THE OFFICIAL MAGAZINE OF THE OCEANOGRAPHY SOCIETY

Oceanography

CITATION

Latorre, M.P., I.R. Schloss, G.O. Almandoz, K. Lemarchand, X. Flores-Melo, V. Massé-Beaulne, and G.A. Ferreyra. 2018. Mixing processes at the pycnocline and vertical nitrate supply: Consequences for the microbial food web in San Jorge Gulf, Argentina. *Oceanography* 31(4):50–59, https://doi.org/10.5670/oceanog.2018.410.

DOI

https://doi.org/10.5670/oceanog.2018.410

PERMISSIONS

Mixing Processes at the Pycnocline and Vertical Nitrate Supply

CONSEQUENCES FOR THE MICROBIAL FOOD WEB IN SAN JORGE GULF, ARGENTINA

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ABSTRACT. Little is known about the base of the food web that could support the high productivity and marine biodiversity found in San Jorge Gulf, Patagonia, Argentina. Here we examine the key components of the microbial food web, including the standing stock and physiological state of the phytoplankton in the context of key oceanographic variables in the gulf. Water samples were collected at 16 stations for biological and chemical analyses, together with measurements of vertical structure and currents. The dynamics of the water column and its impact on nutrient availability for primary producers was evaluated. Our results show that, in spite of the observed low surface nutrient concentrations and low biomass, phytoplankton cells were in good physiological state. This is possible because nutrients are replenished at the pycnocline depth, as estimated by means of Richardson's dynamic stability. Turbulence created by tides and the shear between overlapping water masses favors the disruption of the pycnocline. We suggest that, during summer, San Jorge Gulf maintains not only high primary productivity but also high phytoplankton biomass turnover rate, which is supported by a high C:N ratio, consistent with strong zooplankton grazing and export of organic carbon to deep waters.

INTRODUCTION

The Argentine Patagonian shelf in the southwest Atlantic is one of the most productive marine ecosystems in the Southern Hemisphere (Gregg et al., 2005). There, San Jorge Gulf (SJG; 45°–47°S, 65°30'W), a shallow semi-open basin (~100 m deep), supports a large commercial fishing industry (Góngora et al., 2012) and is an important breeding area for marine mammals and seabirds (Yorio, 2009). Westerly winds (~35 km hr^{-1}; Martin et al., 2016), scarce precipitation (229 mm yr^{-1}), and no significant river inputs characterize this region. Hydrographic properties show that waters in the gulf are a mixture of shelf waters (SW; salinity ranging from 33.4 to 33.8) and low-salinity coastal waters (LSCW; salinity <33.4; Bianchi et al., 2005). Oceanographic models show a counterclockwise circulation with two intense gyres in the south and north extremes that are influenced by bottom topography (Tonini et al., 2006; Matano and Palma, 2018, in this issue). Despite the SJG's great economic and ecological importance, the influence of physico-chemical processes on its microbial ecology is still poorly understood.

The microbial food web contributes to ocean biogeochemical cycles by generating carbon consumed by upper trophic levels or exported to the seafloor (Falkowski et al., 2004). The cycling of organic matter depends on microorganism size structures and trophic interactions, which in turn lead to the development of different types of pelagic food webs (Legendre and Rassoulzadegan, 1995). Herbivorous food webs, which lead to the sequestration of large quantities of carbon (new production), are favored in nutrient-rich, well-mixed environments and are dominated by large autotrophic cells (i.e., diatoms) that are grazed by meso- and macrozooplankton. In contrast, the microbial loop (Azam et al., 1983) usually develops in dynamically stable zones, with little or no nutrient inputs from deep waters, and is dominated by heterotrophs, including bacteria that can remineralize organic nitrogen to ammonium. This ammonium is readily taken up by small phytoplankton, resulting in regenerated production (i.e., production supported by recycling of nutrients in the euphotic zone). In these systems, organic matter is continuously recycled and, therefore, little or no organic carbon is exported to deep waters. Studying the composition and size structure of plankton communities is essential to understand the functioning of pelagic ecosystems.

Previous SJG plankton research focused on the autotrophic component of the community, particularly on phytoplankton composition (Akselman, 1996), biomass (Cucchi Colleoni and Carreto, 2001), toxic algae (Krock et al., 2015), and satellite observations (Glembocki et al., 2015). However, research linking community characteristics with physical and chemical parameters in the area is lacking.

In the SJG, the accumulation of phytoplankton biomass, which usually peaks in spring and fall, is intimately coupled with the formation and rupture of the pycnocline (Akselman, 1996). As in other temperate ecosystems, high summer water column stratification prevents nutrient supply to the euphotic zone. However, turbulent mixing can promote diapycnal (cross-isopycnal) mixing (Thorpe, 2007). This mechanism, resulting from the shear between water masses that lie on top of one another and have different current speeds and directions, cause internal wave breaking and, consequently, turbulence and mixing. This dynamic could bring nutrients to the euphotic zone and stimulate phytoplankton production. Currently, no data exist concerning the impact of this process on summer phytoplankton productivity in the SJG.

Phytoplankton production can be inferred using information about cells' physiological state. The physical and chemical environment not only alters phytoplankton species composition (Margalef, 1978) but also affects the efficiency of photosynthesis (Litchman and Klausmeier, 2008). This fluorescence emission can be used as a proxy for cell physiological state (Suggett et al., 2009). Biophysical properties of photosystem II (PSII), such as the maximum photochemical quantum yield of PSII (estimated as the ratio between variable and maximum fluorescence, F_v/F_m), and the effective absorption cross section of PSII (σ_{PSII}) can be used to characterize the physiological responses of phytoplankton to environmental changes (Suggett et al., 2009).

In this article, we discuss how turbulent mixing and other physical processes that supply nutrients to the surface relate to phytoplankton physiological condition and the microbial food web, with the aim of determining whether the SJG is a productive system for plankton during summer.

MATERIALS AND METHODS

Sampling and Assessment of Oceanographic Conditions

A grid of 16 stations was sampled in February 2014 in the SJG from R/V *Coriolis II*. The expedition was part of the MARine ecosystem health of the San Jorge Gulf: Present status and RESilience (MARES) project (Figure 1a). Water column structure was characterized using a CTD-rosette system (Sea-Bird 9 plus) equipped with photosynthetically available radiation (PAR), dissolved oxygen, and in vivo fluorescence probes. Additionally, CTD casts were performed every two hours during a 36-hour period at a fixed station (FS) located in the gulf's center.

Vertical profiles of currents were acquired with a narrowband 150 kHz acoustic Doppler current profiler (ADCP, RDI Ocean Surveyor) hull-mounted with a 4 m bin size, from 8 m depth to the bottom (~90 m) along the cruise track. Water column stability was assessed by means of the Brunt-Väisälä frequency (N^2), defining the pycnocline depth as the depth of maximum N^2 values (Mann and Lazier, 2006). We evaluated the dynamical stability using the Richardson number (Ri) for turbulent mixing (Thorpe, 2007). The depth of the euphotic zone (Z_{eu}; i.e., depth of 1% of surface incident irradiance) was calculated following the Beer-Lambert law (Mann and Lazier, 2006). Fluorescence data were calibrated against in situ chlorophyll-*a* (Chla) measurements following Parsons et al. (1984).

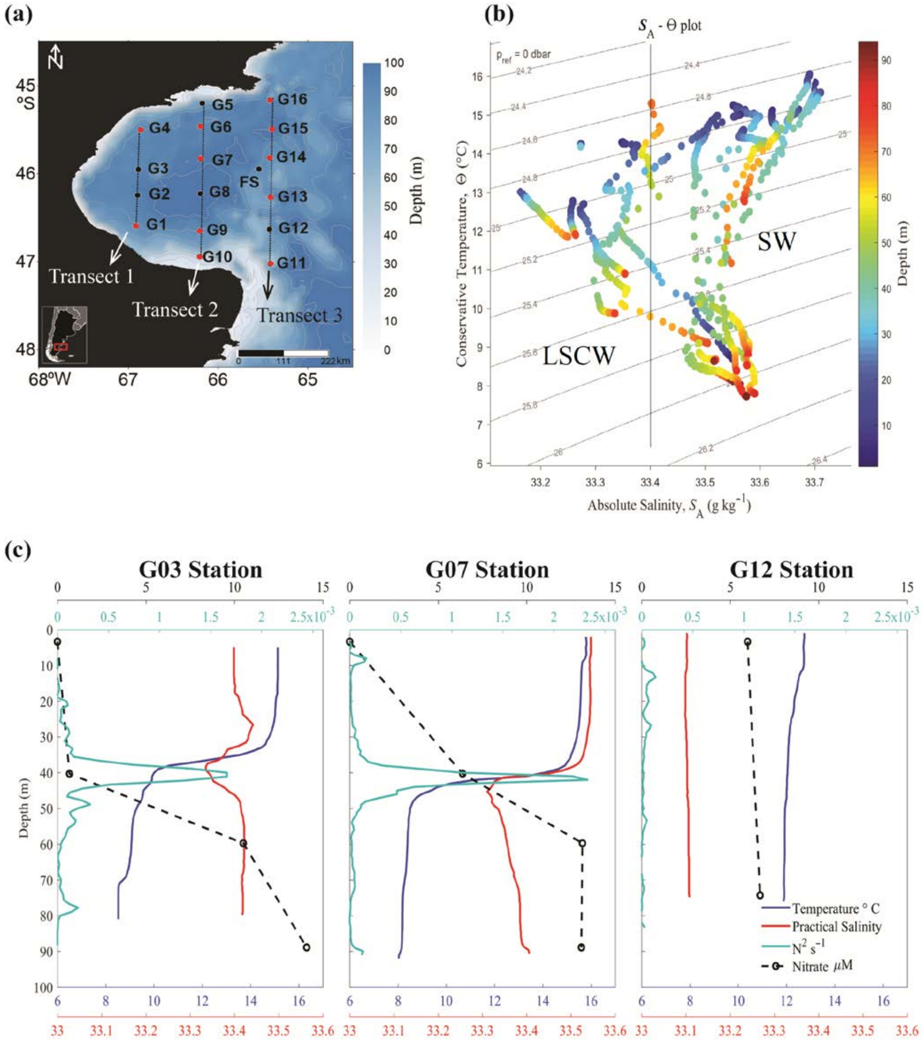

FIGURE 1. (a) San Jorge Gulf (SJG) area with circles indicating CTD casts (G01 to G16) and dotted lines showing inner (1), middle (2), and outer (3) transects. FS = Fixed station. Red circles correspond to stations where water samples were collected with Niskin bottles (n = 11). (b) Temperature-salinity diagram showing the presence of two water masses, low-salinity coastal waters (LSCW) and shelf waters (SW). (c) Vertical profiles of temperature (°C, blue), practical salinity (red), Brunt-Väisälä frequency (N^2, s^{-1}, cyan), and nitrates (μM, black dashed lines) at stations G03, G07, and G12.

Chemical Analyses

To determine nutrient availability (nitrate+nitrite, phosphate, and silicate), seawater samples were collected at four depths with of 12 L Niskin bottles: surface to 2 m depth, subsurface Chla maximum, just below the pycnocline, and at 10 m from the seafloor. Analyses were performed immediately after the cruise using a Skalar Autoanalyzer (Skalar Analytical 2005) at Centro Nacional Patagónico (CENPAT), Argentina. Only nitrate+nitrite data will be analyzed in this work (hereafter "nitrates"). See Torres et al. (2018, in this issue) for a detailed analysis of nutrients in the SJG.

Particulate organic carbon and nitrogen (POC and PON) were determined by first taking 500 ml water samples and passing them through Whatmann GF/F filters (pre-combusted at 450°C, 5 hr) and storing the residue at –80°C in aluminum foil until analysis. Analyses were then performed with continuous-flow isotope ratio mass spectrometry (CF-IRMS) using a DeltaPlus XP mass spectrometer (Thermo Scientific) coupled with an ECS 4010 (Costech Analytical) for elemental analysis.

Microbial Community Composition, Abundance, and Biomass

Samples for picoplankton (bacteria and cyanobacteria) and chlorophyll-containing nanoplankton (2–20 μm) were preserved for flow cytometry in 1% final v/v glutaraldehyde and stored at –80°C. Water samples for microplankton (20–200 μm) analysis were preserved in Lugol solution (final concentration 4%) and stored at 4°C for enumeration and identification with the Utermöhl (1958) method, using a Zeiss Axiovert

100 inverted microscope. Taxonomic identification to the genus level was done following Tomas (1997). Cell biovolume was calculated following Hillebrand et al. (1999) and transformed into carbon, separating diatoms and dinoflagellates according to Menden-Deuer and Lessard (2000) and ciliates according to Verity and Langdon (1984) and Putt and Stoecker (1989). For more detail on its calculation, see Supplementary Material 1.

Pico- and nanoplankton counts were performed with an EPICS ALTRA flow cytometer (Beckman Coulter Inc.) following Belzile et al. (2008) for heterotrophic bacteria (H-BACT) and Tremblay et al. (2009) for cyanobacteria (Pico-CYAN) and eukaryotic phytoplankton (Pico-EUK and nanophytoplankton). The carbon content was calculated according to Zubkov et al. (2000) and Tarran et al. (2006) (see Supplementary Material 1).

The relationships between the microbial community and environmental variables were evaluated with a canonical transformation-based redundancy analysis (tb-RDA) in RStudio© 2015 (Oksanen et al., 2017). Details of this analysis are presented in Supplementary Material 2.

Physiological State of Phytoplankton

The PSII biophysical properties of phytoplankton assemblages were estimated using a Chelsea Instruments (UK) fast repetition rate fluorometer, following the methodology of Kolber et al. (1998), for each station based on 10 replicates collected from the subsurface Chla maximum, as in Sugget et al. (2001).

RESULTS

Characterization of the Water Column

Figure 1b shows that the deepest waters, with density anomalies (σ_θ, gray dotted lines) >25.8 kg m^{-3}, have relatively homogeneous thermohaline characteristics, with low temperatures (~8°C) and high salinities (>33.4). Conversely, heterogeneous thermohaline conditions characterize the two surface water masses, with σ_θ <25.8 kg m^{-3}: low-salinity coastal water (LSCW) and shelf water (SW), separated by the 33.4 isohaline. Salinity was lowest (33.1, Figure 1c, station G12) where the LSCW enters in the southern part of the gulf, then slowly increased as it mixed with inner gulf waters (SW; Figure 1c, station G07). Surface temperatures ranged between 13°C and 15°C across the gulf, with the lowest values recorded in the southern region.

Figure 1c shows profiles of temperature, salinity, Brunt-Väisälä frequency (N^2), and nitrate from the inner, middle, and outer parts of the gulf. Density is not shown because it is highly temperature dependent in this region and its distribution is similar to that of temperature (see Figure S1). At stations located in the central gulf, the thermocline was evident between 40 m and 50 m depth, corresponding to the highest N^2 and coinciding with the position of the nitracline (Figure 1c, stations G03 and G07). Nitrate concentration in deep water (14–17 μM) was higher than in the surface waters (0–5.98 μM), closely following the isotherm profiles. In contrast, both temperature and nitrate concentrations in the southeast zone were homogeneous over the entire water column (Figure 1c, station G12) and related to the LSCW. A remnant signal of this LSCW was detected as a wedge at the pycnocline depth in the inner gulf (Figure 1c, station G07).

The average Chla concentration in the gulf was relatively low (1.03 μg L^{-1} ± 0.53), but showed higher values at the coastal station G01 (maximum value of 2.67 μg L^{-1}) in the western part of the gulf (Figure 2a). Chlorophyll maxima were observed at 20–50 m depth (Figure 2a–c). Station G13 (Figure 2c) was an exception, because Chla (1.70 μg L^{-1} ± 0.085) was uniformly distributed over the first 23 m (25 m pycnocline depth). At all daytime stations where PAR could be measured, Z_{eu} coincided with the pycnocline (white lines in Figure 2).

Particulate Organic Carbon

The mean POC concentration observed for the Gulf was 276 mg m^{-3} ± 98. Highest concentrations were measured throughout the southern coastal waters of the gulf (366–486 mg m^{-3}), with the maximum occurring at station G01. In addition, there was a clear difference between the C:N ratio in coastal stations (values between 2 and 4) and the mouth of the Gulf (>6 at G11–G16), where values approached the Redfield ratio (see Table S1).

Water Column Characteristics During the Time Series Observations

A time series of CTD casts following a diurnal tidal cycle was performed at the fixed station (see Figure 1a for the

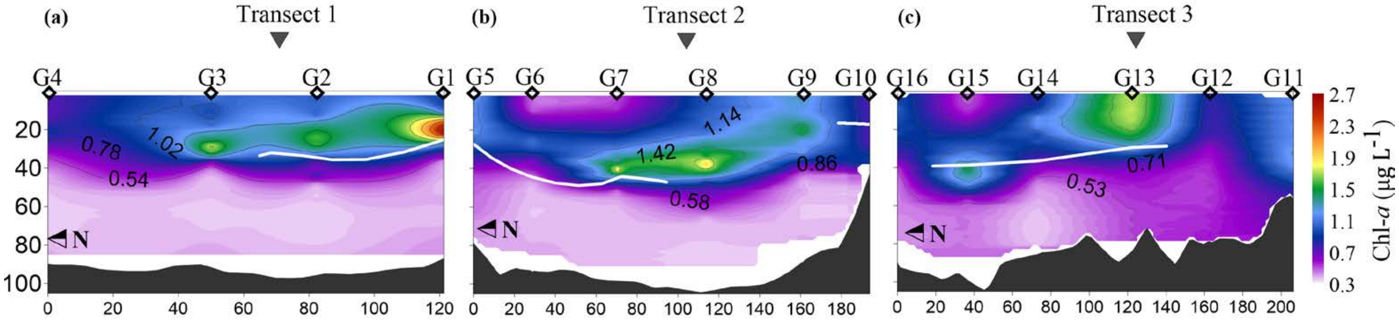

FIGURE 2. Vertical profiles of chlorophyll-*a* (μg L^{-1}). White lines indicate Z_{eu} (depth of the euphotic zone). Transect 1: Inner gulf. Transect 2: Middle gulf. Transect 3: Outer gulf.

location in the central gulf). Only 13 casts from a total of 15 were completed due to weather limitations on marine operations. The vertical white rectangles in Figure 3 indicate no data for CTD cast 5, which was not sampled, and between CTD casts 7 and 8. No significant changes were observed in surface layer temperature and salinity, although the depth of the thermocline varied between low tide (1, 2, 3) and high tide (4, 6), from 46 m to 32 m (Figure 3a,b). By contrast, temperature and salinity changed below the pycnocline. Salinity profiles show that a tongue of low-salinity water (33.2) entered the gulf below the pycnocline when the tide was rising (stations 4, 6, 8, 12, 14) and when the tide was falling (Figure 3b). Chla concentration during one ebb tide had a mean value of 1.03 μg L^{-1} ± 0.18 as in the rest of the gulf. Figure 3d shows how the surface (red) and bottom (blue) current speeds change during one tidal cycle. The different current speed between the two layers can cause shearing and affect the entry of nutrients from the bottom to the top layer.

Potential Vertical Flux of Nutrients Associated with Dynamical Stability

As inorganic nitrogen is the main limiting factor in most temperate marine coastal waters (i.e., Blomquvist et al., 2004), we evaluated mechanisms that could potentially inject nitrate from deeper waters through the pycnocline. We computed the gradient of nitrate (ΔN) in the waters between the surface and below the pycnocline ($\Delta N/\Delta z$) and plotted it as a function of the Richardson number (Ri). In this study, we considered that values between 0.2 and 1.0 indicate turbulent mixing (as in Galperin et al., 2007). Although the Ri was >1 in most cases, an exponential decline of the $\Delta N/\Delta z$ was observed with a decreasing Ri (Figure 4a), suggesting nitrate pumping toward surface waters. Ri <1 values were associated with the southern zone and with one coastal station (G02). Note that our data, based on stations separated in space and time, represent a snapshot of physico-chemical conditions throughout the gulf. Conversely, turbulence is highly intermittent (Carr et al., 1995). We attempted to overcome these limitations using data from the fixed station, where we found the same pattern. In this case, the instability was more evident, with Ri values following the tidal cycle (Figure 4b).

The Relationships of Microbial Community Composition and Physiological State to Environmental Conditions

Phototrophic picoplankton dominated the microbial community biomass, highlighting their importance for summer primary production in the SJG. Pico-EUK comprised the main component of picoplankton (30%), with values ranging between 5.4 and 108.4 μg C L^{-1}, and maxima at stations G01 (64.4 μg C L^{-1}) and G13 (108.4 μg C L^{-1}). Pico-CYAN ranged between 2 and 35.6 μg C L^{-1}, with highest concentrations at G01 and G14 stations (31.2 and 35.9 μg C L^{-1}, respectively). H-BACT varied between 7.23 and 35.5 μg C L^{-1}, with maxima reaching 35.2 and 28.9 μg C L^{-1} at G01 and G14

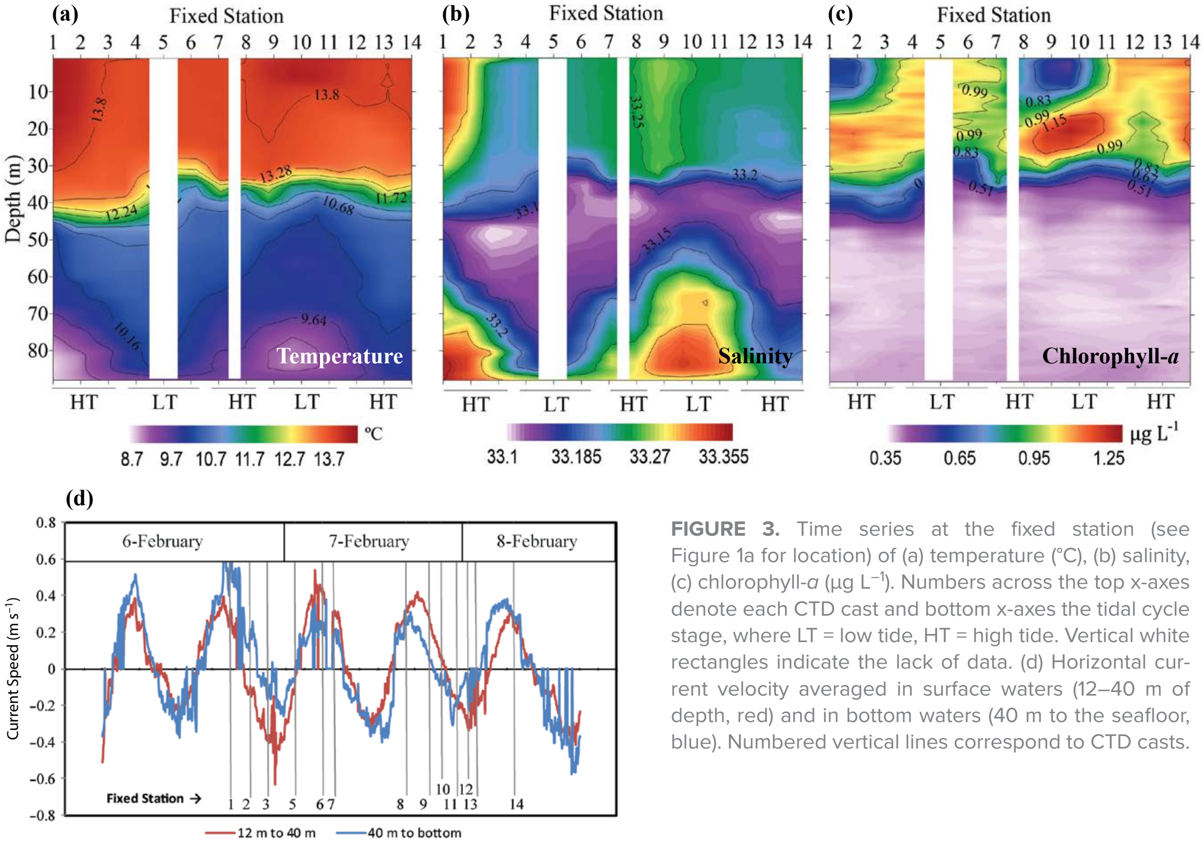

FIGURE 3. Time series at the fixed station (see Figure 1a for location) of (a) temperature (°C), (b) salinity, (c) chlorophyll-*a* (μg L^{-1}). Numbers across the top x-axes denote each CTD cast and bottom x-axes the tidal cycle stage, where LT = low tide, HT = high tide. Vertical white rectangles indicate the lack of data. (d) Horizontal current velocity averaged in surface waters (12–40 m of depth, red) and in bottom waters (40 m to the seafloor, blue). Numbered vertical lines correspond to CTD casts.

stations, respectively (Figure 5a–c).

In the microplankton size class, ciliates were found in all SJG samples, with values between 0.9 and 12.9 μg C L^{-1}. Diatoms (0–24 μg C L^{-1}) were mostly observed in the southern area. Dinoflagellates were detected at the mouth of the gulf, mainly in the northern zone, with values ranging from 0–23 μg C L^{-1} (Figure 5d–f). A complete list of the taxa identified is presented in Table S2. Nanophytoplankton were excluded from the results because their total carbon contribution was negligible (0.003–0.2 μg C L^{-1}) compared to the other groups. This may be due in part to a methodological limitation in the estimation of cellular biovolume (see Supplementary Material 1 for a detailed explanation).

The relationships between the microbial community and environmental variables in the transformation-based redundancy analysis (tb-RDA) suggests that temperature (associated with stratification and, hence, N^2), nutrient availability, and dynamic stability (>Ri) were the main factors controlling the microbial biomass distribution (tb-RDA results $p = 0.002$, Figure 6).

Pico-EUK were associated with low-temperature areas (weak stratification) where nitrate concentrations were high. Interestingly, we found that the Ri was associated with several plankton groups, accompanied by a particular nitrate dynamic: Pico-CYAN were associated with dynamically stable areas (>Ri) where nutrient concentrations were low and temperatures higher (high N^2), while diatoms and dinoflagellates were related to a low Ri and high nutrient availability (Figure 6).

In our results, F_v/F_m and σ_{PSII} were inversely correlated. In areas dominated by picoplankton, F_v/F_m was low (0.4–0.29), with high values of σ_{PSII} (325–355 Å $quanta^{-1}$; Figure 7a,b). Additionally, this combination of physiological parameters was accompanied by the highest values of Chla. In the southeast area where diatoms were found, physiological growth conditions were

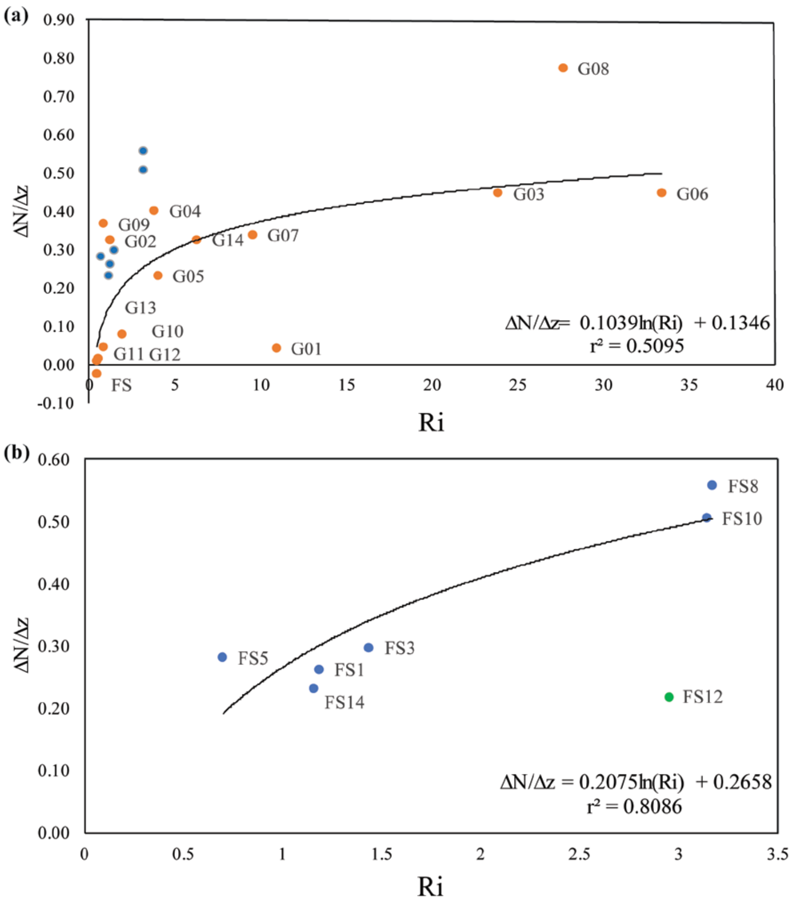

FIGURE 4. Gradient of nitrate (N; ΔN/Δz) vs. Richardson number (Ri) at (a) grid stations (orange dots) and the fixed station (blue dots). (b) Repeated CTD cast at the fixed station (FS). The dotted line shows the logarithmic relationship between the two variables.

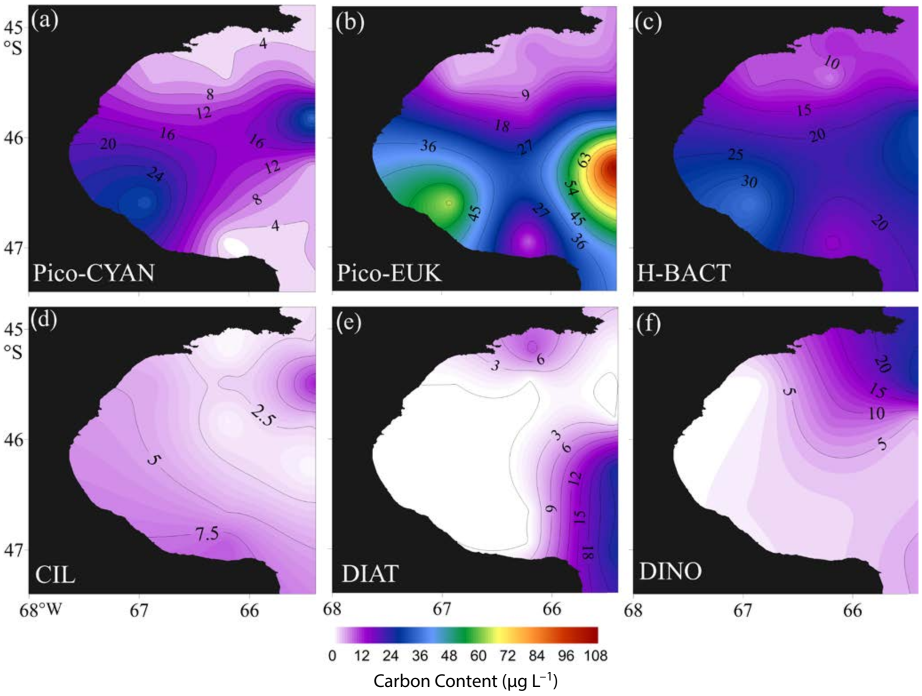

FIGURE 5. Horizontal distribution of carbon content (μg L^{-1}) of (a) picocyanobacteria (Pico-CYAN), (b) picoeukaryotes (Pico-EUK), (c) heterotrophic bacteria (H-BACT), (d) ciliates (CIL), (e) diatoms (DIAT), and (f) dinoflagellates (DINO), estimated using cell biovolume and different carbon conversion factors in the subsurface chlorophyll-*a* maximum.

optimal, with the highest values of F_v/F_m (0.44–0.56) and lowest of σ_{PSII} (300–220 Å quanta^{-1}).

DISCUSSION

In summer, San Jorge Gulf is characterized by strong water column stratification and low nitrate concentrations, conditions related to heavy consumption of nutrients by phytoplankton during the spring bloom (Krock et al., 2015). Picoplankton dominate the area, as they do oligotrophic seas (Lewandowska et al., 2014). However, integrated Chla was higher (>40 mg m^{-2}, data not shown) than in other summer marine ecosystems (i.e., the North Atlantic, 17–27 mg m^{-2}; Mojica et al., 2015) and of the same order as the Gulf of Alaska (39 mg m^{-2}; Childers et al., 2005). We hypothesize that the gulf remains a productive area even during summer, but with a high phytoplankton turnover rate that masks phytoplankton production and avoids its biomass accumulation.

The Role of LSCW in Nitrate Supply to the SJG

Based on salinity, the inner gulf was alternatively dominated by SW and LSCW (Bianchi et al., 2005). LSCW plays an important role in sustaining the high levels of Chla recorded along the Patagonian coast (Romero et al., 2006). Even if nitrate concentration in LSCW were lower (6 µM) than in central bottom waters (16 µM), its significance lies in that this nitrate would be available for phytoplankton uptake in the upper layer due to vertical mixing at the pycnocline. We found that surface nitrate concentrations were higher than those of other coastal (Paparazzo et al., 2010) and shelf break areas at the same latitude (Valiadi et al., 2014).

It is well known that vertical stratification affects the availability of nutrients and light that enable phytoplankton growth (Behrenfeld et al., 2006). Because the euphotic depth coincided with the pycnocline during our study, phytoplankton remained in well-illuminated conditions, so that light was not a limiting factor for growth. Thermal stratification was strong all over the inner gulf (Torres et al., 2018, in this issue). However, some physical processes, such as wind, eddy formation, and internal waves, can disrupt the pycnocline and allow nutrients to be supplied to surface waters (Dave and Lozier, 2013). We analyzed the vertical mixing through the estimation of the dynamical stability by means of the Richardson number. The Ri showed a significant, negative exponential correlation with the vertical nitrate gradient, suggesting that vertical flux of nutrients was possible across the pycnocline. Tidal changes in pycnocline depth (at the fixed station, Figure 3) further suggest that nutrients may reach depths close the surface (10 m above their original position), as we observed during one cycle (time 1 to 7). As shown in the temperature-salinity profiles, nutrient-rich LSCW flows below the pycnocline (Figure 3b). In contrast, Paparazzo et al. (2017) found low nitrate concentrations in LSCW during fall, although they remained high in deep waters (Krock et al., 2015). These results suggest that the contribution of these waters to the nutrient supply is highly variable and probably a key factor during the summer season for the SJG phytoplankton population.

The low vertical resolution of our nutrient data limits our ability to adequately evaluate nitrate fluxes. High-resolution nutrient sampling at the pycnocline, where changes in nutrient concentrations are intense, is recommended to calculate nitrate fluxes (Agusti et al., 2001). Nevertheless, our approach allowed us to highlight the underlying processes associated with vertical nutrient input.

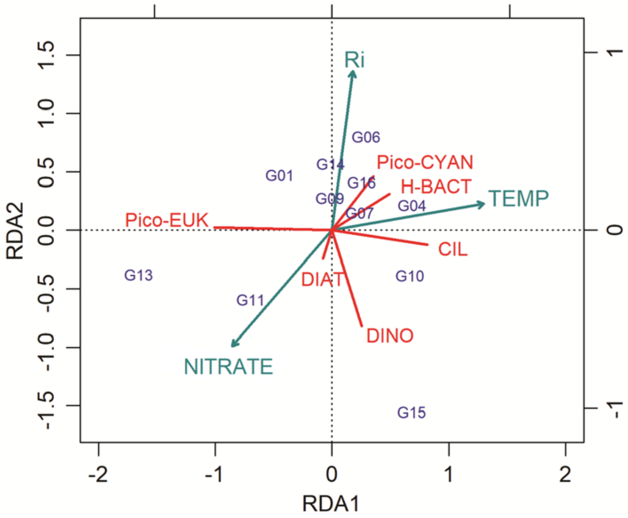

FIGURE 6. Canonical transformation-based redundancy analysis (tb-RDA) triplot of the SJG microbial community represented in terms of carbon content (µg L^{-1}) (red) and environmental variables (green) with samples in blue. The two first axes represent 27% (RDA1) and 17% (RDA2) of total community variability.

Is the SJG a Productive System During Summer?

The environmental characteristics that describe the distribution of pico-EUK and pico-CYAN in the SJG fit nicely with those established in the revision of Margalef's mandala proposed by Glibert (2016). Briefly, it explains that pico-CYAN may grow under low turbulence and warm temperature conditions by using ammonium as a source of nitrogen, while pico-EUK are in the transition between organic and inorganic nitrogen sources. In our study, pico-CYAN dominate in nitrate-poor waters that are highly stratified while pico-EUK dominate in an intermediate area with weak stratification and relatively high nitrate concentrations. We could not analyze ammonium to determine the nitrogen source preferred by each group.

However, it is well known that in ecosystems dominated by small cells, the microbial loop is important for nutrient recycling (Legendre and Rassoulzadegan, 1995). Indeed, the H-BACT and ciliates were closely associated with pico-CYAN, indicating this type of trophic food web.

From a functional-traits perspective, small cells require less nutrient availability to survive and are more efficient at nutrient uptake (Litchman and Klausmeier, 2008). Variations in physiological traits rather than cell size alone allow them to survive in a dynamically stable and nutrient-impoverished environment (Litchman and Klausmaier, 2008). Typically, F_v/F_m is higher in nutrient-replete than in nutrient-poor environments, and is further correlated with higher primary productivity rates (Falkowski and Kolber, 1995). Our cell physiology results agree with values recorded in pico-CYAN or pico-EUK cultures and natural communities, with F_v/F_m ranging between 0.1 and 0.4, and 0.4 and 0.55, respectively (Moore et al., 2006; Sugget et al., 2009). Additionally, these physiological parameters were accompanied by the highest values of Chla. Therefore, in our study, low F_v/F_m seems to be an effect of high pico-CYAN density and their taxonomic signature rather than related to nutrient stress of cells. The community appeared to be in good physiological condition, photosynthetically active and able to accumulate biomass that could eventually be transferred to higher trophic levels.

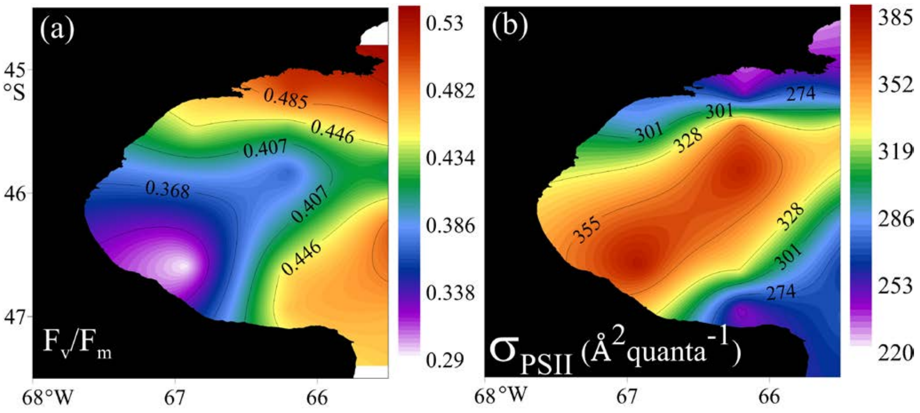

FIGURE 7. (a) Maximum photochemical quantum yield (F_v/F_m) and (b) the effective absorption cross section (σ_{PSII}) at the subsurface chlorophyll-*a* maximum.

Diatoms and dinoflagellates were found in turbulent, low Ri regions with high nutrient availability in the northern and the southern parts of the gulf (Figure 6). Our results are consistent with those reported by Akselman (1996) on microplankton distribution related to nutrient availability in the SJG during summer. The physiological conditions of phytoplankton assemblages in this area were optimal. Although our analysis was carried out with a natural microbial community, where the taxonomic signature of each group would be masked by the presence of others, our values are consistent with those reported in the literature for microphytoplankton in culture (Sugget et al., 2009). However, despite high nutrient availability and good physiological conditions, phytoplankton did not reach high concentrations. This could be due to the presence of intense larval (commercial shrimp) and zooplankton grazing, which would prevent phytoplankton accumulation. The high herbivorous zooplankton density observed in the mouth and center of the gulf (Giménez et al., 2018, in this issue) supports this hypothesis. This means that large cells such as diatoms and dinoflagellates would play a key role in sustaining herbivorous food webs in this zone.

This conclusion is further supported by the C:N ratio (Table S1). Phytoplankton C:N ratios usually range between 6 and 10, zooplankton and bacteria between 3 and 6, and values >12 characterize detrital organic matter (Savoye et al., 2003, and references therein). In the gulf, the ratio was generally <6, highlighting the importance of the heterotrophic components of the system. In addition, results from sediment traps deployed during the same cruise included large concentrations of fecal pellets (Massé-Beaulne, 2017). Furthermore, these pellets contained high amounts of microphytoplankton cells. Consequently, both observations support our hypothesis that high secondary production prevents phytoplankton accumulation (especially microphytoplankton).

SUMMARY AND CONCLUSIONS

Through functional analysis of key components of the microbial food web (i.e., considering size class and physiological condition) and their relationships to prevailing environmental conditions during austral summer, we attempted to better understand the functioning and potential productivity of San Jorge Gulf plankton. The structure of the microbial assemblages typically depended on stratification and inorganic nitrate availability, as previously documented for the gulf (Akselman, 1996; Cucchi Colleoni and Carreto, 2001) and other sectors of the Argentine shelf (Gonçalves-Araujo et al., 2016). For the first time for South Atlantic coastal waters, we detected and described how turbulent processes linked to tides and the entry of the nutrient-rich water masses such as the LSCW favor rupture of the pycnocline and modify the N-limiting conditions, providing a mechanism for nutrient supply to surface waters that could support phytoplankton—and hence, ecosystem—productivity.

Nutrient inputs linked to tides appear to be rapidly consumed by autotrophic cells, resulting in depleted nutrient concentrations in the euphotic zone. The good physiological state of gulf phytoplankton suggests that light and nutrient availability were adequate for growth. Picoplankton have a relevant role during summer because they are the dominant biomass. The presence in the southern zone of large cells in optimal physiological state showed that conditions were adequate for their growth. However, high turnover rates, a result of coupled production and grazing, prevent phytoplankton biomass accumulation. The C:N ratios reported here, the high biomass of zooplankton measured during the same cruise (Giménez et al., 2018, in this issue), and sediment trap results (Massé-Beaulne, 2017) are all consistent with the presence of an intense herbivorous food web. The transition between the two extremes of trophic relationships, the herbivorous food web and the microbial loop (Legendre and Rassoulzadegan, 1995), also occurs during summer, contributing to high productivity in San Jorge Gulf during this season.

SUPPLEMENTARY MATERIALS

Supplementary materials are available online at https://doi.org/10.5670/oceanog.2018.410.

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ACKNOWLEDGMENTS

This research was undertaken in the context of the PROMESse project between Québec (ISMER-UQAR and Québec Océan) and Argentina. Funding for this project was provided by the Ministerio de Ciencia, Tecnología e Inovación Productiva de la Nación, Provincia de Chubut, and CONICET, Argentina. M.P. Latorre received a fellowship from Bec.Ar to undertake her master's studies in oceanography. We thank the crew of R/V *Coriolis II* for data acquisition assistance. We also thank Américo Torres and Pascal Guillot for technical support and Monica Gil for reading and contributing to the manuscript.

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ARTICLE CITATION

Latorre, M.P., I.R. Schloss, G.O. Almandoz, K. Lemarchand, X. Flores-Melo, V. Massé-Beaulne, and G.A. Ferreyra. 2018. Mixing processes at the pycnocline and vertical nitrate supply: Consequences for the microbial food web in San Jorge Gulf, Argentina. *Oceanography* 31(4):50–59, https://doi.org/10.5670/oceanog.2018.410.