

Primary Productivity and heterotrophic activity (Puyuhuapi channel; 44° S, 73° W)

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Primary Productivity and heterotrophic activity in an enclosed marine area of central Patagonia (Puyuhuapi channel; 44° S, 73° W)

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We assessed temporal variability in phytoplankton biomass, Chlorophyll *a*, nutrient availability, Gross Primary Production (GPP), community respiration (CR), and bacterial secondary production (BSP) over a year of monthly observations (October 2007 to October 2008) at a fixed station in the Puyuhuapi fjord, Chilean Patagonia (44° S, 73° W). A set of in situ observations gathered over two consecutive spring-summer seasons, and one autumn-winter season in the middle, has made it possible to connect the two-phase (i.e. productive season/non-productive season) pattern of Chlorophyll *a* (Chl *a*) variability shown by satellite data with a two-phase cycle in GPP, CR, and the composition of phytoplankton assemblages. Estimates of annual GPP and CR, integrated over the top 20 meters of the water column, were 533 and 537 g C m⁻² yr⁻¹, respectively. Low values of *p*CO₂ were measured in mixed layer autotrophic waters (GPP/CR > 1) while high *p*CO₂ levels were measured in mixed layer heterotrophic waters (GPP/CR < 1). Bacterial Secondary Production (BSP) was significantly and positively correlated with GPP ($r = 0.6$, $p < 0.05$, $n = 24$) and Chl *a* ($r = 0.4$, $p < 0.05$, $n = 24$) on an annual cycle basis. The winter drop in bacterioplankton (both bacteria and archaea) activity (from 0.9 ± 0.6 g C m⁻² d⁻¹ to 0.6 ± 0.3 g C m⁻² d⁻¹) was not as pronounced as the winter drop in phytoplankton activity (from 1.1 ± 1.12 g C m⁻² d⁻¹ to 0.1 ± 0.09 g C m⁻² d⁻¹). It is hypothesized that dissolved organic matter (DOM) of terrestrial origin plays an important role (especially in winter) supporting bacterial activity in the Puyuhuapi fjord.

1 Introduction

Fjords and estuaries play an important role in biological productivity and carbon cycles in aquatic ecosystems (González et al., 2010). The Chilean fjords region (41–55° S) spans more than 1600 km of (straight) coastline and over 240 000 km² of highly complex geomorphologic and hydrographic conditions. Oceanographic conditions in this

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region are dominated by a strong interaction between oceanic Sub Antarctic Waters (SAAW), driven into the area as the West Wind Drift reaches the southern coast of Chile, and fjord freshwater from coastal runoff. This large input of freshwater defines a pronounced surface salinity gradient from the inner shores to open ocean environments (Iriarte et al., 2007; and references therein). In addition, the area is characterized by sharp seasonal fluctuations in atmospheric conditions (i.e. solar radiation, changes in wind direction and stress precipitation; Pickard, 1971; Acha et al., 2004; Montero et al., 2011), as well as in freshwater inputs into the fjords, which partially modulate seasonal changes in both biomass and productivity of phytoplankton assemblages.

In situ productivity estimates for the Chilean Patagonian region, are relatively scarce compared with the central-northern coast of Chile (18–37° S). Available data for the northern section of the Chilean fjords (41–48° S), have yielded estimates for surface PP of 1–26 mg C m⁻³ h⁻¹ and Chlorophyll *a* concentrations of 1–12 mg Chl *a* m⁻³ both during spring blooms (Pizarro et al., 2000; Iriarte et al., 2007). The phytoplankton production in the fjord and channel ecosystems of Chilean Patagonia (41–55° S), based on monthly satellite composite images, has been defined in terms of two contrasting seasons: a productive season extending from late winter to late autumn, and a non productive season that predominates during the austral winter (Iriarte et al., 2007). During the productive season, the occurrence of a conspicuous diatom bloom in spring seems to be a common feature in Patagonian ecosystems. However, its intensity, duration and species composition seem to vary along latitudinal and coast to offshore environmental gradients. For instance, in the inner Chiloe Sea (north western Patagonia) the spring diatom bloom is followed by an increase of thecate dinoflagellates in summer (Iriarte and González, 2008) while in the Magellan Strait (southern Patagonia), the spring diatom bloom is followed by the dominance of pico- and nano-phytoplankton during the summer months (Iriarte et al., 2001).

In the majority of aquatic ecosystems, increments of algal activity are usually followed by increments in bacterial activity and subsequent rise in Community Respiration (CR) (Cole et al., 1988; Riemann and Bell, 1990; Williams, 1998; Arístegui and

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Harrison, 2002). It has been noted that heterotrophic bacteria contribute substantially to CR (del Giorgio and Peters, 1993; del Giorgio and Duarte, 2002; Blight et al., 1995; Robinson and Williams, 2005; Carlson et al., 2007; Robinson, 2008), and that a strong relationship between rates of GPP (Gross Primary Production), CR, and BSP (Bacterial Secondary Production) observed in coastal systems indicates a significant degree of coupling between the synthesis of organic matter and its subsequent degradation by the heterotrophic community (Montero et al., 2007, 2011).

Although it is generally recognized that primary and bacterial production are more tightly coupled in oligotrophic systems, it has also been shown that in highly productive ecosystems (e.g. Humboldt Current System, HCS) bacteria are also able to respond rapidly to increments in primary production (PP) (McManus and Peterson, 1988; Troncoso et al., 2003; Cuevas et al., 2004; Montero et al., 2007). Heterotrophic microbes can potentially set an upper limit to the transfer of organic matter to large metazoans, and can substantially modify the total amount of organic carbon that can be exported from the euphotic zone (Legendre and Rivkin, 2002, 2008). Consequently, increased bacterioplankton activity within the mixed layer may reduce the capacity of a given water body to sequester atmospheric CO₂ via photosynthesis.

Although there are virtually no BSP estimates for the Chilean fjord region, observations conducted in Scandinavian fjords have shown peaks in bacterial production in association with peaks in phytoplankton production (Albright and McCrae, 1987), which suggests that algal-derived carbon is an important substrate for bacterial growth (Bukaveckas et al., 2002). Other studies, however, have indicated that organic matter from terrestrial origin is also an important organic source to bacteria in this type of semi-enclosed environments (Newell et al., 1981; Button, 1984; Albright and McCrae, 1987). In fjord ecosystems allochthonous organic matter may be fuelling an important fraction of bacterial production. This subsidy may be especially important during months of low in situ primary production (Albright and McCrae, 1987). Based on these findings some researchers have suggested that enclosed or semi-enclosed marine

systems; such as the fjords of Chilean Patagonia, are dominated by heterotrophic processes (Bukaveckas et al., 2002).

Besides the intricacies of water-column carbon fluxes in these ecosystems, large exchanges of matter and energy (e.g. heat, CO₂, water) take place at the air-sea interface. A recent study (Torres et al., 2011) has shown that minimum values of carbon dioxide fugacity (*f*CO₂) occur in Patagonia during spring-summer (productive period), and that maximum values of *f*CO₂ are observed during austral winter (non productive period). CO₂ utilization by photosynthesis within the mixed layer has the potential to drive a strong flux of CO₂ from the atmosphere into the ocean. However, the strength of this gradient also depends on the release of CO₂ (through heterotrophic processes) by the marine planktonic community. Consequently, the net balance between GPP and CR is expected to be critical to the ability of these marine ecosystems to sequester or release atmospheric CO₂.

In this study, we analyzed the seasonal productivity cycle and their main forcing factors at a fixed station in the Puyuhuapi fjord (44° S, 73° W), Aysén region, southern Chile. By obtaining concurrent measurements of gross primary production (GPP), community respiration (CR) and bacterial secondary production (BSP), we were able to assess the degree of coupling between algal and bacterial production within this system. The consequences of the net balance between organic matter production and its subsequent utilization by heterotrophic processes (mostly bacteria driven) was also analysed in term of the ability of Patagonian fjord and channel ecosystems to sequester atmospheric CO₂. We also analyzed the contribution of the main phytoplankton size fractions, both seasonally and vertically in the water column. To our knowledge, the work presented here represents one of the most comprehensive studies of GPP, CR and BSP over a seasonal cycle for the Patagonian fjord and channel ecosystems.

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2 Materials and methods

2.1 Study area and sampling strategy

The study area corresponds to a fixed station in the Puyuhuapi fjord (44°42.6' S, 72°44.4' W), located at an average depth of 230 m and ca. 5 km N-W of the Cisnes river mouth (Fig. 1). The fjord runs in a N-NE direction and connects directly to the Moraleda channel at its mouth, and through the Jacaf channel near the head (Silva et al., 1997; Fig. 1). Freshwater input to the study area is driven by three main rivers (Ventisqueros north and south, and the Cisnes River), plus additional inputs from several diffuse sources. The freshwater input set an estuarine type of circulation, with a thin layer of freshwater from the continent flowing on top of a thick layer of oceanic Sub-Antarctic Waters (~31.5 psu) that is usually below 15–20 m. Freshwater coming from the continent is loaded with silicic acid while SAAW is loaded with nitrate and phosphate (Silva, 2008).

The station was occupied approximately at monthly intervals between October 2007 and October 2008. Additionally, intensive observations conducted over 5 to 8 consecutive days were undertaken in January 2008 (austral summer), May 2008 (austral autumn), July 2008 (austral winter) and October 2008 (austral spring).

2.2 Variability of atmospheric and sea-surface conditions in the study region

We used ca. 7 yr of satellite-derived data, from 2003 through late 2009, to characterize the regimes of variability in atmospheric forcing and sea-surface conditions near the study site. Data on wind stress measured over a 25 × 25 km coastal pixel were obtained from daily QuikSCAT level-3 images. We used data from a pixel centered at 44°7.5' S, 75°7.5' W, and located ca. 170 km N-W of the fjord's mouth. Out of the 2471 records available for this pixel in 2003–2009, 96.6% contained good data. A time series of Photosynthetically Available Radiation (PAR) for the same period was produced from 8-d composites of SeaWiFS images (level 3) with a 9 km resolution. Data

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5 were acquired for a pixel centered at 44°30' S, 73°25' W, on the Moraleda Channel and ca. 50 km N-W of the fjord's mouth. Out of the 295 PAR images available for this pixel in 2003–2009, 98.0% contained good data. Finally, data on sea surface temperature (SST) and surface Chlorophyll *a* concentration (Chl *a*) were acquired from 8-d composites of MODIS-Aqua images (level 3) with a 4 km spatial resolution. Weekly values of surface Chlorophyll *a* were obtained by averaging data collected over a 5-by-7 pixel area (i.e. 20 km by 35 km) located near the fjord's mouth and encompassing the latitudes 44°47.5'–44°57.7' S and longitudes 73°37.5'–73°22.5' W (see Fig. 1). Out of the 273 Chl *a* and 314 SST images available for this area in 2003–2009, 78% and 94% contained good data. Gaps in all four records of satellite-derived data were filled using linear interpolation.

2.3 Hydrographic measurements, phytoplankton, Chlorophyll *a* and nutrients

15 Profiles of temperature, salinity and dissolved oxygen were gathered during each sampling day using a CTDO (Ocean Seven 304, IDRONAUT, Italy). Water samples for analyses of Chlorophyll *a*, phytoplankton abundance, and inorganic nutrients were collected from 3 discrete depths (2, 10, and 20 m) using a 30-l Niskin bottle.

Water samples for nutrient analyses (nitrate, phosphate, silicic acid) were filtered through GF/F filters and frozen at –20 °C until spectrophotometric analysis in the laboratory. Nitrate, phosphate and silicic acid were determined as in Strickland and Parsons (1968).

25 Samples for phytoplankton cell counts consisted of 250-ml sub-samples collected with a Niskin bottle. Samples were stored in clear plastic bottles, fixed, and preserved in a 1% Lugol iodine solution (alkaline). From each sample, a 10-ml sub-sample was placed in a sedimentation chamber and allowed to settle for 12 h (Utermöhl, 1958) prior to sorting at 40× and 100× under an inverted microscope (Carl Zeiss, Axio Observer A.1).

For total Chl *a* determinations, three 100-ml water samples from each of the same three depths were filtered through MFS glass fiber filters with 0.7-µm nominal pore

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size. Following filtration, samples were immediately frozen (-20°C) until later analysis by fluorometry, using 90 % v/v acetone for pigment extraction and a Turner Design TD-700 fluorometer according to standard procedures (Parsons et al., 1984).

Chlorophyll *a* size fractionation was performed post-incubation in 3 sequential steps: (1) for the nanoplankton fraction (2.0–20 μm), seawater (100-ml) was pre-filtered using 20- μm Nitex mesh and collected on a 2.0- μm Nuclepore; (2) for the picoplankton fraction (0.7–2.0 μm), seawater (100-ml) was pre-filtered using a 2.0- μm Nuclepore and collected on a 0.7- μm MFS (microfiltration system) glass-fiber filter; (3) for the whole phytoplankton community, 100-mL of seawater was filtered through a 0.7- μm MFS glass-fiber filter. The microphytoplankton fraction was obtained by subtracting the Chlorophyll *a* estimated in Steps (1) and (2) from total Chl *a* estimated in Step 3. Chlorophyll *a* size fractionation was only estimated during the intensive sampling campaigns. Discrete-depth estimates of Chl *a* and abundance phytoplankton were integrated down to 20 m, using a polynomial method.

2.4 pH, Total Alkalinity and $p\text{CO}_2$

Samples for pH and Total Alkalinity (A_T) were analyzed following the DOE potentiometric method (1994) and the method of Haraldsson et al. (1997), respectively. The pH, A_T and hydrographic data were used to calculate the seawater $p\text{CO}_2$ using CO_2SYS software (Lewis and Wallace, 1998). Seawater $p\text{CO}_2$ was calculated using Mehrbach solubility constants (Mehrbach et al., 1973) refitted by Dickson and Millero (1987). These experiments were taken during the intensive sampling campaigns of January, May and October 2008. Samples were collected up to 27 m, at intervals of one meter.

2.5 Gross primary production (GPP) and community respiration (CR) experiments

In situ GPP and CR incubations were performed on each field campaign conducted from October 2007 to October 2008, which amounts to 32 experiments. Incubations

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were performed with water samples obtained from the same sampling depths indicated above (2, 10, and 20 m). GPP and CR were estimated from changes in dissolved oxygen concentrations observed after in situ incubation of light and dark bottles (Strickland, 1960). Water from the Niskin bottles was transferred into 125 ml (nominal volume) borosilicate bottles (gravimetrically calibrated) using a silicone tube. Five time-zero bottles, five light bottles, and five dark bottles were used for each incubation depth. Water samples were collected at dawn and were incubated during the whole light period (incubating time was 10 ± 1.3 h in the productive period and 7 ± 0.7 during the non-productive season). Time-zero bottles were fixed at the beginning of each experiment, whereas the incubation bottles were attached to a surface-tethered mooring system. Dissolved oxygen concentrations were determined according to the Winkler method (Strickland and Parson, 1968), using an automatic Metrohom burette (Dosimat plus 865) and by visual end-point detection (problems with the power supply in such isolated locations prevented us from using a photometric end point detector). The mean variation coefficient of the replicate samples was 0.03 ± 0.02 %. Daily GPP and CR were calculated as follows: $GPP = (\text{mean } [O_2] \text{ light bottles} - \text{mean } [O_2] \text{ dark bottles})$; $CR = (\text{mean } [O_2] \text{ time zero bottles} - \text{mean } [O_2] \text{ dark bottles}) / (\text{hours of incubation}) \times 24$. GPP and CR values were converted from oxygen to carbon units using a conservative photosynthetic quotient (PQ) of 1.25 (Williams and Robertson, 1991) and a respiration quotient (RQ) of 1. GPP and CR discrete-depth estimates were integrated down to 20 meters using a polynomial method. The 20 m depth layer roughly corresponded to the main 1 % light depth measured during the productive (21.7 ± 8.2 ; calculated using a Secchi disc as Poole and Atkins, 1929).

2.6 Bacterial secondary production (BSP)

The BSP experiments were carried out using the same water samples obtained for in situ GPP and CR incubations. The experiments were conducted during the intensive campaigns sampling, which amounted to 24 experiments. BSP was estimated through the rate of incorporation of Leu- $[^{14}C]$ -leucine ($300 \text{ mCi mmol}^{-1}$, 50 nM final

5 saturating concentration) into proteins (Simon and Azam, 1989). A blank and three
10 10 ml samples were taken from each sampling depth, and later incubated for one hour.
After incubation, the samples and blank were poisoned with 0.2 μm filtered buffered
formaldehyde. All incubations were stopped by adding cold analytical trichloroacetic
acid (TCA) 50 % w/v. After 10 min, the tube contents were filtered (0.22 μm pore size
GSWP Millipore). Dried filters were transferred to borosilicate scintillation vials, where
they were kept at low temperature until radioisotopic analysis. In the laboratory, vials
were treated with analytical ethyl acetate and 10 ml of liquid scintillate Ecolite (+) (ICN).
All samples were measured in dpm using a Packard (Mod. 1600 TR) liquid scintillation
counter.

Leucine incorporation rates were transformed into bacterial carbon (Bacterial Pro-
duction) using two approaches: the theoretical conversion factor of 1.55 Kg C mol Leu⁻¹
(Simon and Azam, 1989), and the empirical factor calculated for estuaries of
1.3 Kg C mol Leu⁻¹ (Hoch and Kirchman, 1993). BP was converted to Bacterial Carbon
Utilization (i.e., gross bacterial secondary production, BSP) using a Bacterial Growth
Efficiency (BGE). BGE values were derived from the equations of del Giorgio and
Cole (1998) and Kritzberg et al. (2005). Throughout the text, BSP refers to gross bac-
terial secondary production. Discrete-depth estimates of BSP were integrated down
to 20 m. Throughout the text the term “bacteria” and “bacterioplankton” refers to the
pelagic pool of bacteria and archaea.

2.7 Statistical analyses

Seasonal differences in total depth-integrated Chlorophyll *a*, GPP, CR and BSP were
tested using the non parametric Mann-Whitney test (*U*) and Kruskal-Wallis test (*H*).
The degree of association between variables was determined using Spearman Cor-
relation Coefficients (r_s). Cross-correlation analyses were conducted to test for asso-
ciations between satellite-derived time series of meridional wind stress, surface PAR,
SST, and surface Chlorophyll concentration. To assemble a set of data vectors that
were amenable to these analyses, initial and final dates of the composite Chl *a* images

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were used to produce a weekly series of cumulative meridional wind stress. Climatologies were used to convert PAR, SST, and Chl *a* series into anomalies prior to the computation of lagged correlation coefficients. Significance was assessed according to Sciremammano (1979). Finally, and having checked that the highest (and significant) cross-correlations between series corresponded to zero-lag correlations, we used stepwise regression analysis to assess the relative quality and predictive capabilities of wind stress, PAR and SST as predictors of surface Chl *a* concentration in the study area.

In this study we used the 2 m sampling depth to represent upper mixed layer water column conditions since the pycnocline was usually found at 6 m depth.

3 Results

3.1 Variability of atmospheric and sea-surface conditions in the study region

The 7-yr time series of QuikSCAT data on meridional wind stress showed an alternation of periods with equatorward and poleward winds that persisted for several days, with a scale of de-correlation of ca. 5 d, and no apparent annual signal (Fig. 2a). This lack of a clear pattern of seasonal variability in wind forcing, and its high inter-annual variability, became more apparent in the climatology computed for wind stress (Fig. 2e). Contrastingly, surface PAR and SST time series showed a strong annual cycle (Fig. 2b, c), which was also reflected by the low inter-annual variability (i.e. small error bars) obtained for the climatologies (Fig. 2f, g). Surface Chlorophyll concentrations, on the other hand, showed high intra- and inter-annual variability (Fig. 2d, h), and produced a climatology that suggests the existence of 2 distinct seasons: a low-Chlorophyll (presumably less productive) period that spans the autumn and winter months (April–August), and a productive season in the spring and summer (September–March). During this productive season, however, phytoplankton biomass tends to increase rapidly in the spring-early

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summer (September–October), decay in early summer (December–January) and increase again in late summer (February–March, see Fig. 2h).

Surface PAR and SST were highly correlated at lag = 0 ($r = 0.64$, $p < 0.001$) and reached maximum correlation ($r = 0.77$, $p < 0.001$) at ~40-day lags, with increases in PAR leading increases of SST. This high correlation and the lack of a clear annual signal in wind stress variability, confirm that the strong seasonality in SST values near the Puyuhuapi fjord is mostly driven by changes in solar radiation. Weak but significant zero-lag correlations were found for surface Chlorophyll *a* and cumulative meridional wind stress ($r = 0.35$, $p < 0.01$), PAR anomalies ($r = 0.30$, $p < 0.01$) and SST anomalies ($r = 0.23$, $p < 0.01$).

3.2 In situ hydrographic and nutrient measurements

In general, the water column showed a two-layer density structure that to a great extent was determined by salinity, with a pycnocline that was usually found at 6 m (Fig. 3a). Surface temperature decreased from $>18^{\circ}\text{C}$ in January to $<9^{\circ}\text{C}$ in July (Fig. 3b). Thermal stratification decreased over this same period, and a subsequent, winter cooling lead to a thermal inversion that persisted through early spring (October, see 10°C isobath in Fig. 3b). Salinity profiles showed a surface layer (0–10 m) of low-salinity water (<15), particularly in late summer and early spring (Fig. 3a). Below this layer, salinity fluctuated between 30 and 33, with the 33 isohaline deepening in winter (July) and early spring (October). These two instances were associated with an increase in surface oxygen concentration, which increased from warm to cold periods (Fig. 3c).

Nutrient data revealed low concentrations of nitrate and phosphate within the top 20 m in spring and summer, and maximum concentrations in autumn-winter months (Fig. 4a, b). Spring-summer surface concentrations of nitrate and phosphate were $<5\ \mu\text{M}$ and $<0.5\ \mu\text{M}$, respectively; they reached concentrations $>10\ \mu\text{M}$ and $>1\ \mu\text{M}$ during winter months (Fig. 4a, b). Silicic acid concentrations showed a contrasting pattern, with highest surface values ($>20\ \mu\text{M}$) in late summer and autumn-winter, and occasional but moderate increases in spring-summer (Fig. 4c). These increases in surface

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silicic acid coincided with the inputs of low-salinity water (shown in Fig. 3a). The general trend over the top 20 m, however, was for nutrient concentrations to decline sharply from August to February. Correlation analyses revealed a significant relationship between depth-integrated GPP and the concentrations of nitrate ($r = -0.63$, $p < 0.05$, $n = 27$) and silicic acid ($r = -0.5$, $p < 0.05$, $n = 27$).

3.3 Gross primary production (GPP) and community respiration (CR)

Vertical profiles of GPP during the study period showed significant differences between sampling depths ($H = 19$, $p < 0.05$, $n = 98$). The highest values ($4.8\text{--}698.1 \mu\text{g CL}^{-1} \text{d}^{-1}$) were recorded within the surface layer (2 m), while the lowest values ($0.5\text{--}308.6 \mu\text{g CL}^{-1} \text{d}^{-1}$) were observed at 20 m depth (Fig. 5). Vertical profiles of CR showed no significant vertical differences ($H = 2$, $p > 0.05$, $n = 98$).

GPP showed significant differences between the productive and non-productive seasons ($U = 38$, $p < 0.05$, $n = 32$). Depth-integrated GPP rates (down to 20 m) ranged from 0.02 to $4.4 \text{ g C m}^{-2} \text{ d}^{-1}$ over the annual cycle (Fig. 5). The highest GPP values were recorded in April ($3.1 \text{ g C m}^{-2} \text{ d}^{-1}$) and August ($4.4 \text{ g C m}^{-2} \text{ d}^{-1}$), i.e. during early fall and late winter; whereas, low values ($<0.3 \text{ g C m}^{-2} \text{ d}^{-1}$) were observed from May to July. Community respiration rates also showed significant seasonal differences ($U = 51$, $p < 0.05$, $n = 32$), with depth-integrated values ranging from ~ 0 to $2.3 \text{ g C m}^{-2} \text{ d}^{-1}$ over an annual cycle (Fig. 5). Estimates of annual GPP and CR, integrated over the top 20 m of the water column, were 533 and $537 \text{ g C m}^{-2} \text{ yr}^{-1}$, respectively (Table 2).

The 20 m integrated GPP/CR ratio showed significant seasonal differences ($U = 55$, $p < 0.05$, $n = 30$). The mean GPP/CR ratio was <1 throughout the study period: 0.8 ± 0.7 during the productive season and 0.4 ± 0.3 during the non-productive season. Within the surface mixed layer the GPP/CR ratio also showed significant seasonal differences ($U = 15$, $p < 0.05$, $n = 23$). The mixed layer GPP/CR ratio was 1.2 ± 0.7 ; $n = 14$ and 0.33 ± 0.3 ; $n = 9$ during the productive and non-productive season, respectively.

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3.4 Chlorophyll *a* and Phytoplankton abundance

Depth-integrated Chlorophyll *a* (Chl *a*) ranged from 2.8–166.2 mg Chl *a* m⁻² in the productive season to 0.3–15.8 mg Chl *a* m⁻² in the non-productive season. The maximum photosynthetic pigment biomass (166.2 mg Chl *a* m⁻²) was observed in late winter (August, Fig. 7), and coincided with the highest GPP (4.4 g C m⁻² d⁻¹). Depth-integrated Chl *a* and GPP were positively correlated ($r = 0.54$, $n = 28$, $p < 0.05$). Highest Chlorophyll *a* (Chl *a*) concentrations were measured in the surface layers (0.2–19.2 mg m⁻³) while the lowest values (0–3.3 mg m⁻³) were recorded at 20 m depth (Fig. 7)

Estimates of Chl *a* partitioned into three size classes (<2 μm, 2–20 μm, >20 μm) revealed the dominance of picophytoplankton (<2 μm) during the non-productive season (May and July) at 2 and 10 m depth. During the productive season, picophytoplankton was only found to be dominant in a January sample obtained at 20 m depth (Fig. 7). While the nanophytoplankton size class (between 2–20 μm) did not show significant abundance variations over the annual cycle. Strong seasonal variability was observed for microphytoplankton (>20 μm) abundance (Fig. 7). The highest phytoplankton counts (16 000–235 000 cells Leu⁻¹ 10³) were obtained during Spring (October 2008), Summer (January and February) and Autumn (April). The lowest abundances (1600–10 500 cells L⁻¹ 10³) occurred in winter (Fig. 8). During the productive season, diatoms of the genera *Pseudo-nitzschia*, *Skeletonema* and *Chaetoceros* were numerically dominant and represented >50% of the total abundance (Fig. 8). Seasonal fluctuations in GPP values roughly corresponded with the observed changes in diatom abundance, confirming their importance for overall productivity in the Puyuhuapi channel ecosystem. Phytoplankton abundance was also highly and significantly correlated with the concentrations of inorganic nutrients: nitrate ($r = -0.7$, $n = 25$, $p < 0.05$), phosphate ($r = -0.6$, $n = 25$, $p < 0.05$) and silicic acid ($r = -0.8$, $n = 25$, $p < 0.05$).

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3.5 Bacterial production (BP), bacterial growth efficiency (BGE) and bacterial secondary production (BSP)

Estimates of Bacterial Production (BP) obtained for each sampling depth using two different conversion factors did not differ significantly ($U = 1454$, $p > 0.05$, $n = 61$). Bacterial Growth Efficiency (BGE) estimates calculated according to Kritzberg et al. (2005) and del Giorgio and Cole (1998) ranged between 0.02–0.32 and 0.04–0.31, respectively. There was marked seasonal difference in BGE ($U = 259$, $p < 0.05$, $n = 61$), with high values (mean 0.2 ± 0.05 , $n = 30$) during productive months, and low values (mean 0.08 ± 0.04 , $n = 31$) during the non-productive season.

Rates of Bacterial Secondary Production (BSP) ranged from 0.001 to $1.81 \text{ g C m}^{-2} \text{ d}^{-1}$, and showed significant differences between productive and non-productive seasons ($U = 528$, $p < 0.05$, $n = 96$) (Fig. 9). Maximum BSP rates ($>0.6 \text{ g C m}^{-2} \text{ d}^{-1}$; Fig. 9) were observed during two intensive sampling campaigns in January and October 2008. BSP rates $<0.1 \text{ g C m}^{-2} \text{ d}^{-1}$ were recorded in October 2007 (Fig. 9). There were significant correlations between BSP and GPP ($r = 0.6$, $p < 0.05$, $n = 24$), and between BSP and Chl *a* ($r = 0.4$, $p < 0.05$, $n = 24$).

3.6 $p\text{CO}_2$ and GPP/CR ratios

Water column $p\text{CO}_2$ estimates derived from pH and alkalinity measurements conducted in January (summer), May (late autumn), and October (spring 2008) showed substantial seasonal differences. The lowest and highest surface $p\text{CO}_2$ values were observed in October ($93.5 \mu\text{atm}$), and May ($298 \mu\text{atm}$), respectively. The depths where $p\text{CO}_2$ was $>380 \mu\text{atm}$ (roughly corresponding to atmospheric $p\text{CO}_2$ concentration) varied from 14 m in October to 10 and 2 m in January and May, respectively (Fig. 10). Within the upper mixed layer GPP/CR showed values >1 when $p\text{CO}_2$ levels in the water column were lower than $380 \mu\text{atm}$. On the contrary GPP/CR values <1 were observed when $p\text{CO}_2$ levels were higher than $380 \mu\text{atm}$ (Fig. 10).

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We have documented sharp seasonal changes in the atmospheric and water-column conditions that determine nutrient availability for primary production, phytoplankton biomass and composition, and the overall metabolic balance of the Puyuhuapi fjord ecosystem. A set of in situ observations gathered over two consecutive spring-summer seasons, and one autumn-fall season in the middle, has made it possible to connect the two-phase pattern (i.e. productive season/non-productive season) of Chl-*a* variability shown by satellite data (Iriarte et al., 2007) with a two-phase cycle in GPP, CR, and the composition of phytoplankton assemblages.

Given the hypothesized role of fjord ecosystems in this part of world as sinks for atmospheric CO₂ (Torres et al., 2011), resolving temporal and vertical patterns of these processes, and connecting them with larger-scale patterns detected through remote sensing, is highly relevant for future climate-change scenarios.

The annual productivity cycle of the study area is influenced by nutrient availability, water column stabilization and seasonal variations in the light regime. The joint analysis of our in situ data and longer records of satellite-derived surface Chl *a* suggests that the “productive season” in the Puyuhuapi fjord begins in late winter (August) and extends until autumn (April). The shorter “non-productive season”, on the other hand, spans the May–July period, i.e. from late autumn to early winter. These results, together with recently acquired data from a distant and contrasting fjord ecosystem (Puyuhuapi fjord, Lat. 41° S; Montero et al., 2011), may indicate that common larger-scale forcing factors modulate productivity cycles and the overall metabolism of marine ecosystems in Patagonia. The switching times between productive and non-productive conditions that we observed in our study are also consistent with previous observations (Pizarro et al., 2005; Iriarte et al., 2007) indicating that an improvement in light conditions towards the end of winter is the main factor triggering phytoplankton blooms in the Chilean fjord region.

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Although changes in the light field, play an important role in determining the extent of the productive season, other factors, such as freshwater input and fjord hydrodynamics are equally important. The Puyuhuapi fjord usually receives a high amount of freshwater from the Cisnes River, which co-occur with the seasonal increase in concentrations of silicic acid (20–40 μM). The first diatom bloom in our study area was recorded during late August and coincided with a $\sim 50\%$ drop in the Cisnes river discharge (from $379 \text{ m}^3 \text{ s}^{-1}$ in July to $166 \text{ m}^3 \text{ s}^{-1}$ in August). In contrast, the late autumn decline in phytoplankton productivity was associated with increased river discharge (from $100 \text{ m}^3 \text{ s}^{-1}$ in March to $>200 \text{ m}^3 \text{ s}^{-1}$ between April and July). Influences of river outflow patterns on the occurrence and spatial distribution of phytoplankton blooms have also been reported by Goebel et al. (2005) who documented a connection between higher irradiance attenuation in sub-surface waters and periods of increased freshwater input. Freshwater input stabilizes the water column and sets an estuarine type of circulation, with a buoyant fresher layer on top of a nutrient-rich subsurface layer characteristic of open ocean environments in these latitudes (i.e. Sub-Antarctic Surface Water; Chaigneau and Pizarro, 2005). This layout of hydrographic properties exerts a strong influence on rates of vertical mixing and water column stability, on the sensitivity of local productivity and metabolism to large-scale forcing, and ultimately on the fjord's role in the exchange of carbon across the air-sea and water-sediment interfaces.

The high variability of integrated GPP values observed during the productive season reflects the pulsed nature and spatial heterogeneity of productivity cycles in the Patagonian fjord region. Productivity cycles are modulated by a combination of biological and hydrodynamical controls, both top down (e.g. grazing by predators; González et al., 2011) and bottom-up processes associated to photic layer nutrient depletion and replenishment as a consequence of turbulent eddy formation (Farmer and Freeland, 1983), wind stress (Gibbs, 2001), and tidal currents (Cloern, 1982).

The annual depth-integrated Gross Primary Production (GPP) estimated for the Puyuhuapi study site ($533 \text{ g C m}^{-2} \text{ yr}^{-1}$) amounts to ca. 50% of the yearly GPP estimated for the exceptionally productive upwelling system off Concepción, in central

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Chile (Daneri et al., 2000; Montero et al., 2007) and compares well with estimates made in other highly productive ecosystems fjord such as the Howe sound ($563 \text{ g C m}^{-2} \text{ yr}^{-1}$) on the southern coast of British Columbia (Albright and McRae, 1987). The range of daily measurements of GPP obtained during the productive season at Puyuhuapi (0.02– $4.4 \text{ g C m}^{-2} \text{ d}^{-1}$) is also in good agreement with high productivity estimates reported by previous studies conducted in the inner sea of Chiloé (41.5° – 43° S; Iriarte et al., 2007), the Reloncaví fjord (41° S; Montero et al., 2011), the Aysén region (43° – 46° S; Pizarro et al., 2005) and the Aysén fjord (45° S; Daneri et al., unpublished data). Lowest GPP and Chl *a* values were obtained during the non-productive season (0.04 to $0.3 \text{ g C m}^{-2} \text{ d}^{-1}$ and 0.3 to 16 mg m^{-2} respectively). The phase change between productive and non productive season was also reflected in changes on the relative dominance of phytoplankton size fractions. During the productive season, large phytoplankton ($>20 \mu\text{m}$; mainly diatoms) was dominant, while the non-productive season was dominated by the picophytoplankton size fraction ($<2 \mu\text{m}$). These results support the notion that diatoms tend to dominate under conditions of higher nutrient availability and surface irradiance, while small photosynthetic cells become more important under harsher environmental conditions.

Within the large phytoplankton community species succession is recurrent in the southern fjord region. In our study *Skeletonema costatum* dominated at the beginning of the productive season (late winter), while *Chaetoceros* spp. and *Pseudo-nitzschia* spp. became dominant during the spring and summer-autumn season, respectively. The three main diatoms observed in this study have been described as dominant species within phytoplankton assemblages in several Chilean fjords (Iriarte et al., 2007; Alves-de-Souza et al., 2008; Iriarte and González, 2008; Montero et al., 2011). In terms of cell abundance maximum counts of phytoplankton cells were observed when *Pseudo-nitzschia* spp. were dominant (January to April; $80\,000$ – $235\,000 \text{ cells L}^{-1} 10^3$) however, the highest GPP values were associated with *Skeletonema costatum* during late winter (August; $16\,000$ – $71\,000 \text{ cells L}^{-1} 10^3$) when the concentrations of silicic acid (and river input), were highest. The high GPP, lower biomass condition

associated to the late winter *Skeletonema costatum* bloom may be the result of top-down controls (e.g. grazing) being exerted on this species by zooplankton that peaks in the area at the beginning of the productive season (González et al., 2011).

A significant degree of association between diatom abundance and nutrient concentration, has been reported for the fjords and channels of southern Chile. *Pseudo-nitzschia* spp. and *Chaetoceros* spp. have been mainly correlated with nitrate, whereas *Skeletonema costatum* has been associated with enhanced levels of silicic acid (Alves-de-Souza et al., 2008). During this study, phytoplankton abundance was significantly correlated with nitrate, phosphate and silicic acid. Nutrient concentrations were highest during the winter and lowest during the rest of the year. Despite the marked fall in nutrient concentration that occurs during the productive season nutrient levels are rarely limiting (i.e. they rarely fall below the known half saturation constant of several diatoms, Eppley et al., 1969) as a result of periodic water entrainment processes already discussed above. Continuous nutrient availability is probably the main cause of the exceptionally extended productive season (from late winter to late autumn), observed for the Puyuhuapi fjord (this study) and Reloncaví fjord (Montero et al., 2011). Besides nutrient replenishment by oceanic water entrainment, the levels of silicic acid in Patagonian fjords are enhanced by river input which results in higher than normal Redfield ratios for $\text{Si}[\text{OH}]_4:\text{NO}_3(2)$ and $\text{Si}[\text{OH}]_4:\text{PO}_4(20)$. The $\text{NO}_3:\text{PO}_4$ ratio (10) also shows a deviation from Redfield (this study and Iriarte et al., 2007) indicating that nitrate could eventually be more limiting than phosphate.

The productivity of bacterioplankton (both bacteria and archaea) in most aquatic ecosystem depends mainly on the quantity and quality of organic matter produced by phytoplankton (Cole et al., 1988), although in coastal environments terrestrial organic matter may also be important (Albright and McCrae, 1987). During this study Bacterial Secondary Production (BSP) was positively correlated with GPP and Chl *a* on an annual cycle basis. However the winter drop in bacterioplankton activity was not as pronounced as the winter drop in phytoplankton activity. BSP fell from $1 \pm 0.6 \text{ g C m}^{-2} \text{ d}^{-1}$ to $0.6 \pm 0.3 \text{ g C m}^{-2} \text{ d}^{-1}$ while GPP values dropped from $1.1 \pm 1.12 \text{ g C m}^{-2} \text{ d}^{-1}$ to

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0.1 ± 0.1 g C m⁻² d⁻¹. As a result of this, bacterial carbon utilization (integrated to 20 m) increased on average from 116 % of GPP during the productive season to >500 % of GPP during the non productive season indicating that an important amount of BSP is being sustained independently of algal production. Dissolved organic matter (DOM) of terrestrial origin entering the Puyuhuapi fjord through point and diffuse freshwater sources is probably the main source of allochthonous DOC supporting bacterial activity in excess of algal production. This hypothesis is supported by the positive correlations observed between BSP and Cisnes River flow ($r = 0.66$, $p < 0.05$, $n = 11$), and between surface DOC concentration and Cisnes River flow ($r = 0.72$, $p < 0.05$, $n = 12$) (see Fig. 11).

Our estimates of Bacterial Growth Efficiency (BGE) were high during the productive season when in situ algal production was probably the main substrate supporting bacterial activity. BGE values were low during the non-productive season when bacteria was mainly supported by allochthonous organic matter. These results support the notion that bacterioplankton grow more efficiently (high BGE) on autochthonous rather than on allochthonous (in our case terrestrial) organic matter. Similar results have been reported for the Reloncaví fjord in southern Chile (Montero et al., 2011), the Hudson River estuary (Findlay et al., 1991) and the Kentucky Lake in the United States (Bukaveckas et al., 2002). Low BGE values imply that a large proportion of the assimilated DOC is directly respired to meet bacterial metabolic needs, thus reducing the amount of organic matter of bacterial origin available to higher trophic levels.

Estimates of annual GPP and CR, integrated over the top 20 m of the water column (that roughly corresponded to the photic layer), were 533 and 536 g C m⁻² yr⁻¹, respectively and the mean GPP/CR ratio was <1 throughout the study period indicating that overall, on an annual basis, the surface layer was heterotrophic. It should be pointed out however that during the productive season GPP/CR was closer to unity than during the non-productive season (0.8 ± 0.7 during the productive season and 0.4 ± 0.3 during the non-productive season respectively). Within the surface mixed layer (roughly 6 m deep) the mean GPP/CR ratio was >1 during the productive season and <1 during the

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non productive season. Within this layer the significant correlation recorded between GPP/CR and GPP during the productive season, and between GPP/CR and CR during the non-productive season, is indicative that the trophic status of the mixed layer at our Puyuhuapi fjord station is controlled by both GPP (during the productive season) and by CR (during the non productive season). CR control of trophic balance can only occur in ecosystems with an important subsidy of organic carbon which would be the case of the Puyuhuapi fjord. CR control of GPP/CR has rarely been reported; most work (albeit generally undertaken in less productive environments) indicates that the GPP/CR ratio is controlled by GPP (Aristegui and Harrison, 2002; Serret et al., 2009).

The dominant metabolic status (autotrophic or heterotrophic) of surface waters is directly related to the ability of a system to sequester or release atmospheric CO₂. In the Puyuhuapi fjord, the seasonal transition from autotrophic to heterotrophic metabolism (and vice versa) within the upper mixed layer is reflected in the pCO₂ content of the surface waters. Thus, low values of pCO₂ were measured in autotrophic waters (GPP/CR > 1) while high pCO₂ levels were measured in heterotrophic waters (GPP/CR < 1). These results are in agreement with those reported by Torres et al. (2011), who have indicated that the Patagonian eco-region is a net sink of atmospheric CO₂. Such condition holds at the Puyuhuapi fjord during the extended productive season documented for the Patagonian fjord and channel ecosystems in southern Chile.

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Table 1. Rates of Bacterial Secondary Production (BSP) estimated for the Puyuhuapi station with different BGE, Gross Primary Production (GPP) and % GPP utilization by bacteria in the study area.

Date	BSP (BGE by Kritzberg et al., 2005)					BSP (BGE by del Giorgio and Cole, 1998)				
	GPP	Simon and Azam	utilization	Hoch and Kirchman	utilization	Simon and Azam	utilization	Hoch and Kirchman	utilization	
	g C m ⁻² d ⁻¹	g C m ⁻² d ⁻¹	%	g C m ⁻² d ⁻¹	%	g C m ⁻² d ⁻¹	%	g C m ⁻² d ⁻¹	%	
13 October 2007	0.62	0.05	9	0.05	8	0.03	4	0.02	4	
14 October 2007	0.24	0.05	22	0.07	28	0.04	16	0.03	13	
15 October 2007	0.05	0.01	22	0.01	19	0.01	11	0.01	20	
22 January 2008	0.81	0.99	123	0.95	118	1.33	164	1.21	149	
23 January 2008	0.52	1.24	239	1.19	228	1.57	302	1.43	275	
24 January 2008	0.95	1.53	161	1.45	153	1.81	191	1.63	172	
26 January 2008	0.63	1.14	182	1.09	174	1.45	230	1.32	209	
27 January 2008	0.64	0.91	143	0.94	146	1.32	206	1.20	188	
28 January 2008	0.77	0.84	109	0.81	105	1.18	153	1.08	140	
12 May 2008	0.10	0.72	723	0.70	701	1.00	1000	0.90	905	
13 May 2008	0.09	0.73	813	0.71	786	1.00	1107	0.90	1004	
15 May 2008	0.23	0.83	361	0.80	348	1.13	491	1.03	447	
16 May 2008	0.17	0.56	331	0.55	323	0.73	429	0.65	381	
17 May 2008	0.06	0.53	887	0.52	864	0.66	1106	0.58	971	
18 May 2008	0.06	0.002	3	0.002	3	0.001	2	0.001	2	
19 May 2008	0.04	0.45	1132	0.44	1100	0.52	1292	0.45	1121	
28 July 2008	0.06	0.40	670	0.39	650	0.40	672	0.34	568	
29 July 2008	0.27	0.49	182	0.48	177	0.59	217	0.51	188	
30 July 2008	0.33	0.43	131	0.42	128	0.46	140	0.39	120	
31 July 2008	0.16	0.21	133	0.20	126	0.15	93	0.12	76	
6 October 2008	1.03	1.10	107	0.97	95	1.36	132	1.24	121	
7 October 2008	0.95	0.97	102	0.87	92	1.25	131	1.14	120	
8 October 2008	2.53	1.31	52	1.14	45	1.52	60	1.38	55	
9 October 2008	0.02	1.14	5702	1.00	5023	1.39	6969	1.27	6367	

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Table 2. Monthly averaged values of depth-integrated primary production and community respiration at the Puyuhuapi station.

Month	Primary Production (g C m ⁻² d ⁻¹)	<i>n</i>	Community Respiration (g C m ⁻² d ⁻¹)	<i>n</i>
January	0.7 ± 0.1	7	1.2 ± 0.6	7
February	0.5 ± 0.4	2	0.9 ± 0.8	2
March*	1.1 ± 0.5	3	1.9 ± 0.7	3
April	3.1	1	2.3	1
May	0.1 ± 0.1	7	0.3 ± 0.2	7
June	0.1	1	2.0	1
July	0.2 ± 0.1	5	0.7 ± 0.5	5
August	4.4	1	2.1	1
September	0.95	1	2.2	1
October	0.8 ± 0.8	7	1.1 ± 0.8	7
November*	4.2	1		
December				
Average	1.46 ± 1.6		1.47 ± 0.7	

* The experiment conducted in March and November was not included in the rest of the analysis.

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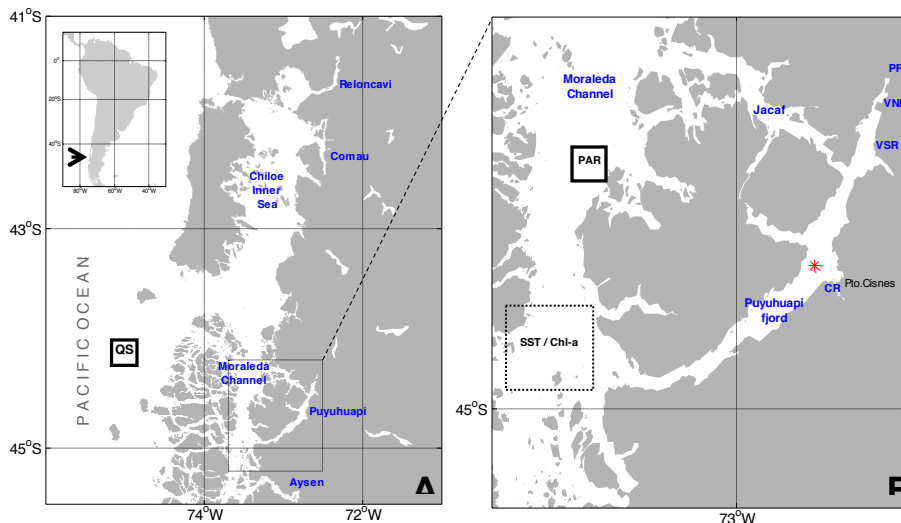


Fig. 1. Location of the study area in Chilean Patagonia ((A), dashed line) and position of the time series station in the Puyuhuapi fjord ((B), asterisk). Solid squares in (A) and (B) indicate the points/areas for which satellite data on wind stress (QS), PAR radiation (PAR), Sea Surface Temperature (SST) and surface Chlorophyll *a* concentration (Chl *a*) were obtained (see methods for details). Positions of the rivers are indicated in (B) and correspond to rivers Cisnes (CR), Ventisquero Sur (VSR), Ventisquero Norte (VNR), and Pascua (PR).

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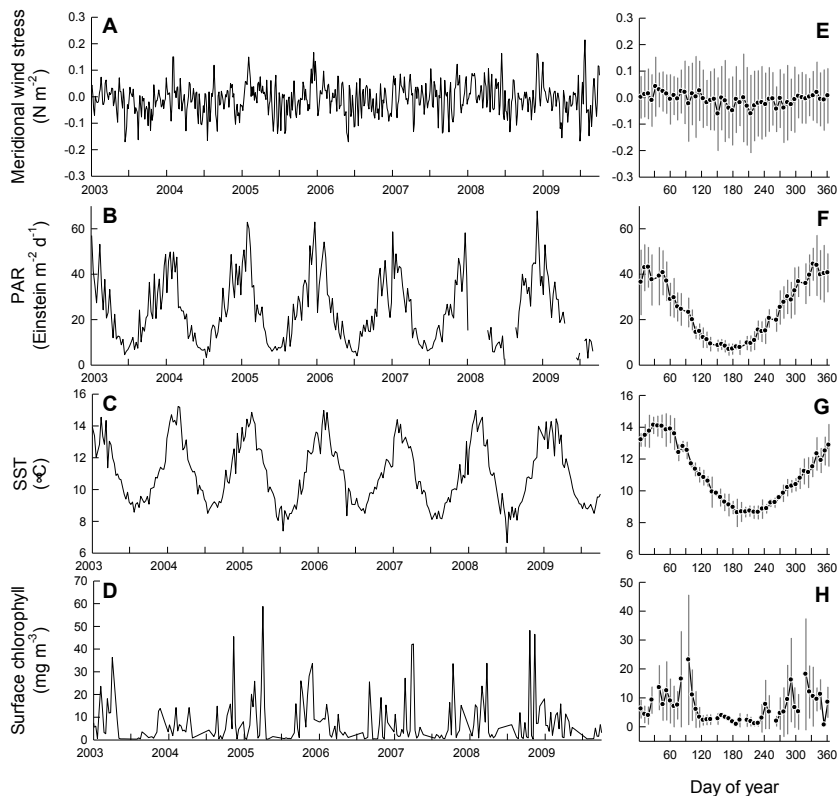


Fig. 2. Satellite-derived time series (A–D) and climatologies (E–H) of meridional wind stress (A, E), surface PAR, i.e. Photosynthetically Available Radiation (B, F), Sea Surface Temperature (C, G), and surface Chlorophyll *a* concentration (D, H). Wind stress data were obtained from daily QuikSCAT level-3 images with ~ 25 km spatial resolution, PAR data were produced from 8-d composites of SeaWiFS images with 9 km resolution, whereas SST and Chl *a* were extracted from 8-d composites of MODIS-Aqua images with 4 km resolution. See methods for more details. Symbols and error bars in (E–H) correspond to the mean ± 1 SD.

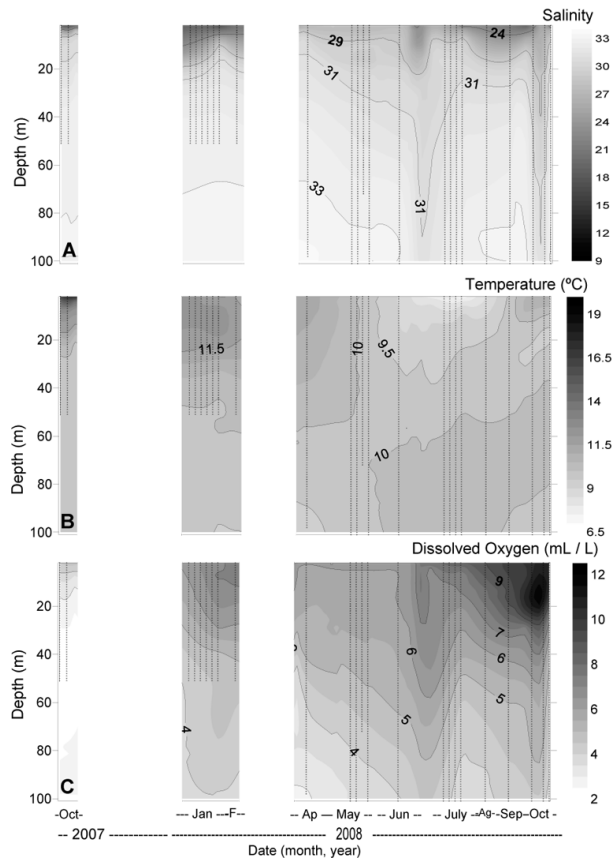


Fig. 3. Temporal variability of hydrographic profiles at the Puyuhuapi fjord station: **(A)** salinity, **(B)** temperature, and **(C)** dissolved oxygen. Sampling times and depth range are indicated by dotted vertical lines.

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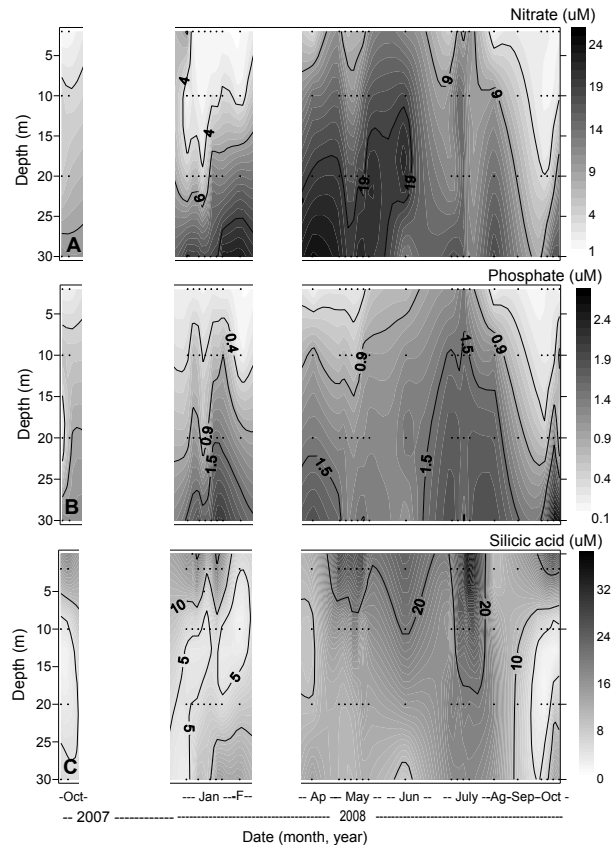


Fig. 4. Temporal variability of dissolved inorganic nutrient profiles at the Puyuhuapi station: **(A)** nitrate, **(B)** phosphate, and **(C)** silicic acid. Sampling times and depths are indicated by dots.

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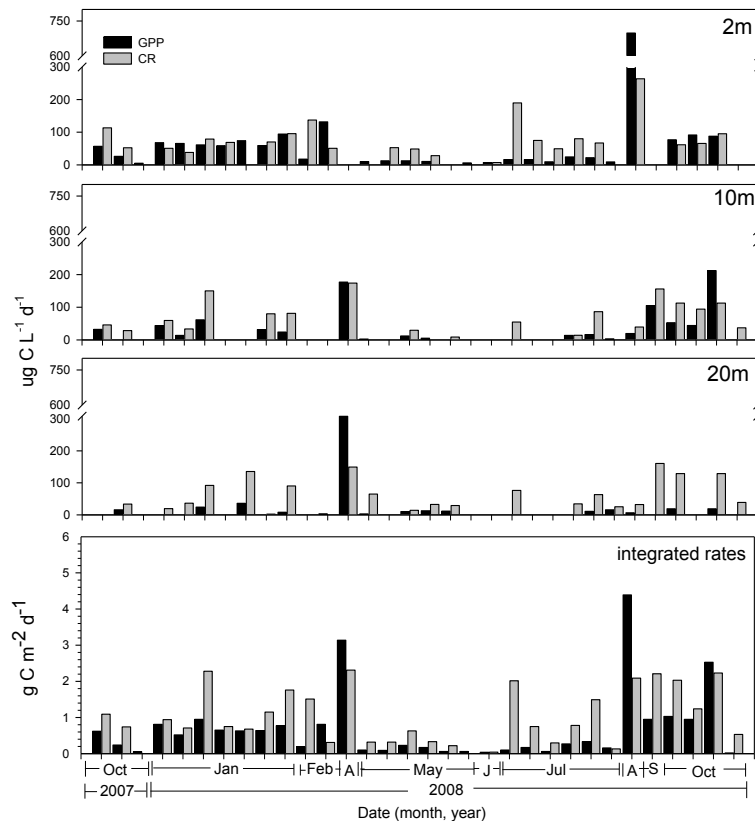


Fig. 5. Temporal and vertical variability of gross primary production (GPP) and community respiration (CR) rates at the Puyuhuapi station.

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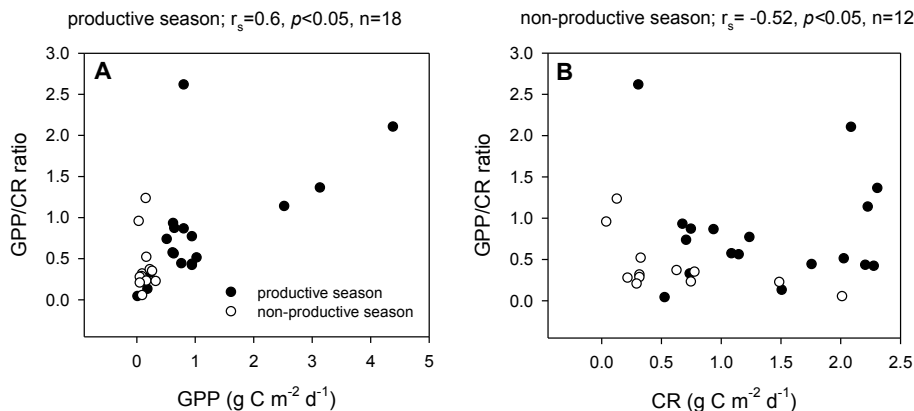


Fig. 6. Correlation between GPP/CR ratio and GPP rates **(A)** and between GPP/CR ratio and CR rates **(B)**, during the productive (filled circles) and non-productive periods (open circles).

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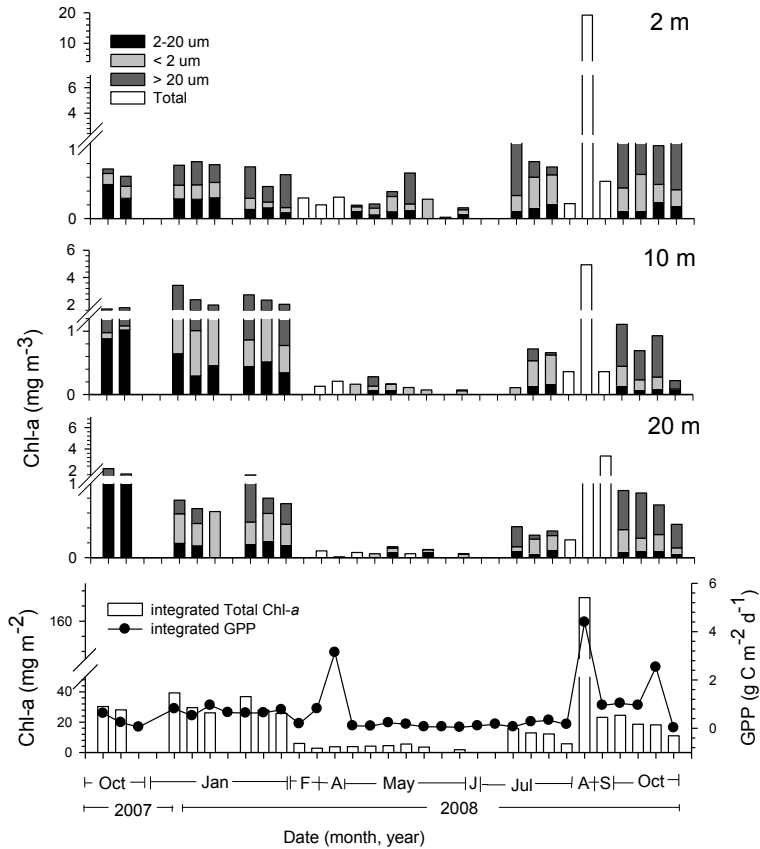


Fig. 7. Temporal and vertical variability of fractionated and total Chlorophyll *a* at the Puyuhuapi station. The bottom panel shows depth-integrated (0–20 m) total Chlorophyll *a* and GPP.

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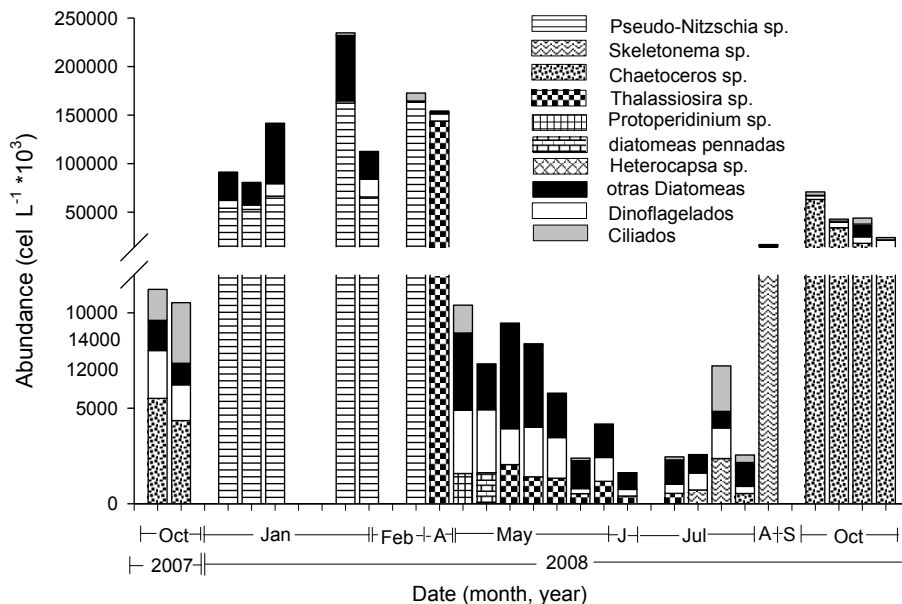


Fig. 8. Seasonal variability of phytoplankton abundance and composition at the Puyuhuapi station.

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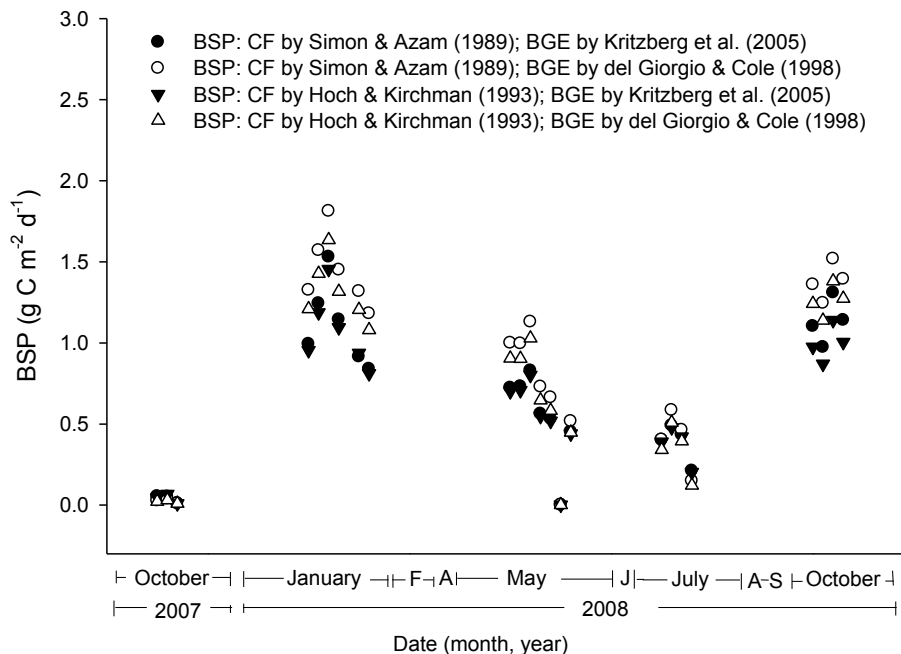


Fig. 9. Seasonal variability of Bacterial Secondary Production rates (BSP) and Bacterial Growth Efficiency (BGE), estimated using two different conversion factors (CF). Symbols show all four possible combinations of estimates obtained from these factors.

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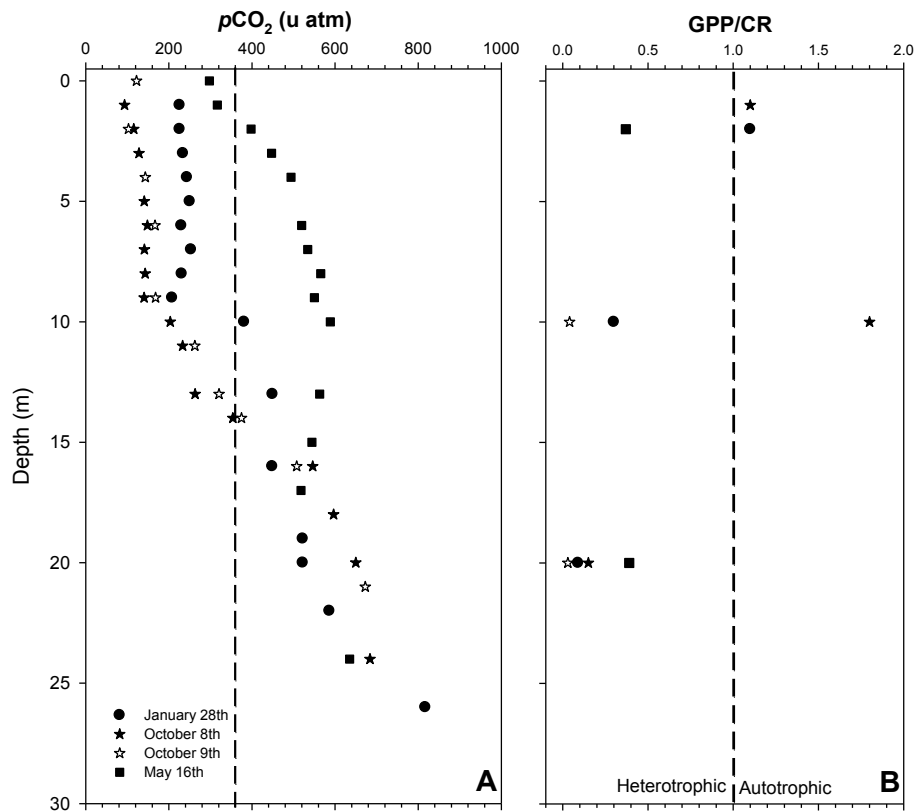


Fig. 10. Depth profiles of $p\text{CO}_2$ at the Puyuhuapi station during three seasonal campaigns **(A)**. Depth distribution of GPP/CR ratios estimated during campaigns where $p\text{CO}_2$ was measured **(B)**. Dotted lines correspond to **(A)** atmospheric $p\text{CO}_2$ concentration (380 μatm), and **(B)** trophic system in balance (GPP = CR).

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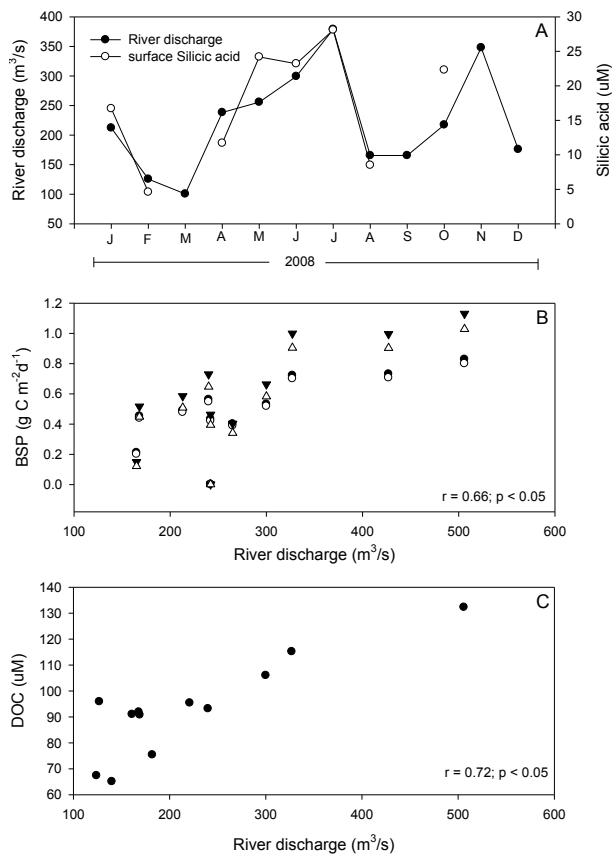


Fig. 11. Cisnes River discharge and its association with **(A)** average monthly supply of silicic acid to surface waters, **(B)** bacterial secondary production (BSP) during winter, and **(C)** surface dissolved organic carbon (DOC).

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