bonada et al., 2006; Minshall, 1988). In the study region they comprise the main components of fish diet (Macchi et al., 1999; Oscoz et al., 2005; Buria et al., 2007). Because no data existed prior to the eruption on benthic macroinvertebrates, we studied their availability throughout time (i.e. 8, 19 and 30 months after the eruption) within the seven study streams.

For each sampled reach, five random samples were taken along transects set perpendicular to the stream flow and located over a riffle using a 30 × 30 cm y 200 μm mesh Surber net. Samples were preserved in 80% ethyl alcohol and macroinvertebrates later separated in the laboratory under a binocular microscope (10×). All specimens were identified to the family level, except for the Hyrudinea and Oligochaeta classes.

2.4. Fish assemblages characterization

Characterization of pre-eruption fish assemblages in tributaries of the Nahuel Huapi Lake was accomplished by comparing fish count data from snorkel surveys of the 5 streams sampled in 2007 and electroshocking catches from the Chacabuco stream (Lippolt, 2004). The snorkel surveys were necessitated by extremely low pre-eruption conductivity of the western streams. By contrast, increased turbidity of the streams due to fallen volcanic ash transport made it impossible to use snorkeling counts in the post-eruption samplings, which were done instead using an electroshocker (Pick-i Fish A400, CENITEC) adjusting voltage to stream conductivity values. In order to be able to compare pre and post eruption fish densities estimated as catch per unit of effort per 100 m^2 (CPUE), we fitted a curve between catch data concurrently obtained with the two methodologies in 7 reaches in the 2007 exploratory samplings. Because catch data did not comply with the normality assumption they were $\log_{10}$ transformed. We thus obtained the model equation: $y = 0.779\ x + 0.027$ ($R^2 = 0.72$) by which fish species snorkeling counts (x) for each stream were allocated to electroshocking CPUE data (y) (Fig. 2).

In post-eruption samples fish were collected with dip nets by electroshocking the selected segments working upstream using settings between 500 and 1000 V. All caught fish were identified to the species level. Electroshocking efficiency was estimated by comparing electrofishing catch numbers with snorkeling count numbers. Pre-eruption electrofishing density data for the Chacabuco stream were taken from Lippolt, 2004 and included in the analysis. In order to evaluate the volcanic impact on total and specific recruitment to the streams young of the year specimens (YOY), defined as those less than 60 mm of standard length, were also identified and counted.

2.5. Data analysis

2.5.1. Environment characterization
Gross channel and riparian environmental changes were evaluated through in situ observation and pre- and post-eruption visual assessment of publicly available Google Earth satellite imagery (2009–2014). Possible differences between pre- and post-eruption water quality environmental data sets and amount of deposited ash were analyzed using the non-parametric Kruskal–Wallis test.

2.5.2. Macroinvertebrate community
Total density of organism per date and site were estimated, as well as that of Chironomidae specimens, a family considered characteristic of environments with high sediment loads (Fesl, 2002; De Haas et al., 2006). The Ephemeroptera, Plecoptera and Trichoptera index (EPT) was also estimated because their orders are considered to be susceptible to contaminants (Carrera and Fierro, 2001).

2.5.3. Fish assemblages
Total and per species densities were estimated as catch per unit of effort per 100 m^2 (CPUE). Density comparison between sampling dates were performed using Before - After models following Wiens and Parker, 1995 and Murphy et al., 1997. For density analysis we grouped streams into high (i.e. Acantuco, Estacada and Ragintuco streams) and low (i.e. Castilla, Casa de Piedra, Chacabuco streams) impact levels in terms of ash deposition levels in upslope catchments. To compare change in densities we excluded young of the year caught by electrofishing because this life stage was not included on the pre-eruption stream count data. We then transformed all catch per unit of effort data into their natural logs, adding a constant of 0.167 to all density estimates to avoid calculating a ln of zero (Mosteller and Tukey, 1977). For each species we calculated the change in densities that

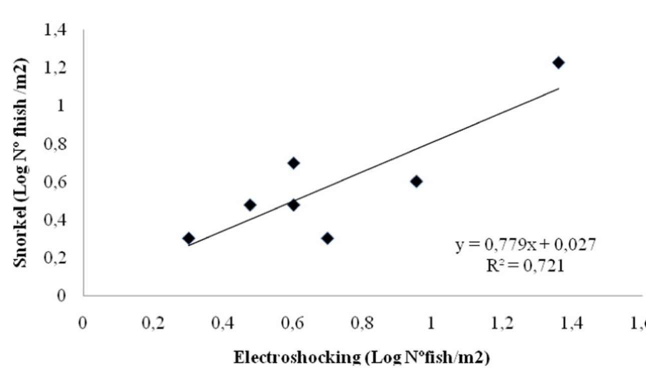

Fig. 2. Fitted curve between Total electroshocking catch data (number of fishes/m^2) and Snorkel counts (number of fishes/m^2) done in 7 reaches in the 2007 exploratory samplings.

occurred in each stream for each sampling date after the eruption relative to the pre-eruption baseline as:

$$\Delta_{im} = \ln \text{density (post} - \text{eruption)} - \ln(\text{pre} - \text{eruption}),$$

where i = species and m = post-eruption sampling month.

For each species and ash deposition level, a Mann–Whitney U test was used to evaluate whether there was a significant change in densities between pre- and post-sampling dates (i.e. 8, 19 and 30 months after the eruption). Overall abundance was considered to have changed (decrease – increase) across all streams of the two impact levels for any sampling if the mean change in densities was significantly lower or higher than zero, to aid in the interpretation of the results we considered α levels of 0.1 and 0.05.

Variations in recruitment through the post-eruption samplings were analyzed based on YOY densities (YOY number per 100 m^2). Possible relationships between environmental variables (TDS, Conductivity, Temperature, NTU, pH and ash particles %) and fish catches (total, species specific and YOY catches) were investigated through correlation analysis.

3. Results

3.1. Pre and post-eruption stream characterization

In general terms all streams were characterized by fast, oxygen saturated, slightly alkaline and cold waters, with very low conductivity and turbidity values (Table 2). Streams towards the western extreme of the climatic gradient tended to have higher flows, bottoms with higher proportions of boulders and parent rock and lower TDS values. Streams located towards the East generally had lower flows, and higher proportions of cobbles, gravel, sand and fines covering the bottom as well as higher TDS values.

According to the ash deposition map of Gaitán et al. (2011) the Puyehue Cordon Caulle eruption provoked differential ash fallout over the Limay river basin (Fig. 1). These differences were brought about both by volume and particle size deposited. Of the seven studied streams, the Acantuco was the closest stream to the volcano (30 km to the East) having also, its main flow axis following a northwest to southeast direction coincidental with the ash fallout gradient and with a broader upper catchment converging downstream. This stream was the only one that showed extensive channel modifications due to ash deposition (15–30 cm) and channel clogging by transported ash and logs in lahars type processes. Sediment transport problems led to obliteration of the historic channel and the opening of new ones through the surrounding riparian area (Fig. 3a). As a result, extensive tree deaths were evident 19 months later in woodland flooded areas (Fig. 3b). The Estacada, Ragintuco and Huemul watersheds (7.5–10 cm ash deposition) have predominantly north to south orientations perpendicular to the main axis of the ash deposition gradient (Fig. 1). The first two catchments have steep longitudinal profiles in their lower reaches, whereas the latter one has a concave profile at its confluence with Nahuel Huapi Lake (our data). These three streams did not show extensive channel modifications, even though resuspension and transport of ash sediments was observed during the study period. The Castilla and Chacabuco (1.5–3.0 cm ash deposition) with lower longitudinal gradients and, respectively, north to south and west to east orientation did not experience channel modifications. This was also the case for the

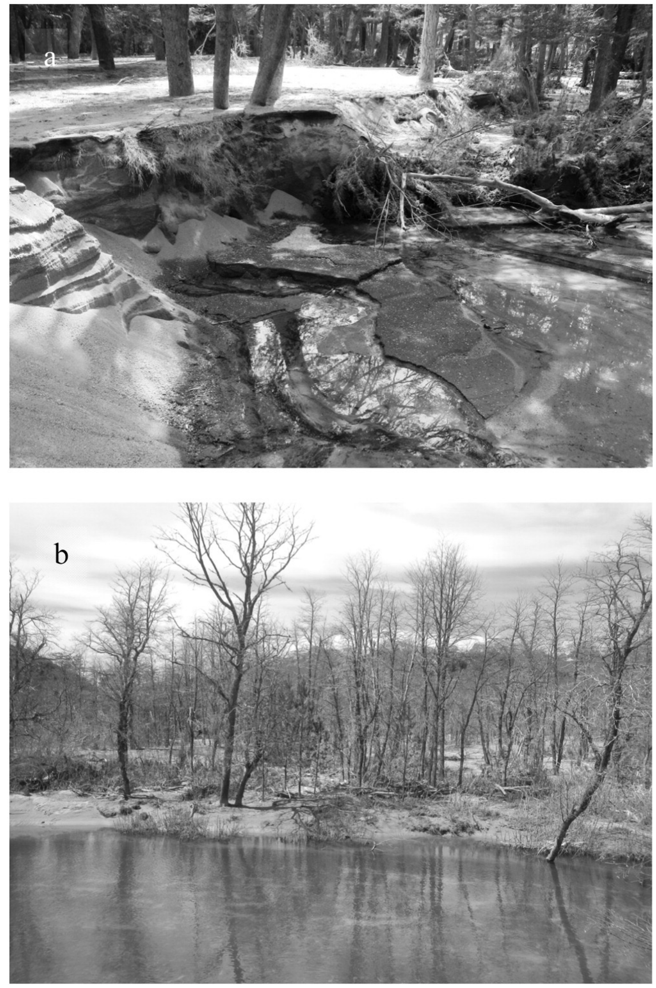

Fig. 3. a. Acantuco main channel deactivation due to the ash deposition, October 2011. b. Downstream Acantuco with dead riparian vegetation 30 months after the Puyehue eruption.

Table 2
Pre (2007) and post-eruption (2012–2013) percentage values of ash particles (<2 mm) in stream beds and water quality parameter values. TDS: Total Dissolve Solids, NTU: Nephelometric Turbidity Units. ND: no data available, Pre; pre-eruption, 8, 19 and 30 months after the eruption.

	Ash (%)				Conductivity (μS/cm)				pH				TDS (mg/l)				NTU			
Stream	Pre	8	19	30	Pre	8	19	30	Pre	8	19	30	Pre	8	19	30	Pre	8	19	30
Acantuco	8	96	90	60	44.4	74.9	65.7	39.4	7.63	8.35	7.83	7.78	31.9	53.3	41.5	28.0	ND	99.5	4.1	5.1
Estacada	13	60	10	10	46.9	46.4	61.7	55.7	7.37	8.20	8.13	7.87	30.0	23.5	43.2	39.3	ND	44.8	1.1	0. 9
Ragintuco	8	60	15	5	45.3[a]	54.2	56.4	47.7	7.50[a]	7.94	8.13	7.93	20.0	40.4	40.0	23.8	ND	34.4	2.4	2.4
Huemul	ND	40	39	2	55.1[a]	60.6	60.5	63.1	6.85[a]	8.40	7.99	7.75	ND	30.5	43.0	44.9	ND	4.5	2.7	1.3
Castilla	5	10	1	1	75.9	87.8	92.6	89.3	7.52	8.45	8.40	8.04	53.4	62.3	65.8	63.3	ND	1.2	0.7	1.5
Chacabuco	1	1	1	1	90.5[b]	125.8	135.5	126.2	6.90	8.21	7.85	7.88	65.8	90.8	96.8	82.3	ND	3.4	2.5	0.4
Casa de Piedra	2	10	5	2	51.3[a]	64.0	53.3	27.3	7.69	8.10	8.06	7.8	30.0	45.4	38.0	19.5	ND	0.6	0.2	0.1
Average	6	39.6	23.0	11.6	58.5	73.4	75.1	64.1	7.5	8.2	8.1	7.9	38.5	49.4	52.6	43.0	0.01–2[c]	26.9	1.9	1.7

[a] Pedrozo et al. (1993).
[b] Lippolt (2004).
[c] Range of values taken from 7 streams in the area not affected by the volcanic eruption.

Casa de Piedra watershed (0.2–1.5 cm ash deposition), which has a largely southwest to northeast orientation.

Eight months after the eruption, pH values were significantly higher (KW; n = 21, $X^2 = 19.33$; $p < 0.0001$) than those recorded in pre-eruption dates. Conductivity and TDS, although also somewhat higher than those recorded in pre-eruption dates, did not differ significantly (Table 2). In general, all variables declined in subsequent samples. Despite a lack pre-eruption turbidity, this variable appeared the most responsive, with NTU values decreasing sharply across space from west to east and through time from 8 to 19 months after the initial eruption. By month 30, all turbidity values approximated the normal range for unaffected streams (0.01–2 NTU). Variation in accumulated ash particles (<2 mm) over stream substrates varied with time (Table 2). The Acantuco stream, extensively modified by ash deposition, retained great amounts of ash on its substrate, covering 96% of the examined area even 30 months after the initial eruption. Eight months after the eruption, Ragintuco, Estacada and Huemul channels had ash accumulations covering between 60% and 40% of the study reaches, gradually decreasing to <5%. Ash accumulation in Castilla, Chacabuco and Casa de Piedra streams did not produce extensive deposits and never exceeded 10% of the study reaches. Resuspension, transport, and resedimentation processes were observed during the study period, especially in the western streams.

3.2. Macroinvertebrate characterization

A total of 1518 specimens belonging to 31 macroinvertebrate taxa were collected in all seven streams. The eight months samples of the Chacabuco and Casa de Piedra streams were lost due to bad preservation. Densities by stream and date varied extensively (Fig. 4), with overall macroinvertebrate densities higher on the first sampling date (8 months) after the eruption for all streams, yet decreasing sharply in subsequent samplings.

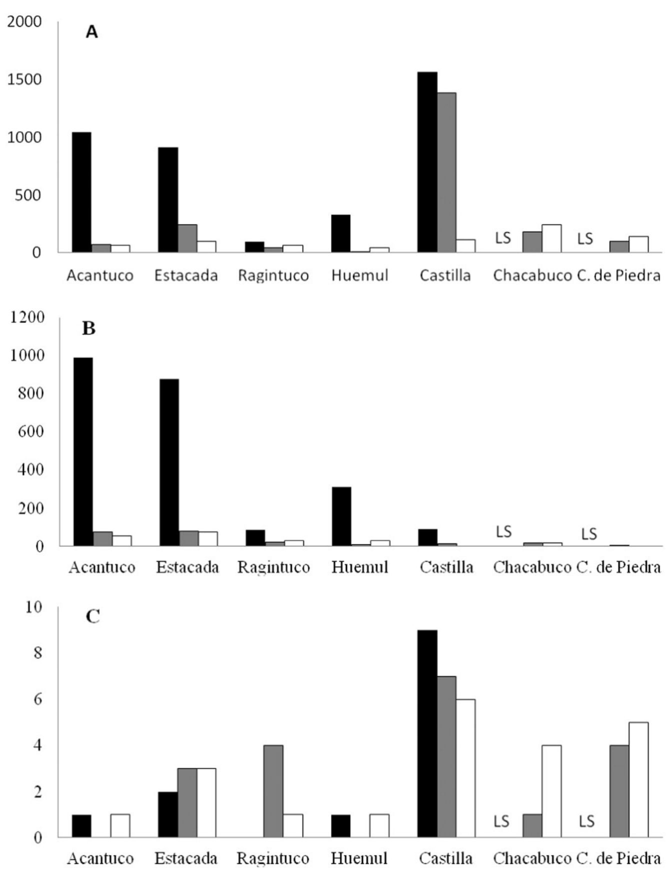

Fig. 4. Density of benthic macroinvertebrate organisms per m^2. A) Overall macroinvertebrate densities, B) Chironomid densities and C) EPT index; 8 (black bars), 19 (gray bars) and 30 (white bars) months after the initial eruption. LS: lost samples.

Chironomid densities were extremely high 8 months after the eruption in streams nearest to the volcano, with high turbidity and ash values, varying between 33% and 100% of total macroinvertebrate densities. Chironomid densities decreased sharply in subsequent samples, especially for streams farther away from the eruption center (Castilla, Chacabuco and Casa de Piedra, Fig. 4B). In streams nearest to the volcano, the EPT index was initially low after the eruption, and increased as time passed (Fig. 4C). The Castilla stream appears to not have been substantially affected by the eruption, showing high overall macroinvertebrate densities and EPT index values as well as low Chironomid densities (Fig. 4). In these more eastern streams, overall macroinvertebrate values and EPT values were related to high conductivity and TDS parameters (Fig. 4).

3.3. Fish assemblages characterization

Examination of pre- and post-eruption catch data (Table 3) showed that only three salmonid species were present on the sampled streams, *Oncorhynchus mykiss* (rainbow trout), *Salmo trutta* (brown trout) and *Salvelinus fontinalis* (brook trout). No native fish were caught in any of the sampled streams and dates. The baseline fish assemblage characterization showed that assemblages varied between catchments, and were composed of one, two, or three species. Pre-eruption total fish densities per stream showed two distinctive patterns; the three western-most streams had lower densities than the three eastern-most streams (Fig. 4). The most widely distributed species was rainbow trout, which dominated all streams except for Chacabuco and Castilla, where brown trout was the most abundant species. Across all streams, brown and brook trout were the second and least abundant, respectively.

Environmental changes caused by the eruption had a clear impact on stream fish assemblages, affecting both species composition and fish densities (Table 3, Fig. 5). The three western and heavily impacted streams showed a sharp decrease in total fish densities 8 month following the eruption. Of these three, only Acantuco and Estacada showed signs of increasing fish densities after 19 and 30 months. Ragintuco

Table 3
Total and young of the year fish densities (number of fishes per 100 m^2) in sampled streams before and after 8, 19 and 30 months of the eruption. RBT = rainbow trout, BRT = brown trout, BKT = brook trout, ND = no data available.

	Pre/post	Total densities			YOY density		
		RBT	BRT	BKT	RBT	BRT	BKT
Acantuco	Pre	4.14	2.48	0.29	ND	ND	ND
	8	0.3	0.15	0	0	0	0
	19	5.2	0.52	0.43	2.43	0.09	0
	30	2.29	0.53	0.04	0.49	0.22	0
Estacada	Pre	1.82	0.21	0.07	ND	ND	ND
	8	0.36	0	0	0	0	0
	19	4.32	0	1.32	3.18	0	0
	30	2.95	0	0	0.34	0	0
Ragintuco	Pre	9.53	0	0	ND	ND	ND
	8	0.15	0	0	0.15	0	0
	19	0.53	0	0	0.27	0	0
	30	1.69	0	0	0.12	0	0
Castilla	Pre	3.87	17.17	0.17	ND	ND	ND
	8	15.67	3.38	0	10.45	2	0
	19	41.91	16.91	0	30.88	6.62	0
	30	14.62	45.18	0	9.3	10.63	0
Chacabuco	Pre	0.62	6	0	ND	ND	ND
	8	14.02	26.52	0	7.95	11.36	0
	19	7.82	23.15	0	2.28	8.15	0
	30	13.33	53.33	0	7.92	27.5	0
Casa de Piedra	Pre	12.1	0	0.63	ND	ND	ND
	8	5.05	0	0.07	3.94	0	0
	19	17.71	0	0.76	9.87	0	0.25
	30	10.31	0	1.09	3.75	0	0.16
Huemul	Pre	ND	ND	ND	ND	ND	ND
	8	0.27	0	0	0	0	0
	19	2.46	0	0	1.68	0	0
	30	7.12	0	0	4.15	0	0

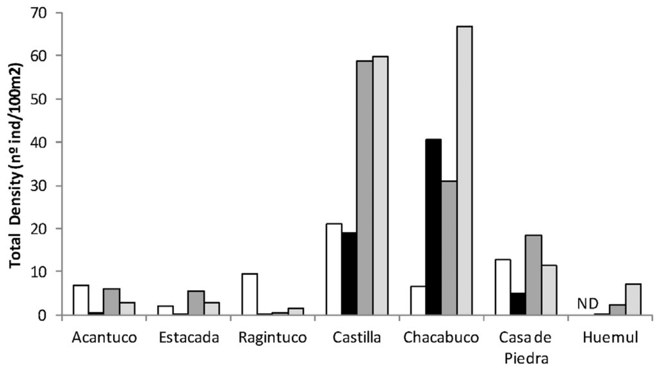

Fig. 5. Pre (white bars) and post-eruption total fish density in the seven sampled streams at 8 months: Black bars, 19 months: dark gray bars, 30 months: light gray bars. ND: no data available.

remained below the pre-eruption densities (Fig. 5). By contrast, the less impacted streams to the east did not follow a similar trend. Castilla showed a decrease in brown trout densities after 8 months, with densities increasing 19 and 30 months later. However, the opposite trend was observed for rainbow trout. For all sampling dates, the Chacabuco showed higher densities than those of pre-eruption. Casa de Piedra showed only slight decreases in fish densities followed by a return to pre-eruption levels. Even though, we did not have pre-eruption data for the Huemul stream, located in-between the high and low impacted streams, we observed post eruption samples with very low initial values that gradually increased in numbers as time passed (Table 3) consistent with an impact and recovery process.

After the eruption rainbow trout remained the overall most abundant species surveyed; with the exception of the Castilla and Chacabuco, which by month 30 had brown trout dominated assemblages. Percent variation in fish densities per species between periods for the streams highly impacted by fallen ash (i.e. Acantuco, Estacada and Ragintuco) showed a decrease in the overall response of fish density difference values (Table 4). Rainbow trout was the only species that by month 19 seemed to have recovered within highly impacted streams. The overall decrease of brown trout density values was significant for all considered sample periods. Overall values of brook trout showed a highly variable oscillation in values. In contrast, streams with lower ash impacts did not show significant changes in density (Table 4).

Overall salmonid and rainbow trout catches decreased sharply in relation to the amount of ash particles on stream bottoms (salmonid total densities: Spearman, $N = 21$, $R = -0.49$, $P = 0.025$; rainbow trout densities: Spearman, $N = 21$, $R = -0.48$, $P = 0.029$), (Fig. 6A and B). Brown and brook trout followed the same pattern despite the fact that

Table 4
Percentage differences, results of Mann–Whitney U test and overall responses of relative changes in fish densities, in streams grouped by impact level as high ($n = 3$) and low ($n = 3$), in terms of fallen ash. A negative or positive percentage difference, indicates that densities were lower or higher during a particular post eruption sampling period. Significance codes for Mann–Whitney U test: $^{*} \leq 0.1$; $^{**} \leq 0.05$.

Species	Pre-eruption density	Percentage change			Overall response
		After8	After19	After30	
High impact level streams					
Onchorynchus mykiss	5.16	−92.09**	−72.97	−51.46	Decrease
Salmo trutta	0.90	−62.43*	−53.60*	−56.94*	Decrease
Salvelinus fontinalis	0.12	−36.38*	101.62*	−31.66*	Decrease
Low impact level streams					
Onchorynchus mykiss	5.53	3.26	135.90	74.15	None
Salmo trutta	7.67	−39.47	14.05	103.61	None
Salvelinus fontinalis	0.06	−47.18	−25.06	−11.97	None

they did not yield significant correlations (Fig. 6). We also found that densities appeared to increase for total salmonids and *S. trutta* in relation to conductivity (Salmonid total densities: Spearman, $N = 21$, $R = 0.74$, $P = 0.0001$; Brown trout densities: Spearman, $N = 21$, $R = 0.77$, $P = 0.0001$; Fig. 6).

Analysis of post-eruption recruitment data showed that YOY catches decreased with the amount of fallen ash. In the three streams closest to the volcano (Acantuco, Estacada and Huemul) YOY of the three salmonid species were completely absent until 19 months after the initial eruption (Fig. 7, Table 3). Ragintuco, Castilla, Chacabuco and Casa de Piedra streams had YOY on all sampling dates. Of these streams, Ragintuco, the closest of the remaining four streams to the volcano, showed very low YOY density values. Meanwhile Castilla, Chacabuco and Casa de Piedra showed higher numbers of YOY, varying between sampling dates with no discernible pattern. Brown trout YOY did not recruit in the Acantuco 8 months after the eruption, but YOY specimens were present in later samples. No brown trout YOY were observed in Estacada, Ragintuco, Huemul and Casa de Piedra, whereas Castilla and Chacabuco showed YOY specimens on all sampling dates (Fig. 7). Brook trout YOY specimens were absent for all streams and dates except for the Casa de Piedra, where they were caught in the final two samples (Table 3).

4. Discussion

The Puyehue Cordón–Caulle eruption of June 4, 2011 modified watersheds characteristics and stream habitats by shear accumulation of ash fallout particles. Impact variations between watersheds were related to distance to the emission point and the amount and granulometry of fallout ash particles (Gaitán et al., 2011; Wilson et al., 2012), as well as by watershed characteristics such as shape, orientation and gradient, which appeared to influence local patterns of ash accumulation. Massive ash fallout led to decreased physical habitat quality for both, macroinvertebrates and fish, in terms of changes in channel morphology, riparian vegetation, substrate, and habitat availability. As a result, decrease in habitat and food base quality likely was responsible for the decrease in fish densities.

Due to its proximity to the volcano as well as its overall geomorphology and general orientation, the Acantuco catchment funneled large quantities of volcanic ash to the sampling reach causing extensive channel modifications. At intermediate and lower ranges of ash deposition, such changes progressed from reduced to negligible, not only because of the lower amounts of ash deposited at greater distances, but also because of distinct catchment morphologies.

Remobilization of deposited sediments, continuous prolonged volcanic emission (6 months), westerly winds and overland transport by surface runoff may have also prolonged stream instability. This was reflected by the variation in physico-chemical parameters recorded across sampling dates (Table 2). Lagged effects such as those described here have also been reported for other volcanic events in the region (Martin et al., 2009; Miserendino et al., 2012; Brand and Miserendino, 2014) and in other parts of the world (Dorava and Milner, 1999). Prolonged perturbations can have consequences for both, stream geometry and hydrologic processes, as well as habitat availability and quality, which in turn can lead to modifications in community composition and trophic structure.

Decreases in the transport of suspended ash particles brought about by sedimentation, cessation of volcanic emissions, and channel evacuation, resulted in decreased turbidity in later post-eruption samples. Short-duration turbidity spikes and sedimentation processes unrelated to volcanic events are a common occurrence in mountainous streams, triggered by precipitation or snowmelt runoff events. Detrimental effects upon biota are dependent on both the duration of disturbance and the nature of transported particles (Shaw and Richardson, 2001; Ramezani et al., 2014). Streams that were more impacted by the eruption differed most from pre-eruption conditions; however fish population's densities were similar to pre-eruption after 30 months, suggesting that the disturbance created a shift from the pre-existing

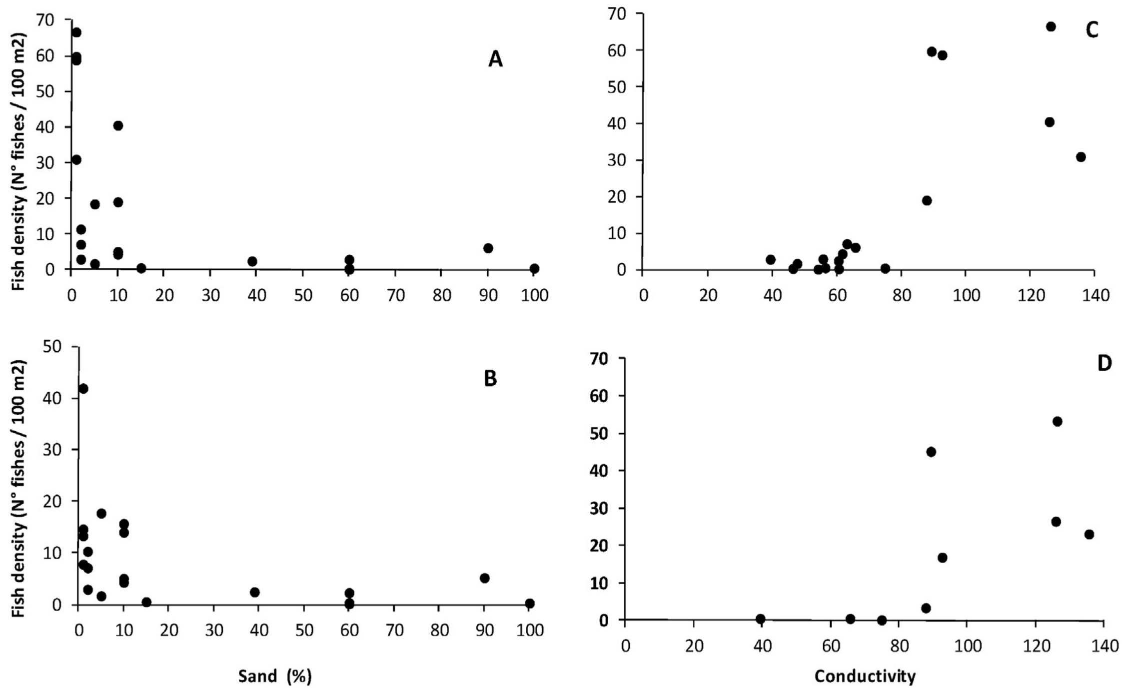

Fig. 6. Post eruption Total fish (A) and rainbow trout (B) densities (n° fishes/100 m2) according to the amount of Sand (%). Total fish (C) and brown trout (D) densities (number of fishes/100 m^2) according to conductivity values (μS/cm).

equilibrium recovering towards previous densities as conditions improved.

Removing impact factors may lead a system to return to its original state or to find a new one, and such changes should be reflected in changes to biotic diversity and abundance (Del Moral, 1981; Brand and Miserendino, 2014; Elizalde, 2014). Lack of pre-eruption benthic data does not allow us to determine whether the macroinvertebrate prey base returned to its original composition or density. Yet, contrary to our initial expectations, the highest overall macroinvertebrate densities were found in streams nearest to the volcano in our earliest post-eruption sample. However, the density pattern was almost entirely attributable to an anomalous dominance of Chironomids, group which has been mentioned as an indicator of bad habitat conditions (Carrera and Fierro, 2001; Edwards and Sugg, 2005).

Although Chironomids are typically absent from tephra layers of volcanic events around the world (Araneda et al., 2007), they were also found to be the dominant taxa in recovery phases in lakes and streams affected by Mt. Saint Helens eruption (Anderson and Wisseman, 1987; Edwards and Sugg, 2005). Araneda et al. (2007) found a similar pattern of post-eruption dominance for an Andean Chilean Lake. Thus, although ash deposition may obliterate Chironomids, they appear to recover rapidly after deposition is over, perhaps taking advantage of the organic material trapped in new sediments (Massaferro et al., 2005). Therefore, we suggest that 8 months after the eruption, Chironomids that find suitable conditions in accumulated fine sediments proliferated in streams with the most ash deposition. As fallout was evacuated, conditions in the studied streams resulted in the replacement of Chironomids by other taxa.

Members of the orders Ephemeroptera, Plecoptera, and Trichoptera (EPT) are considered generally susceptible to sedimentation (Harrison et al., 2007). Increases in EPT densities may indicate improving environmental conditions as sediments are washed away. Recolonization leading to increased EPT index scores could be brought about either from nearby population sources or from reaches that managed to avoid serious impacts as reported for other eruptions (Hawkins and Sedell, 1990). Stream recovery with more benthic macroinvertebrates taxa and numbers would improve potential for successful recolonization by fish species that depend on macroinvertebrates for food. Generally high macroinvertebrate densities and EPT index values coupled with low Chironomid numbers for the eastern study streams indicates that ash fallout did not have a marked effect on their benthic fauna.

Pre and post-post eruption fish assemblages of sampled stream were formed only by salmonids. The absence of native fish in these streams is in accordance with data from 22 other streams of the Nahuel Huapi basin (unpublished data). Whether this is due solely to mountain stream characteristics or to the presence of salmons in them or the combination of both factors requires further investigation. Post-eruption salmonid assemblage structure varied from those known prior to the eruption in terms of species composition and overall abundances (Table 3). Fish density responses could be separated into two groups: (1) the less impacted streams towards the east with increase in fish densities in some of them and (2) highly impacted streams towards the west that experienced a sharp decrease in densities 8 months after the eruption and increases later on.

Higher overall catches after the eruption could be due to higher electroshocking efficiency related to higher conductivity values (Reynolds, 1996) in relation to the iron content in the ash fallout. However, in some of the most western streams catches increased or did not vary widely through time despite decreases in conductivity. The less impacted eastern streams where ash fallout was lower and conductivities are normally higher than those on the western streams, showed noticeable density increases (e.g. Castilla and Chacabuco) throughout time. Such increases cannot be attributed sensu stricto to a recovery process, because there is no evidence that the eruption disrupted habitat availability, fish assemblages, or their food base. Furthermore, the continued presence of YOY just 8 months after the eruption indicates that recruitment was unaffected. Instead, increased fish densities might reflect an increase in stream production from nutrient-rich ash deposition. If so, low level inputs from eruptions may result in benefits to fish further increasing the differential impacts depending on the spatial arrangement of streams relative to the eruption event. However we cannot ascertain that this is our case, because it takes time for increased production to pass through the food chain up to the fish. We believe it to be more likely that allochthonous organic matter and normal processes provided for a better food base for immigrants and recruitment. Other auto-correlated factors associated with the eastern most catchments may

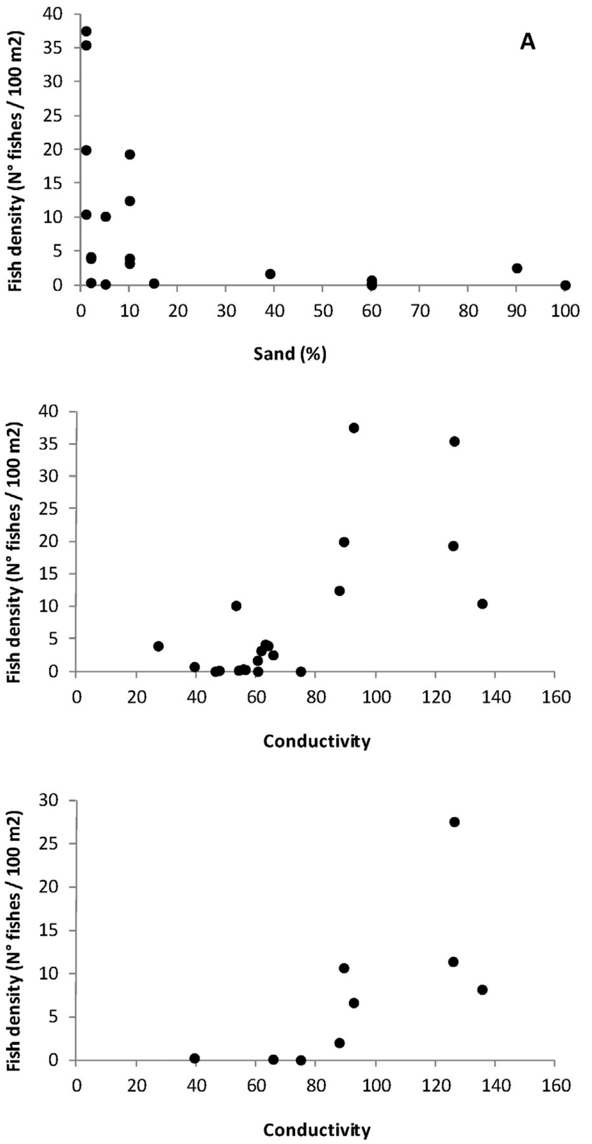

Fig. 7. Post-eruption Total YOY densities (A) (number of fishes/100 m^2) according to the amount of sand (%). Total YOY (B) and brown trout YOY densities (C) (number of fishes/100 m^2) according to conductivity values (μS/cm).

also explain differences in fish density such as low gradient channels that originate in wetlands and flow more slowly through wider valleys and thus receive greater sun exposure and achieve higher annual average temperatures.

Within the most impacted western streams, ash-choked channels from the initial ash deposition likely killed a large proportion of fish by mechanical means, as revealed by lack of catches and visual inspections four months after the eruption. Moreover, surviving individuals would also be subject to stress from gill abrasion (Newcomb and Flagg, 1983), changes in homing behavior (Whitman et al., 1982) and impaired vision leading to reduced predation success (Shaw and Richardson, 2001).

Due to the temporal extent of ash emissions (June–November 2011) and each species' life history, differential effects in relation to spawning success and survival of the different life stages could be expected. In North Andean Patagonia, juvenile salmonids remain in the streams where they hatched for 1 to 3 years (unpublished data). For each salmonid species, spawning success in the studied streams after the volcanic eruption was probably related to their spawning times. Brown trout in the region migrate into streams for spawning by mid May (Rechencq, 2003); brook trout migrates between May and June (Báez, 2007), whereas rainbow trout spawn from June to December (*our data*). Therefore it is highly probable that, in the most affected streams, deposition from the initial emission (June 4, 2011) destroyed all eggs and developing embryos of both fall spawning species in most of the study streams. This would occur due to physical and chemical disruption of interstitial spaces within spawning redds by burial (Sternecker and Geist, 2010). Even in less impacted streams, both brown and brook trout hatchlings would have to successfully emerge from the ash covered spawning redds and then survive in ash laden waters (Sternecker and Geist, 2010). By contrast, due to the spawning period of rainbow trout it is probable that many individuals of this species had not yet spawned by the initial eruption. Therefore, they could have avoided the affected streams, migrating mainly into watersheds that exhibited slightly or no impacts (75% of the watersheds in the region). Assuming that spawning was possible, hatchling and juvenile survival may have been impacted by reductions in benthic biomass due to ash accumulation.

The observed increase in both numbers and species of fish 19 months after the volcanic event indicate a shift towards more suitable conditions for all three species favoring stream recolonization. Because we analyzed variation in stream response within local reaches, we cannot ascertain the origin of fish recolonization. Due to the physical extent of ash deposition in streams closest to the emission point, it seems unlikely that local refugia would provide the main source of individuals for fish recolonization. The primary source for most recolonization processes of disturbed streams is far more likely from the Nahuel Huapi Lake, consistent with a highly connected network of lakes and their tributaries acting as common pool for all three salmonid species. Within this system, rainbow trout is the most abundant and widely dispersed salmonid. Brown trout is the second most common species, but more commonly found in the east, whereas brook trout is more common towards the western portions of the watershed (Pascual et al., 2002; Macchi et al., 2008, this study). Consistent with our observations, extant patterns of fish density alone would make it more likely that rainbow trout would be the first species to recolonize affected streams, followed by brown trout and then brook trout.

Species plasticity might also explain patterns of recolonization, as species with greater tolerance to adverse conditions such as turbidity and suspended sediments should have an advantage over species with narrower tolerance ranges (Southwood, 1977). According to Rowe et al. (2003) rainbow trout juvenile can feed normally at turbidity levels as high as 160 NTU, meanwhile both brown and brook trout's alter their feeding pattern with high turbidity levels (Raleigh, 1982; Stuart-Smith et al., 2004). In this sense rainbow trout, the most widely distributed salmonid in the world would be considered quite plastic (Fausch, 2008; Halverson, 2010). Therefore, considering rainbow trout plasticity and its dominance throughout the Nahuel Huapi watershed, it is hardly surprising that this species appears to have recolonized affected streams more rapidly than brown or brook trout. Variation in numbers of fish and species present at different sites along the study period would then be the result, for each site, of the interplay throughout time of habitat changes in terms of refuge and food availability, propagule pressure, species plasticity and species specific interactions.

5. Conclusions

Ejected material, particle size, duration, and intensity are widely acknowledged as important factors determining the effects of volcanic eruptions (Turner et al., 1997; Annen and Wagner, 2003; Martin et al., 2009). Ecological consequences of eruptions may extend in time over broad geographic areas (Bisson et al., 2005; Ruggieri et al., 2012). In this paper we analyzed the effects of ash deposition upon fish assemblages in streams, in relation to concurrent habitat and macroinvertebrate benthic community changes. Ash deposition generated varying types and degrees of impact that included abiotic and biotic factors at different spatial and temporal scales. The observed macroinvertebrate taxa replacement throughout time, especially in the more affected streams, seem to indicate an initial high impact on the macroinvertebrate fauna and a gradual replacement as streams returned towards pre-eruption conditions. Less impacted eastern streams were not altered enough by deposited ash to disrupt fish populations and other processes were likely responsible for observed changes in fish densities. In the highly impacted western streams, environmental consequences of ash deposition and subsequent transport persist 30 months after the initial eruption of the Puyehue Cordon–Caulle. In general, evidence suggests that recovery is well underway, but whether this recovery returns affected streams to preexisting conditions or whether the channels and their fish assemblages establish a new dynamic equilibrium remains to be seen. However, it does seem reasonable to conclude that salmonids are effectively recolonizing affected streams from the common pool that is the Nahuel Huapi watershed, making re-stocking unnecessary.

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