

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

5933

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.

5934

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

5947

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

5948

- Haraldsson, C., Anderson, L. G., Hassellöv, M., Hulth, S., and Olsson, K.: Rapid, high precision potentiometric titration of alkalinity in ocean and sediment pore waters, *Deep-Sea Res. I*, 44, 2031–2044, 1997.
- Hoch, M. P. and Kirchman, D. L.: Seasonal and inter-annual variability in bacterial production and biomass in a temperate estuary, *Mar. Ecol. Prog. Ser.*, 98, 283–295, 1993.
- Iriarte, J. L. and Gonzalez, H. E.: Phytoplankton bloom ecology of the inner Sea of Chiloé, Southern Chile, *Nova Hedwigia*, Beiheft, 133, 67–79, 2008.
- Iriarte, J. L., Kush, A., and Ruiz, M.: Phytoplankton biomass in the sub-Antarctic area of the Straits of Magellan (53°S); Chile during spring–summer 1997–1998, *Polar Biol.*, 24, 154–162, 2001.
- Iriarte, J. L., González, H. E., Liu, K. K., Rivas, C., and Valenzuela, C.: Spatial and temporal variability of Chlorophyll and primary productivity in surface waters of southern Chile (41.5–43°S), *Estuar. Coast. Shelf S.*, 74, 471–480, 2007.
- Kritzberg, E. S., Cole, J. J., Pace, M. M., and Granéli, W.: Does autochthonous primary production drive variability in bacterial metabolism and growth efficiency in lakes dominated by terrestrial C inputs?, *Aquat. Microb. Ecol.*, 38, 103–111, 2005.
- Legendre, L. and Rivkin, R. B.: Fluxes of carbon in the upper ocean: regulations by food-webs control nodes, *Mar. Ecol. Prog. Ser.*, 242, 95–109, 2002.
- Legendre, L. and Rivkin, R. B.: Planktonic food webs: microbial hub approach, *Mar. Ecol. Prog. Ser.*, 365, 289–309, 2008.
- Lewis, E. and Wallace, D. W. R.: Program Developed for CO₂ System Calculations. ORNL/CDIAC-105, Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy, Oak Ridge, Tennessee, 1998.
- McManus, G. and Peterson, W. T.: Bacterioplankton production in the nearshore zone during upwelling off central Chile, *Mar. Ecol. Prog. Ser.*, 43, 11–17, 1988.
- Mehrbach, C., Culberson, C. H., Hawley, J. E., and Pytkowicz, R. M.: Measurement of the apparent dissociation constants of carbonic acid in seawater at atmospheric pressure, *Limnol. Oceanogr.*, 18, 897–907, 1973.
- Montero, P., Daneri, G., Cuevas, L. A., González, H. E., Jacob, B., Lizárraga, L., and Menschel, E.: Productivity cycles in the coastal upwelling area of Concepción: The importance of diatoms and bacteria in the flux of organic carbon, *Prog. Oceanogr.*, 75, 518–530, 2007.
- Montero, P., Daneri, G., González, H. E., Iriarte, J. L., Tapia, F. J., Lizárraga, L., Sanchez, N., and Pizarro, O.: Seasonal variability of primary production in a fjord ecosystem of the Chilean

5953

- Patagonia: implications for the transfer of carbon within pelagic food webs, *Cont. Shelf Res.*, 31, 202–215, 2011.
- Newell, S. Y. and Christian, R. R.: Frequency of dividing cells as an estimator of bacterial productivity, *Appl. Environ. Microb.*, 42, 23–31, 1981.
- Parsons, T. R., Maita, R., and Lalli, C. M.: Counting, media and preservatives. A manual of chemical and biological methods for seawater analysis (1–163), Pergamon Press, Toronto, 1984.
- Pickard, G. L.: Some physical oceanographic features of inlets of Chile, *J. Fish. Bd. Canada*, 28, 1077–1106, 1971.
- Pizarro, G., Iriarte, J. L., Montecino, V., Blanco, J. L., and Guzman, L.: Distribución de la biomasa fitoplanctónica y productividad primaria máxima de fiordos y canales australes (47°–50° S) en octubre 1996, *Ciencia y tecnología del 23 Marzo*, 25–48, 2000.
- Pizarro, G., Astoreca, R., Montecino, Paredes, M. A., Alarcon, G., Uribe, P., and Guzman, L.: Patronos espaciales de la abundancia de la clorofila, su relacion con la productividad primaria y la estructura de tamaños del fitoplancton en Julio y Noviembre de 2001 en la region de Aysén (43°–56°S), *Rev. Cien. Tecn. Mar.*, 28, 27–42, 2005.
- Poole, H. H. and Atkins, W. R. G.: Photo-electric measurements of submarine illumination throughout the year, *J. Mar. Biol. Ass., UK*, 16, 297–324, 1929.
- Riemann, B. and Bell, R. T.: Advances in estimating bacterial biomass and growth in aquatic systems, *Arch. Hydrobiol.*, 25, 385–402, 1990.
- Rivkin, R. B. and Legendre, L.: Biogenic carbon cycling in the upper ocean: effects of microbial respiration, *Science*, 291, 2398–2400, 2001.
- Robinson, C. and Williams, P. J. LeB.: Respiration and its measurement in surface marine waters, in: *Respiration in Aquatic Ecosystems*, edited by: del Giorgio, P. A. and Williams, P. J. LeB., Oxford University Press, 147–180, 2005.
- Robinson, C.: Heterotrophic bacterial respiration, in: *Microbial Ecology of the Ocean*, edited by: Kirchman, D. L., 2 Edn., 299–334, 2008.
- Sciremammano, F.: A suggestion for the presentation of correlations and their significance levels, *J. Phys. Oceanogr.*, 9, 1273–1276, 1979.
- Serret, P., Robinson, C., Fernández, E., Teira, E., Tilstone, G., and Pérez, V.: Predicting plankton net community production in the Atlantic Ocean, *Deep-Sea Res. II*, 56, 941–953, 2009.
- Silva, N.: Dissolved oxygen, pH, and nutrients in the austral Chilean channels and fjords. Progress in the oceanographic Knowledge of Chilean interior waters, from Puerto Montt to

5954

- Cape Horn, edited by: Silva, N. and Palma, S., Comité Oceanográfico Nacional – Pontificia Universidad Católica de Valparaíso, Valparaíso, 37–43, 2008.
- Silva, N., Calvete, M., and Sievers, H.: Características oceanográficas físicas y químicas de canales australes chilenos entre Puerto Montt y Laguna san Rafael (Crucero CIMAR-Fiordo 1), *Cienc. Tecnol. Mar.*, 20, 23–106, 1997.
- Simon, M. and Azam, F.: Protein content and protein synthesis rates of planktonic marine bacteria, *Mar. Ecol. Prog. Ser.*, 51, 201–213, 1989.
- Strickland, J. D. H.: Measuring the production of marine phytoplankton, *Bull. Fish. Res. Board Can.*, 122, 1–72, 1960.
- Strickland, J. D. H. and Parsons, T. R.: Determination of reactive nitrite, in: *A Practical Handbook of Seawater Analysis*, *Bull. Fish. Res. Board Can.*, 167, 71–75, 1968.
- Torres, R., Pantoja, S., Harada, N., González, H., Daneri, G., and Frangopulos, M.: Air-sea CO₂ fluxes along the coast of Chile: from CO₂ outgassing in central-northern upwelling waters to CO₂ sequestering in southern Patagonian fjords, *J. Geophys. Res.*, 116, C09006, doi:10.1029/2010JC006344,
- Troncoso, V. A., Daneri, G., Cuevas, L. A., Jacob, B., and Montero, P.: Bacterial carbon flow in the Humboldt Current System off Chile, *Mar. Ecol. Prog. Ser.*, 250, 1–12, 2003.
- Utermöhl, H.: Zur Vervollkommnung der quantitativen Phytoplankton. Methodik, *Mitt. Int. Ver. Theor. Angew. Limnol.*, 9, 1–39, 1958.
- Williams, P. J. LeB.: The balance of plankton respiration and the photosynthesis in the open ocean, *Nature*, 394, 55–57, 1998.
- Williams, P. J. LeB. and Robertson, J. E.: Overall planktonic oxygen and carbon dioxide metabolisms: the problem of reconciling observations and calculations of photosynthetic quotients, *J. Plankton Res.*, 13, 153–169, 1991.

5955

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	
	gC m ⁻² d ⁻¹	gC m ⁻² d ⁻¹	%	gC m ⁻² d ⁻¹	%	gC m ⁻² d ⁻¹	%	gC 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	

5956

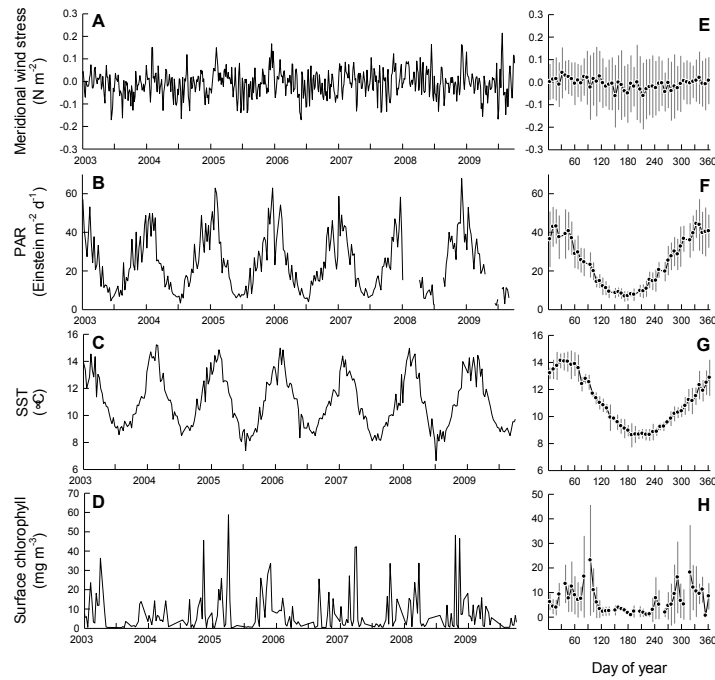


Fig. 2. Satellite-derived time series (A–D) and climatologies (E–H) of meridional wind stress (A, E), surface PAR, i.e. Photosynthetically Available Radiation (B, F), Sea Surface Temperature (C, G), and surface Chlorophyll *a* concentration (D, H). Wind stress data were obtained from daily QuikSCAT level-3 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.

5959

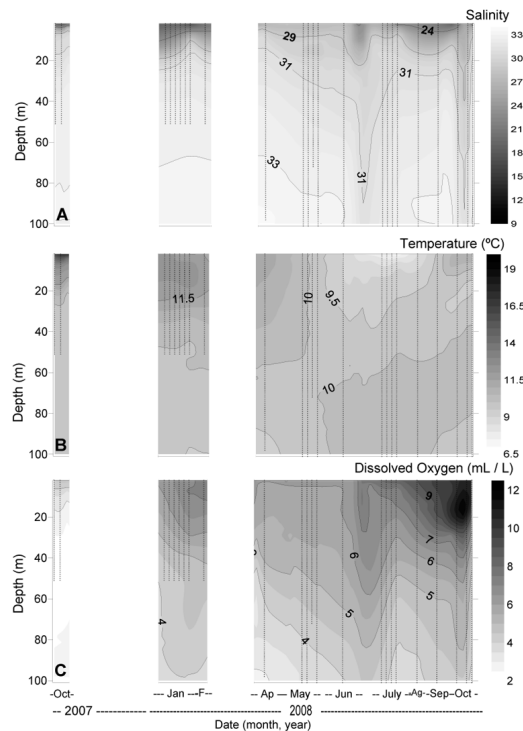


Fig. 3. Temporal variability of hydrographic profiles at the Puyuhuapi fjord station: (A) salinity, (B) temperature, and (C) dissolved oxygen. Sampling times and depth range are indicated by dotted vertical lines.

5960

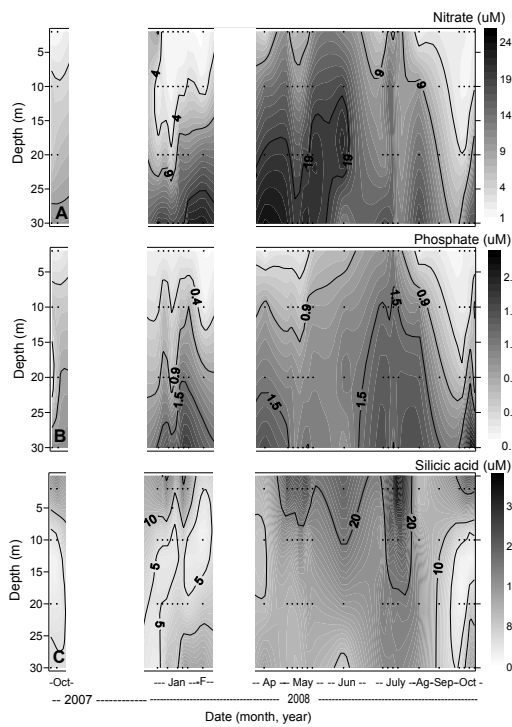


Fig. 4. Temporal variability of dissolved inorganic nutrient profiles at the Puyuhuapi station: **(A)** nitrate, **(B)** phosphate, and **(C)** silicic acid. Sampling times and depths are indicated by dots.

5961

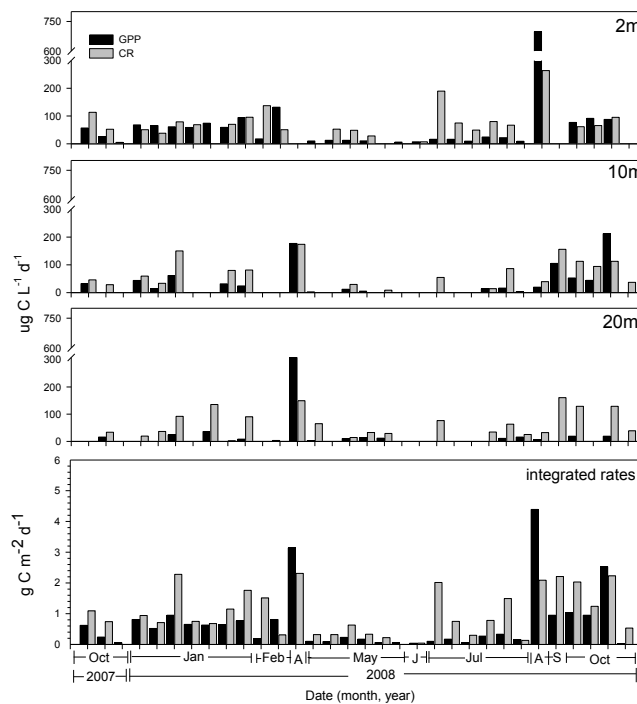


Fig. 5. Temporal and vertical variability of gross primary production (GPP) and community respiration (CR) rates at the Puyuhuapi station.

5962

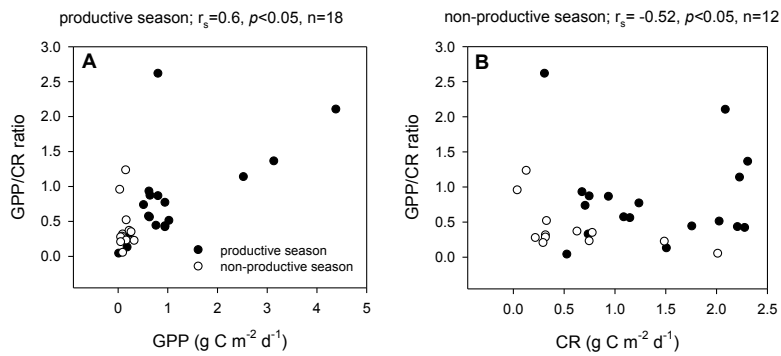


Fig. 6. Correlation between GPP/CR ratio and GPP rates (A) and between GPP/CR ratio and CR rates (B), during the productive (filled circles) and non-productive periods (open circles).

5963

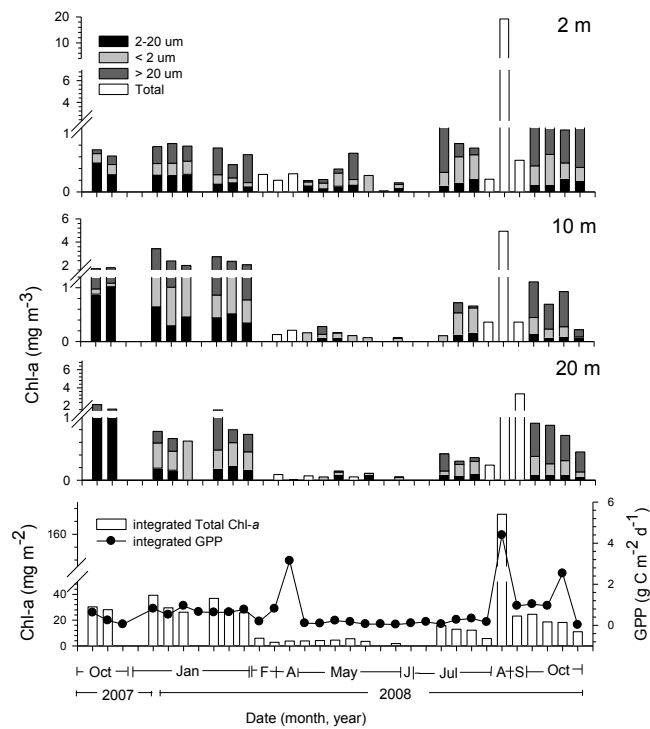


Fig. 7. Temporal and vertical variability of fractionated and total Chlorophyll *a* at the Puyuhuapi station. The bottom panel shows depth-integrated (0–20 m) total Chlorophyll *a* and GPP.

5964

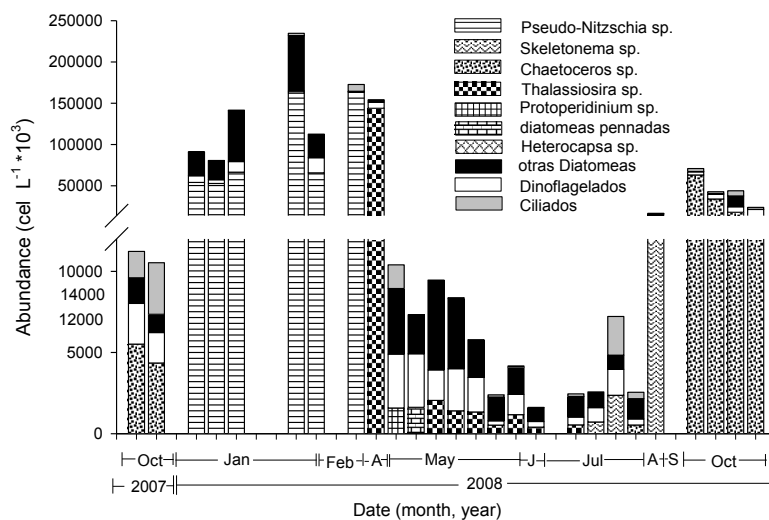


Fig. 8. Seasonal variability of phytoplankton abundance and composition at the Puyuhuapi station.

5965

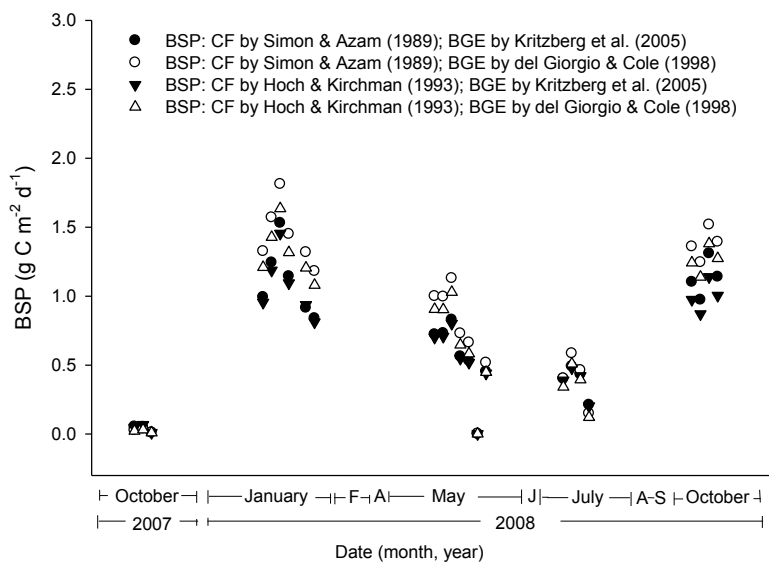


Fig. 9. Seasonal variability of Bacterial Secondary Production rates (BSP) and Bacterial Growth Efficiency (BGE), estimated using two different conversion factors (CF). Symbols show all four possible combinations of estimates obtained from these factors.

5966

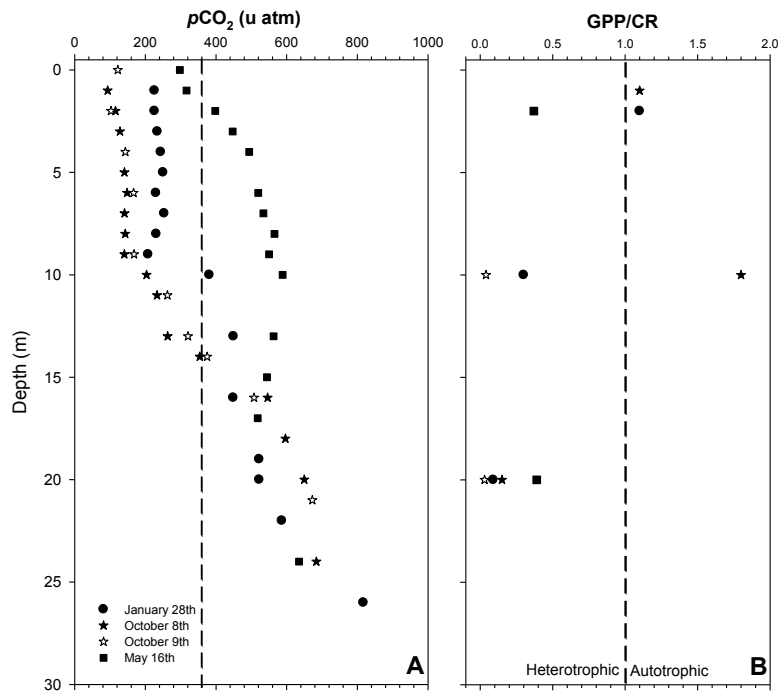


Fig. 10. Depth profiles of pCO_2 at the Puyuhuapi station during three seasonal campaigns **(A)**. Depth distribution of GPP/CR ratios estimated during campaigns where pCO_2 was measured **(B)**. Dotted lines correspond to **(A)** atmospheric pCO_2 concentration (380 μatm), and **(B)** trophic system in balance (GPP = CR).

5967

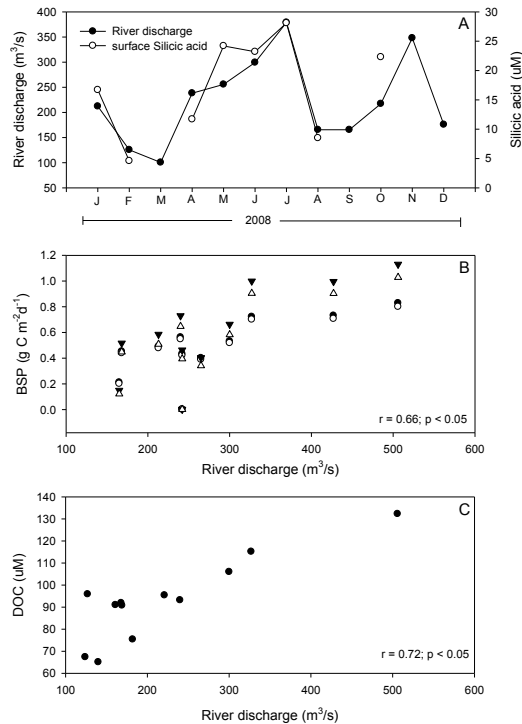


Fig. 11. Cisnes River discharge and its association with **(A)** average monthly supply of silicic acid to surface waters, **(B)** bacterial secondary production (BSP) during winter, and **(C)** surface dissolved organic carbon (DOC).

5968