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The susceptibility of cladocerans in North Andean Patagonian lakes to volcanic ashes

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SUMMARY

1. Explosive volcanic eruptions are one of the few natural phenomena that can produce global catastrophic effects. On 4 June 2011, an eruption in the Puyehue volcanic complex (40°35′S, 72°06′W, Chile) discharged massive amounts of ash and pumice into the surrounding landscape in Argentina (North Andean Patagonia). The ejected material affected nearby aquatic environments, producing an increase in total suspended solids.
2. We combined field data and laboratory experiment data to determine the effect of the volcanic ashes suspended in the water column on cladoceran populations.
3. During the summer of 2011–2012 (6 months after the eruption), zooplankton populations in these lakes decreased, mainly due to the disappearance of cladocerans. This decrease in zooplankton was not caused by food shortage; chlorophyll *a* concentrations in the lakes were higher than in previous years or in the following season, and no change in phytoplankton size was observed. By the following summer (2013), 18 months after the eruption, a recovery of cladoceran populations was observed, with a concomitant decrease in total suspended solids.
4. We performed a life-table experiment, examining *Daphnia commutata* survival and fecundity at a series of ash concentrations. Ash concentrations of 2, 3, 5 and 8 mg L^{-1} negatively affected survival and fecundity. Populations exposed to 8 mg L^{-1} of ash cannot persist; these organisms fail to produce offspring because they die before reaching reproductive age.
5. We conclude that the disappearance of cladocerans was due to the presence of ash. As the sedimentation process occurs, ash concentrations decrease, favouring population recovery, as observed the following summer. When the lakes recovered their original transparency with low total suspended solids values, the cladoceran populations also returned to their historical abundances.
6. Previous data on other explosive volcanic eruptions and the present data indicate that immediately after ash fall, the zooplankton suffer reduced abundance, particularly of non-selective filter feeders such as daphnids. However, recovery of zooplankton population growth can be expected within a few years.

Keywords: *Ceriodaphnia*, *Daphnia*, demography, filter feeders, lakes, volcanic eruption

Introduction

Explosive volcanic eruptions cause intense ash fallout, and this ash is deposited in terrestrial and aquatic environments. Hugely explosive volcanic eruptions are one of the few natural phenomena that can produce global catastrophic effects (Self, 2006). Volcanic eruptions may have contrasting effects on biota, since ashes can differentially supply elements that may promote primary producers growth (Frogner, Gíslason & Óskarsson, 2001; Hamme *et al*., 2010; Lin *et al*., 2011), or ashes may result in heavy shading and reduce photosynthesis (Hirano, Kiyota & Aiga, 1995) or plant growth rates (Battipaglia *et al*., 2007). In addition, stratospheric aerosols of volcanic origin modulate the incident radiation and significantly affect the timing of ice break-up of high-altitude lakes (Livingstone, 1997). The June 2011 eruption of Puyehue-Cordón Caulle (40°30′S, 72°07′W, Chile) discharged massive amounts of ash and pumice into the surrounding landscape in Chile and Argentina.

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The Puyehue-Cordón Caulle volcanic complex consists mainly of basaltic to andesitic lava that formed two broad shield volcanoes between 314 and 70 kya and has become much more explosive over time Singer *et al.* (2008). In particular, the ash cloud from the 2011 Puyehue eruption completely circled the globe in the Southern Hemisphere (Klüser, Erbertseder & Meyer-Arnek, 2013). The major components of the ashes from the Puyehue-Caulle eruption were O, Si, Al, Fe, Na and K (Buteler *et al.*, 2011; Caneiro *et al.*, 2011).

The type and magnitude of effects of ash in aquatic environments depend on both its chemical and physical properties. Studies of the impacts of eruptions on aquatic ecosystems have shown that ash-borne elements such as phosphorus and iron may act as fertilisers (Frogner *et al.*, 2001; Hamme *et al.*, 2010; Lin *et al.*, 2011), increasing the concentrations of chlorophyll (a proxy of phytoplankton biomass) (Hamme *et al.*, 2010; Lin *et al.*, 2011). As a consequence of the 2011 Puyehue eruption, lakes in the area received these volcanic ash particles, increasing the suspended solid concentration values from about 0.5 mg L^{-1} before the eruption to 14 mg L^{-1} immediately afterwards, and concentrations of about 5 mg L^{-1} persisted for several months (Modenutti *et al.*, in press-a). North Patagonian Andean lakes (40°–42°S) are extremely transparent environments and typically have very low nutrient concentrations (Morris *et al.*, 1995; Markert *et al.*, 1997; Balseiro *et al.*, 2007). Because volcanic ash precipitation from the 2011 event came from the north-west (Chile), there was a gradient in the impact of these ashes, with western-most lakes receiving more particles (Modenutti *et al.*, in press-a).

This increase in inorganic particles may affect cladocerans because suspended ash particles, which are within the range of their food spectrum, can be ingested by filter-feeding zooplankton. Several authors (DeMott, 1982, 1986) have shown that cladoceran daphnids feed non-selectively on various mixtures of algae and flavoured and untreated microspheres across a wide range of food types and sizes, while other zooplankton, such as copepods, are more selective (Balseiro, Modenutti & Queimaliños, 2001).

Cladocerans are considered key organisms in aquatic ecosystems because they connect upper trophic levels with lower levels (McQueen *et al.*, 1989). Cladoceran survival and development are influenced by many features of their natural environments, such as predator activity (Gliwicz, 1986a; Vanni, 1987), food quality (Lynch, 1989; Boersma & Vijverberg, 1996; Brett, Müller-Navarra & Park, 2000), ultraviolet radiation (Siebeck *et al.*, 1994) and other factors. In particular, cladocerans of the genus *Daphnia* exert a significant grazing pressure on different components of micro- and nanophytoplankton assemblages due to their ability to filter a large size spectrum (1–30 μm) of food particles (Geller & Müller, 1981; Jürgens, 1994). Earlier studies indicated that *Daphnia* can ingest suspended clay particles during feeding (Gliwicz, 1986b), and an increase in the concentration of inorganic particles (above 50 mg L^{-1}) reduces fecundity, survival and fitness (McCabe & O'Brien, 1983; Kirk & Gilbert, 1990). Therefore, the appearance of ash particles due to volcanic eruption may be expected to cause a decrease in cladoceran populations as a consequence of a decrease in food quality.

Based on the limited ability of daphnids to avoid the ingestion of small inorganic particles, we assumed that cladocerans, and in particular daphnids, would ingest volcanic ash when it was mixed with food (nanoflagellates). In addition, volcanic ash has a crystalline structure (Caneiro *et al.*, 2011) that might have an abrasive effect on the gut, affecting the digestive process. Therefore, our main hypothesis was that ash particles would negatively affect cladoceran populations at the concentrations observed in natural environments after volcanic eruptions. To assess this hypothesis, we performed a field study in three affected lakes (Espejo, Correntoso and Nahuel Huapi), comparing the abundance and composition of crustacean zooplankton populations in the summer immediately following the eruption (6 months) with that in the subsequent summer (18 months). In addition, because population parameters provide only basic information about the reasons for success or failure of a zooplankton species in a community (Urabe & Sterner, 2001), we further analysed the survival and fecundity of a cladoceran of the genus *Daphnia* (*D. commutata*) under a gradient of ash concentration, using laboratory life-table experiments.

Methods

Field Study

We studied three lakes: Lakes Espejo (maximum depth, $Z_{\max}$ 245 m), Nahuel Huapi ($Z_{\max}$ 464 m) and Correntoso ($Z_{\max}$ >120 m) located between 40°00′S and 40°26′ S and 71°33′W and 71°42′W at 764–800 masl in the North Andean Patagonian region (Argentina) (Fig. 1), corresponding to the glacial lakes district of the Southern Andes (Iriondo, 1989). The lakes are deep, very clear and with low nutrient concentrations and exhibit a warm, monomictic thermal regime, with stable thermal stratification during late spring and summer (Callieri

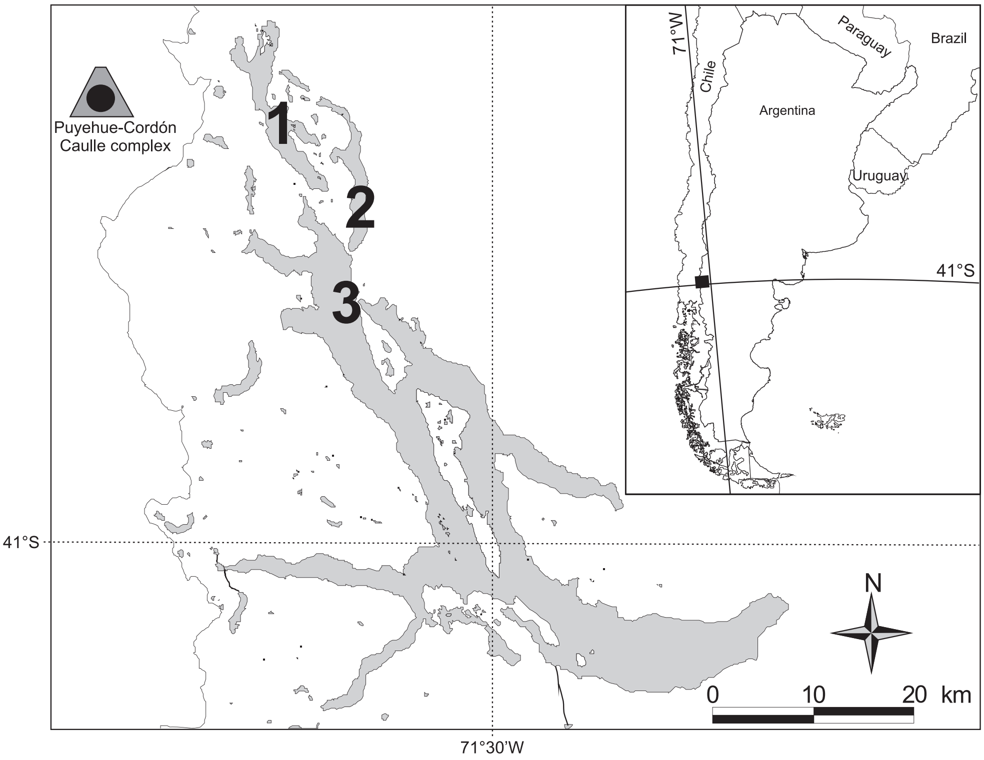

Fig. 1 Map of the sampling area and the location of the Puyehue-Cordón Caulle volcanic complex. (1) Lake Espejo, (2) Lake Correntoso and (3) Lake Nahuel Huapi.

et al., 2007; Modenutti *et al.*, in press-a). The climate in the region is temperate and cool with an annual precipitation of 1500 mm and a mean annual temperature of 8.7 °C (Paruelo *et al.*, 1998).

We compared data from summer surveys in three different periods: pre-eruption, eruption and post-eruption. Each of the three lakes was sampled during summers 2002–2007 (January–February), spring–summer 2011–2012 (October–March) after the initial event in June 2011, which was still during the eruption period, and in summer 2013 (January–February), when the eruption was completely finished. In each summer period, sampling was performed at approximately two-week intervals. Samples were obtained from a central sampling point located at the deepest part of each lake basin. All samplings were carried out at mid-day, 1 h before astronomic noon. Water samples of 12 L were obtained with a Schindler–Patalas trap from depths of 0, 10, 20, 30 and 45 m. These were transferred to 5 L polypropylene containers (HCl washed), which were kept in the dark and thermally isolated, and immediately carried to the laboratory for nutrient and chlorophyll *a* concentration determination. In the field, direct measurements of pH and conductivity were carried out with a Hanna 8424 and YSI 85, and 250 mL of lake water was immediately fixed with acid Lugol's solution for phytoplankton examination. Zooplankton from each lake were sampled with vertical tows from 50 m to the surface with a Bongo net (55 μm mesh size) with a closing mechanism.

In the laboratory, direct measurements of chlorophyll *a* concentration were carried out by filtering 500 mL of the lake water from each depth onto GF/F Whatman filters (Whatman, Maidstone, UK). Chlorophyll *a* concentration was determined fluorometrically with a Turner AU10 Fluorometer (Turner Designs, Sunnyvale, CA, U.S.A.) by extraction with hot 90% ethanol (Nusch, 1980). Phytoplankton quantification was performed according to the Utermöhl technique with an inverted microscope (Olympus IX70, Olympus, Japan)) using 50 mL Utermöhl chambers. Chlorophyll *a* was considered a measure of food quantity for zooplankton, while phytoplankton quantification was performed to evaluate the food size spectrum. Crustacean zooplankton were examined under a stereomicroscope in 5 mL Bogorov chambers.

The release of phosphorus from the ash material was measured in the laboratory, from ashes that were freshly collected in Bariloche, Argentina, during the initial ash fall of June 2011. We suspended 1 g of ash in 50 mL of MilliQ™ water for 1 h and then measured soluble reactive phosphorus (SRP) using the molybdate reaction (APHA, 2005).

Life-table experiments

A clonal population of *D. commutata* was established from a single female isolated from the population of Lake Mascardi (same lake district and very close to the affected lakes, Nahuel Huapi National Park, Patagonia, Argentina) (Balseiro *et al.*, 2008). The clone was maintained under laboratory conditions (16 ± 1 °C and 85 μmol photons m^{-2} s^{-1} with a 14 : 10 light/dark photoperiod) and fed with *Chlamydomonas reinhardtii* for at least 50 generations prior to starting the experiment. We chose this species for our experiments because during the eruption, we did not observe the presence of cladocerans in the affected lakes and we have this species in a laboratory culture.

Egg-carrying females were carefully sorted under a dissecting microscope and placed in beakers with a freshwater culture medium named COMBO (Kilham *et al.*, 1998) and food (*C. reinhardtii*). On the following day, all neonates (<24 h old) were separated and transferred to 50 mL Erlenmeyer ground glass stoppers. Each flask contained four neonates, and all the flasks were filled with COMBO and *C. reinhardtii* as food (1 mg L^{-1} carbon) and one of six ash concentrations: 0 (Control), 1, 2, 3, 5 and 8 mg L^{-1}. Each treatment group included 15 replicates. The ash concentrations used in the experiment corresponded to the concentrations observed in different impacted lakes after the eruption (Modenutti *et al.*, in press-a). The flasks were completely filled with medium to decrease the risk that the neonates would be caught in the surface tension. The carbon concentrations in the *C. reinhardtii* cultures were estimated based on *in vivo* fluorescence on a Turner AU10 fluorometer against direct carbon measurements on a Thermo Finnigan EA1112 CHN elemental analyser (Thermo Fisher, Cambridge, U.K.).

To prepare the ash for the experiments, 10 g of sterile ash (combusted at 450 °C for 1 h) was placed in 1000 mL sterile distilled water and stirred for 1 h, then allowed to settle for 1 h (to eliminate large particles). After that, we took just the supernatant 750 mL. Total suspended solid (TSS) concentrations were measured to obtain the concentration of this stock suspension, and then, dilutions were made to reach the desired concentrations. TSS was obtained by filtering a known volume of the supernatant suspended ashes in previously weighed glass fibre filters (GF/F Whatman filters). The filters were dried at 60 °C for 48 h and then weighed again. The difference between the weight and the filtered volume was used to calculate TSS. Throughout the experiment, whenever new ash was added, the suspended ash preparation was sterilised again at 1.5 atmospheres for 20 min. Subsequent analyses confirmed that sterilization did not change the chemical composition of ashes.

The experiments were run in a walk-in incubator at 16 ± 1 °C and 85 μmol photons m^{-2} s^{-1} with a 14 : 10 light/dark photoperiod. Animals were transferred to fresh medium every 4 days using a clean 5-mL glass pipette. Survival and egg production were checked every 24 h under a stereomicroscope. Live and dead individuals were photographed by taking lateral images to determine whether the gut had been affected by the ash. We compared the gut of individuals reared with and without ashes (increasing concentrations), and we were able to distinguish normal guts (filled with algae – green coloured foregut and midgut) from two levels of damaged gut: (i) gut filled with ashes no visible algae (black coloured gut), sometimes with an empty foregut indicating a reduction in feeding and (ii) broken gut with disappearance of the gut wall (Fig. 2). The experiments were continued for 35 days (maximum) or until all the organisms of the treatment had died.

Data analysis

All data were analysed in Sigma Plot.12 (Systat Software Inc., San Jose, CA, USA). The Kaplan–Meier (Gehan–Breslow) method (Kaplan & Meier, 1958) and all Pairwise Multiple Comparison Procedures (Holm–Sidak method) were used for survival analysis. The Gehan–Breslow test gives more weight to early deaths (Pyke & Thompson, 1986), which were frequently observed in our experiment. Friedman RM ANOVA on rankings method and all Pairwise Multiple Comparison Procedures (Tukey's Test) were used to analyse the fecundity data.

ANOVA (One Way Analysis of Variance) was used to evaluate R_0 and m_x, while T_c was analysed with a Kruskal–Wallis ANOVA on rankings and all Pairwise Multiple Comparison Procedures (Tukey's Test).

To obtain the TSS values, we followed Strickland & Parsons (1968).

The life-table parameters calculated were as follows:

x = Age in days.
n_x = Number of individuals at age x.
l_x = Survival probability from age 0 to age x (n_x/n_0).
m_x = Average fecundity per female at age x.
R_0 = Net reproductive rate: $R_0 = \sum l_x m_x$
T_c = Cohort generation time: $T_c = \frac{\sum x l_x m_x}{R_0}$

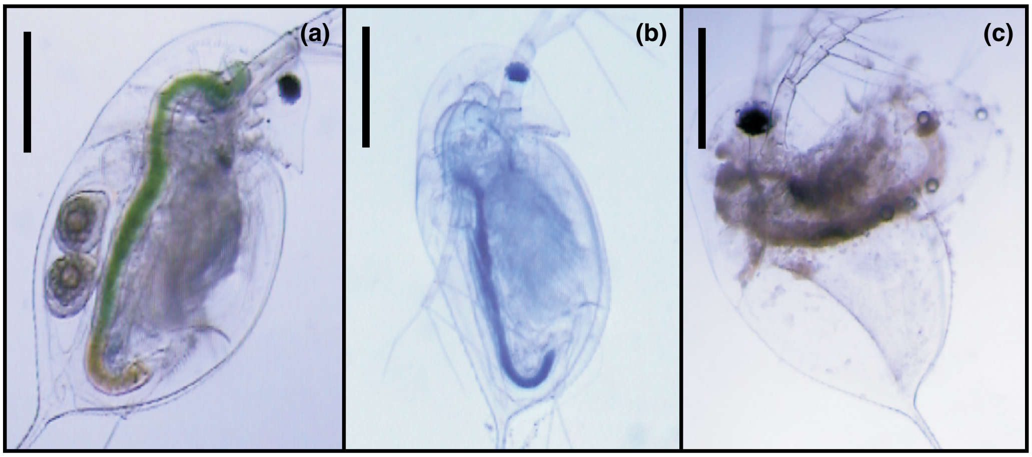

Fig. 2 Photographs taken 10 days into the *Daphnia commutata* experiment. (a) Control (no ash) group, (b) 2 mg L^{-1} treatment group (note the change in the gut due to the presence of the ash and the empty foregut) and (c) 5 mg L^{-1} treatment group (note the damage in the gut). Black bars: 0.5 mm.

Results

Field study

During the summer of 2011–2012 (5–8 months after the eruption), TSS in lakes affected by the eruption was consistently above 1 mg L^{-1}, with values ranging from 1 to 8 mg L^{-1} Fig. 3(a–c). Lake Espejo was the most affected by ash input, with higher TSS values than Nahuel Huapi Lake and Correntoso Lake (Fig. 3a). Conductivity and pH did not vary in the different studied periods, remaining between 45 and 60 μS cm^{-1} and 7–7.3, respectively. Based on the phosphorus content of the volcanic material measured in the laboratory, each gram of pumice contained 90 μg of P.

Chlorophyll *a* concentrations during the eruption period were between 1.5 and 2.5 μg L^{-1}, which are up to 2- to 3-fold higher than previous data Fig. 3(d–f). The phytoplankton samples were dominated by nanoflagellates (*Chrysochromulina parva* (Haptophyceae); average cell length = 3.78 ± 0.5 μm) and Cryptophyceae, particularly *Rhodomonas lacustris* (average cell length = 8.7 ± 0.7 μm).

In the summer of 2013, 18 months after the eruption, concentrations of total suspended solids and chlorophyll *a* had decreased compared with the previous summers, and these values were very similar to those recorded prior to the eruption (Fig. 3). Phytoplankton composition was always dominated by the same species of nanoflagellates.

In the summer of 2011–2012, immediately after the eruption event, zooplankton declined, with an absence of cladocerans in the 50 m vertical tows. However, by the following summer (2013), the zooplankton population had recovered, and cladoceran daphnids, with *Ceriodaphnia dubia* as the dominant species, were again observed as in pre-eruption summers (Fig. 4). Due to the ash fall, water transparency decreased and the deep chlorophyll maxima moved upwards (Modenutti *et al.*, in press-a, in press-b). Although it is possible that cladocerans were not captured in the 50-m vertical tows because of the transparency decrease and upward movement of phytoplankton, it seems unlikely that the cladocerans would have moved downwards compared with clear water summers (cladocerans between 30–40 m) (E. Balseiro, personal observation).

Life-table experiments

While feeding, *D. commutata* effectively captured ash particles that, depending on the concentration, filled the gut tract in a few days (Fig. 2). Consequently, ingestion of algae was affected as evidenced by empty foreguts, indicating that feeding had ceased (Fig. 2b). Moreover, in the higher concentration treatments, the gut wall was not detectable in the photographs (Fig. 2c), indicating irreversible damage and subsequent death.

In the survival experiments, about 50% of individuals in the treatments with 0 mg L^{-1} (Control) or 1 mg L^{-1} ash survived for up to 35 days, whereas no animal in any of the other treatments survived for longer than 31 days (Fig. 5). We observed significant differences in survival among the treatments (Breslow–Gehan, Log-Rank = 212.8, d.f. = 5, $P < 0.001$). In the 8 mg L^{-1} ash group, all exposed individuals died within 5 days, while in the 2, 3 and 5 mg L^{-1} ash groups, individuals survived for up to 30 days. Nevertheless, we recorded a

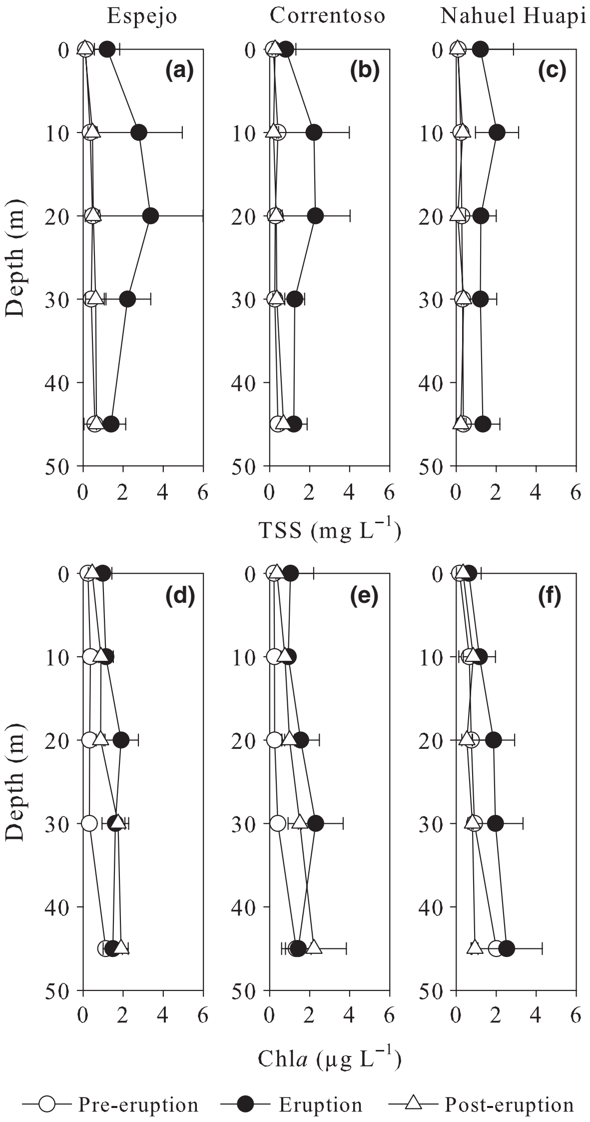

Fig. 3 Vertical profiles of total suspended solids (TSS) (a, b and c) and total chlorophyll *a* (Chl*a*) (d, e and f) in the pre-eruption summers (2002–2007), during the eruption (2011–2012) and 18 months later (summer 2013). (a) and (d) Lake Espejo, (b) and (e) Lake Correntoso and (c) and (f) Lake Nahuel Huapi. Error bars represent 1 standard error.

larger number of early deaths in the 3 and 5 mg L^{-1} groups. Accordingly, the *a posteriori* Holm–Sidak method indicated that there were four homogeneous groups, one represented by the Control (0 mg L^{-1}) and 1 mg L^{-1} treatments, the second by the 2 mg L^{-1} treatment, the third group by the 3 and 5 mg L^{-1} treatments and the fourth group by the 8 mg L^{-1} treatment (Fig. 5).

During the experiment, all individuals reproduced by parthenogenesis, except for one case in the 1 mg L^{-1} treatment group, in which one diapause egg (ephippium) was observed. The 8 mg L^{-1} treatment group was not analysed due to the early deaths of all the individuals before reproduction took place. The highest number of eggs per clutch and the largest number of eggs produced during the experiment were observed in the 1 mg L^{-1} treatment group (Fig. 6), while the Control (no ash) group produced a slightly lower number of total eggs (Fig. 6). The other three treatments showed much lower numbers of eggs and almost no new eggs after 25 days (Fig. 6).

The gross reproductive rate (total number of eggs produced by a female = Σm_x) was also found to differ significantly among treatments (ANOVA $F_{4,10}$=9.23, P = 0.002). The *a posteriori* Tukey test indicated two homogeneous groups (Fig. 7a).

Net reproductive rate (R_0), which simultaneously considers the survival and average fecundity of the population, was significantly different among treatments (ANOVA $F_{4,10}$ = 17.10, P < 0.001). The *a posteriori* Tukey test revealed two homogeneous groups. The first included the 1 mg L^{-1} ash treatment, which had the highest value (R_0 = 18.967), and the Control treatment (R_0 = 14.473) (Fig. 7b). The other group included all the other analysed treatments (2, 3 and 5 mg L^{-1}) (Fig. 7b).

The cohort generation time is defined as the average time between two successive generations in a population with discrete reproductive periods and without overlapping generations. Analysis (ANOVA $F_{4.10}$ = 2.99, P = 0.07) showed no differences in this parameter among treatments, indicating that the onset and duration of the reproductive period was not particularly affected by the ashes (Fig. 7c).

Discussion

The deposition of volcanic ash in the lakes affected by the eruption caused a remarkable decrease in cladoceran populations. Previous data on the zooplankton composition of Lakes Espejo, Correntoso and Nahuel Huapi show *Ceriodaphnia dubia* as the dominant cladoceran, followed by *Bosmina chilensis* (Balseiro *et al.*, 2007). However, data collected during the summer of 2011–2012 revealed an absence of cladoceran populations and a decrease in all zooplankton compared with previous years and compared with data collected 18 months after the eruption. Chlorophyll *a* concentrations were similar to or higher than those from the pre-eruption period (Callieri *et al.*, 2007; Modenutti *et al.*, in press-a) and in the summer of 2013. Phytoplankton compositions in both summers were dominated by nanoflagellates, which are the main resource for zooplankton in Andean Patagonian lakes (Balseiro, Modenutti & Queimalinos, 1992; Balseiro *et al.*, 2001). Because the food resources in the summer of

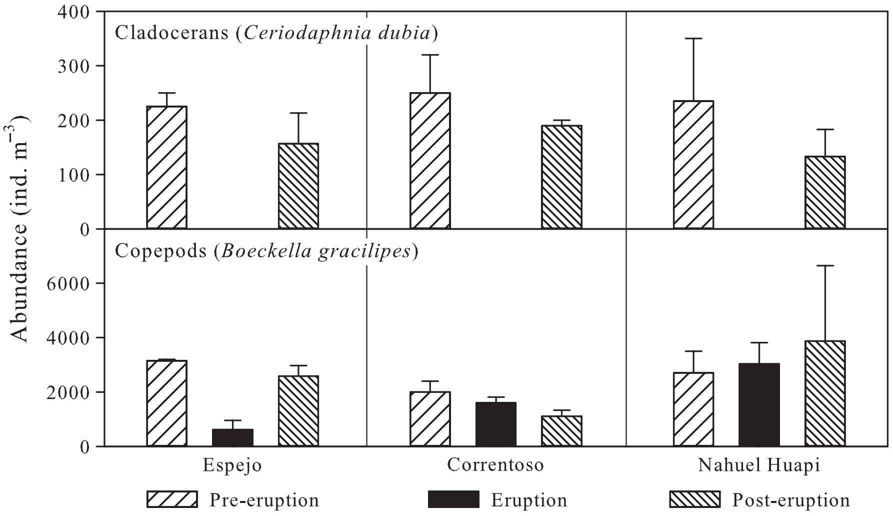

Fig. 4 Abundances of cladocerans (*Ceriodaphnia dubia*) and copepods (*Boeckella gracilipes*) in the pre-eruption summers (2002–2007), during the eruption (2011–2012) and the post-eruption summer (2013). Values are given in ind.m^{-3}. Error bars represent 1 standard error.

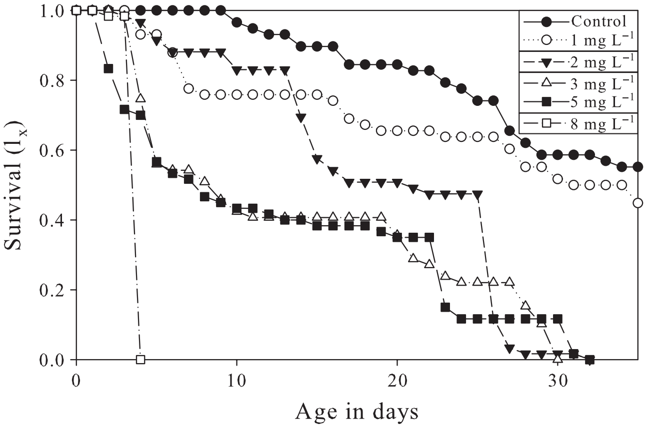

Fig. 5 Survival curves for each treatment group in the life-table experiment. Statistically homogeneous groups are indicated by legend boxes.

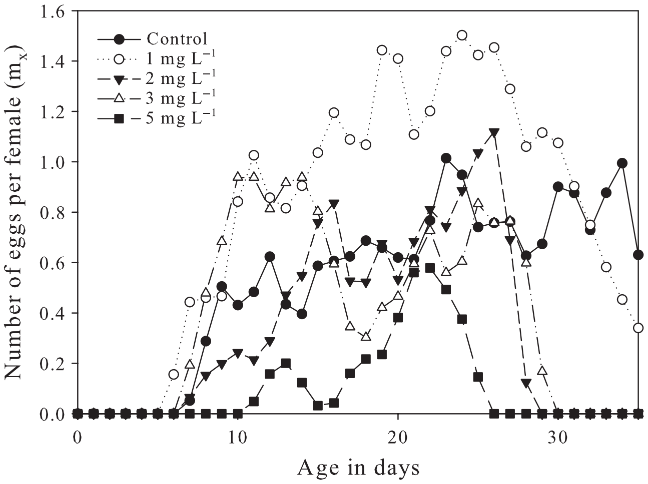

Fig. 6 Mean number of eggs per female in each treatment group in the life-table experiment. Note that only the organisms in the Control and 1 mg L^{-1} treatments continued laying eggs after 28 days.

2011–12 seemed to have been sufficient, or at least not lower than historical concentrations, we concluded that food shortages or changes in phytoplankton cell size could not be the cause of the failure of cladoceran populations. Neither conductivity nor pH was affected by the eruption so the decrease in cladoceran populations was not due to changes in these parameters. However, total suspended solids in the lakes increased during that period due to ash input, and our laboratory experiments showed that cladocerans are negatively affected by ash at the concentrations found in the lakes during the summer after the eruption.

Our experiments showed that different ash concentrations were associated with different survival curves in *D. commutata*. The ash that fell in June 2011 was an abrasive material due its composition (mainly silica) and crystalline structure (Caneiro *et al.*, 2011). This material was observed to be captured by *D. commutata* during the feeding process, resulting in a gut completely filled with ashes (Fig. 2b,c), causing a decrease in food uptake as shown by empty foreguts in animals exposed to ashes and a decrease in reproduction and survival in the experimental treatments. Particle size analysis showed that the volcanic ashes in the lakes affected by the 2011 eruption were in the size range of *Daphnia* food particles (2.55 μm ± 2.00, mean ± SD) (Modenutti *et al.*, in press-a). Because the morphology and feeding strategy of *Daphnia* limit its ability to manipulate individual particles (DeMott, 1986), this non-digestible material was ingested along with the food. In short-term experiments (10 min), it has been observed that grazing rates of *Daphnia* on *Cryptomonas* were not significantly altered by the presence of partic-

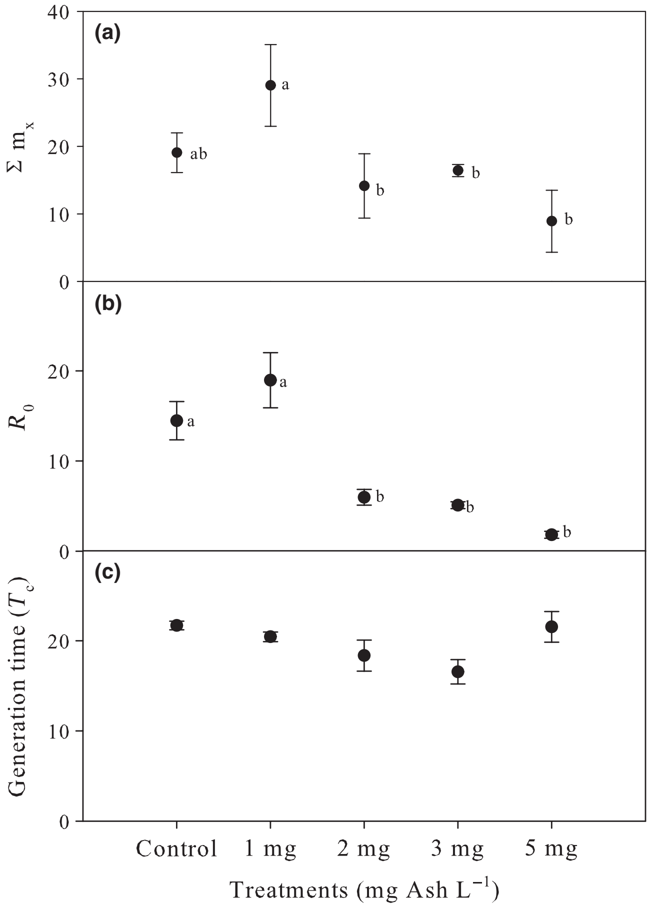

Fig. 7 (a) Gross reproductive rate (Σm_x), (b) net reproductive rate (R_0) and (c) generation time (T_c) in the different treatment groups in the life-table experiment. Letters inside the graphs indicate statistically homogeneous groups. Error bars represent one standard error.

ulate ash (Gaddy & Parker, 1986). However, in our long-term experiments, the ashes affected *D. commutata* survival after 5 days in the higher concentration treatment and for as long as twenty days in the low concentration treatment. Accordingly, we can conclude that feeding rates in the first 10 min were not affected, but the ashes affected *D. commutata* performance through its life span. Earlier studies indicated that *Daphnia* cannot efficiently eliminate non-digestible and harmful suspended sediments because this interrupts its feeding and is associated with a great energy cost (Porter & Mc Donough, 1984). Thus, inorganic particles (suspended clay) are implicated as an important factor that can reduce fertility, survival and fitness in cladocerans (McCabe & O'Brien, 1983; Kirk & Gilbert, 1990). Experiments using inorganic clay particles reported that *Daphnia* survival decreased at 50 mg L^{-1} of suspended clay (Kirk & Gilbert, 1990) or 734 mg L^{-1} of kaolinite (Robinson, Capper & Klaine, 2010). However, this represents a much higher particle concentration than was used in our experiments (ashes 2–8 mg L^{-1}), suggesting that the damage caused by the volcanic ashes in the gut was greater than that of the clay and was sufficiently harmful to affect survival and reproduction. The concentration of 8 mg L^{-1} of ashes induced a sharp decrease in the *D. commutata* population, causing its early disappearance (within 5 days of the start of the experiment). This result highlights the importance of the presence of ash particles in aquatic environments affected by volcanism because cladoceran populations may experience a sudden decrease after the eruption, when the highest ash concentrations (from 8 up to 14 mg L^{-1}) are observed. Populations exposed to 8 mg L^{-1} of ash or more could not succeed because these organisms die before reaching reproductive age and thus fail to produce offspring.

Population fitness is defined as the combination of reproductive potential and survival; thus, a population that has higher values of these parameters will have better fitness (Lampert & Sommer, 2007). An analysis of the parameter R_0, which links average fertility with survival, revealed two groups with significant differences: a no or very low ($\leq$1 mg L^{-1}) ash group and a medium or high ($\geq$2 mg L^{-1}) ash group. Therefore, the fitness of *D. commutata* was significantly lowered when 2 mg L^{-1} or more of suspended volcanic ash was present in the lake water. Although population fitness was similar in the Control and 1 mg L^{-1} ash groups, which formed one group in the analysis, the latter group exhibited slightly, although not significantly, higher egg production per female. Because survival in the 1 mg L^{-1} ash group was slightly lower than that in the Control group, but this group produced a slightly higher number of eggs per female, the net result was a similar population fitness in the 1 mg L^{-1} ash and Control groups. This suggests that the addition of ash may have provided some limiting component for *D. commutata* reproduction that compensated for the lower survival. In previous experiments, phosphorus was observed to be a key element in the life history of *Daphnia* (Elser *et al.*, 1996). In particular, in Andean lakes with extreme P limitation (Balseiro *et al.*, 2007), growth rate of *D. commutata* was observed to depend inversely on the elemental C/P ratio of its food (Balseiro *et al.*, 2007, 2008). Because the ash contained P, it may be that cladoceran growth was favoured by the ash-borne P. Nevertheless, the addition of P to the experimental system could be considered negligible because COMBO has a high molar concentration of P (50 μM P), and the P added by the ash should have no effect.

Our experimental results also have important ecological implications. Most ecological changes are gradual; however, extensive changes in ecosystems can sometimes occur over short periods of time (Holling, 1973; Scheffer & Carpenter, 2003; Walker & Meyers, 2004). Volcanic eruptions are one cause of such sudden and rapid ecological changes. Early studies indicated that the fertilisation of lake waters in western Alaska by volcanic ash during eruptions may be an important factor in determining the abundance of sockeye salmon (*Oncorhynchus nerka*) (Eicher & Rounsefell, 1957). In addition, studies of the effect of volcanic eruptions on aquatic ecosystems have mainly focused on the fertilisation effect of ash-borne elements such as phosphorus and iron (Frogner *et al.*, 2001; Hamme *et al.*, 2010; Lin *et al.*, 2011). Palaeolimnological evidence shows that in lake sediments, tephra deposition is followed by an increase in chlorophyll-derived pigments, indicating an increase in phytoplankton biomass after volcanic ash deposition (Einarsson, Óskarsson & Haflidason, 1993). Because zooplankton has an intermediate position in the food web, changes at this level may in turn affect fishes and phytoplankton (Carpenter *et al.*, 1987). The presence of volcanic ash is associated with differences in *Daphnia* survival and fecundity, depending on the magnitude of ash concentration. A decrease in cladoceran populations may be expected immediately after an eruption (high ash input, corresponding to the 8 mg L^{-1} ash treatment). Indeed, our data from the natural systems affected by the ash input show disappearance of cladocerans and critical reductions in calanoid copepod abundances. It has been shown that daphnid filter feeders cannot efficiently eliminate non-digestible and harmful suspended particles (Porter & Mc Donough, 1984) that cause a reduction in fertility, survival and fitness in its populations (McCabe & O'Brien, 1983; Kirk & Gilbert, 1990). On the other hand, copepods seem to be much less affected since we only observed a notable decrease in the most affected lake (Lake Espejo). Arendt *et al.* (2011) showed that calanoid copepods were affected by suspended sediments reducing gut passage rate, although no effect in egg production was found.

Although *D. commutata* in treatments with medium concentration of ash survived and reproduced, their contribution to the next generation (R_0) was sharply reduced, so populations under these conditions may not be able to compensate for other mortality factors, such as predation. However, as the settlement process occurs, the ash concentration decreases, favouring population recovery. This phenomenon was observed the following summer when the lakes nearly recovered their original transparencies with low TSS values and cladoceran populations also returned to their historical abundances. A similar pattern of recovery was observed for crustaceans and rotifers in Soap Lake and Lake Lenore, Washington (Edmondson & Litt, 1984), following heavy ash fall. In lakes of the Kamchatka region, Russia, it was also reported that after eruptions, there was a decrease in zooplankton that recovered after 3 years (Kurenkov, 1966). In conclusion, previous data on other explosive volcanic eruptions and the present data suggest that immediately after ash fall, the zooplankton suffer reductions in abundance, in particular non-selective filter feeders, such as daphnids. However, a few years after the eruption, a recovery in zooplankton population growth may be expected. The net result of these changes in the grazer trophic level may affect resource quantity and quality for organisms at higher trophic levels, such as fish. This may account for an adverse effect on the yield of sockeye salmon in lakes of Alaska in the first years after ashfall (Eicher & Rounsefell, 1957). However, the fertilising effect of volcanic ash improved plankton development in subsequent years in Lake Asabatchye (Kamchatka) and sockeye salmon increased in number due to favourable changes in conditions affecting reproduction (Kurenkov, 1966). The effect on upper trophic levels will depend on predator type and generation time. For long-lived fish, this effect may be dampened, but a greater effect may be expected for short-lived fish or larvae and juveniles.

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