



Low spring primary production and microplankton carbon biomass in Sub-Antarctic Patagonian channels and fjords (50–53°S)

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ABSTRACT

It is relevant to understand the processes and factors that modulate the efficiency of the carbon pump throughout the ecosystem of Patagonian fjords. Spatial variability of primary productivity and bacteria-microplankton biomass was assessed in relation to inorganic nutrients and stratification across nearshore zones of southern Patagonia (50–53°S) in austral spring 2009. Estimates of primary productivity ($300\text{--}500\text{ mg C m}^{-2}\text{ d}^{-1}$) and phytoplankton biomass ($9\text{--}180\text{ mg chlorophyll-}a\text{ m}^{-2}$) were low at offshore and inshore waters. Synergistic effects of low silicic acid concentrations and poor light penetration because of salinity-driven stratification of glacier meltwater in springtime appeared to negatively affect phytoplankton carbon biomass and primary production in this sub-Antarctic region. The knowledge of the relative importance of nutrient sources and light is especially significant for Patagonian glacier-fjord systems that are expected to receive higher freshwater inputs and will be more stratified in the future.

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Plankton carbon; fjords system; Patagonia primary production; freshwater haline stratification

Introduction

Patagonian fjord systems are responsible for a significant portion of primary productivity (PP; Iriarte et al. 2007; González et al. 2010; Torres et al. 2011). Sub-Antarctic water (SAAW) enters the fjords of Chile's Patagonian region (41–55°S), and strong seasonal climatic changes (e.g., solar radiation, West Wind Drift, heavy freshwater streamflows, and precipitation; Dávila, Figueroa, and Muller 2002; Pickard 1971; Torres et al. 2014) affect the pelagic biota, causing seasonal/cyclic shifts in abundance, biomass, and productivity. Coupling between freshwater inputs (from rivers and glaciers), nutrients, and biological responses of coastal systems in the outflow region of Patagonia's inner seas has been a major oceanographic issue in the past fifteen years, especially given actual scenarios of climatic-driven

hydrological regime changes (León-Muñoz et al. 2018). Early studies have pointed out that Patagonian fjords are thought to be sinks for atmospheric CO₂ (Torres et al. 2011), and they are important aquatic systems where high concentrations of organic matter and biogenic opal contents in the sediments have been associated with high primary productivity estimates (Aracena et al. 2011; Silva and Prego 2002). A combination of physical (stratification) and chemical (nutrients) properties has been reported to determine high primary production in spring and summer (up to $4\text{ g C m}^{-2}\text{ d}^{-1}$) in the inner sea of northern Patagonia (Iriarte et al. 2007; Jacob et al. 2014). There, primary production and phytoplankton biomass are dominated by highly silicified chain-forming diatoms (Iriarte and González 2008). Increasingly, mesoscale studies

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have been used to explore the spatial variability of phytoplankton biomass in the Patagonian fjord region and the physical and chemical forcings that modify this biomass (Lara et al. 2016; Lutz et al. 2016). Phytoplankton of different size classes could support different pathways of materials (such as biomass) in the food web (Legendre and Rassoulzadegan 1995). In the Patagonian fjord system, smaller phytoplankton (cell size less than 20 μm : pico- and nanoplankton, such as cyanobacteria and flagellates, respectively) fuel a microbial food web within the photic layer, while larger microphytoplankton (cell size greater than 20 μm : diatoms and dinoflagellates) are an important component of the “classical” food chain (González et al. 2010, 2011). Diatoms are a large-cell-sized phytoplankton species, dominant in spring and summer months and they constitute the principal biomass (e.g., carbon) source of matter and energy through food chains in the northern highly productive fjord region (41–43°S; González et al. 2010; Jacob et al. 2014). The dominance of large-size phytoplankton is often related to optimal-growth environmental conditions (i.e., radiation and nutrient availability); if nutrients and light are low, any increase in cell surface/volume ratio should give a clear competitive advantage to pico- and nanoplankton size groups (Kjørboe 1993). In addition, an influx of dissolved organic matter from rivers as well as inorganic nutrients from deep waters could significantly enhance the growth of bacterioplankton and bacterial secondary production in the fjord region (Montero et al. 2011; Olsen et al. 2014) and augment the eventual transfer of this organic matter to higher trophic levels (e.g., heterotrophic nanoflagellates, micro- and mesozooplankton; Vargas, Martínez, and González 2008).

Previous results from the northern section of Patagonia (41–43°S) strongly suggest that nitrogen sources (mainly inorganic sources, such as nitrate and ammonia) could play a major role in sustaining relatively large spring and summer primary production (2–4 $\text{g C m}^{-2} \text{d}^{-1}$), thereby acting as a “limiting” nutrient for phytoplankton growth (Iriarte et al. 2007; Olsen et al. 2014). However, coastal waters in the southern section of the Patagonian fjords (50–53°S) are poor in silicic acid (González et al. 2013; Torres et al. 2014). In this context, we hypothesize that low silicic acid waters (low Si:N ratio) could lead to lesser growth of diatoms (cell numbers, biomass, primary production), and thus the whole phytoplankton assemblage structure. Furthermore, a deviation from N to Si (or vice versa) limitation may lead to blooms of harmful diatom

and dinoflagellate species (e.g., *Pseudo-nitzschia* spp., and *Alexandrium catenella*), a situation in which toxin production may also be triggered as the silicic acid-to-nitrate ratio changes (Ryan et al. 2017). The aim of this study was to assess the spring variability in microplankton biomass and the productivity of phytoplankton along several transects of the inner sea of south Patagonia, which is influenced by freshwater inputs from coastal rivers and glaciers. Microplankton biomass (both microzooplankton and phytoplankton cell carbon and chlorophyll-*a*) and primary production were analyzed and combined in order to better understand the magnitude of primary production rates and interpret the springtime spatial variability of microplankton biomass within the freshwater-driven system of Patagonian fjords and channels.

Methods

Study area and field-sampling design

Chile’s southern Patagonia (41–54°S) consists of an extensive inner sea that includes channels, fjords, and bays. As is typical of most high-latitude fjord ecosystems, the physical and chemical conditions of the upper layers of the water column are strongly influenced by freshwater input, primarily from several rivers (streamflows greater than 1,000–2,500 $\text{m}^3 \text{s}^{-1}$) and abundant rainfall (2,000–6,000 mm) throughout the year (Calvete and Sobarzo 2011; Dávila, Figueroa, and Muller 2002). River streamflow regimes ranged mainly from winter pluvial regimes in the northern section (41–43°S) to spring and summer nival regimes in the southern section (43–54°S; Dávila, Figueroa, and Muller 2002). Glacial melting is another important source of freshwater. Indeed, the central section of Chilean Patagonia (46–50°S) is home to the Northern and Southern Icefields in the Southern Hemisphere. There, the marine ecosystem is a positive estuarine system in which the oceanic SAAW, with relatively high salinity (31–33 psu) and high nutrient loads, enters the fjord area below a surface layer of fresher water (2–20 psu; González et al. 2010; Sievers and Silva 2008).

Samples were taken during a synoptic field survey, CIMAR 15 Fiordos (Ciencias Marinas C15F) cruise, which covered the region from 50–53°S. Oceanographic samples were taken from several channels and fjords (Concepción, Inocentes, Collingwood, Unión, Sarmiento, Smyth, Kirke, Valdes, Almirante Montt, Señoret) during austral spring, from October 11 to November 19, 2009 (Figure 1). For comparative analyses of post-spring bloom conditions we considered the primary productivity estimates collected at three oceanic stations located at the northern sites of

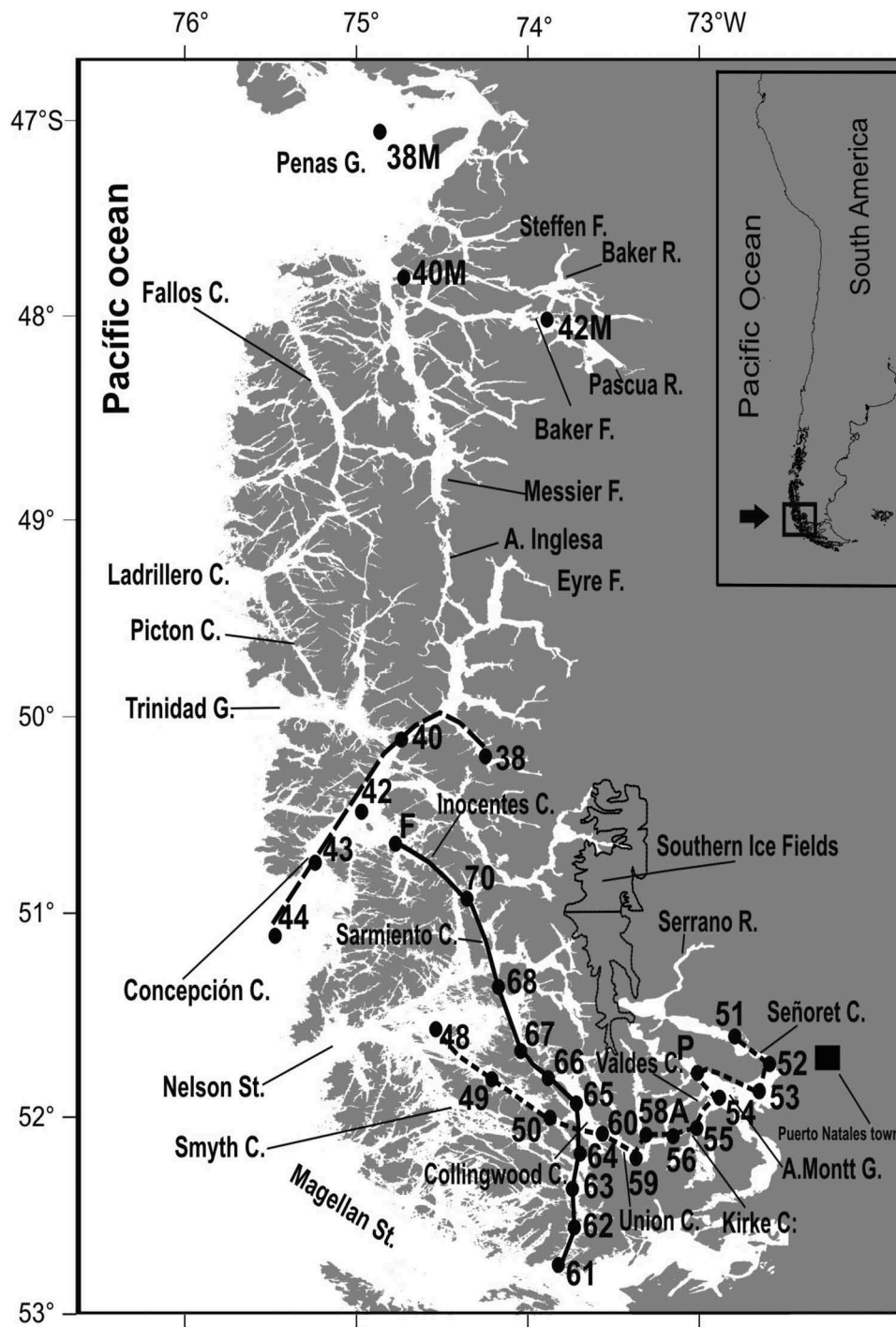


Figure 1. Map of the study area showing the stations sampled along three transects during CIMAR15 (dashed and continued lines): Concepción Channel, Sta. 40–44; Inocentes Channel to Smyth Channel, Sta. F-61; Smyth Channel to Señoret Channel, Sta. 52–59 and Sta. 48–50, including the processes station (P). The three stations sampled during the MIRAI (MR08-06) cruise are located in the northern section of the map (38M, 40M, 42M).

the main study area (Golfo de Penas, 47–48°S) during an earlier MIRAI (MR08-06; JAMSTEC: Japan Agency for Marine-Earth Science and Technology) research cruise carried out in March 2009 (austral fall). Given the geographic and environmental complexities as well as the paucity of spatial mesoscale information of

southern Patagonia (replication in time and space), we assumed that any significant relationship among biological and environmental variables would apply across the entire region covered in this study. In this context, the C15F and MR08-06 observations covered a wide range of spatial scales and were used to investigate the

influence of freshwater inputs on water-column stability, variability in nutrient concentrations, and regional-scale plankton biomass. Data on plankton biomass (bacteria, nanoflagellates, phytoplankton, microzooplankton), carbon pools (POC), sea temperature, salinity, dissolved oxygen, inorganic nutrients, and chlorophyll-*a* concentrations were estimated during basin-wide oceanographic transects that crossed the inner sea of southern Patagonia. Additionally, biological rates for primary production (oxygen evolution) and respiration from the plankton community (community respiration = CR) were estimated at a selected station (P = processes station).

Physical and chemical properties

Twenty-seven oceanographic stations were sampled during C15F on board the R/V *Vidal Gormaz*. Three transects were sampled in the upper 100 m (Figure 1): two with a north-south orientation (Sta. 40 to Sta. 44; Sta. 61 to Sta. F) and one with an east-west orientation (Sta. 48 to Sta. 51). During the oceanographic cruise, temperature and conductivity profiles were recorded with a CTD Seabird (model SBE 25). Water samples for dissolved oxygen, orthophosphate (PO_4^{-3}), nitrate (NO_3^{-}), and silicic acid ($\text{Si}(\text{OH})_4$) were taken with twenty-four Niskin bottles in a rosette at standard depths (0, 2, 5, 10, 25, 50, 75, 100 m). Samples for dissolved oxygen were analyzed according to Carpenter (1965), and nutrient samples were analyzed with a nutrient auto-analyzer following Atlas et al. (1971). CTD-salinity records were corrected using the results of a calibrated bench salinometer for analysis of discrete samples collected in the water column during the CTD casting. Buoyancy frequency (N^2) was computed to infer the water-column stability (IOC et al. 2010).

Microplankton biomass

To analyze nanoplankton (cell size less than 20 μm) and microplankton (cell size greater than 20 μm) abundance and biomass, water samples (1 L) were collected from discrete depths (0, 5, 10, 25, 35 m) with twenty-four Niskin bottles in a rosette. Nanoplankton samples (heterotrophic and autotrophic flagellates) were preserved in plastic tubes (50 mL) with 2.5 percent glutaraldehyde (final concentration). Different-sized cells were counted using a stratified design (Booth 1988) and were viewed under a blue light using a microscope equipped for epifluorescence (100 W Mercury light, reflector 505 nm, excitation 465–495 nm, barrier filter 515–555 nm). Flagellate abundance was observed using proflavine staining (Hass 1982) and by concentrating

cells in a 0.8 μm black polycarbonate filter. Flagellate biomass was measured by estimating the cell volume per flagellate and multiplying this volume by a volume-carbon conversion factor of 220 $\text{fg C } \mu\text{m}^{-3}$ (Borsheim and Bratbak 1987).

Microplankton samples were preserved in a 1 percent alkaline Lugol solution (Levinsen and Nielsen 2002). Biomass was estimated using a size-dependent carbon:volume ratio, as suggested by Verity et al. (1992). Subsamples (50 mL) were allowed to settle for 24 h in sedimentation chambers (Utermöhl 1958), after which the diatoms (>10 μm cell size), dinoflagellates (>10 μm cell size), and ciliates were identified, counted, and measured using an inverted microscopy. We assumed carbon:plasma volume ratios of 0.11 $\text{pg C } \mu\text{m}^{-3}$ for diatoms (Edler 1979), 0.3 and 0.19 $\text{pg C } \mu\text{m}^{-3}$ for heavily thecate and atehcate dinoflagellate forms (E. J. Lessard unpublished data from Gifford and Caron 2000), and 0.148 $\text{pg C } \mu\text{m}^{-3}$ for ciliates (Ohman and Snyder 1991).

Water samples (15 mL) for bacterial abundance were preserved in cold glutaraldehyde (2.5% final concentration) and kept in the dark until bacterial counting under an epifluorescence microscope. Bacterial abundance (cell mL^{-1}) was estimated using fluorochrome DAPI (Porter and Feig 1980) and by concentrating bacterial cells in a 0.2 μm black polycarbonate filter. Bacterial biomass was estimated by multiplying the abundance by the conversion factor (20 fg C cell^{-1}), as suggested by Lee and Fuhrman (1987).

To determine particulate organic carbon (POC) and nitrogen (PON) in spring, water samples (200 mL) were filtered through precombusted filters (MFS glass fiber filters with 0.7 μm nominal pore size) and stored frozen until later analysis. Measurements were conducted in a continuous-flow isotope ratio mass spectrometer (Europa Hydra 20/20) following combustion at 1,000°C at the UC Davis Stable Isotope Facility Laboratory (USA), using acetanilide as a standard (Bodungen, Wunsch, and Furderer 1991). Size-fractionated chlorophyll-*a* concentration was measured also within the euphotic zone and for three different size classes: nanophytoplankton fraction (2.0–20 μm), picophytoplankton fraction (0.7–2.0 μm), and microphytoplankton fraction (>20 μm). Filters were immediately frozen (–20°C) until later fluorometric analysis, using acetone (90% v/v) for the pigment extraction (Turner Design TD-700) according to Parsons, Maita, and Lalli (1984). For all plankton biomass variables, depth-integrated values were estimated over an euphotic zone from the surface down to 25 m. The extent of light (photosynthetically active radiation, PAR) penetration to calculated photic

layer (mostly between 20 m and 25 m) was determined using a submersible sensor (QSP 200-D, Biospherical Instrument).

Primary productivity (PP) and community respiration (CR) experiments

Gross primary production (GPP) and community respiration (CR) incubations (in situ and on-deck) were conducted during C15F (spring 2009) and MR08-06 (fall 2009) cruises. Here, GPP refers to the total rate of organic carbon production by phytoplankton, while CR refers to the oxidation of organic carbon back to carbon dioxide by phytoplankton plus heterotrophic organisms. Both of these terms refer to the rate at which the full metabolism of phytoplankton produces biomass. In situ incubations were performed with water samples obtained from standard depths, with a depth range of 1–25 m at Sta. P (the “processes” station). On-deck incubations were carried out with water obtained at three stations (38M, 40M, 42M) north of the main studied region (Figure 1).

Gross primary production and CR estimates were based on changes in dissolved oxygen concentrations observed after incubation in light and dark bottles (Strickland 1960). Water from GoFlo bottles (General Oceanic) was transferred using a silicone tube to gravimetrically calibrated borosilicate bottles with a nominal volume of 125 mL. Winkler titration was carried out with a motorized burette (Metrohm) and by visual end-point detection. The average coefficient of variation for replicate samples was 0.03 percent. Gross primary production values were converted from oxygen to carbon units using a conservative photosynthetic quotient (PQ) of 1.25 (Williams and Robertson 1991), and the CR values were converted from oxygen to carbon units using a respiration quotient (RQ) of 1.

Statistical analyses

Environmental variability associated with biological variables was characterized through nonparametric correlation analysis (Spearman’s rho test) of the set of physical-chemical measurements (temperature, salinity, dissolved oxygen, nutrient concentrations) and biological variables (microplankton biomass) taken at several stations during the C15F cruise. A statistical test of correlation was performed to detect tendencies and relationships between biomass and main environmental factors such as salinity (negative relationship with salinity) and inorganic nutrients (positive relationship with nitrate and silicic acid). Depth-integrated plankton biomass (phytoplankton, bacteria, nanoflagellates, microzooplankton) and mean values at 25 m water-column depth were used in correlation analyses.

Results

Oceanographic conditions and nutrient distribution

Salinity was strongly stratified in the surface layer (50 m) and was almost homogeneous in the subsurface layer (50–100 m; Figure 2A, B, C). This vertical structure was due to important differences in salinity between fresher surface estuarine waters (15–32 PSU) and saltier subsurface marine waters (32–33 PSU). The spring 2009 data showed a very stable surface layer in the water column throughout most of the studied area, with vertical salinity gradients approximately $0.1\text{--}0.6\text{ m}^{-1}$ and buoyancy frequency values of $20\text{--}60 \times 10^{-3}\text{ s}^{-2}$. Because of the shallow western continental sill (50–100 m depth) along the western border of the entire Patagonian archipelago system (Figure 2A), SAAW penetrated the region mainly through Concepción Channel, at the center of the study area (Sievers, Calvete, and Silva 2002; Sievers and Silva 2008). As SAAW penetrated the channel network, it mixed with freshwater in different proportions depending on the freshwater contributions (river discharge, glacial melting, coastal runoff, precipitation) and their proximity. Resulting waters had salinities between 31 and 33 (Modified Sub-Antarctic Water, MSAAW) and between 2 and 31 (Estuarine Water, EW) in this region.

Overall, the surface layer of the study area was well oxygenated and generally above 6 mL L^{-1} (90–110% saturation; Figure 2a, b, c), due mainly to oxygenated freshwater inputs and cold ocean–atmosphere exchanges (González et al. 2011; Silva 2008). In the subsurface layer, dissolved oxygen dropped to below 5 mL L^{-1} (<60% saturation), as previously recorded in the area (Torres et al. 2011). Nutrients were also distributed differently in two layers, with very low contents in the surface layer (orthophosphate $<0.8\text{ }\mu\text{M}$, nitrate $<8\text{ }\mu\text{M}$, silicic acid $<4\text{ }\mu\text{M}$; Figure 3a, b, c) and high contents in the subsurface layer (orthophosphate $>1.4\text{ }\mu\text{M}$, nitrate $>16\text{ }\mu\text{M}$, silicic acid $>5\text{ }\mu\text{M}$). One exception was found in Almirante Montt Gulf (Sta. P); there, the subsurface layer had the lowest dissolved oxygen levels ($<2\text{ mL L}^{-1}$, <25% saturation) and the highest nutrient contents (orthophosphate $>1.6\text{ }\mu\text{M}$, nitrate $<16\text{ }\mu\text{M}$, silicic acid $>60\text{ }\mu\text{M}$) found at 100 m depth.

Primary productivity (PP) and plankton biomass

With few exceptions, phytoplankton biomass in the studied fjord region was low ($0.5\text{--}2.0\text{ mg chlorophyll-}a\text{ m}^{-3}$; $5\text{--}180\text{ mg chlorophyll-}a\text{ m}^{-2}$; Figure 4, upper panel), as were PP estimates ($300\text{--}500\text{ mg C m}^{-2}\text{ d}^{-1}$) at fjord-channel stations for spring (Table 1) as well as at MIRAI stations for fall (Table 2). The gross primary productivity/community respiration ratio (GPP/CR),

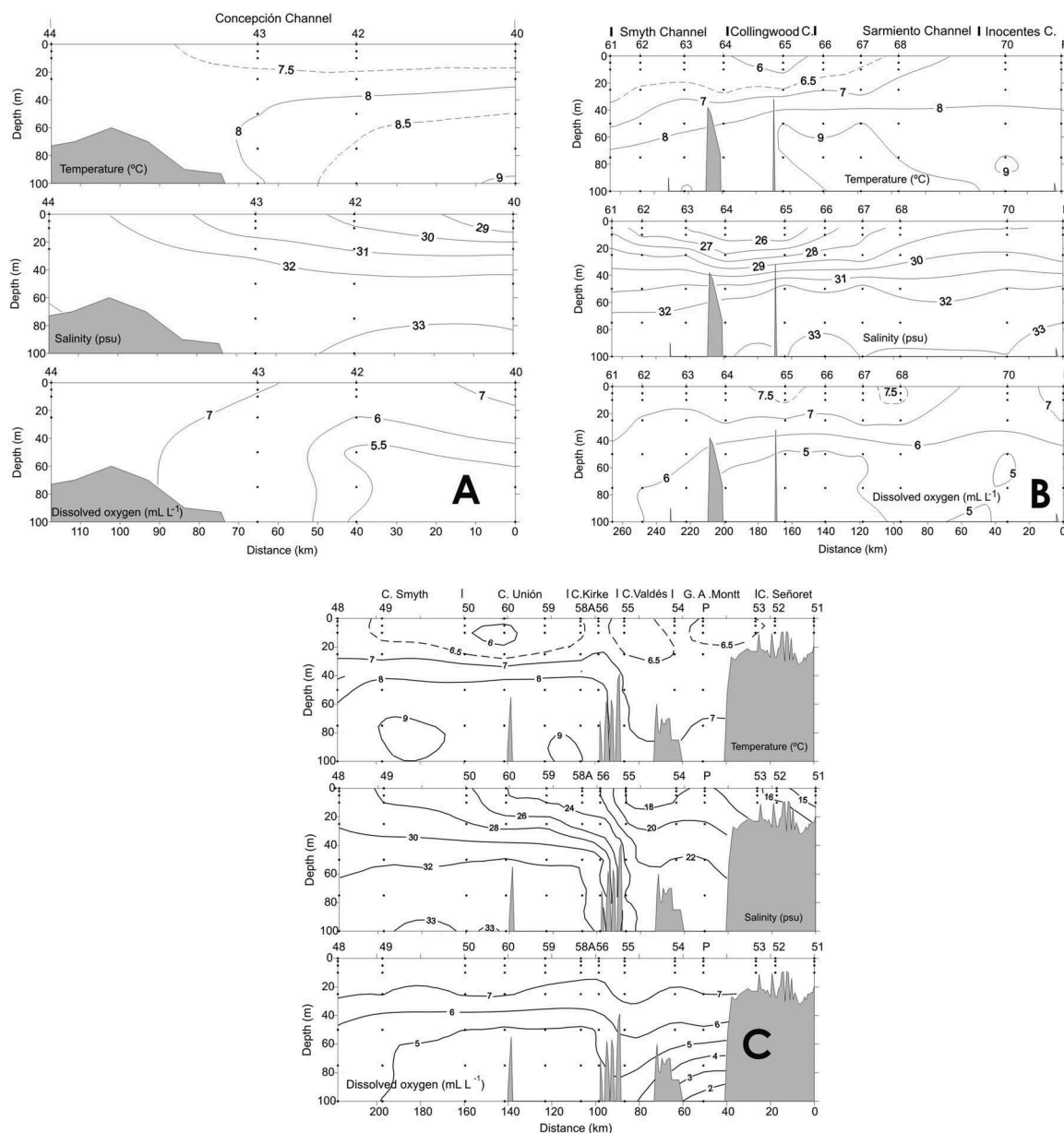


Figure 2. Vertical distribution of the physical (temperature, °C) and chemical (salinity, dissolved oxygen in mL L⁻¹) conditions along the main transects throughout the first 100 m during CIMAR15.

which was used as an index for the trophic status of the system, ranged from 0.1 to 2.3 (Tables 1 and 2; with the exception of the 40.5 value), and averaged 0.8 ± 0.7 for both study areas. This ratio, combined with significant correlation between GPP and CR rates ($r = 0.9$, $p < 0.05$, $n = 19$), indicated a close coupling between the synthesis of organic matter and its usage by the heterotrophic community in the study area. Furthermore, results that were obtained between depths of 10 m and 25 m in the water column (Sta. P) showed a marked heterotrophic metabolism ($GPP/CR < 1$; Tables 1 and 2).

Stations located in more open waters (Concepción and Smyth channels) were dominated by large-sized microphytoplankton taxa ($>20 \mu\text{m}$). *Chaetoceros* spp., *Guinardia* sp., *Leptocylindrus minimus*, and *Skeletonema* spp. diatom species contributed nearly 90 percent of cell abundances in austral spring. Inner stations, which received more freshwater contributions (Almirante Montt Gulf, Kirke Channel, Smyth Channel at Sta. 62, 63, 64), had chlorophyll-*a* concentrations less than 2 mg m^{-3} and were dominated by pico- and nanophytoplankton (10–30 μm cell size nonidentified dinoflagellates species) in terms of chlorophyll-*a* ($>40\%$).

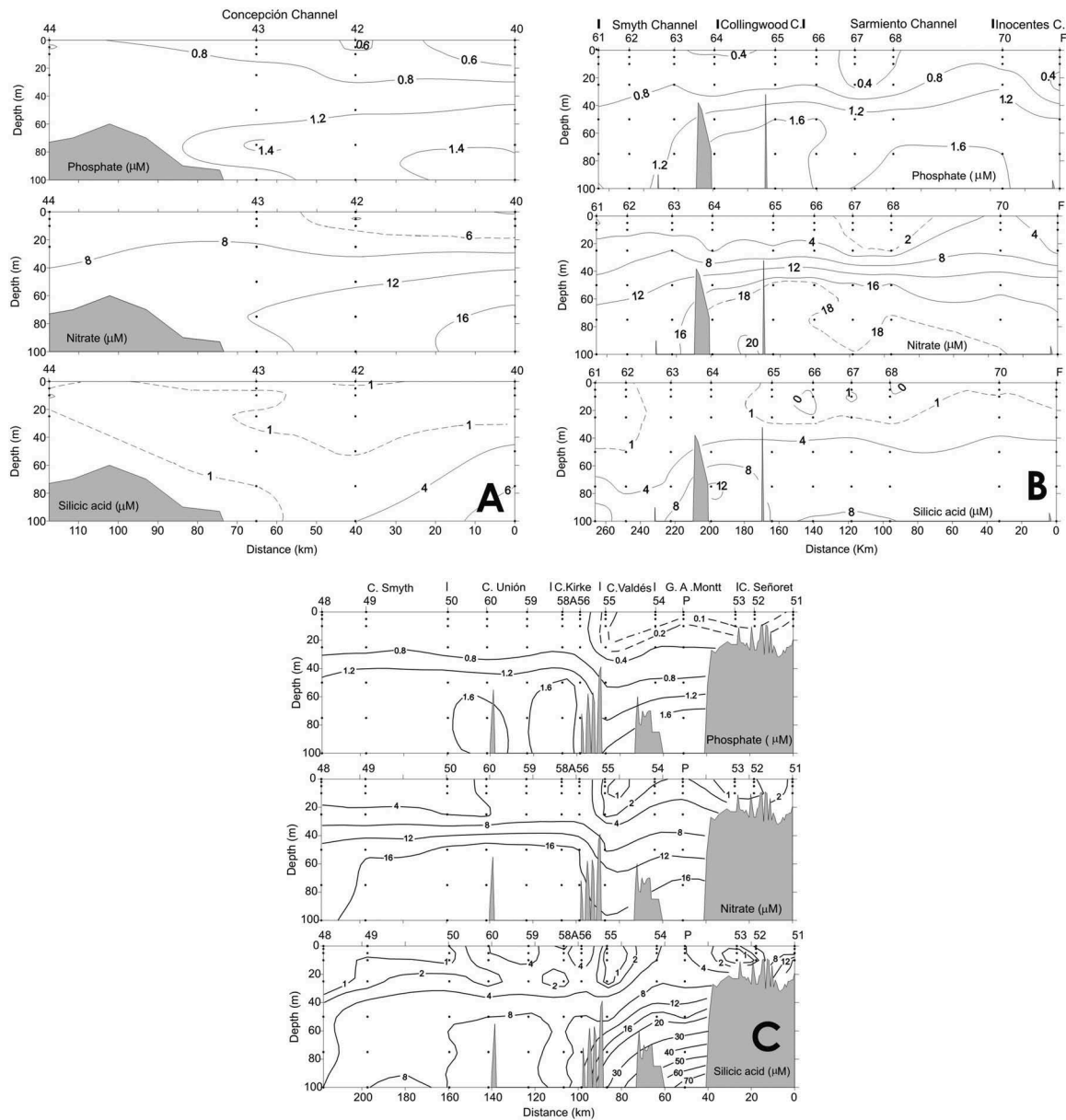


Figure 3. Vertical distribution of dissolved inorganic nutrient (nitrate in μM , orthophosphate in μM , silicic acid in μM) conditions along the main transects (A, B, C) throughout the first 100 m during CIMAR15.

Correlation analyses of depth-integrated plankton biomass and physical-chemical properties revealed differences between stations (e.g., inner-sea stations versus oceanic stations: mean $r_{\text{Micro+Bact}} = 0.7$, $p < 0.006$, $n = 21$). The biomass of microphytoplankton and bacteria was greater at the more oceanic stations (Figure 4), which had high salinity and nutrient-rich waters. The ratio of particulate carbon to nitrogen (C:N) for the near-surface plankton community ranged from 4.5 to 8.5 (POC 1,500–7,500 mg C m^{-2} ; PON 200–1,000 mg N m^{-2} ; Figure 5). High POC values were found at both oceanic and channel stations and coincided with high chlorophyll-*a* and microplankton cell

biomasses (dinoflagellates, nauplii, heterotrophic nanoflagellates; Figure 6).

Discussion

Rivers and glaciers reaching the fjord and channel regions of southern Chile might regulate the silicic acid input to coastal waters. Therefore, horizontal (fronts) and vertical (pycnocline) buoyancy features impinged by freshwater runoff may have an important effect on phytoplankton primary productivity and biomass (Iriarte et al. 2016; Meire et al. 2017; Torres et al. 2014). Our results suggest that inputs of silicic acid and nitrate from freshwater sources

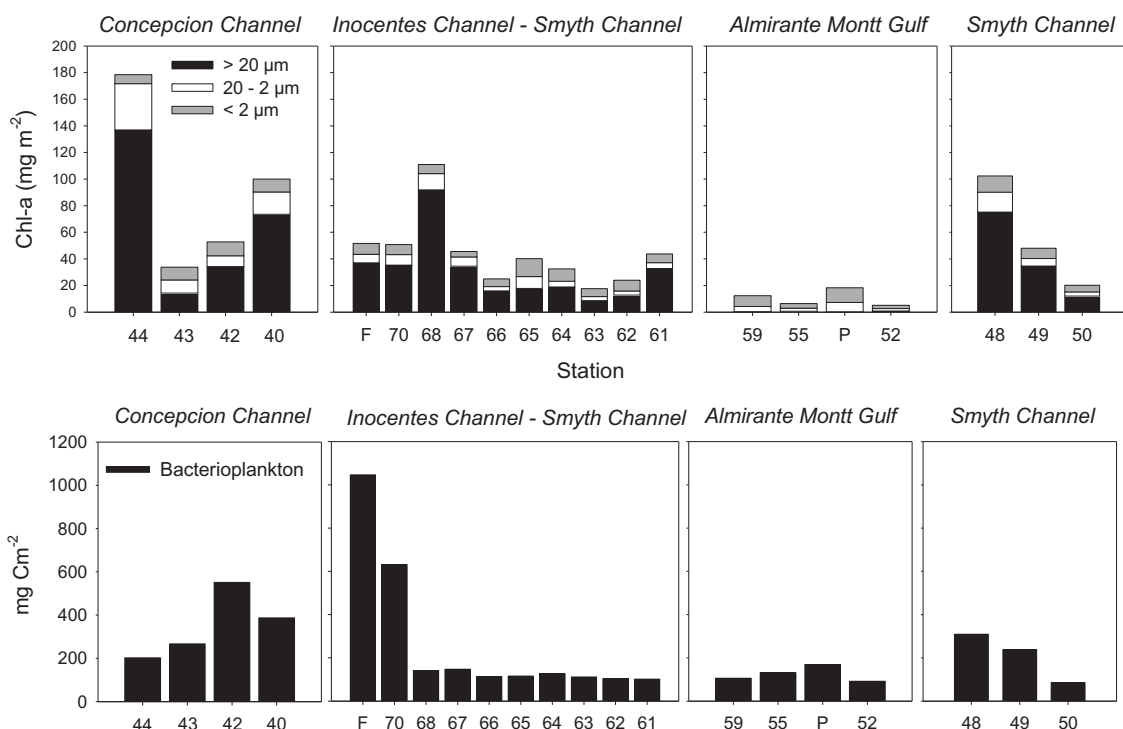


Figure 4. Upper panel: fractionated chlorophyll-*a* concentrations integrated at 25 m depth for picoplankton (<2 μm), nanoplankton (2–20 μm), and microphytoplankton (>20 μm) along the transects during CIMAR15. Lower panel: bacterioplankton biomass (mg C m⁻²) integrated at 25 m depth along the transects during the spring sampling period.

Table 1. Estimates of gross primary production (GPP), community respiration (CR), and GPP/CR ratio during the CIMAR15 cruise.

Date	Lat S	Long W	Station	Depth (m)	GPP (ug C l ⁻¹ d ⁻¹)	CR (ug C l ⁻¹ d ⁻¹)	GPP/CR
October 25, 2009	50° 47.55'	75° 12.80'	43	1	43.4	33.4	1.3
November 3, 2009	51° 47.60'	72° 51.00'	P1	1	42.1	18.5	2.3
				5	30.0	16.5	1.8
				10	10.7	54.1	0.2
				25	0.3	6.0	0.1
				1	63.4	46.5	1.4
November 5, 2009	51° 47.60'	72° 51.00'	P2	5	30.3	26.2	1.2
				10	17.3	29.5	0.6
				25	3.9	0.0	
				1	6.1	6.7	0.9
November 9, 2009	51° 39.25'	73° 58.00'	67	1	16.6	12.1	1.4

Table 2. Estimates of gross primary production (GPP), community respiration (CR), and GPP/CR ratio during the MIRAI MR08-06 cruise.

Date	Lat S	Long W	Station	Depth (m)	GPP (ug C l ⁻¹ d ⁻¹)	CR (ug C l ⁻¹ d ⁻¹)	GPP/CR
March 18, 2009	47°0'10.8"	74°45'5.39"	38 M	1	87.1	191.1	0.5
				5	6.5	216.7	0.0
				10	45.3	302.0	0.2
				15	5.5	65.1	0.1
				25	4.1	69.8	0.1
March 19, 2009	47°59'53.88"	73°45'57.6"	42 M	1	52.8	39.6	1.3
				5	29.5	84.2	0.4
				10	34.3	0.0	
				15	36.0	0.9	40.5
March 20, 2009	47°42'31.52"	74°44'17.87"	40 M	1	255.9	131.9	1.9

(rivers, glaciers) could be deficient in nutrients for diatom growth in the coastal waters of southern Patagonia. This coastal region has already been previously considered to be a low-productive system

with low primary productivity estimates and low chlorophyll-*a* biomass (Aracena et al. 2011; Pizarro et al. 2000). The stability aspect was a main feature of this Patagonian region, and similar patterns were

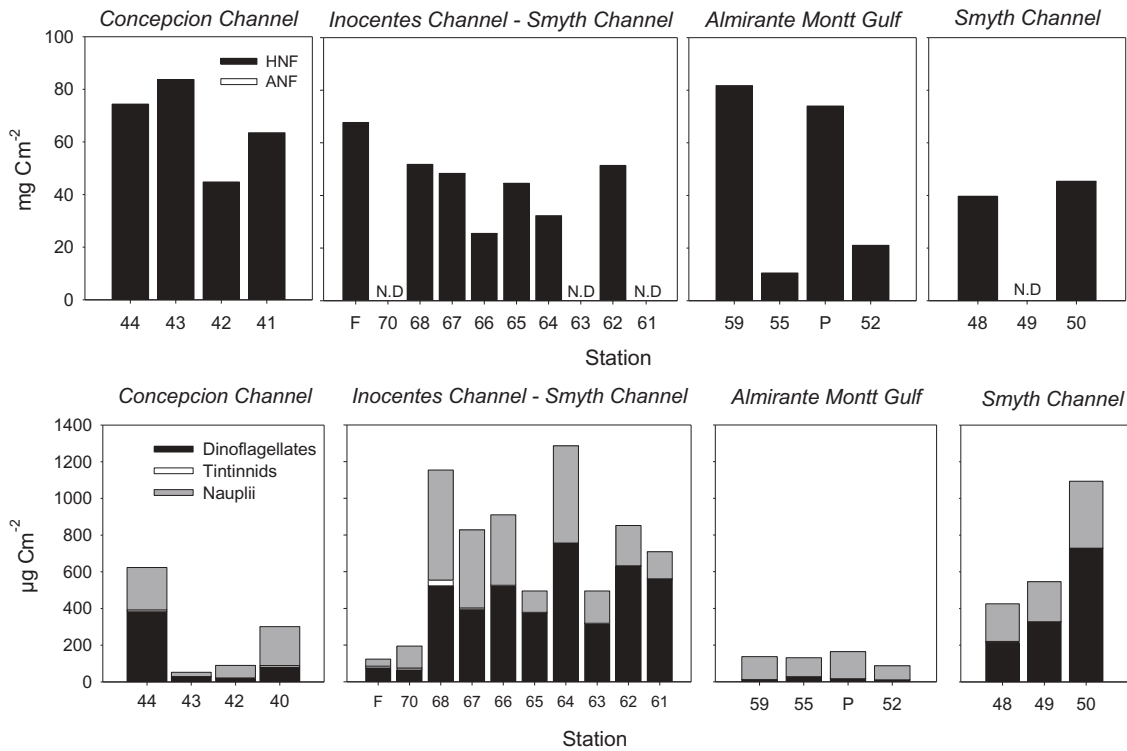


Figure 5. Particulate organic carbon concentration (POC; mg C m^{-2} ; white bars), particulate organic nitrogen (PON; mg N m^{-2} ; black bars), and the POC:PON ratio (solid line) integrated at 25 m depth along the transects during CIMAR15.

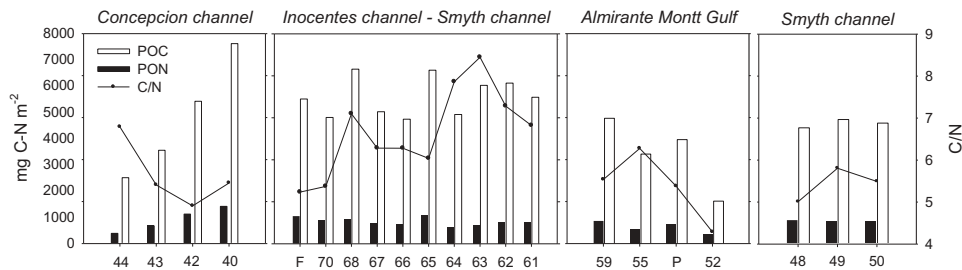


Figure 6. Upper panel: Heterotrophic (HNF) and autotrophic (ANF) nanoflagellate biomass integrated at 25 m depth along the transects during CIMAR15. Lower panel: total and differentiated microzooplankton biomass for dinoflagellates, tintinnids, and copepod nauplii integrated at 25 m depth along the transects during CIMAR15.

also found during earlier studies, such as HUDSON Chile 70 and CIMAR 2 Fiordos (Pickard 1971; Sievers, Calvete, and Silva 2002; Sievers and Silva 2008). Here, strong haloclines were created when freshwater from local rivers and glacial melting mixed with marine SAAW coming from the adjacent Pacific Ocean (Pickard 1971; Sievers and Silva 2008). In this type of fjord system, the vertical density distribution was governed mainly by salinity, which created stability in the water column (Pickard 1971). The low levels of orthophosphate and nitrate in the surface layer of the Chilean fjord region have been mainly attributed to fast uptake by phytoplankton in spring (González et al.

2011; Iriarte et al. 2007) and the input of low-nutrient freshwater from local rivers (Serrano River: nitrate $0.8 \mu\text{M}$, phosphate $0.01 \mu\text{M}$; Silva 2008). Although rivers in northern Patagonia have been shown to carry high levels of dissolved silicic acid (González et al. 2010), relatively low silicic acid concentrations ($<4 \mu\text{M}$) were detected near the surface (20 m) at almost all studied stations.

Low estimates of PP ($<500 \text{ mg C m}^{-2} \text{ d}^{-1}$; Tables 1 and 2) toward oceanic stations were similar in magnitude to those reported for the adjacent Pacific Ocean at the mouth of the Strait of Magellan (Saggiomo et al. 1994) and they were at the low end for those found in central Patagonia for the spring

season ($91\text{--}1,093\text{ mg C m}^{-2}\text{ d}^{-1}$; Aracena et al. 2011). Under low PP rates for the fall season (Table 2, MIRAI cruise), phytoplankton community composition was dominated by a combination of nanoflagellates ($10\text{--}20\text{ }\mu\text{m}$ cell size) and diatom species *Skeletonema* spp. and *Chaetoceros* spp. Nanoplankton biomass also has been quantified in stratified coastal waters (Iriarte et al. 2012), where low-salinity surface waters and high stratification in the photic layer resulted in low total chlorophyll-*a* and a large contribution of small-sized phytoplankton. Thus, the combined effects of low light and nutrient availability in the upper water column may further explain the dominance of small-cell phytoplankton ($<20\text{ }\mu\text{m}$) along this region, mainly driven by glacier-derived freshwater inputs (Jacob et al. 2014).

In this southern region, diatom species have been observed to be predominant in the spring and summer and are associated with mixed nitrate-rich waters, whereas intermediate cell-sized dinoflagellates (e.g., Peridinians) were correlated with stratified and reduced water mass exchange conditions (Alves-de-Souza et al. 2008). Although some similarities in the main species groups were observed, hydrographic variability (i.e., temperature and salinity) by way of seasonal changes in stratification (thermo and haline structure conditions) and the interplay between riverine and marine influences on the two main inorganic nutrients (nitrate and silicic acid) appeared to modulate differences in microphytoplankton composition at the regional scale. In the case of more oceanic waters, such as station 38M (MIRAI), we suggested that the phytoplankton community would be dominated by small dinoflagellate and diatom species under oceanographic conditions of low Si:N nutrient ratio (<1) and a deep mixed layer (Alves-de-Souza et al. 2008; Iriarte et al. 2001). Our primary productivity estimates (Tables 1 and 2) and autotrophic biomass results contrasted with estimates for the fjords and channels of northern Patagonia ($41\text{--}48^\circ\text{S}$) for spring: autotrophic biomass ($>5\text{ mg chlorophyll-}a\text{ m}^{-3}$) and PP values ($2\text{--}4\text{ g C m}^{-2}\text{ d}^{-1}$; González et al. 2011; Iriarte et al. 2007). The low estimates of PP and chlorophyll-*a* biomass associated with the drastic reduction in nitrate ($<4\text{ }\mu\text{M}$, Figure 3A, B, C) and low levels of silicic acid ($<1\text{ }\mu\text{M}$ Figure 3A, B, C) that were observed at shallow depths suggested a potential nutrient “limitation” on phytoplankton productivity in spring. Although Si(OH)_4 has been identified as one of the primary nutrients “limiting” diatom productivity at N:Si ratios of 4:1 (Gilpin, Davison, and Roberts 2004), the availability of Si(OH)_4 has probably been an important factor influencing the dynamics of diatom blooms in sub-Antarctic coastal

areas (Iriarte et al. 2001; Torres et al. 2014). Egge and Aksnes (1992) and Escaravage and Prins (2002) showed that diatom dominance ceased when silicic acid concentrations remained below $2\text{ }\mu\text{M}$ in the coastal waters of Norway and The Netherlands. Thus, the effects of silicic acid could be an additional “limiting” nutrient in the surface waters of southern Patagonia ($50\text{--}53^\circ\text{S}$). In fact, the PP and autotrophic biomass observed near poor silicic acid surface waters ($<4\text{ }\mu\text{M}$) were relatively lower than those found in the northern fjords region ($41\text{--}46^\circ\text{S}$, $20\text{--}80\text{ }\mu\text{M}$; Iriarte et al. 2013; Torres et al. 2014).

Hydrography in northern Patagonia is greatly influenced by the Northern and Southern Patagonian Ice Fields. Glaciers descend to the tide-water and release turbid meltwater and icebergs into the fjords. It has been reported that glacial influence affects the inputs of silicic acid into fjord and channel systems (Torres et al. 2011). Our results of biomass and PP rates were estimated in coastal areas heavily influenced by those glaciers. The influence of freshwater inputs (usually salinities in the range of $15\text{--}30$ PSU) to the surface waters coincided with low silicic acid ($<1\text{ }\mu\text{M}$) and nitrate ($<4\text{ }\mu\text{M}$) at almost all studied stations. It had been recently suggested that nutrient upwelling induced by subglacial freshwater discharge could have positive effects as a mechanism to resupply nutrients into the photic layer and promote coastal phytoplankton blooms (fjord-type marine-terminating glaciers; Meire et al. 2017). However, meltwater may also have a diluting effect on fjord surface nutrient concentrations as well as on the runoff of suspended material as “glacial silt” that attenuates PP because of decreasing light penetration (Montencino and Pizarro 2008; Pizarro et al. 2000). Low production has been explained by the absence of a mechanism to supply nutrients to surface waters under strong haline stratification in Greenland’s fjord system (fjord-type land-terminating glaciers; Meire et al. 2017). From our results, we reinforced Pizarro’s hypothesis (Pizarro et al. 2000) that despite a strong haline-driven stratification to promote spring phytoplankton blooms, poor light availability and silicic acid–nitrate surface-water depletion are main combined factors working simultaneously to restrict the development of microphytoplankton.

Conclusion

Our results suggest that in the inner sea of sub-Antarctic fjords and channels ($50\text{--}53^\circ\text{S}$), the horizontal buoyancy impinged by freshwater inputs with high suspended particle loads from glaciers has an important

negative effect on spring primary production and autotrophic biomass, isolating microphytoplankton (cells larger than 20 μm) from their principal source of light above the pycnocline. In addition, stable halocline and low inorganic nutrient inputs (mainly silicic acid) near the surface created unfavorable conditions for the typical spring growth of microphytoplankton species. We conclude that freshwater-induced stratification in austral spring may lead to reduced nutrient and light availability in surface waters, favoring the high contribution of smaller cells to total autotrophic biomass.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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