



# Influence of precipitation, landscape and hydrogeomorphic lake features on pelagic allochthonous indicators in two connected ultraoligotrophic lakes of North Patagonia

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## ABSTRACT

We investigated the terrestrial influence on two chained deep ultraoligotrophic lakes of North Patagonia (Argentina) through the seasonal analysis of two pelagic allochthonous indicators: i) water color, as a proxy of allochthonous dissolved organic matter in lakes; and ii) the color to chlorophyll *a* ratio (Color:Chl<sub>a</sub>), as an indicator of the relationship between allochthonous and autochthonous carbon pools. We also evaluated the potential transfer pathways of the allochthonous dissolved organic matter into the pelagic food webs of these deep lakes, including the natural zooplankton  $\delta^{13}\text{C}$  in the analysis. The dynamics of the allochthonous indicators were related to the precipitation regime, water level fluctuations, and hydrogeomorphic and catchment features of lakes Moreno East and Moreno West. The water color (absorbance at 440 nm) was extremely low ( $<0.28 \text{ m}^{-1}$ ) in both lakes regardless of the season. However, precipitation and snowmelt regimes drove the increase and decrease of water color, respectively. A significant positive relationship between the zooplankton bulk  $\delta^{13}\text{C}$  with the water color would suggest an input of allochthonous organic carbon into the pelagic consumers. The incorporation of the dissolved allochthonous material into higher trophic levels is likely favored by the bacterivorous behavior of planktonic organisms, mixotrophic flagellates and ciliates, which dominate the pelagic food webs of these Patagonian lakes. Morphometric aspects, mainly the higher water residence time, led to lower values of allochthony in Moreno East compared to Moreno West, probably accentuated by its upper position in the lake chain. Overall, our results suggest that these allochthonous signals can bring insight into the magnitude of the interaction between terrestrial environments and lake ecosystems, even in extremely clear and ultraoligotrophic systems, such as the Andean Patagonian lakes.

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## 1. Introduction

The terrestrial environment provides inputs of allochthonous dissolved and particulate organic carbon from vegetation and soils to aquatic ecosystems (Polis et al., 1997; Pace et al., 2004; Williamson et al., 2009), supporting differentially their secondary production (Wetzel, 2001; Cole et al., 2011). In lakes, the dissolved allochthonous organic carbon enters the pelagic food webs directly by bacterial consumption, and transfers to zooplankton either via direct feeding on bacteria, or through intermediate bacterial consumers; e.g., bacteria-flagellate-macrozooplankton food chain (Jones, 1992; Bergström and Jansson, 2000; Karlsson et al., 2003). Several studies have suggested that allochthonous organic carbon should be relatively more important in supporting planktonic food webs in humic lakes compared to relatively shallow clear-water lakes (Jones, 1992; Jansson et al., 2007; Pace et al., 2007). According to Karlsson et

al. (2003), the dependency of zooplankton on allochthonous carbon is more associated to the heterotrophic energy mobilization in the pelagic food webs rather than to a high content of allochthonous carbon in the lake water. They found that even clear subarctic lakes dominated by heterotrophic energy mobilization, have zooplankton populations that rely on allochthonous carbon.

Water color, determined as the absorbance of light at 440 nm, has been demonstrated to be proportional to the amount of terrestrially derived organic carbon potentially available to consumers, and thus is a reliable proxy of allochthonous dissolved organic matter in lakes (Rasmussen et al., 1989; Hessen and Tranvik, 1998; Carpenter et al., 2005). Moreover, the chlorophyll *a* (Chl<sub>a</sub>) is proportional to phytoplankton biomass, and can be used as an indicator of the amount of autochthonous carbon available to consumers (Carpenter et al., 2005). In this sense, the Color:Chl<sub>a</sub> ratio, as an indicator of the relationship between allochthonous and autochthonous carbon pools, is a useful predictor of allochthony. In fact, the Color:Chl<sub>a</sub> ratio has been applied to indirectly measure the relative importance of the allochthonous carbon

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inputs to a wide and diverse range of north-temperate lakes (Webster et al., 2008). Moreover, Webster and colleagues found that the among-lake variation of this ratio could be explained by certain hydrogeomorphic (HGM) features, such as water retention time (WRT) and lake area.

Inputs of allochthonous dissolved organic matter in lakes are strongly affected by precipitation (Pace and Cole, 2002; Adrian et al., 2009), which is also associated with water level fluctuations. As a result of water inputs and outputs, water levels fluctuate dynamically, positively correlated with precipitation, surface runoff and inflows, and inversely correlated to outflows and evaporation (Sellinger et al., 2007). Thus, climate-driven forces may have profound effects on physical, chemical, and biological lake properties (Adrian et al., 2009).

Over the last few decades, the use of stable carbon isotope analysis has provided insight regarding the organic matter fluxes in aquatic food webs, since the  $\delta^{13}\text{C}$  values of consumers reflect quite closely those obtained from their diet (Jones et al., 1998). Thus, carbon isotope ratios of  $^{13}\text{C}$  to  $^{12}\text{C}$  are useful to identify the sources of organic matter to the food webs (Meili et al., 1996; Jones et al., 1998; Grey et al., 2001). In recent years, experimental whole-lake manipulation using  $^{13}\text{C}$ -enriched additions indicated that  $\delta^{13}\text{C}$  data can be used to quantify the contribution of the allochthonous organic carbon to several trophic levels of the pelagic food webs of small lakes including bacteria (Kritzberg et al., 2004), phytoplankton, zooplankton, and fish (Cole et al., 2002; Pace et al., 2004; Carpenter et al., 2005). These experiments demonstrated that terrestrial organic matter support to zooplankton was greater than 30% in most cases, except when internal primary production was enhanced by nutrient enrichment, thus increasing autochthonous sources (Carpenter et al., 2005).

The Andean region of North Patagonia comprises a wide lacustrine district with numerous deep clear water lakes of glacial origin. These Andean Patagonian lakes are extremely clear systems, with dissolved organic carbon concentrations below  $0.7 \text{ mg L}^{-1}$  (Morris et al., 1995) and maximum depths greater than 90 m. In these systems, the role of the terrestrial inputs and their influence on the pelagic food webs remain still unknown. The Lake Moreno complex within the Glacial Lake District (Iriondo, 1989) includes two connected, ultraoligotrophic deep lakes known as Moreno East and Moreno West (Alonso et al., 2004). The regional precipitation regime is characterized by a strong temperate seasonality including winter snowfall, and dry summers (Paruelo et al., 1998).

The aim of this study was to evaluate the influence of the terrestrial environment on these chained ultraoligotrophic lakes of North Patagonia (Argentina). We focused our analysis in two pelagic indicators of allochthonous influence (hereinafter allochthonous indicators): the water color and the Color:Chl *a* ratio. Our main objectives were to: (1) determine possible seasonal variations in the allochthonous indicators and their relationship with the precipitation regime; (2) associate the HGM and catchment features of each lake with the dynamics of the allochthonous indicators; (3) discuss the potential transfer pathways of the allochthonous dissolved organic matter into the pelagic food webs of these North Patagonian deep lakes, including the natural zooplankton  $\delta^{13}\text{C}$  in the analysis. In order to address our second objective, we performed for the first time a detailed analysis of the HGM and catchment features of both Moreno lakes. Overall, we hypothesize that: (1) even in extremely clear lakes such as most ultraoligotrophic Patagonian lakes, the influence of the terrestrial environment in the water column could be detected through allochthonous indicators; (2) the seasonal dynamics of these allochthonous indicators will track the regional precipitation regime; and (3) lake morphometry will ultimately determine the strength of the landscape-lake interactions.

## 2. Materials and methods

### 2.1. Study area

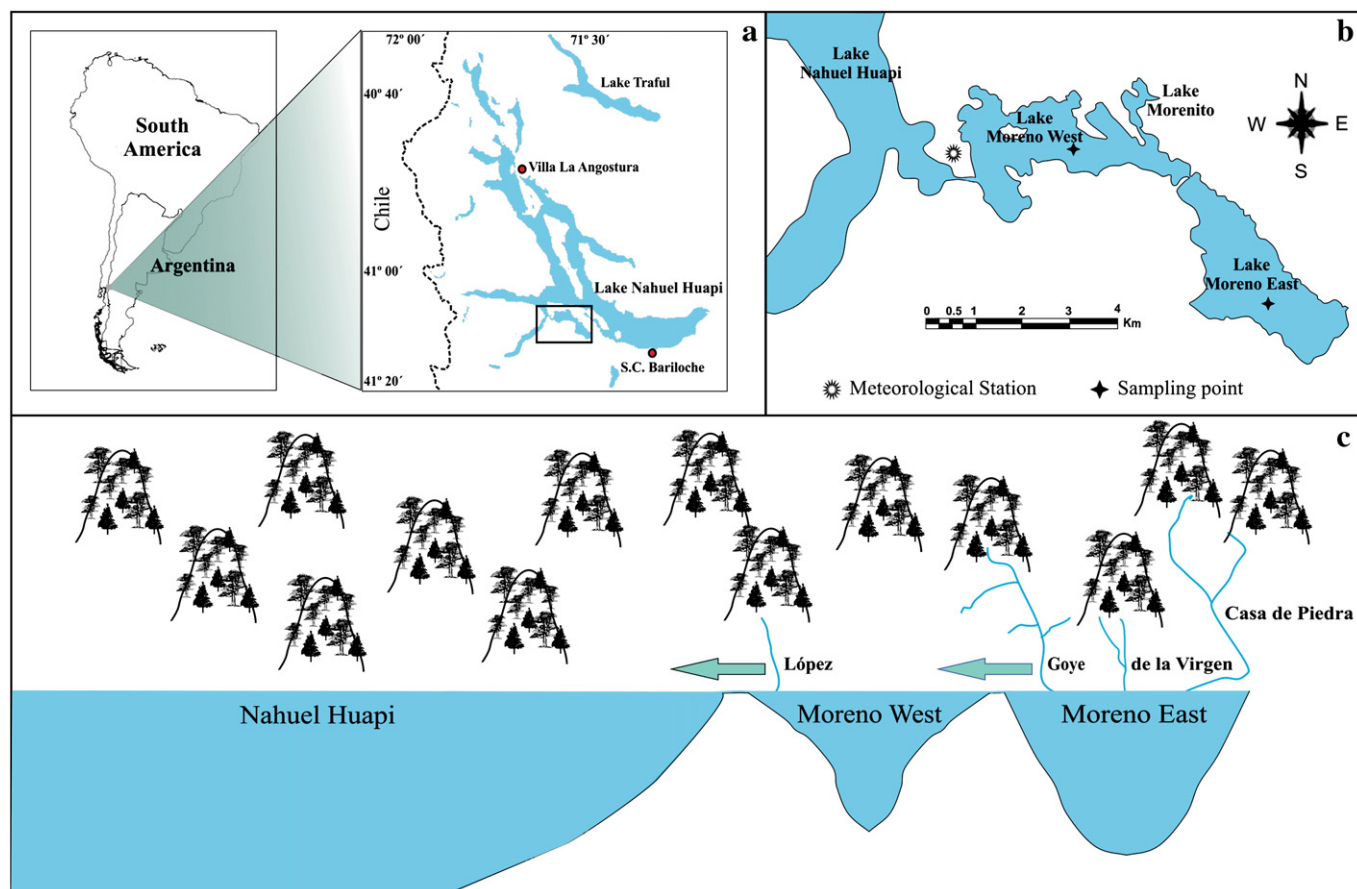
Lakes Moreno East (ME) and Moreno West (MW) are located in the Glacial Lake district of the Southern Andes (Iriondo, 1989), inside

the Nahuel Huapi National Park (North Patagonia, Argentina), ~20 km West to the city of San Carlos de Bariloche (Fig. 1a). The Lake Moreno complex ( $45^\circ 04' \text{ S}$ ,  $71^\circ 31' \text{ W}$ ) includes both deep lakes ( $Z_{\text{max}} \geq 90 \text{ m}$ ), as well as the shallow Lake Morenito ( $Z_{\text{max}} = 12 \text{ m}$ ) (Alonso et al., 2004) (Fig. 1b). The three lakes have narrow connections between each other, which become enhanced with rising water levels (Fig. 1b). ME and Morenito flow into MW, which discharges through a narrow channel (0.5 km long) into Lake Nahuel Huapi, the largest freshwater lake in northern Patagonia (Area =  $557 \text{ km}^2$ ; Fig. 1b, c). These piedmont lakes (768 m asl) belong to mountainous catchment areas (up to 2200 m asl), with relatively low anthropogenic influence, and mostly covered by mixed forests of *Nothofagus dombeyi* (Mirb.) Blume and *Austrocedrus chilensis* (D. Don) Florin et Boutleje from lake level (768 m asl) to 900 m asl, and *Nothofagus pumilio* (Poepp. Et Endl.) Krasser from 900 to 1600 m asl (Bessera and Moretti, 1993). In this scenario, ME and MW are part of a chained lake series, with ME upper in the mixed forest montane landscape (Fig. 1c).

The Andean region of Patagonia is continental and humid cold-temperate (Pedrozo et al., 1993), with 73% of annual precipitation concentrated in the fall–winter period (Paruelo et al., 1998). In this Austral region, the fall season (April–June) is dominated by rainfall, while in the winter (July–September) precipitation includes both rain and snow. Thus, in this region rainfall and snowfall co-dominate during the wet seasons. The snow falling in high altitudes contribute to the formation of a snowpack, which remains frozen until the springtime snowmelt. Moreover, this Patagonian region is exposed to persistent westerly winds, which present their maximum speed between September and January (Paruelo et al., 1998).

Lake water storage (positively related to water level fluctuations) of the connected Lake Nahuel Huapi is monitored with high temporal resolution by AIC (Autoridad Interjurisdiccional de Cuencas, Río Negro, Argentina). Long-term lake water storage datasets indicate that the maximum variation in water level in Lake Nahuel Huapi attains 3.2 m, with the lowest levels occur during summer (from December to March), followed by an increment from April (fall), and reaching the highest values between July and November (AIC, 2009). The changes in water levels are also reflected in Moreno lakes, with the lowest levels occurring in the drier summer season.

Both ME and MW are ultraoligotrophic, characterized by low total phosphorus concentrations ( $<4 \mu\text{g L}^{-1}$ ; Queimaliños et al., 1999, 2002). The lakes are warm monomictic, thermally stratified during late spring and summer, with a thermocline usually between 30 and 40 m (Queimaliños et al., 1999; Pérez et al., 2002), and epilimnetic temperature around  $16\text{--}17^\circ\text{C}$  (this study). Specific conductance is very low in both lakes (Díaz et al., 2007) with ME having somewhat consistently lower values ( $38\text{--}40 \mu\text{S cm}^{-1}$ ) compared to those in MW ( $41\text{--}43 \mu\text{S cm}^{-1}$ ) (data obtained in this study). Due to the typically low dissolved organic carbon (DOC) concentrations ( $<0.7 \text{ mg L}^{-1}$ ), light penetration is high in deep North Patagonian Andean lakes (Morris et al., 1995). In particular, a spring-summer study in MW revealed that the photosynthetically active radiation diffuse extinction coefficients ( $K_{\text{dPAR}}$ ) varied between 0.121 and  $0.154 \text{ m}^{-1}$ , leading to an euphotic zone extending up to 38 m depth, slightly more than one-third of the total depth (Queimaliños et al., 2002). Summer vertical distribution of chlorophyll *a* in MW demonstrated metalimnetic peaks, mainly constituted of *Ophrydium naumanni*, a large mixotrophic ciliate, and the dinoflagellate *Gymnodinium paradoxum* (Queimaliños et al., 1999). Mixotrophic behavior is widespread in these lakes considering that phytoplankton is dominated by mixotrophic nanoflagellates like *Chrysochromulina parva* and *Plagioselmis lacustris* (Queimaliños et al., 2002), while another mixotrophic ciliate, *Stentor araucanus*, prevails in epilimnetic waters of MW (Modenutti et al., 2008). In this context, the microzooplankton community of Moreno lakes is characterized by the presence of these large mixotrophic ciliates in addition to rotifer species; while the crustacean fraction is mainly constituted by the copepod *Boeckella gracilipes*



**Fig. 1.** (a) Geographic location of Lake Moreno complex inside the Nahuel Huapi system (North Patagonia, Argentina); (b) map of Lake Moreno complex showing the narrow connection between Moreno East (ME) and Moreno West (MW) and the drainage to Lake Nahuel Huapi; (c) landscape position of Lakes ME, MW and Nahuel Huapi, included in mountainous catchment areas.

and the cladocerans *Bosmina longirostris* and *Ceriodaphnia dubia* (Modenutti et al., 1998).

## 2.2. Water and plankton sampling

Sampling was performed seasonally between May 2008 and February 2009 (Southern fall and summer, respectively). Water samples were obtained with a 12-L Schindler–Patalas trap at a sampling point located at the deepest part of each lake every 10 m between surface and 100 m in ME, and between surface and 80 m in MW. The winter profile of ME was the only one comprising 0 to 60 m because a strong storm forced us off the lake at the time of sampling. In each profile, temperature and conductance were measured with multiparameter probes. Samples for color and chlorophyll *a* (Chl*a*) determinations were transferred to 5 L polypropylene containers, which were acid-washed and pre-rinsed with the water sampled at the beginning of the collection. To enumerate mixotrophic ciliates, a 250-mL sample of the lake water at each depth was preserved with acid Lugol's solution and immediately put in darkness. Crustacean zooplankton samples were obtained by sieving of 24-L water samples through a 53- $\mu$ m mesh and preserved with 4% formaldehyde.

## 2.3. Laboratory analyses

In the laboratory, water color was determined as the absorbance at 440 nm ( $a_{440}$ ) of the dissolved fraction of each sample, with a Hewlett-Packard photodiode array 8453E spectrophotometer in a 10 cm pathlength cell following Carpenter et al. (2005). Distilled water was used as a reference blank. The dissolved fractions were

obtained by gentle filtration through pre-ashed Whatman GF/F glass fiber filters. Chl*a* concentration was determined spectrophotometrically by extraction with hot 90% ethanol following Nusch (1980).

Mixotrophic ciliates were enumerated in 50 mL Utermöhl chambers under an inverted microscope, by scanning the entire chamber surface at 100 $\times$ . Crustaceans were quantified under stereomicroscope in a 5-mL Bogorov chambers, and rotifers in a 1-mL Sedgwick–Rafter chamber under direct microscope. The biomass of the mixotrophic ciliate *O. naumannii* was determined through biovolume calculations after Balseiro et al. (2001), assuming a specific gravity of one between fresh weight and volume. Wet weight of *S. araucanus*, 1  $\mu$ g ind $^{-1}$ , was taken from Kamjunke et al. (2009). The specific dry weight for key zooplanktonic species was obtained either from the literature (Bottrell et al., 1976) or by direct measurement of pooled and dried individuals collected from Moreno lakes. These dry weight values were properly converted to fresh weight data following the conventionally accepted conversion factor 10:1.

## 2.4. Determination of HGM features and catchment areas

Lake perimeters, areas, volumes (*V*), and maximum and mean depths ( $Z_{\max}$  and  $Z_{\text{mean}}$ ) of ME and MW were determined from existing bathymetric maps (Rechencq et al., 2011). The volume of each lake was calculated integrating the area delimited by the hypsographic curves depth-area (Wetzel, 2001). The mean annual water discharge of each lake [ $Q_{\text{mv}}$  ( $\text{m}^3 \text{s}^{-1}$ )] was calculated using precipitation data, evaporation volumes and runoff water inputs obtained by hydrometeorological processed data. Water retention time (WRT) was estimated as  $V/Q_{\text{mv}}$  (Håkanson, 2005).



Catchment or drainage areas (DA) and the ratio of drainage area to lake area (D/A) were calculated applying Digital Terrain Models based on maps published by ASTER-GDEM.<sup>1</sup> In the case of MW, the drainage area was calculated including the area of the upstream lakes (ME and Morenito). In order to characterize the catchment areas of ME and MW in terms of substrate composition (i.e. rocky and forested), wetland and urban areas, we calculated the proportions of each one using maps published by Pereyra (2007).

### 2.5. Precipitation regime and water level fluctuations

The temporal variation in precipitation values was analyzed through data obtained from an AIC meteorological station at the outlet stream of MW (Fig. 1b). The snowpack data (in mm as equivalent rain units) from a reference mountain within the Nahuel Huapi basin was obtained from published hydrometeorologic reports ([www.aic.gov.ar](http://www.aic.gov.ar)). Water level fluctuations were inferred from the variation of the lake water storage (LWS) of Lake Nahuel Huapi (AIC, 2009), assuming a positive relation between both variables. The AIC provides the LWS data as percentages of the maximum water storage historically registered for the Lake Nahuel Huapi (AIC, 2009). We extrapolated these values to both Moreno lakes, since they share the same large basin with co-fluctuating water levels (Fig. 1a).

### 2.6. Plankton sampling for $\delta^{13}\text{C}$ analyses

Plankton samples for  $\delta^{13}\text{C}$  measurements were collected by vertical tows from 100 and/or 80 m to surface (ME and MW respectively), with nets of two different mesh sizes (53 and 200  $\mu\text{m}$ ), and further sieved in the laboratory into two fractions: Fraction 1 ( $\geq 53$  and  $< 200$   $\mu\text{m}$ ), and Fraction 2 ( $> 200$   $\mu\text{m}$ ). Subsamples of the Fraction 1 were examined for the eventual presence of larger phytoplankton species and their proportion was always found to be negligible. Additionally, in summer samples, the largest dominant zooplankton species (*B. gracilipes* and *C. dubia*) were separated from living samples under a dissecting microscope for  $\delta^{13}\text{C}$  analysis. The abundance of *B. longirostris* and cyclopoid copepods was too low to perform their manual separation. All sorted samples were handled by means of titanium and Teflon® devices, frozen at  $-40$  °C and freeze-dried until constant weight. Carbon isotope samples were analyzed by gas chromatography mass spectrometry using a DELTAplusXP continuous flow stable isotope ratio-mass spectrometer at the Queen's University, Kingston, Canada. All  $\delta^{13}\text{C}$  data are represented as  $\delta$  values in per mil units following the equation:

$$\delta^{13}\text{C} = 1000 \times [(R/0.0112372) - 1]$$

where R is the ratio of  $^{13}\text{C}$  to  $^{12}\text{C}$  in the sample, and 0.011237 is the same ratio of  $^{13}\text{C}$  to  $^{12}\text{C}$  in the standard reference material Vienna Pee Dee Belemnite (VPDB). The  $\delta^{13}\text{C}$  signature denotes the ratio of  $^{13}\text{C}$  to  $^{12}\text{C}$  expressed as deviation from the recognized isotopic standard reference material. Increases in  $^{13}\text{C}$  relative to  $^{12}\text{C}$  is therefore reflected by higher (i.e. less negative)  $\delta^{13}\text{C}$  values; decreases in  $^{13}\text{C}$  relative to  $^{12}\text{C}$  is reflected reciprocally by lower (i.e. more negative)  $\delta^{13}\text{C}$  values.

### 2.7. Data analyses

Mean color, Chla concentration, Color:Chla ratio and zooplankton biomass at each sampling date were calculated averaging the values obtained across all depths to present an integrated lake pattern. With the purpose of comparing in-lake and among-lake statistical differences in these variables we averaged the data from the depths

belonging to each of the layers observed during summer stratification: 0–20 m (mixed layer), 30–40 m (metalimnion), and 50–maximum depth sampled (hypolimnion). In the case of Chla concentration and the Color:Chla ratio, the comparisons were made only considering the data obtained in the photic layers.

Two-way ANOVA was applied to assess the variability of color, Chla concentration, Color:Chla ratio and the zooplanktonic  $\delta^{13}\text{C}$  among seasons and lakes, and among strata within each lake and between both lakes. Whenever the effects of these factors were significant, contrasts were performed applying post hoc Bonferroni tests. Pearson product moment correlation was applied to study the relationship between color and the bulk zooplanktonic  $\delta^{13}\text{C}$  of Fraction 2. For evaluating the seasonal variation in the zooplanktonic  $\delta^{13}\text{C}$  of Fraction 2, we included previous data obtained during the period 2006–2007 (Arcagni, unpubl.).

## 3. Results

### 3.1. HGM and catchment features

Moreno lakes have surface areas close to 6 km<sup>2</sup> each, with slightly different maximum depths: 106 m in ME and 90 m in MW (Table 1). However, our own estimations pointed out that ME has twice the volume of MW (Table 1), despite the similar areas and the comparable  $Z_{\text{max}}$ . This difference is attributable to ME having a very steep and fjord-like basin shape with higher  $Z_{\text{mean}}$  values, while MW has a more conical basin (Figs. 1c, 2a,b; Table 1). Considering 40 m depth as the highest limit of the euphotic zone in these lakes (Queimaliños et al., 2002), those different lake shapes promote aphotic zones around 47 and 22% in ME and MW, respectively. As a result, ME has a “dark” volume 4.2-fold larger than that of MW (Table 1). Perimeter and perimeter-lake area ratio are higher in MW, implying a greater contact between the lake and the terrestrial environment, and a potential greater influence of allochthonous carbon in this lake, while the WRT was 2.34-fold higher in ME compared to MW (Table 1, Fig. 2a).

ME has a very large drainage area, almost 5-fold greater than that of MW, and as a result has a larger drainage ratio (D/A) since both lakes have a similar surface area (Table 1, Fig. 3). Moreover, both drainage areas exhibit high elevations ( $> 2000$  m asl, Fig. 3) with large portions located above the timberline ( $\approx 1600$  m asl, Pereyra,

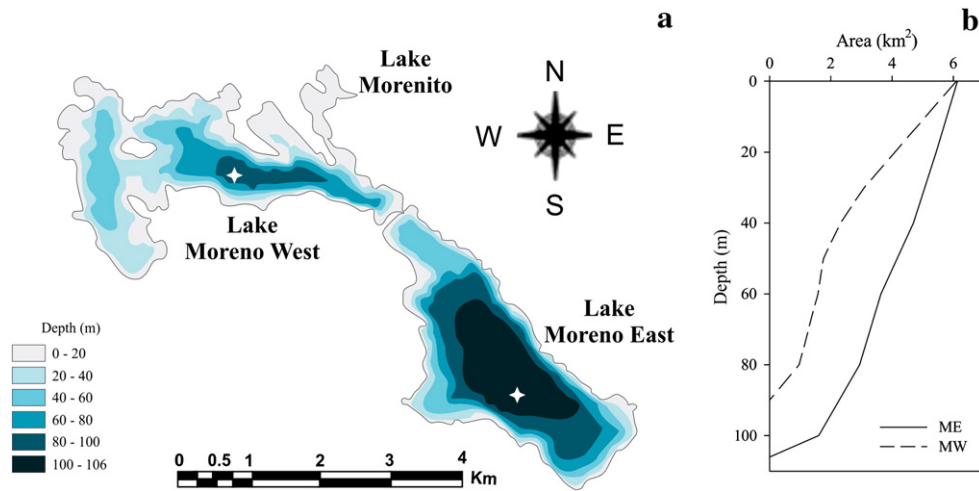
**Table 1**

Geographic location, and hydrogeomorphic and catchment features of Lakes Moreno East and Moreno West. Abbreviations are as follows: Qmv, mean annual water discharge; WRT, water retention time.

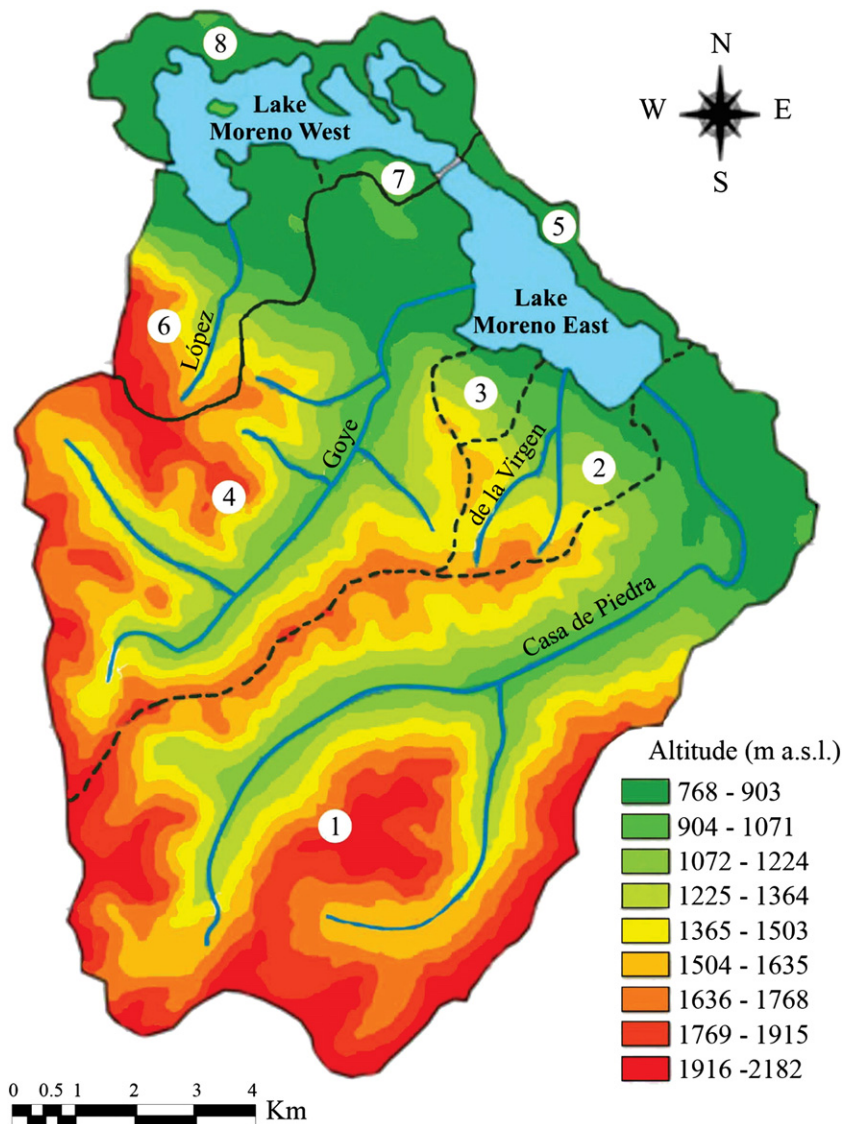
	Moreno East	Moreno West	Ratios ME:MW
Geographic location	41°05'51" S 71°29'23" W	41°03'33" S 71°32'24" W	
<i>Lake hydrogeomorphic features</i>			
Lake Area (km <sup>2</sup> )	6.14	6.10	1.01
Lake Volume (V) (km <sup>3</sup> )	0.41	0.20	2.01
Maximum depth ( $Z_{\text{max}}$ ) (m)	106	90	1.18
Mean depth ( $Z_{\text{mean}}$ ) (m)	67.0	33.5	2.00
Perimeter (km)	13.3	19.3	0.69
Perimeter:lake area ratio (km <sup>-1</sup> )	2.17	3.16	0.69
Euphotic Volume (hm <sup>3</sup> )	216.93	158.75	1.37
Aphotic volume (hm <sup>3</sup> )	194.20	45.79	4.24
Qmv (m <sup>3</sup> s <sup>-1</sup> )	5.68	6.60	0.86
WRT (years)	2.29	0.98	2.34
<i>Catchment features</i>			
Drainage area (D) (km <sup>2</sup> )	116.93	23.77	4.92
Drainage ratio (D/A)	19.04	3.90	4.89
% Forest	68.40	72.50	0.94
% Rock	29.84	12.70	2.35
% Wetland	0.30	5.50	0.05
% Urban area	1.50	9.30	0.16

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<sup>1</sup> Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model (GDEM) was developed jointly by the Japan Ministry of Economy, Trade, and Industry (METI) and the United States National Aeronautics and Space Administration (NASA)



**Fig. 2.** (a) Bathymetric maps of Moreno lakes [adapted from Rechencq et al. (2011)]; (b) hypsographic curves of Lakes Moreno East (ME) and Moreno West (MW). White stars indicate the sampling points.



**Fig. 3.** Catchment areas of Lakes Moreno East (ME) and Moreno West (MW) and their main lotic tributaries. Numbers indicate sub-areas within catchments of Lakes ME (1 to 5) and MW (6 to 8). ME receives three main lotic tributaries: the streams “Casa de Piedra” and “Goye”, originated in small high altitude lakes, and the first order stream “de la Virgen”. MW has a smaller drainage area with a distinctive pattern: it receives the first order stream “López”, as well as the waters of the Lakes ME and Morenito.

2007), and typified by rocky substrates (Bessera and Moretti, 1993). These sectors are larger in the drainage area of ME compared to MW (Table 1).

### 3.2. Precipitation regime and water level fluctuations

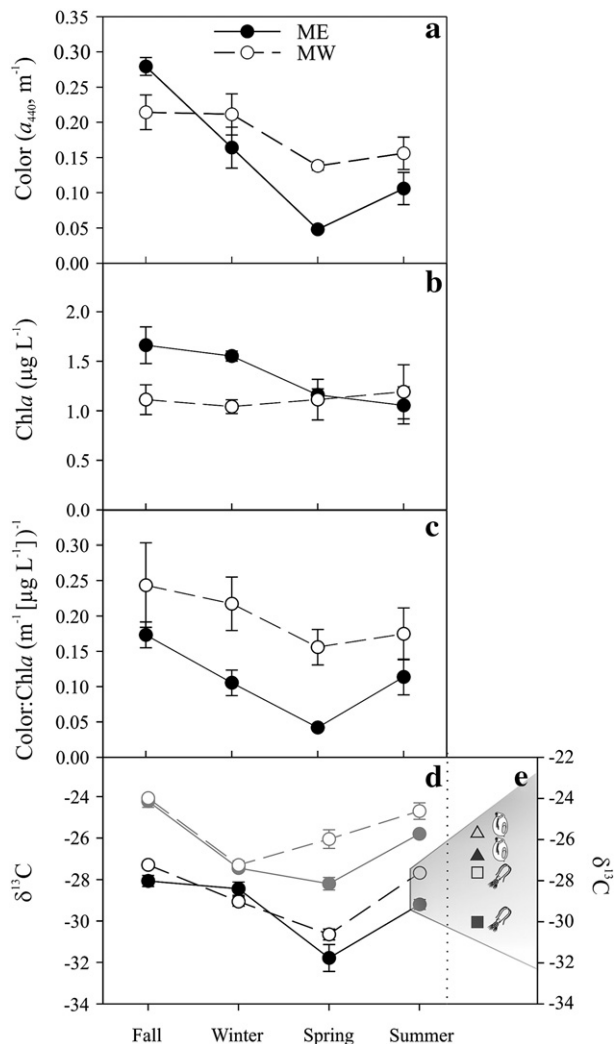
During the study period (April 2008–March 2009), the annual precipitation in the Moreno lakes' area totaled 1243 mm with 82% occurring during the fall–winter seasons (April–September; Fig. 4). The volume of the snow pack was greatest during September (late winter) diminishing afterward until its complete melting by the end of November (late spring) (Fig. 4). The increased water levels observed during fall and winter in Moreno lakes reflect the stronger precipitation episodes while the high levels registered during spring are likely associated with snowmelt inputs (Fig. 4). Conversely, low water levels coincided with warmer temperatures and higher evaporation losses prevailing in the dry summer season (Fig. 4). The temporal dynamics of the LWS during the study period is in line with its documented historical behavior (AIC, 2009) (Fig. 4).

### 3.3. Seasonal dynamics of allochthonous indicators and the zooplankton $\delta^{13}\text{C}$ signatures

In both lakes, the two allochthonous indicators presented their highest values during fall (Fig. 5a, c and d) which coincided with the beginning of more intense precipitation (Fig. 4) and surface runoff in the fall.

Water color values were very low in both lakes ( $0.05\text{--}0.28\text{ m}^{-1}$ ) (Fig. 5a), and were similar across strata in the two lakes regardless of the season (ANOVA  $p > 0.05$ ). In contrast, water color showed a strong seasonal variability within each lake (ANOVA  $p < 0.001$ ), with the lowest values during spring snowmelt (Fig. 5a). Even though a similar color pattern was found in both lakes (ANOVA  $p > 0.05$ ), ME showed a stronger variation in water color than MW (Fig. 5a). MW had higher mean color values than ME, except in the fall (Fig. 5a). Among lake differences in color were significant in fall and in spring (Bonferroni  $p = 0.026$  and  $p = 0.003$ , respectively), due to differences observed in the hypolimnion in fall (Bonferroni  $p = 0.018$ ), and in the three depth strata in spring (Bonferroni  $p < 0.001$  in all cases).

The mean vertical Chla concentration showed small fluctuations across seasons in both lakes (Fig. 5b). In MW the concentrations were similar across seasons (ANOVA  $p > 0.05$ ), fluctuating around  $1.1\text{ }\mu\text{g L}^{-1}$ . In contrast, Chla concentrations in ME varied seasonally, with levels up to  $1.65\text{ }\mu\text{g L}^{-1}$  in fall and winter, significantly higher than those of MW (Bonferroni  $p = 0.048$  and  $p = 0.006$ , respectively), but similar in spring and summer (Bonferroni  $p > 0.05$  (Fig. 5b). The differences among lakes were due to differences in epilimnetic values in fall (Bonferroni



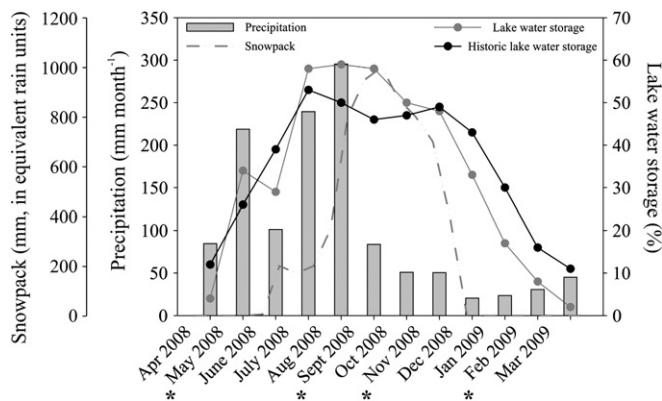
**Fig. 5.** Allochthonous indicators and Chlorophyll *a* concentration (Chla) in Moreno lakes during the study period: (a) water color ( $a_{440}, \text{m}^{-1}$ ); (b) Chla concentration ( $\mu\text{g L}^{-1}$ ); (c) Color:Chla ratio ( $\text{m}^{-1} [\mu\text{g L}^{-1}]^{-1}$ ); (d)  $\delta^{13}\text{C}$  in the zooplankton, Fraction 1: data comprising 2008–2009 (gray), and Fraction 2: data comprising 2006–2009 (black); and (e) Specific  $\delta^{13}\text{C}$  of *Ceriodaphnia dubia* (triangle) and *Boeckella gracilipes* (square) collected in summer 2009. References: Lake Moreno East (ME), filled symbols; Lake Moreno West (MW), empty symbols). Symbols and error bars: vertical mean  $\pm$  SE.

$p = 0.009$ ), and contrasting differences in the epilimnetic and metalimnetic layers in winter (Bonferroni  $p = 0.042$  and  $p = 0.032$ , respectively).

The Color:Chla ratio ranged between 0.04 and 0.18 in ME and between 0.16 and 0.25 in MW, with the lowest ratios occurring during spring in both lakes (Fig. 5c). The Color:Chla ratio showed a consistent seasonal variability in both lakes, although it was significant only in ME (ANOVA  $p < 0.001$ ). The ratios were significantly higher in MW than in ME in winter and in spring (Bonferroni  $p = 0.017$  and  $p < 0.001$ , respectively) (Fig. 5c). The differences between lakes during spring were observed in the metalimnion (Bonferroni  $p = 0.025$ ).

The stable C isotope ( $\delta^{13}\text{C}$ ) for both zooplankton size fractions exhibited a marked seasonal variability in both lakes (ANOVA Fraction 1,  $p < 0.001$ ; Fraction 2,  $p < 0.001$ ), with the lowest values in spring, except those corresponding to Fraction 1 ( $\geq 53$  and  $< 200\text{ }\mu\text{m}$ ) in MW (Fig. 5d). Remarkably, the seasonal pattern for Fraction 2 ( $> 200\text{ }\mu\text{m}$ ) appears to be interannually consistent, as inferred through the low deviations from the mean obtained from seasonally-pooled  $\delta^{13}\text{C}$  values for three consecutive years (2006–2009) (Fig. 5d) (previous data from M. Arcagni unpubl., and this study).

In order to understand the potential transfer pathways of the allochthonous dissolved organic matter into the pelagic food webs,



**Fig. 4.** Precipitation pattern in Moreno lakes' catchment areas. Monthly precipitation, lake water storage and snowpack contribution during the study period (April 2008–March 2009). The asterisks indicate the sampling dates. Historic lake water storage is also presented.



we performed a detailed study of the zooplankton structure in both Moreno lakes (Table 2). The results of this analysis showed that: i) the zooplankton community was dominated by adult copepods of *B. gracilipes* most of the year, particularly during winter; ii) the rotifer biomass was highest during fall in both lakes, co-dominating with *B. gracilipes*; iii) the cladoceran *C. dubia* increased considerably during the summer period, especially in Lake Moreno East; iv) *B. longirostris* and cyclopoid copepods were present at low densities throughout the study period; v) the mixotrophic ciliate *S. araucanus* had its maximum biomass during spring; vi) *O. naumanni* showed a different pattern among lakes, fairly constant in ME, and with a higher biomass in fall and spring in MW (Table 2).

The smaller zooplankton of Fraction 1 was constituted by four rotifer species (*Polyarthra vulgaris*, *Synchaeta pectinata*, *S. kitina* and *Conochilus unicornis*), the large mixotrophic ciliates *O. naumanni* and *S. araucanus* and nauplii of *B. gracilipes* (Table 2). In this fraction the species composition was different among lakes, with a greater proportion of ciliates and nauplii in MW than in ME. *S. araucanus* prevailed in MW above 15 m depth all year round, with the highest biomass during spring, while it occurred mostly in the spring-summer period in ME (Table 2). Zooplankton Fraction 2 (>200 µm) was also different between lakes, with a greater proportion of *B. gracilipes*, *B. longirostris* and cyclopoids in MW, whereas the cladoceran *C. dubia* was more important in ME, mainly during summer when this species co-dominated with *Boeckella* (Table 2).

The Fraction 1 had significantly higher  $\delta^{13}\text{C}$  values (e.g. enriched in  $^{13}\text{C}$  relative to  $^{12}\text{C}$ ) compared to Fraction 2 in both lakes (ANOVA ME  $p < 0.001$ , MW  $p < 0.001$ ). Isotopic carbon signatures of both fractions were different among lakes (ANOVA Fraction 1,  $p = 0.002$ ; Fraction 2,  $p = 0.002$ ). The  $\delta^{13}\text{C}$  values were higher in MW during spring in Fraction 1 (Bonferroni  $p = 0.016$ ), and during summer in Fraction 2 (Bonferroni  $p = 0.013$ ) (Fig. 5d). The species-specific  $\delta^{13}\text{C}$  analysis of summer samples revealed that *C. dubia* had higher  $\delta^{13}\text{C}$  values compared to *B. gracilipes*, and the cladoceran values were close to those of Fraction 1 (Fig. 5d,e). In contrast, the summer  $\delta^{13}\text{C}$  values for the calanoid copepod *B. gracilipes* was ~3‰ and ~4‰ lower relative to Fraction 1 in MW and ME, respectively (Fig. 5e).

The  $\delta^{13}\text{C}$  values of bulk crustacean zooplankton samples (Fraction 2) reflected the result of a different species composition among lakes. As the copepod *B. gracilipes* is the dominant species in both lakes, the variation in  $\delta^{13}\text{C}$  values for the bulk zooplankton samples was likely related to copepod proportions. However, in the summer, Fraction 2 was constituted by a combination of copepods and *C. dubia* (Table 2) which may have influenced the  $\delta^{13}\text{C}$  values, since they have contrasting  $\delta^{13}\text{C}$  values (Fig. 5e). Interestingly, the  $\delta^{13}\text{C}$  values of summer crustacean zooplankton in MW were close to those of *B. gracilipes* due to its dominance in summer samples (Table 2, Fig. 5d,e). In contrast, in ME the  $\delta^{13}\text{C}$  values were higher since they were more influenced by

*C. dubia* signatures because of its higher biomass in this lake (Table 2, Fig. 5d,e).

We found a positive significant correlation between the water color and the carbon isotopic signatures of crustaceans (Pearson correlation  $r = 0.710$ ;  $p = 0.048$ ;  $n = 8$ ) (Fig. 6), by pooling the data obtained in both Moreno lakes.

#### 4. Discussion

##### 4.1. Seasonal dynamics of the allochthonous indicators and the zooplankton $\delta^{13}\text{C}$ signatures

Water color, the Color:Chla ratio and the zooplankton  $\delta^{13}\text{C}$  fluctuated concomitantly and consistently in both lakes, even considering that the Color:Chla ratio and the zooplankton  $\delta^{13}\text{C}$  values are independent measurements analyzed using different methods. Overall, the seasonal pattern observed in water color dynamics (Fig. 5a) was closely reflected by changes in the Color:Chla ratio and by the zooplankton  $\delta^{13}\text{C}$  in Moreno lakes (Fig. 5c,d).

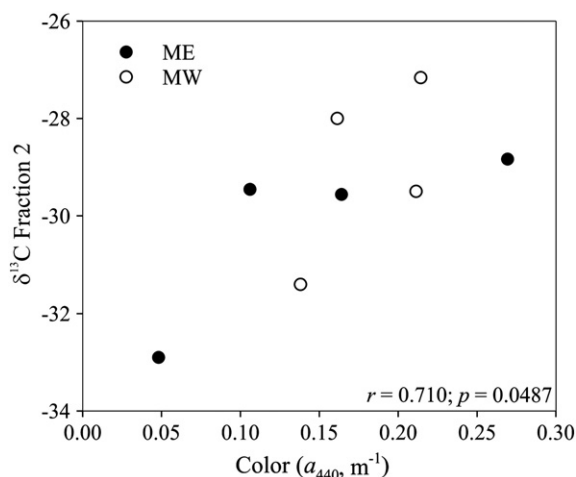
It is accepted that major water inflows are the primary source of allochthonous material to lakes by increasing the runoff and stream discharges, by flushing accumulated dissolved organic matter from upper soil horizons (Hongve et al., 2002; Pace and Cole, 2002; Eimers et al., 2008). In both Moreno lakes, the relative high values of water color registered in fall were related to the beginning of the precipitation events (Figs. 4, 5a). The increment of water level observed during fall and winter in Moreno lakes was closely associated with strong precipitation episodes in the catchments of both lakes (Fig. 4). However, the high levels recorded during spring were likely due to snowmelt, since precipitation diminished drastically (Fig. 4). The spring snowmelt period was associated with the lowest color values in both lakes (Fig. 5a), and there are several factors that could account for the spring decrease in water color. On the one hand, these low color values might reflect a low incidence of new terrestrial inputs of organic matter during spring snowmelt. This also suggests that the snowpack at high-altitude rocky substrates of the catchments do not contribute substantial organic material to the lake during snowmelt. Extremely low color values obtained in the four lotic tributaries of the Moreno lakes in spring supported this assertion (data not presented). The input of these clear streams likely produced a “dilution effect” in the lakes by decreasing the color values. This contrasts to the effect of the torrential autumn rainfall which enhances the runoff from forested soils, transporting dissolved organic materials from the terrestrial environment to the lakes.

A regionally significant factor might also account for the low color values observed in spring. The high levels of solar radiation (especially ultraviolet radiation, UVR) experienced in Patagonia from early spring are known to exert profound effects on whole lake dynamics including the transformation of dissolved organic matter (Zagarese et al., 2001;

**Table 2**

Seasonal structure and biomass ( $\mu\text{g L}^{-1}$  of fresh weight) of zooplankton from Lakes Moreno East (ME) and Moreno West (MW). Fraction 1: 50–200 µm, Fraction 2: > 200 µm. Mean zooplankton biomass at each sampling date was obtained averaging biomasses across sampled depths. Standard errors are not shown for clarity. Winter data of rotifers and crustaceans from ME is lacking due to sampling constraints explained in the Method section. Dominant biomass is indicated in bold.

Group	Species	Fall		Winter		Spring		Summer	
		ME	MW	ME	MW	ME	MW	ME	MW
Fraction 1	Nauplii of calanoid copepods	1.45	1.57	–	<b>9.30</b>	4.68	1.80	0.80	1.32
	Rotifers	<b>68.49</b>	<b>58.00</b>	–	<b>9.01</b>	<b>25.56</b>	<b>16.58</b>	<b>18.59</b>	<b>16.97</b>
	Protozoa	<i>Polyarthra vulgaris</i> , <i>Synchaeta pectinata</i> , <i>S. kitina</i> and <i>Conochilus unicornis</i>							
		10.17	17.45	10.66	5.24	11.78	13.02	8.07	8.99
Fraction 2	Cladocera	<i>Ophrydium naumanni</i>							
		0.95	12.22	0.37	2.62	10.21	<b>33.45</b>	3.20	2.62
	Copepoda	<i>Stentor araucanus</i>							
		6.25	2.64	–	5.29	2.11	7.05	<b>17.44</b>	<b>10.57</b>
		1.45	5.57	–	5.52	2.23	5.90	1.03	0.21
	Cyclopoids	<i>Ceriodaphnia dubia</i>							
		<b>80.36</b>	<b>80.65</b>	–	<b>164.33</b>	<b>73.34</b>	<b>93.90</b>	<b>22.58</b>	<b>18.82</b>
		1.17	4.55	–	0.71	3.21	3.33	3.21	7.86



**Fig. 6.** Relationship between water color ( $a_{440}$ ,  $m^{-1}$ ) and  $\delta^{13}C$  in the zooplankton Fraction 2 in Lake Moreno East (ME) and Moreno West (MW),  $r$  = Pearson product moment correlation coefficient.

Pérez et al., 2003). The breakdown of the organic molecules by direct light absorption and/or indirectly due to the action of photoproducted oxidants progressively reduces water color, which in turn determines a higher penetration of UVR, thereby creating a positive feedback loop (Zagarese et al., 2001; Neale et al., 2003). Furthermore, the wind stress affecting temperate lakes of Patagonia in spring produces major heat losses and deeper mixed layers, flushing unexposed labile molecules from deep and dark layers to near surface, leading to increasing photobleaching due to a higher molecular vulnerability to UVR (Neale et al., 2003).

In contrast, the moderate increase observed in the values of water color during summer coincided with a different hydrological scenario, characterized by a drastic diminution of lake level. The decreasing lake levels are apparently caused by lower inputs of water and higher evaporation losses. Indeed, in the Moreno lakes region, the evaporation exceeds precipitation during summer (R. Rapacioli, unpubl. data). The summer increase in water color was unexpected considering the potential impact of photobleaching due to high PAR and UVR at that time of the year (Alonso et al., 2004). However, photooxidation levels in late summer could be low due to the cumulative exposure to conditioning solar radiation during spring and early summer, as has been reported by Lindell et al. (2000). Even so, new inputs of organic matter from the landscape during summer should not be ruled out. In fact, streams continue flowing into lakes, although the water input is noticeably lower. Furthermore, the summer rainfall in this region, even scarce in volume, is concentrated in short periods of time producing occasionally torrential events, eroding dry soils and ultimately producing pulses of allochthonous matter inputs into lakes. Overall, these findings provide insight into the natural interaction of the terrestrial surrounding with these large and deep clear lakes.

In this scenario, the positive correlation between the water color and the zooplankton  $\delta^{13}C$  (Fig. 6), led us to infer the existence of inputs of allochthonous organic carbon into the pelagic consumers. This rationale seems plausible even though we lack the  $^{13}C$  signatures for end members, phytoplankton and terrestrially derived carbon. In fact, several studies have pointed out that allochthonous organic matter has greater  $\delta^{13}C$  values than those from phytoplankton (del Giorgio and France, 1996; Jones et al., 1998; Pulido-Villena et al., 2005). Thus, we propose that the high  $\delta^{13}C$  values registered during fall in both Moreno lakes could be indicative of a greater allochthony in the zooplankton, associated to the external inputs of dissolved organic carbon enhanced by precipitation and runoff. In addition, the lowest  $\delta^{13}C$  values observed during spring coincided with the lowest color values in both lakes (Fig. 5a).

The transfer of allochthonous dissolved organic matter into the food webs largely depends on bacteria, leading to heterotrophic energy mobilization, which is a process analogous to the autotrophic energy mobilization by phytoplankton (Karlsson et al., 2003; Jansson et al., 2007). The allochthonous dissolved organic carbon incorporated into bacterial biomass is then transferred into higher trophic levels by zooplankton grazers (Jansson et al., 2007). Bacteria are efficiently consumed by phagotrophic organisms such as flagellates and ciliates and also by certain filter feeding zooplankton, such as cladocerans. Interestingly, in the Lake Moreno West, the mixotrophic nanoflagellate *C. parva* can feed on bacteria with high ingestion rates (Queimaliños, 2002). Additionally, the mixotrophic ciliates *O. naumanni* and *S. araucanus* also ingest bacteria although they are primarily photosynthetic organisms (Woelfl and Geller, 2002; Modenutti et al., 2008). The transfer of the allochthonous organic carbon to rotifers of the smaller Fraction 1 could have occurred either by direct feeding on bacteria, or through intermediate bacterial consumers, such as the bacterivorous nanoflagellates prevailing in the Moreno lakes (Queimaliños, 2002). Thus, mixotrophic ciliates and rotifers could constitute a link between the dissolved organic matter and higher trophic levels in the Moreno lakes.

In our study, the larger zooplankton of Fraction 2 had lower  $\delta^{13}C$  values than those of Fraction 1, probably suggesting a lower terrestrial carbon subsidy (Table 2, Fig. 5d). We interpreted that the “lighter”  $\delta^{13}C$  values observed in the case of Fraction 2 might reflect that *B. gracilipes* feeds on “lighter”  $\delta^{13}C$  plankton. This idea is based on the assumption that the higher  $\delta^{13}C$  of allochthonous carbon sources are likely diluted by the contribution of a lower  $\delta^{13}C$  algal component (del Giorgio and France, 1996; Pulido-Villena et al., 2005). This is supported by the fact that *B. gracilipes* of MW consumes mixotrophic nanoflagellates and small ciliates, as well as the autotrophic dinoflagellate *G. paradoxum* (Balseiro et al., 2001). These feeding features could involve the alternative use of autochthonous and allochthonous carbon, and may help to explain the “lighter”  $\delta^{13}C$  values found in Fraction 2. A more detailed analysis of the summer  $\delta^{13}C$  values in the crustacean community could also indicate species-specific differences in food sources. While the calanoid copepod *B. gracilipes* appeared linked to an algal carbon source associated with lighter  $\delta^{13}C$  values, the isotopic signatures of the cladoceran *C. dubia* would indicate a higher contribution of carbon of terrestrial origin, probably due to its bacterivorous behaviour. The differences observed in the  $\delta^{13}C$  measured in *Boeckella* and *Ceriodaphnia* coincided with the pattern obtained by Karlsson et al. (2007). These differences may be based on their feeding behavior, more selective and raptorial in the case of the copepod in contrast to the cladoceran which has a less discriminative filter-feeding behavior (Lampert and Sommer, 2007).

Allochthony in zooplankton can also be influenced by direct consumption of particulate organic matter (POM) (Grey et al., 2001; Pace et al., 2004; Masclaux et al., 2011), as well as by the inputs of non-pigmented low molecular weight compounds (LMWC) of terrestrial origin into the microbial food web (Berggren et al., 2010). Even though we lack information about the actual inputs of POM and non-pigmented LMWC in Moreno lakes, we suspect that these fractions are also incorporated through precipitation, ultimately contributing to the potential allochthony in their pelagic food webs. Nevertheless, further studies are necessary to confirm if the natural zooplankton  $\delta^{13}C$  signature can act as other allochthonous indicator in these ultraoligotrophic lakes.

#### 4.2. Among-lake variations of allochthonous indicators

HGM features, the catchment aspects and the relative position of Moreno lakes in the lake chain, in general, led to higher allochthonous indicators in MW compared to ME.

The higher WRT in ME likely explains its lower color values (Table 1), due to the fact that longer residence times lead to higher processing of dissolved substances. Indeed, it has been demonstrated



that photobleaching and microbial breakdown, processes (likely co-occurring in Moreno lakes), are favored by longer WRT and are responsible for the internal loss of colored substances (Rasmussen et al., 1989; Kratz et al., 1997; Håkanson, 2005; Webster et al., 2008). Furthermore, the particular morphometry of ME (a deeper fjord-like lake) determines a comparatively higher total volume and a 4.24-fold greater tropholytic zone (Table 1, Fig. 2b), responsible for the contrasting values of the hypolimnetic water color among lakes. Thus, we propose that the differences in water color between Moreno lakes are mainly given by their different WRT. Moreover, these differences could be accentuated because they are positioned within a chain, as it has been stated by Soranno et al. (1999). Other variables as  $Z_{\text{mean}}$  and the slope of the drainage area have been found to correlate negatively with water color (Rasmussen et al., 1989), adding explanation to the general lower values in water color of ME. At the same time, the higher Color:Chl $a$  ratio found in MW could respond indirectly to WRT through its influence on water color, as has been pointed out by Webster et al. (2008).

As far as we know, this is the first study which integrates processes in the water column of lakes with those occurring in the terrestrial environment in the remote Patagonian region. Undoubtedly, further investigations are needed to better understand in-lake processes responsible for the metabolism of terrestrial inputs in Moreno lakes. Nevertheless, the monitoring of the changes in allochthonous indicators appears as a useful tool to capture variations in the landscape induced by continuous and/or eventual processes.

## 5. Conclusions

In two ultraoligotrophic lakes of North Patagonia we found a seasonal variability in two allochthonous indicators, water color and Color:Chl $a$  ratio, as well as in the natural zooplanktonic  $\delta^{13}\text{C}$  signatures. Overall, the dissolved organic matter of terrestrial origin (water color) was low according to the trophic condition, and timed with precipitation and snowmelt. We found that the highest values of allochthony coincided with the beginning of the precipitation events in the fall and winter, when the runoff and stream discharges increased washing out dissolved organic matter from upper soil horizons. In contrast, the lowest values of allochthony in the lakes corresponded to the snowmelt period in the spring, suggesting that the snowpack at high-altitude rocky substrates contributed little with organic material during melting, producing accordingly a “dilution effect”. Furthermore, allochthony was usually higher in MW compared to ME, and the WRT appeared as the main factor explaining the differences among lakes, together with the higher perimeter-lake area ratio of MW. Seemingly, Color:Chl $a$  and zooplankton  $\delta^{13}\text{C}$ , tracked the dynamics of water color consistently in both lakes. The obtained positive correlation between water color and the crustacean zooplankton  $\delta^{13}\text{C}$ , led us to infer the existence of inputs of allochthonous organic carbon in pelagic consumers of these ultraoligotrophic lakes. The incorporation of this dissolved allochthonous material into higher trophic levels might be favored by relevant regional features of pelagic food webs, such as the dominance of bacterivorous planktonic organisms in these Patagonian lakes. Allochthony values were likely shaped by in-lake processes with a high impact at a regional level, such as photobleaching. Thus, our results point out to local morphometric, hydrologic and climatic conditions as critical factors controlling the magnitude of the allochthonous inputs to the Moreno lakes, and underscore the seasonal timing of the terrestrial subsidy to aquatic food webs in ultraoligotrophic lakes of Patagonia. Overall, we propose that due to their high sensitivity, ultraoligotrophic lakes of Patagonia are amenable for monitoring the impact of climate-driven forces and eventual alterations in the catchment.

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