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SHORT COMMUNICATION

Influence of seasonal freshwater streamflow regimes on phytoplankton blooms in a Patagonian fjord

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ABSTRACT

Large-scale regional phenomena and global climate trends may alter the freshwater discharge of large Patagonian rivers and could modify local circulation patterns in ways that influence phytoplankton dynamics. Modifications detected in the streamflow regime of the Puelo River (41.5° S, Patagonia, Chile) in recent decades may affect the regularity of seasonal phytoplankton blooms in Reloncaví Fjord. We examined the occurrence/frequency of spring–summer and autumn phytoplankton blooms in Reloncaví Fjord with respect to seasonal and inter-annual changes in freshwater streamflows from 2003 to 2011. Surface chlorophyll-a derived from satellite-ocean colour and phytoplankton abundances revealed that significant recurrences of autumn phytoplankton blooms ($> 2 \text{ mg Chl-a m}^{-3}$, $> 500 \text{ cell mL}^{-1}$) were associated with historical low mean freshwater streamflows, mainly in autumn ($< 350 \text{ m}^3 \text{ s}^{-1}$). On the other hand, the occurrence of spring–summer blooms was related to high streamflows ($> 470 \text{ m}^3 \text{ s}^{-1}$) that increased mixing in the upper photic layer enough to enhance phytoplankton growth. Our findings imply that the intensity of autumn blooms in Reloncaví Fjord could be modulated by streamflow strength.

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Chlorophyll-a; hydrological regimes; Patagonian fjords; phytoplankton blooms; satellite-ocean colour

Introduction

The coastal system of the Chilean Patagonia (41–53° S) has a highly complex geography composed of channels, islands and fjords. Subantarctic Waters (SAAW) interact strongly with freshwater input from precipitation and the discharge of large rivers, producing sharp horizontal and vertical salinity gradients (Clément 1988; Dávila et al. 2002; Iriarte et al. 2014). In this large region, the impingement of horizontal buoyancy input by freshwater runoff has an important effect on spatio-temporal patterns on phytoplankton dynamics including distribution of biomass. Stratifying effect of buoyancy is a key regulator of primary production: it limits the depth of turbulent mixing, thereby keeping phytoplankton cells within the photic zone. On the other hand, stratification isolates algae from their

principal source of macronutrients (mainly nitrate, orthophosphate) below the pycnocline, thus leading to the eventual shutdown of production after short blooms. Southern Patagonian fjords (48–53° S) are strongly influenced by snow and glacial melting. As a result, these fjords receive significantly higher loads of fine suspended sediments, which may limit the light available for photosynthesis in near-surface waters (González et al. 2013; Jacob et al. 2014).

Large-scale remote phenomena (e.g. Pacific Decadal Oscillation [PDO], El Niño and La Niña [ENSO], Southern Annular Mode [SAM]) and global climate trends may alter the freshwater discharge of large rivers such as the Puelo River. Dendrochronological reconstructions of Chile's North Patagonia have identified variable climatic and hydrological cycles over the last seven decades that are a function of global change (Lara et al. 2005, 2008). These cycles are characterised by marked declines in precipitation and streamflows, with high inter-annual variability. Recent paleoceanographic and dendrochronological studies have indicated the same pattern for Reloncaví Fjord, more southerly rivers (Baker River) and other northern fjords (Sepulveda et al. 2005; Rebolledo et al. 2011, 2015; Lara et al. 2016).

Although changes in climate are expected to alter the regional atmospheric (e.g. West Wind Drift) and local oceanic circulation in this region (Garreaud et al. 2013), the impact of these basin-scale changes on biogeochemical and phytoplankton community properties are still unclear (Lara et al. 2016). One major issue, especially under future scenarios of climate-driven changes on Patagonian hydrological regimes, is the coupling between freshwater fluxes and biological responses of the near coastal system in the outflow region of continental shelves. Increased rates of primary production and autotrophic biomass, together with the timing and development of algal blooms associated with freshwater inputs to the surface ocean, have been documented for major productive coastal areas; for example, Mississippi (Liu et al. 2004), Oregon (Frame & Lessard 2009) and the Concepción upwelling region (Iriarte et al. 2012). However, this classic pattern may not hold for the coastal waters of Patagonia. Freshwater input and flow to fjords, modulated mainly by pluvial and nival seasonal regimes, have been shown to be highly variable between years, with a historical decreasing trend (León-Muñoz et al. 2013). Seasonal bloom pulses in northern Patagonia are driven mainly by vertical mixing and the exchange of nutrients between the low-salinity, low-nutrient (except for silicic acid [Si]) surface layer and the more saline, nutrient-rich sub-surface layer (Iriarte et al. 2014 and references thereafter). In addition to light, any change or anomaly in the interplay between these two layers may affect phytoplankton growth.

Inorganic nutrient concentrations show a strongly seasonal signal associated mainly with intrusion of oceanic waters to inner waters of Patagonia: nitrate and orthophosphate are higher in winter and lower in spring–summer, caused by a sharp increase in primary productivity when light availability is greater in near-surface waters (González et al. 2011; Iriarte et al. 2013; Jacob et al. 2014). A second autotrophic biomass (as chlorophyll-a [Chl-a]) peak occurs in autumn months (March–April) following summertime nutrient replenishment (Iriarte et al. 2007). Recent evidence shows that the intensity of spring–summer phytoplankton blooms may vary strongly on inter-annual scales in association with variability in remote signals (e.g. PDO, ENSO, SAM; Lara et al. 2016). The aim of this study was to examine the relationship of surface phytoplankton biomass and dynamics with river streamflows in Reloncaví Fjord from 2003 to 2011. We tested the hypothesis that

intra-annual modifications in the streamflow regime of the Puelo River affected the frequency of seasonal blooms during this period. An 8 year analysis of satellite chlorophyll and phytoplankton abundances is insufficient to characterise long-term trends in coastal areas, and determining relationships between variables of land-ocean origins is very difficult. Our analysis was intended to document current trends in phytoplankton biomass and potential hydrological relationships in Patagonian fjords.

Methods

Study area

The estuarine condition of Reloncaví Fjord (41.5° S–72.5° W) is closely linked to high freshwater contributions from the drainage basin, particularly from the Puelo River (Figure 1). Incidental precipitation in the Puelo River drainage basin and Reloncaví

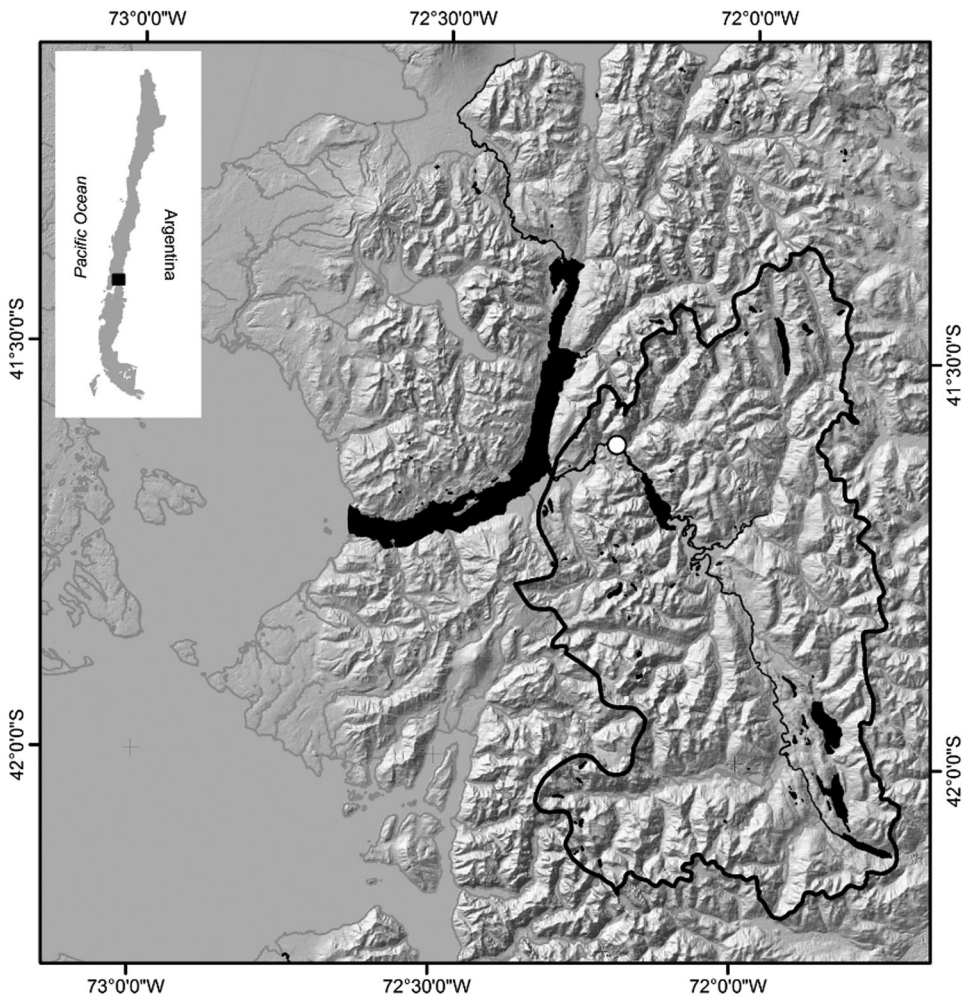


Figure 1. Reloncaví Fjord (black area) as part of the northern section of the marine system of Patagonia. The circle indicates the site used to measure streamflow at the mouth of the Puelo River.

Fjord is dominated by seasonal variations of the Southern Pacific Subtropical Anticyclone gyre off the Chilean coast, with mean precipitation of 2800 mm y^{-1} . The monthly streamflow of the Puelo River fluctuates widely, averaging c. $650 \text{ m}^3 \text{ s}^{-1}$ ($Q = 150\text{--}2350 \text{ m}^3 \text{ s}^{-1}$), and its hydrological year lasts from April of one year to March of the next. The river has a pluvio-nival regime (Figure 2) characterised by greater pluvial concentrations in winter and a higher influence from snowmelt in spring (Niemeyer & Cereceda 1984, León-Muñoz et al. 2013; Castillo et al. 2016). The temporal streamflow pattern of the Puelo River is significantly related ($r^2 = \text{c. } 0.9$, $P < 0.05$) to the other two main tributary rivers that empty into the middle sector (Cochamó River $Q = \text{c. } 100 \text{ m}^3 \text{ s}^{-1}$) and head (Petrohué River $Q = \text{c. } 350 \text{ m}^3 \text{ s}^{-1}$) of Reloncaví Fjord. To analyse the freshwater influence of the Puelo River on Reloncaví Fjord, we compiled data bases containing information on both the river (streamflow in $\text{m}^3 \text{ s}^{-1}$) and the fjord (surface satellite Chl-a in mg m^{-3} , phytoplankton abundance in cell mL^{-1}). We obtained detailed time series for abundances and composition of phytoplankton species between 2003 and 2011 from the data base of the 'Phytoplankton Monitoring Program' of Plancton Andino. Discrete quantitative samples were collected monthly from the surface photic layer. However, sampling was done more often and at more stations in spring, summer and fall. Phytoplankton samples were analysed for total abundances using standard inverted microscopy.

Chlorophyll-a satellite time series

Data on Chl-a concentrations between 2003 and 2011 (MODIS L3, 8 day, 4 km resolution) were obtained from the NASA website (<http://modis.gsfc.nasa.gov>). The OC3-MODIS standard product is a band-ratio algorithm that uses a ratio of the blue to green spectral regions to estimate Chl-a concentrations (Blondeau-Patissier et al. 2014). The data were

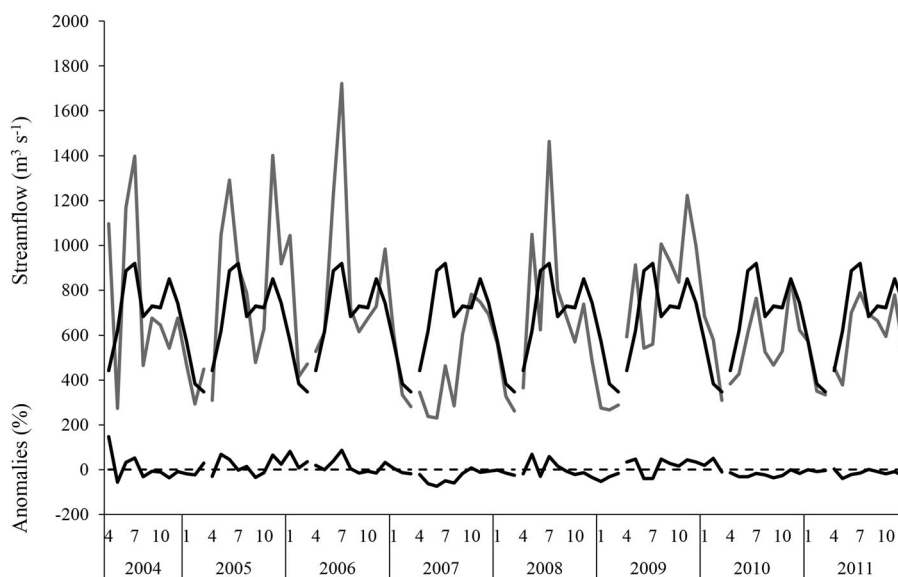


Figure 2. Puelo River streamflow (grey line) for this study period and historic means 1950–2015 (black line). The lower solid line corresponds to streamflow anomalies recorded during the study period.

processed using ENVI/IDL (version 4.8) software and converted into monthly time series of spatially averaged Chl-a in the study area (Lara et al. 2016). To avoid turbid pixels where the MODIS Chl-a is likely to be contaminated by anthropogenic effects and other substances (e.g. CDOM), we excluded all data from MODIS images situated less than 8 km from the coast from the analysis.

Puelo River streamflow time series

Streamflow information was obtained from the hydrological station Carrera Basilio (41.6° S; 72.2° W) of the Dirección General de Aguas de Chile (General Water Office of Chile). This database consists of the daily streamflow for the hydrological years 1944–to date. Carrera Basilio is the gauging station closest to the mouth of the Puelo River in the Reloncaví Fjord and offers a representative view of the total contributions from this river's drainage basin. The trend of the streamflow series was analysed using the non-parametric Mann-Kendall trend test and the regression of the Sen slope (Gilbert 1987; Helsel & Hirsch 1992). These statistical methods have been used to analyse seasonal data without a normal distribution (Zhang et al. 2001).

The data were processed in the MAKESENS application (Salmi et al. 2002) and analysed at the level of three seasonal scales: 1. hydrological years; 2. months; and 3. ratios between months. Satellite Chl-a data and phytoplankton abundances were analysed in function of the frequency of occurrence of the Puelo River streamflows. For this, we generated a flow duration curve (FDC) with the streamflow data gathered between 1944 and 2015. This approach is commonly used to analyse streamflow series with large data (Liucci et al. 2014). Later, each measurement of satellite Chl-a and phytoplankton abundance was paired with the percentage of excess/residual obtained from the FDC; that is, with the percentage of time that the specific streamflow on the day of monitoring would have been equal to or greater than during the last seven decades. In order to analyse the freshwater influence of the Puelo River on the Reloncaví Fjord, we performed continuous wavelet transform (CWT) and cross wavelet transform (XWT) analyses (Grinsted et al. 2004; Cazelles et al. 2008). This approach evaluates the associations (time-frequency) between variables at the seasonal level (Labat 2005; Marcé et al. 2010). Specifically, the application of XWT allows us to determine the common power of two CWT decompositions, identifying when two series oscillate in a common frequency, be it in phase (e.g. simultaneous maxima) or in anti-phase (e.g. simultaneous maxima and minima). The areas of significance in the wavelet graphs were estimated using Monte Carlo techniques (Grinsted et al. 2004). The CWT and XWT analyses were developed using software provided by Aslak Grinsted (<http://www.pol.ac.uk/home/research/waveletcoherence/>).

Results and discussion

Current trends in the Puelo River streamflow

During the study period (December 2003–December 2011), we observed high intra-annual variability in the Puelo River's hydrological regime (Figure 2). The hydrological years ranged from mixed regimes with high volumes of freshwater in the winter (rain) and spring (snowmelt) to years with streamflows that fell below the historic ranges

(Figure 2), resulting in nival regimes (as occurred in springtime 2007). León-Muñoz et al. (2013) reported a decreasing pattern for the Puelo River streamflow over the last six decades. This tendency has been tied mainly to the summer months (January–February) and especially autumn (May) (Table 1). Considering the global prognoses for precipitation in the coming decades (Polade et al. 2014), the rivers of northern Patagonia can be expected to register a greater recurrence of years with slow summertime–autumn streamflows, as already have been observed during the hydrological years 2007, 2010 and 2011 (Figure 2). River discharge remains primarily dependent on the climate conditions that determine a river's hydrological processes. Large Patagonian rivers have experienced minimal hydro-morphological intervention, and their drainage watersheds retain vast coverage by native forests, which have high levels of nutrient recycling and streamflow controls (Oyarzún et al. 2011). These conditions determine the course of oligotrophic waters, with natural discharge that transport low concentrations of inorganic nitrogen (Perakis & Hedin 2001). Inorganic nutrients through the top 15 m at the fjord showed a marked seasonal variability during summer and winter seasons. The upper surface layer (5 m) were remarkably poor in NO_3^- ($< 3 \mu\text{M}$) and PO_4^{3+} ($< 0.7 \mu\text{M}$) in the summer (January–February), increasing at the 15 m depth below the halocline (NO_3^- : 10–22 μM ; PO_4^{3+} : 0.8–1.8 μM); whereas the vertical distribution of Si showed maximum values of 50–100 μM in the surface layer (0–10 m). During winter months Si concentrations were high ($>30 \mu\text{M}$), and NO_3^- and PO_4^{3+} were also high at 6–22 μM and $>1 \mu\text{M}$, respectively.

Relationships between streamflow and phytoplankton

The satellite Chl-a and phytoplankton abundances observed in Reloncaví Fjord between December 2003 and December 2011 described clear seasonal patterns (Figure 3) as a function of the ranges of the Puelo River streamflow (Figure 4). The phytoplankton abundance, normally dominated by *Skeletonema* spp., revealed a marked springtime peak, with maximum values near 20,000 cells mL^{-1} and a mean of 6500 cell mL^{-1} . In spring, several species of the microphytoplankton size-fraction ($>20 \mu\text{m}$) is dominated by chain-forming diatoms of the genera *Skeletonema*, *Chaetoceros*, *Thalassiosira* and

Table 1. Non-parametric Mann-Kendall trend test and the regression of the Sen slope for the Puelo River monthly average streamflow (1950–2013).

Month	Z test	Significance level	Estimated Sen slope
Annual	−2.31	*	−1.59
January	−2.47	*	−2.87
February	−2.69	**	−1.89
March	−1.93	+	−0.98
April	−0.84		−0.59
May	−2.82	**	−5.24
June	0.05		0.21
July	−0.34		−0.72
August	−1.07		−1.83
September	0.16		0.16
October	−0.32		−0.27
November	−1.69	+	−2.75
December	−0.99		−1.64

Data source: Dirección General de Aguas de Chile.

** if trend at $\alpha = 0.01$ level of significance.

* if trend at $\alpha = 0.05$ level of significance.

+ if trend at $\alpha = 0.1$ level of significance.

Rhizosolenia. Phytoplankton abundances declined from summer to autumn to winter, with greater recurrences in spring and summer, when the Puelo River presented streamflows between 470 and 620 m³ s⁻¹. In winter a few diatoms belonging largely to the genera *Skeletonema* and *Navicula* as well as the species *Thalassionema nitzschioides* are present in surface waters. Likewise, in autumn, important occurrences of high phytoplankton levels were also observed when streamflows were lower than 350 m³ s⁻¹ (Figure 4B). Species such as *Rhizosolenia setigera* and *Thalassiosira subtilis*, and genera *Coscinodiscus* and *Leptocylindrus*, dominate during autumn months. Although both freshwater and marine diatoms are abundant in fjord sediments, a decreasing trend in freshwater diatom relative abundances during the 20th century have been associated with a decrease in river streamflows and the occurrence of El Niño events (Rebolledo et al. 2011, 2015).

Satellite measurements of Chl-a showed a seasonal pattern with mean values between 2 and 4 mg m⁻³ in spring, summer and autumn (Figure 3). The analysis performed on the bi-weekly data revealed a marked peak in autumn, when the distribution of concentrations was greater than that recorded in spring and summer (e.g. maximum value: 11.1 mg m⁻³; mean value: 2.4 mg m⁻³) (Figure 3). Satellite Chl-a presented a greater occurrence of measurements with concentrations between 2 and 12 mg m⁻³ during autumn months that coincided with Puelo River streamflows lower than 350 m³ s⁻¹. In spring, we noted a second grouping of measurements with high satellite Chl-a concentrations, this one associated with greater streamflows, in the order of 700 m³ s⁻¹ (Figure 4A–B).

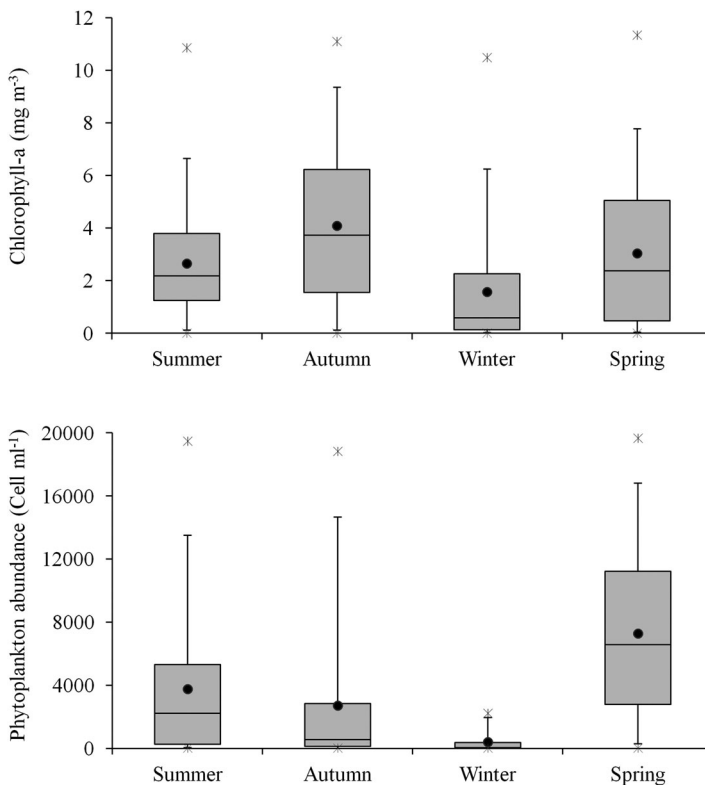


Figure 3. Seasonal mean satellite chlorophyll-a (mg m⁻³) and phytoplankton abundances (cell mL⁻¹) between December 2003 and December 2011.

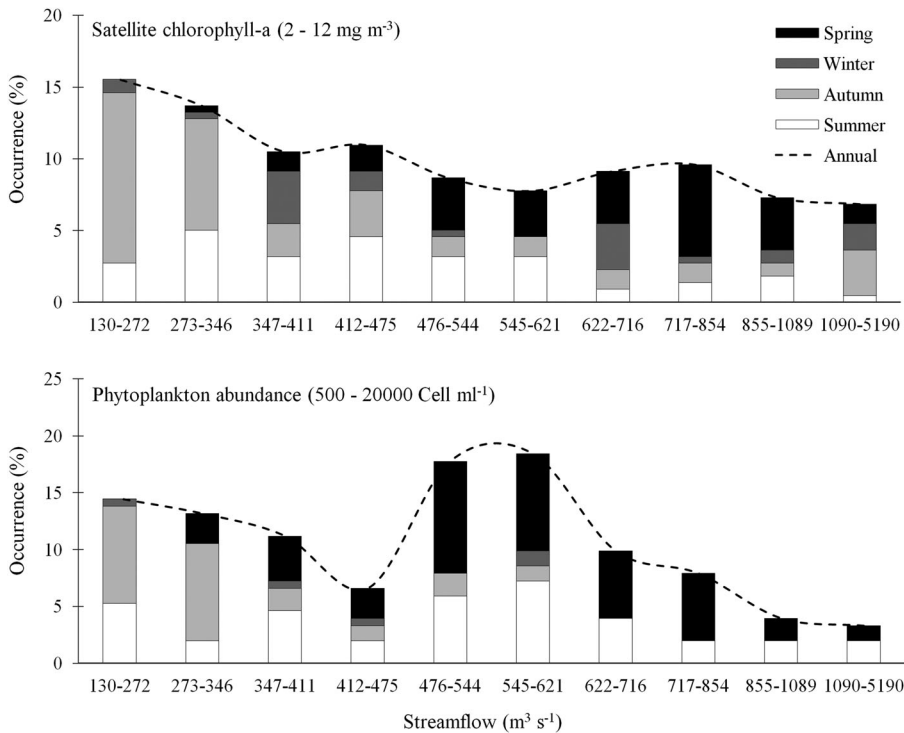


Figure 4. Seasonal variability of satellite chlorophyll-a (mg m^{-3}) and phytoplankton abundances (cell mL^{-1}) as a function of the frequency of occurrence of the Puelo River streamflows ($\text{m}^3 \text{s}^{-1}$).

The XWT analysis showed significant coupling between the Puelo River streamflow record ($\text{m}^3 \text{s}^{-1}$) and Reloncaví Fjord satellite Chl-a concentrations at different periods (Figure 5). A significant common annual oscillation was present from 2004 to 2010, but missing during 2011 and 2012, coinciding with the absence of peak streamflows larger than $1500 \text{ m}^3 \text{s}^{-1}$. Significant common oscillations at lower periods (c. 6 months, c. 80 days, c. 40 days and c. 1 day) were intermittent, appearing only in particular years in the time series. In general, there was an inverse relationship between streamflow and Chl-a concentration (series in anti-phase, see green arrows pointing to the left in Figure 5). The coupling between streamflow and Chl-a concentration moments was stronger during high streamflow periods (winter 2005, 2006, 2008). Specifically, the significant coupling between these two variables were noted mainly in late autumn and winter, with streamflow records near or above the historic averages, when the Puelo River reached its highest discharge levels (Figures 2 and 5).

During dry autumns (as occurred in 2007, El Niño phase: January–June 2007), the low streamflows of the Puelo River ($<350 \text{ m}^3 \text{s}^{-1}$) and satellite Chl-a records were uncoupled. Those results indicated more frequent high Chl-a concentrations and phytoplankton abundances in surface waters during drier autumns (Figure 6). Therefore, the following conceptual model could explain the pattern observed in temperate phytoplankton blooms: the development of phytoplankton autumn blooms and diminished streamflows lead to a significant shallowing of the freshwater mixed layer, which coincides with the summer remineralisation/recycling of nitrate (mean = $10 \mu\text{M}$) and orthophosphate

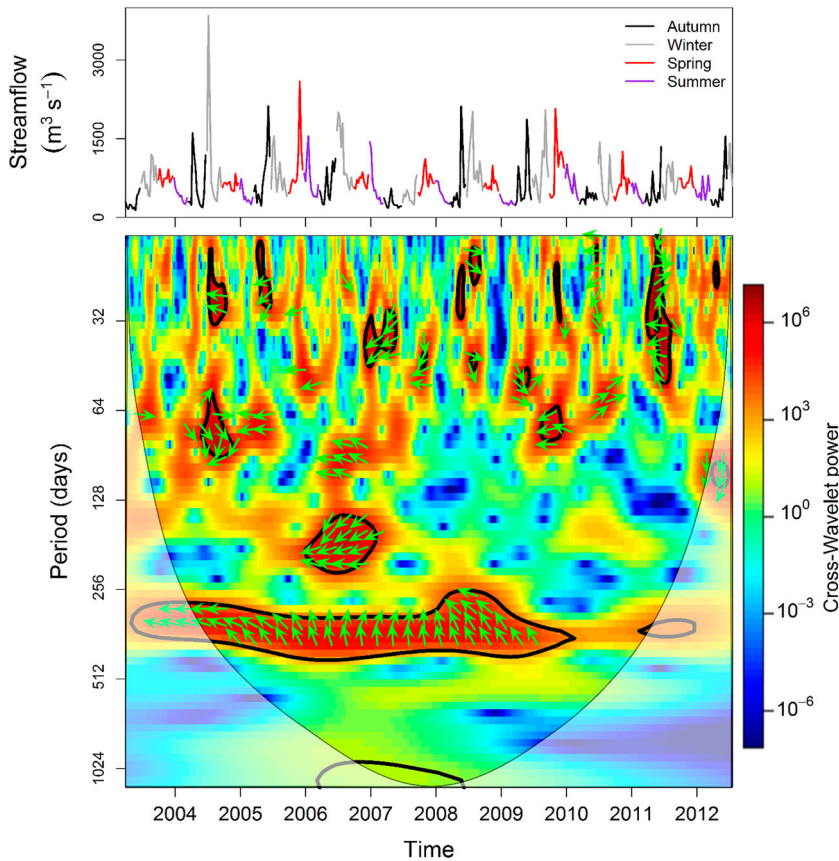


Figure 5. Spectral cross-wavelet power between the Puelo River streamflow and chlorophyll-a in Reloncaví Fjord. The black contour lines indicate coherent oscillations at significance levels of $P < 0.05$; the arrows identify the phase of the ratio between the variables (right = phase, left = anti-phase).

(mean = $1.5 \mu\text{M}$) concentrations coming from oceanic water in the upper layer. Sudden high irradiation in late winter and early spring, in combination with the seasonal change in direction of the south winds, will allow advection of waters of high nutrient concentrations into the photic layer along with intermediate and high freshwater flows. All these factors create optimal conditions for high spring phytoplankton growth, leading to assemblages dominated by chain-forming diatoms, high primary productivity rates and high autotrophic biomass.

Conclusion

According to the conceptual model detailed herein: high (low) fresher streamflows cause the formation of deep (shallow) mixed layer and strong (weak) pycnocline, leading to rapid water column fluctuations in irradiance (high near the surface, low near the pycnocline) and nutrients (low near the surface, high near the pycnocline), which may enhance phytoplankton growth through the photic layer. As we stated in our general hypothesis, the freshwater input to the Patagonian fjords is modulated by both pluvial and nival

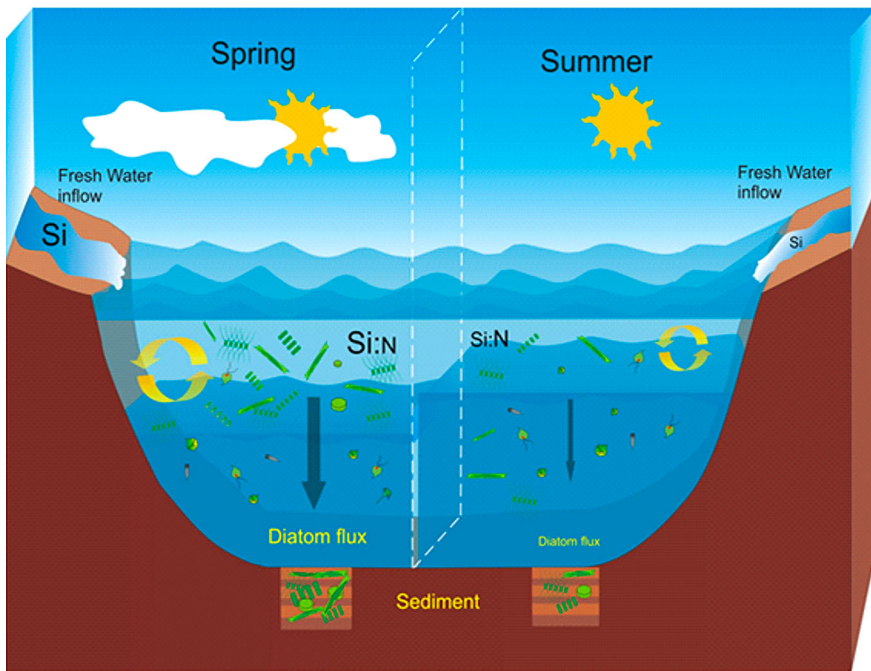


Figure 6. Conceptual model for the north section of the Patagonian fjord showing higher freshwater inflows (winter–spring) and lower freshwater inflows (summer–autumn) to the fjords. We hypothesise that seasonal low freshwater discharge could decrease Si (silicic acid) concentrations in the northern Chilean fjords, thereby explaining partially future scenarios of low dissolved Si:N ratio, favouring non-siliceous-requiring phytoplankton species at the expense of diatoms. Reduced autumn streamflows might result in a dominance of flagellate species in coastal waters of southern Chile.

seasonal regimes, which have been highly variable between years during the last 15 years. Therefore, future changes in streamflow patterns linked to changes in the regional atmospheric circulation (e.g. decreasing the West Wind Drift) and most probably local ocean circulation in this region, including the expansion to the north of SAAW (Cubillos et al. 2014), could have major implications for spring–autumn bloom dynamics in high-latitude fjord systems.

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Disclosure statement

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