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# Bacterial carbon flow in the Humboldt Current System off Chile

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ABSTRACT: During this study, bacterial secondary production (BSP) was measured at 3 coastal upwelling sites (Antofagasta, latitude 23° S; Coquimbo, latitude 30° S; and Concepción, latitude 36° S) within the Humboldt Current System (HCS) off Chile. The data show that bacteria are an important component of pelagic food webs in these areas. The coastal area of Antofagasta had the highest level of bacterial activity (1722 ± 1362 mg C $m^{-2}$ $d^{-1}$), the coastal area of Coquimbo the values (77 ± 56 mg C $m^{-2}$ $d^{-1}$). The low levels observed in Coquimbo are in agreement with the observation that Coquimbo is an oligotrophic area of persistent upwelling that persistently shows low primay production (PP) values. A BSP value of ca. 5000 mg C $m^{-2}$ $d^{-1}$ measured during this study in the coastal area of Antofagasta constitutes the highest BSP value ever reported in the literature. In the 3 upwelling areas sampled a significant proportion of the PP was utilised by bacteria (ca. 63 to 96 % in Antofagasta, 16 to 34 % in Coquimbo and 10 to 24 % in Concepción). A strong correlation between BSP and PP was found during this study ($r^2$ = 0.57, n = 51), reflecting a tight coupling between carbon synthesis and bacterial consumption. The high correlation between PP and BSP, coupled with the lack of correlation between temperature and BSP ($r^2$ = 0.0, n = 420), indicates that in the HCS off Chile substrate availability seems to be more important than temperature in limiting bacterial activity and abundance.

KEY WORDS: Bacterioplankton · Biomass · Production · Humboldt Current · Upwelling



## INTRODUCTION

The Humboldt Current System (HCS) of Chile is an eastern boundary current system typified by the occurrence of coastal upwelling, the presence of a shallow nutrient-rich oxygen-depleted subsurface water mass, and interannual variations associated with El Niño events. The upwelling of subsurface waters triggers a vigorous exchange of $CO_2$ and heat. Subsequently, water stabilisation, due to lateral mixing and solar surface heating, stimulates the growth of phytoplankton. The primary production levels are among the highest reported in the literature (Daneri et al. 2000).

The high fish production in upwelling systems has been primarily associated with recurrent upwelling pulses and with the predominance of short, thermodynamically efficient food chains (Ryther 1969, Ryther et al. 1971). This early view, based on a simplified structure and functioning of the food chain in upwelling systems, is now under revision. Central to this has been a re-evaluation of the importance of bacteria in a variety of marine environments (McManus & Peterson 1988). Bacterioplankton constitutes an important fraction of the total carbon biomass in pelagic ecosystems. In oligotrophic waters bacterial biomass can be 2 to 3 times more abundant than phytoplankton (Cho & Azam 1990), and in meso- and eutrophic environments 0.5 to 2 times greater (Azam et al. 1983). Bacteria are an important pelagic mineralizer of organic matter. It has been reported that, depending on environmental conditions, bacterial secondary production (BSP), as a percentage of primary production (PP), can fluctuate between 2 and 1101 % (Andrews & Williams 1971, Sieburth et al. 1977, Hagström et al. 1979, Fuhrman &

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Azam 1982, see also references in Table 1). This may represent an underestimation, as most of the estimates of BSP/PP % do not take into consideration that bacterial activity continues at night (McManus & Peterson 1988).

Bacterial production and abundance in coastal upwelling ecosystems is similar to that reported for other coastal environments and seems to be closely coupled to upwelling cycles (Field et al. 1980, Zimmermann et al. 1980, Gocke et al. 1983, Rheinheimer & Schmaljohann 1983, Hanson et al. 1986, McManus & Peterson 1988). In the Benguela upwelling system, BSP has been shown to increase a few days after the peak of PP (Painting et al. 1993). A similar decoupling between PP and BSP has been reported by McManus & Peterson (1988) for the Concepción upwelling ecosystem in the HCS off Chile. McManus & Peterson (1988) showed that PP was lowest during periods of active upwelling and highest during subsequent periods of calm or light northerly winds, with BSP showing the greatest increase 1 or 2 d after the peak in phytoplankton production.

Watson (1978) estimated ocean global production to be 25 to 75 g C $m^{-2}$ $yr^{-1}$ for open ocean areas, 100 g C $m^{-2}$ $yr^{-1}$ for coastal areas and up to 300 g C $m^{-2}$ $yr^{-1}$ for upwelling ecosystems. Higher values of 1 kg C $m^{-2}$ $yr^{-1}$ and 0.93 kg C $m^{-2}$ $yr^{-1}$ have been estimated for the Peruvian upwelling (Walsh 1981) and for the southern Chilean upwelling (Daneri et al. 2000), respectively. While the PP in oligotrophic areas depends mostly on regenerated ($NH_3$-based) nitrogen in upwelling or highly productive coastal areas, PP is mainly supported by the injection of $NO_3$ into the photic layer. New production in highly productive ecosystems is typically in the order of 50 to 70% of the total production, indicating the dependence of primary production on nutrients advected from subsurface waters. Although in these productive areas, dependence of PP on epipelagically produced nutrients is not as crucial as in oligotrophic areas, absolute rates of nutrient regeneration by the heterotrophic community are not insignificant (C. Morales pers. comm.). It is now accepted that a high proportion of the organic carbon produced by the phytoplankton may flow through the bacteria in a variety of marine environments, including upwelling areas. A significant amount of carbon flowing through the bacterioplankton may imply that the carrying capacity for fishes in upwelling ecosystems is considerably less than that which might be anticipated for a simple herbivore-dominated food chain (Newell & Turley 1987).

Table 1. Summary of primary production (PP), bacterial secondary production (BSP) and bacterial abundance (BA), BSP/PP% reported in the literature for contrasting marine ecosystems. Spaces: no data

| PP | BSP | BA | BSP/PP | Comments | Source |
|---|---|---|---|---|---|
| (mg C $m^{-2}$ $d^{-1}$) | | ($\times 10^9$ cells $l^{-1}$) | (%) | | |
| 150–3470 | 50–780 | <1–14 | 3–1101 | Northern and southern Benguela, euphotic zone | Brown et al. (1991)[a] |
| 160–2670 | | 1.2–8.8 | | Upwelling centre, southern Benguela (summer) | Painting et al. (1993)[b] |
| 300–500 | | | 30–42 | Darwin Stns 3, 5, 7, oligotrophic | Ducklow (1993) |
| 1400–2700 | | | 10–22 | Darwin Stns 14, 16 upwelling | |
| 970 | 200 | | 20.6 | Equatorial Pacific, El Niño conditions | Kirchman et al. (1995) |
| 1390 | 240 | | 17.3 | Equatorial Pacific, non-El Niño conditions | |
| 500–1100 | 150–220 | 1.1–2.5 | 9–28 | Oligotrophic SW, monsoon Somali Basin | Wiebinga et al. (1997)[c] |
| 700–2800 | 80–100 | 1.0–2.1 | 9–30 | Upwelling SW monsoon, Gulf of Aden | |
| 400–1000 | 130–140 | 1.1–2.5 | 14–22 | Oligotrophic NE monsoon, Somali Basin | |
| 600–2200 | 180–260 | 1.0–2.1 | 10–34 | Upwelling, NE monsoon, Gulf of Aden | |
| | 50–160 | 0.1–2 | 12–22 | Southern Ocean | Lochte et al. (1997)[d] |
| | 30–530 | 0.9–1.6 | 10–30 | NW Arabian Sea | Pomroy & Joint (1999)[e] |
| 90–2130 | 30–330 | 0.1–2.5 | 6–42 | Continental shelf of southern East China Sea | Shiah et al. (2000)[b] |
| (µg C $l^{-1}$ $d^{-1}$) | | ($\times 10^9$ cells $l^{-1}$) | (%) | | |
| 2.06–276 | 0.01–20.8 | 0.06–2.08 | | Euphotic zone, Southern California Bight, USA | Fuhrman et al. (1980)[b] |
| | 0–152 | 1–8 | 6–32 | Delaware estuary, winter and summer | Coffin & Sharp (1987) |
| 24–240 | 4.8–31.2 | 2–4 | 3–55 | Active upwelling, Concepción shelf | McManus & Peterson (1988)[a] |
| 120–1320 | 19.2–33.6 | 2.8–3.7 | 2–13 | Relaxation, Concepción shelf | |
| | 0.2–2.6 | 0.6–1.8 | 3–21 | Subartic NE Pacific during winter, spring and summer, euphotic zone | Sherry et al. (1999)[b] |

Conversion fac–rs for BSP:
[a]17.2–24 fg C $cell^{-1}$ (Painting et al. 1989), [b]20 fg C $cell^{-1}$ (Lee & Fuhrman (1987), [c]34 fg C $cell^{-1}$ (Fry 1990), [d]18.7 fg C $cell^{-1}$, [e]20 fg C $cell^{-1}$ (Ducklow 1993)

In this paper, the relationship between bacterial production and abundance and phytoplankton biomass and production in 3 upwelling ecosystems in the HCS off Chile (Antofagasta, 23° S; Coquimbo, 30° S; Concepción, 36° S) and adjacent oceanic areas is examined. Based on estimated bacterial growth yields, the total carbon flux through the bacteria was assessed under a range of environmental conditions. The large amount of data allowed, for the first time, a comprehensive understanding of the role of bacterioplankton in the HCS of Chile.

## MATERIALS AND METHODS

**Cruises and stations.** The study was carried out at 3 coastal upwelling sites in the HCS off Chile. Sampling took place off Antofagasta (23° S), during January (summer) and July (winter) 1997 on board the RV 'Abate Molina' as part of the Sectorial Antofagasta (CONICYT-Chile) research programme. The Antofagasta stations were sampled within a grid bounded by 22° 40′ to 24° 00′ S and 70° 30′ W to 71° 52′ W. During July 1997 stations were sampled in a transect from the coast to 200 miles offshore (Fig. 1). Sampling at Coquimbo (30° S) was undertaken as part of a series of short research cruises of the JGOFS-Chile program on board the RV 'Abate Molina' and the AGOR 'Vidal Gormaz'. The JGOFS-Chile (Coquimbo area) results are from a fixed transect from the coast to offshore, running from the Coquimbo coastal station (COSMOS) (30° 20′ 90″ S, 71° 47′ 40″ W) to OCEMOS (29° 58′ 02″ S, 73° 19′ 18″ W) (Fig. 1). In the shelf upwelling area of Concepción (36° S), 2 multidisciplinary intensive research cruises (MIRC I and MIRC II) took place in October (spring) 1998 and July (winter) 1999 as part of the FONDAP-Humboldt research program. Sampling took place in a quasi-synoptic M-type grid during both cruises along a coast-to-offshore transect starting 5 nautical miles (n miles) from the coast and ending 200 n miles offshore (Fig. 1).

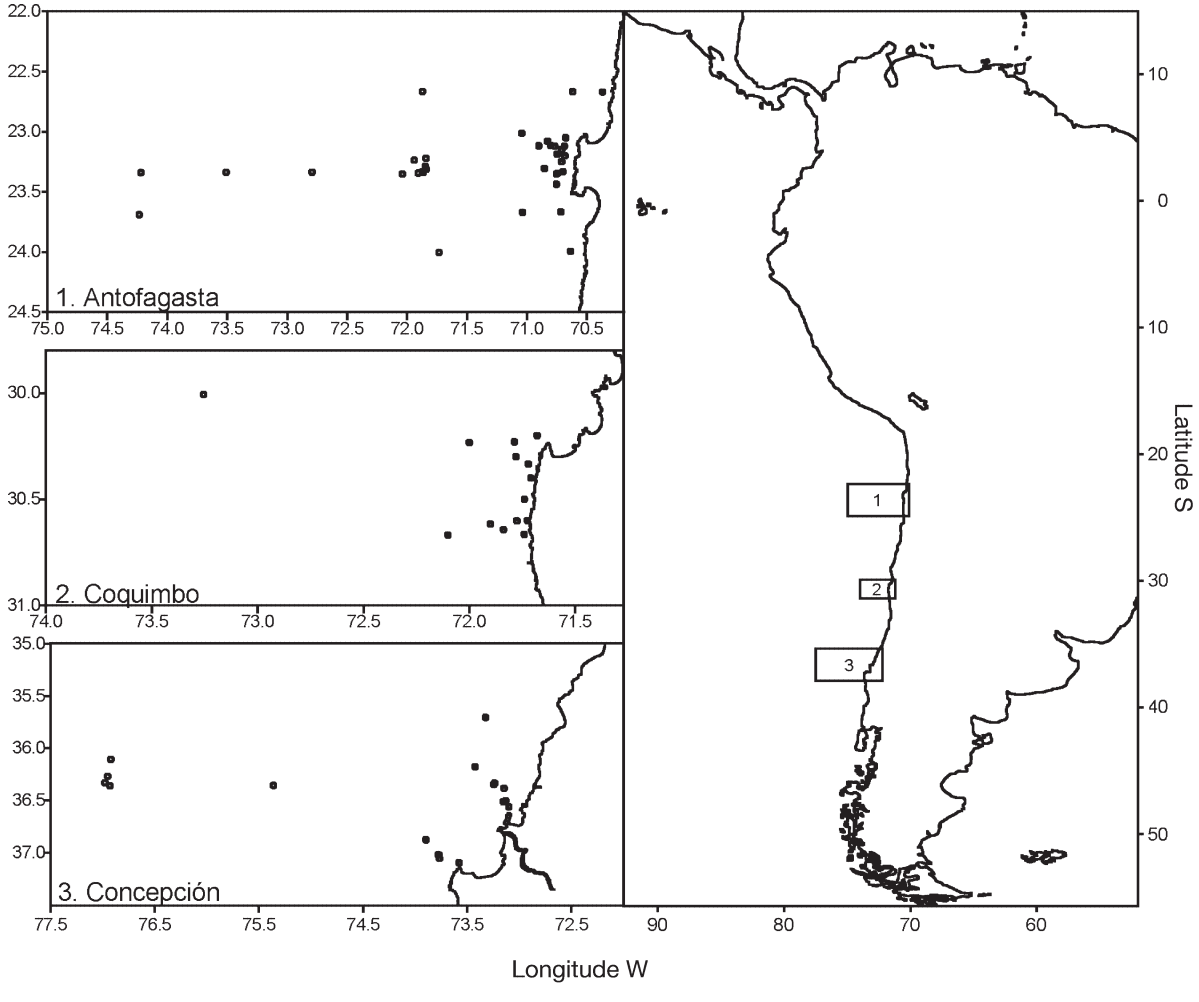


Fig. 1. Area sampled. (1) Antofagasta upwelling, (2) Coquimbo upwelling, (3) Concepción upwelling

In this study, the terms 'inshore' or 'coastal' refer to areas within 40 n miles of the coast, while 'offshore' or 'oceanic' refer to stations sampled at distances >100 miles from the coast for Coquimbo and Concepción and >60 miles for Antofagasta.

The highly dynamic nature of the HCS allowed us to sample upwelling areas under contrasting oceanographic conditions (Table 2). The January cruise to the Antofagasta upwelling system took place during an unusual period of low wind stress which preceded the 1997-98 El Niño event. This resulted in a weakening of upwelling and a decrease in the productivity of the system (Daneri et al. 2000). The second cruise to the Antofagasta region took place while the area was being affected by the 1997-98 El Niño event, one of the strongest ever recorded. The spring (upwelling season) and winter (non-upwelling season) cruises to the Concepción shelf area took place in the period after the 1997-98 El Niño under oceanographic conditions associated with La Niña. The Coquimbo area was sampled during oceanographic periods regarded as normal. Coquimbo, however, is an area of persistent upwelling but consistently low water productivity (Daneri et al. 2000) (Table 2).

**Sample collection and hydrographic measurements.** During the cruises on board the RV 'Abate Molina' and the AGOR 'Vidal Gormaz', water samples for primary production (PP), bacterial secondary production (BSP), and chlorophyll *a* (chl *a*) were obtained within the photic zone using Niskin bottles attached to a CTD rosette sampler. Samples for bacterial abundance (BA) and bacterial biomass (BB) were collected only during the Sectorial Antofagasta and MIRC I and MIRC II cruises to the area of Concepción. Data on basic water-column structure was obtained from continuous CTD records using a Neil Brown (MK III) instrument equipped with oxygen sensors, *in vivo* fluorescence Sea-Tech (FL 3000), and a scalar (photosynthetically active radiation) PAR sensor (Biospherical Instrument, Model QSP-200L). The General Oceanic rosette sampler was equipped with 12 Niskin bottles of 5 l capacity ('Abate Molina' cruise), and a Sea-bird CTD installed in a General Oceanic rosette sampler equipped with 24 Niskin bottles of 1.5 l capacity in the (AGOR 'Vidal Gormaz' cruise).

**Bacterial abundance.** Discrete seawater samples from the euphotic zone were collected directly from Niskin bottles in sterile tubes (50 ml capacity, Costar 3252) and preserved in the dark with cold glutaraldehyde (2% W/V final concentration). Bacterial counting was performed with epifluorescence microscopy following the methodology of Porter & Feig (1980). Samples (2 to 5 ml) were stained with DAPI (4, 6-diamidine 2-fenilindol, Sigma D-1388) to 72 µM final concentration, and collected on black 25 mm polycarbonate filters (0.2 µm pore size; Millipore GTBP). Ten random fields and a total of at least 400 cells were counted at 1000× with a Zeiss-Axioskop epifluorescence microscope equipped with quartz optics.

**Bacterial biomass and biovolume.** Bacterial cellular carbon was estimated using the equation $C\,(\mathrm{fg}) = 90.06 \times V\,(\mu\mathrm{m}^3)^{0.59}$, where $V$ = bacterial volume (Simon & Azam 1989, Riemann & Bell 1990); 2 epifluorescence microscopy pictures were taken for each sample. The cell volume was determined by measuring the longest cell axis on enlarged microphotographs (12 500×). Between 100 to 200 cells were measured. Care was taken to measure the size of the bacterial cell wall and not the fluorescent halo around the bacteria. The biovolume was calculated using the equation $V(\mu\mathrm{m})^3 = (d^2 \times \pi/4) \times (l - d) + (\pi \times d^3/6)$, where $d$ = diameter and $l$ = length (Watson et al. 1977). Bacterial cell carbon was determined at 8 stations in the Antofagasta region (summer/winter). For the Concepción samples, bacterial cell carbon was determined at 1 coastal station during spring and 2 stations (coastal and oceanic) during winter. Significant differences between the summer (54 fg C) and winter (41 fg C) average cell-carbon amounts were found for Antofagasta (Mann-Whitney $U = 131.5$, $p < 0.0001$). In the spring cruise off Concep-

Table 2. Summary of research cruises and oceanographic conditions during present study

| Research programme | Vessel(s) | Date | Season | Conditions |
|---|---|---|---|---|
| Antofagasta 23° S Sectorial | RV 'Abate Molina' | January 1997 | Summer | Low wind stress; preconditions; 1997-98 El Niño event |
| | | July 1997 | Winter | 1997-98 El Niño event |
| Coquimbo 30° S JGOFS-Chile | RV 'Abate Molina' | 1992, 1993, 1994, 1996, 1997 | Summer | Persistent upwelling but low subsequent |
| | AGOR 'Vidal Gormaz' | 1992, 1995, 1996 | Winter | Water productivity |
| Concepción 36° S FONDAP-Humboldt | RV 'Abate Molina' | October 1998 | Spring | After the 1997-98 El Niño event; upwelling season |
| | | July 1999 | Winter | Conditions associated with La Niña event; non-upwelling season |

ción (MIRC I), the average bacterial cell carbon was 27 fg C, while in the winter cruise (MIRC-II) the average was 22 fg C at the coastal stations and 16 fg C at the oceanic station (Mann-Whitney $U = 2$, $p < 0.01$). Based on these results, we used values of 54 and 41 fg C for the summer and winter cruises off Antofagasta, 27 fg C for the spring in Concepción and 22 and 16 fg C for the coastal and oceanic stations in the winter cruise of Concepción, respectively. Water-column bacterial organic carbon (BOC) or biomass was estimated by multiplying bacterial cellular carbon by the water column bacterial abundance.

**Bacterial secondary production (BSP).** BSP was measured through the incorporation of [methyl-$^3$H]-thymidine to the DNA (Fuhrman & Azam 1982, as modified by Wicks & Robarts 1987). Discrete seawater samples were collected from the process study stations at 6 light depths from the surface to the 1% light depth for the simultaneous measurement of PP and BSP. Within 15 min of collection, 10 ml from each depth sample was transferred to sterile tubes (Falcon 2051) of 15 ml capacity (3 replicates and 1 blank). The blanks were poisoned with formalin (Merck) which had been sterilised using 45 mm Nuclepore 0.2 µm pore-size polycarbonate filters. The samples were incubated with [methyl-$^3$H]-thymidine (50.1 Ci mmol$^{-1}$ specific activity, Sigma T-6527) to a final concentration of 10 nM and maintained in the dark in a water bath provided with running surface seawater. In Antofagasta and Coquimbo the incubation time was 2 h; in Concepción it was 1 h. The incubation was stopped with the addition of 2.8 ml of cold trichloroacetic acid (TCA) (p.a.) grade (50% w/v, J. T. Baker) Following the procedure of Wicks & Robarts (1987), after filtration (<200 mm Hg) the sample was treated with 5 ml of phenol-chloroform solution pro-analysis (p.a.) grade (50% w/w) and re-filtered with 5 ml of cold ethanol p.a. (80% v/v). After extraction of the DNA, the dried filters were kept cool until radioisotopic analysis. In the laboratory the vials were treated with ethyl acetate p.a. and 10 ml Ecolite (+) (ICN). The incorporation of [methyl-$^3$H]-thymidine was measured in dpm using a Packard (Model 1600 TR) liquid scintillation counter. The counting efficiency was calculated from the non-quenched standard of $^3$H-toluene. Moles of thymidine incorporated were transformed into cell production using a constant of $2 \times 10^{18}$ (Furhman & Azam 1982). Simultaneous with the determination of BSP, samples from the same Niskin bottles were collected for bacterial abundance and biomass.

**Chlorophyll *a* (chl *a*).** Chl *a* was estimated using a Turner Designs fluorometer Model 10AU calibrated against pure chl *a* (Sigma) following the method of Holm-Hansen et al. (1965). Pigments were extracted on boardship in cold acetone (90%) for 24 h, and fluorescence was measured before and after acidification.

**Primary production (oxygen and $^{14}$C method).** Primary production for the Antofagasta and Coquimbo upwelling ecosystem were estimated measuring the $^{14}$C uptake by planktonic microalgae. Samples for PP experiments were collected at 10 stations using 5 l PVC Niskin water-sampling bottles. Water samples were incubated in 100 ml borosilicate glass for 4 h (mainly between 10:00 and 14:00 h). Temperature was regulated by running surface seawater over the incubation bottles. Sodium bicarbonate (40 µCi $NaH^{14}CO_3$) was added to each bottle. After incubation the bottle content was filtered, placed in 20 ml scintillation vials and kept at –15°C until reading (usually 15 d later). To remove excess inorganic carbon, filters were treated with HCl fumes for 4 h. During the 2 MIRC cruises to the Concepción upwelling area, PP was estimated from changes in dissolved oxygen concentrations during incubation of *in vitro* light and dark bottles. The $^{14}$C procedure and results are fully described in Iriarte et al. (2000), the $O_2$ method is fully described in Daneri et al. (2000).

## RESULTS

### Antofagasta upwelling ecosystem

#### Summer (pre-El Niño)

The Antofagasta upwelling ecosystem was visited during January 1997 under 'pre-El Niño' oceanographic conditions. Although the average PP measured at the inshore stations was relatively high (4853 ± 5261 mg C m$^{-2}$ d$^{-1}$, n = 10, range 632 to 14984 mg C m$^{-2}$ d$^{-1}$) (Table 3) it is possible that the anomalous drop in wind stress (under pre-El Niño conditions) did not allow the area to reach the full productivity potential expected for this time of the year. The average offshore PP was ca. 5 times lower than the PP inshore (1076 ± 405 mg C m$^{-2}$ d$^{-1}$, n = 5, range 745 to 1723 mg C m$^{-2}$ d$^{-1}$). At the inshore stations, daily average BSP was 1722 ± 1362 mg C m$^{-2}$ d$^{-1}$ (n = 19, range 269 to 4999 mg C m$^{-2}$ d$^{-1}$), while offshore it was almost half these values (850 ± 292 mg C m$^{-2}$ d$^{-1}$, n = 7, range 469 to 1279 mg C m$^{-2}$ d$^{-1}$). The average BA inshore was $17.5 \pm 7.2 \times 10^9$ cells m$^{-2}$ (n = 19, range 5.2 to $27.8 \times 10^9$ cells m$^{-2}$ ), while offshore it was $20.8 \pm 3.7 \times 10^9$ cells m$^{-2}$ (n = 7, range 16.3 to 26.6 × $10^9$ cells m$^{-2}$). The average BOC inshore was 941 ± 386 mg C m$^{-2}$ (n = 19, range 277 to 1497 mg C m$^{-2}$) while offshore it was 1114 ± 198 mg C m$^{-2}$ (n = 7, range 873 to 1428 mg C m$^{-2}$). Inshore the average BSP as percentage PP was 63 ± 43% (n = 10, range 20 to 145%) while offshore it was 83 ± 9% (n = 5, range 74 to 99%).

Table 3. Summary of integrated primary production (PP), bacterial secondary production (BSP), bacterial abundance (BA), bacterial organic carbon (BOC) and BSP/PP% measured during this study. n = no. of samples

| Area and season | | | | PP (mg C $m^{-2}$ $d^{-1}$) | BSP (mg C $m^{-2}$ $d^{-1}$) | BA ($10^9$ cells $m^{-2}$) | BOC (mg C $m^{-2}$) | BSP/PP (%) |
|---|---|---|---|---|---|---|---|---|
| Antofagasta | Summer | Coast | Avg | 4853 | 1722 | 17.5 | 941 | 63 |
| | | | SD | 5261 | 1362 | 7.2 | 386 | 43 |
| | | | Range | 632–14984 | 296–4999 | 5.2–27.8 | 277–1497 | 20–145 |
| | | | n | 10 | 19 | 19 | 19 | 10 |
| | | Ocean | Avg | 1076 | 850 | 20.8 | 1114 | 83 |
| | | | SD | 405 | 292 | 3.7 | 198 | 9 |
| | | | Range | 745–1723 | 469–1279 | 16.3–26.6 | 873–1428 | 74–99 |
| | | | n | 5 | 7 | 7 | 7 | 5 |
| | Winter | Coast | Avg | 1215 | 490 | 9.6 | 391 | 478 |
| | | | SD | 1594 | 178 | 4.4 | 178 | 726 |
| | | | Range | 23–3800 | 291–867 | 3.8–19.9 | 157–815 | 18–1811 |
| | | | n | 7 | 16 | 16 | 16 | 7 |
| | | Ocean | Avg | 848 | 450 | 7.4 | 262 | 96 |
| | | | SD | 628 | 267 | 2.6 | 136 | 78 |
| | | | Range | 122–1799 | 243–1144 | 2.5–10.7 | 91–438 | 22–238 |
| | | | n | 7 | 13 | 13 | 13 | 7 |
| Coquimbo | Summer | Coast | Avg | 1264 | 294 | | | 34 |
| | | | SD | 656 | 160 | | | 19 |
| | | | Range | 605–2224 | 90–639 | | | 13–64 |
| | | | n | 5 | 13 | | | 5 |
| | | Ocean | Avg | 425 | 145 | | | 34 |
| | | | SD | 46 | 36 | | | 8 |
| | | | Range | 392–457 | 110–182 | | | 28–40 |
| | | | n | 2 | 3 | | | 2 |
| | Winter | Coast | Avg | 807 | 77 | | | 16 |
| | | | SD | 290 | 56 | | | 18 |
| | | | Range | 602–1012 | 34–173 | | | 3–29 |
| | | | n | 2 | 5 | | | 2 |
| | | Ocean | Avg | 1034 | 109 | | | 3 |
| | | | SD | 897 | 39 | | | 15 |
| | | | Range | 399–1668 | 66–144 | | | 9–29 |
| | | | n | 2 | 39 | | | 2 |
| Concepción | Spring | Coast | Avg | 4540 | 421 | 22.7 | 621 | 11 |
| | | | SD | 2531 | 196 | 16.2 | 444 | 7 |
| | | | Range | 1200–8740 | 239–760 | 12.7–58.8 | 348–1612 | 4–22 |
| | | | n | 6 | 7 | 7 | 7 | 6 |
| | | Ocean | Avg | 430 | 97 | 20.9 | 573 | 24 |
| | | | SD | 156 | 8 | 2.4 | 65 | 7 |
| | | | Range | 320–540 | 93–102 | 19.2–22.6 | 527–618 | 19–29 |
| | | | n | 2 | 2 | 2 | 2 | 2 |
| | Winter | Coast | Avg | 874 | 70 | 57.7 | 1274 | 10 |
| | | | SD | 477 | 8 | 9.6 | 211 | 4 |
| | | | Range | 481–1710 | 63–80 | 48.3–71.4 | 1067–1579 | 5–14 |
| | | | n | 6 | 6 | 6 | 10 | 6 |
| | | Ocean | Avg | 573 | 97 | 44.7 | 733 | 19 |
| | | | SD | 253 | 19 | 14.2 | 233 | 8 |
| | | | Range | 415–865 | 75–111 | 35.9–61.1 | 589–1002 | 12–27 |
| | | | n | 3 | 3 | 3 | 3 | 3 |

### Winter (El Niño)

The July 1997 Antofagasta upwelling cruise took place during the strong 1997/1998 El Niño event, which in all probability enhanced the expected seasonal drop in productivity of this system. This was evidenced by a decrease by an approximate factor of 5 in PP during the winter cruise at the inshore stations (1215 ± 1594 mg C $m^{-2}$ $d^{-1}$, n = 7, range 23 to 3800 mg C $m^{-2}$ $d^{-1}$) compared to the summer cruise. This drop in PP was not, however, observed offshore, where the PP values (848 ± 628 mg C $m^{-2}$ $d^{-1}$, n = 7, range 122 to

1799 mg C $m^{-2}$ $d^{-1}$) were similar to those measured during the summer cruise (Table 3). The drop in the overall productivity of the Antofagasta upwelling ecosystem was also reflected in an almost 4-fold decrease in the daily average inshore BSP (490 ± 178 mg C $m^{-2}$ $d^{-1}$, n = 16, range 291 to 867 mg C $m^{-2}$ $d^{-1}$) and an almost 2-fold decrease in the daily average offshore BSP (450 ± 267 mg C $m^{-2}$ $d^{-1}$, n = 13, range 243 to 1144 mg C $m^{-2}$ $d^{-1}$). Inshore, the average BA was 9.6 ± 4.4 × $10^9$ cells $m^{-2}$ (n = 16, range 3.8 to 19.9 × $10^9$ cells $m^{-2}$), while offshore it was 7.4 ± 2.6 × $10^9$ cells $m^{-2}$ (n = 13, range 2.5 to 10.7 × $10^9$ cells $m^{-2}$). Inshore BOC averaged 391 ± 178 mg C $m^{-2}$ (n = 16, range 157 to 815 mg C $m^{-2}$), while offshore the average BOC was 262 ± 136 mg C $m^{-2}$ (n = 13, range 91 to 438 mg C $m^{-2}$). The average BSP/PP inshore was 478 ± 726 % (n = 7, 18 to 1811 %). The high variance of the inshore BSP/PP can be attributed to 2 stations with high bacterial production and low PP. Were the data from these stations to be excluded, the average BSP/PP would be 67 ± 55 %. Offshore, the average BSP as percentage PP was 96 ± 78 % (n = 7, range 22 to 238 %).

### Coquimbo upwelling ecosystem

#### Summer (non-El Niño)

The Coquimbo upwelling ecosystem is an oligotrophic area of persistent upwelling. This is reflected in the low average PP values measured at the inshore stations (1264 ± 656 mg C $m^{-2}$ $d^{-1}$, n = 5, range 605 to 2224 mg C $m^{-2}$ $d^{-1}$) (Table 3). Offshore, the average PP was 425 ± 46 mg C $m^{-2}$ $d^{-1}$ (n = 2, range 392 to 457 mg C $m^{-2}$ $d^{-1}$). The oligotrophic conditions of Coquimbo were also reflected in the low levels of BSP measured both inshore (294 ± 160 mg C $m^{-2}$ $d^{-1}$, n = 13, range 90 to 639 mg C $m^{-2}$ $d^{-1}$) and offshore (145 ± 36 mg C $m^{-2}$ $d^{-1}$, n = 3, range 110 to 182 mg C $m^{-2}$ $d^{-1}$). Inshore, the average BSP/PP was 34 ± 19 % (n = 5, range 13 to 64 %), while at the offshore stations it was 34 ± 8 % (n = 2, range 28 to 40 %).

#### Winter (non-El Niño)

The lowest inshore values of PP were measured during winter cruises to the Coquimbo upwelling area (807 ± 290 mg C $m^{-2}$ $d^{-1}$, n = 2, range 602 to 1012 mg C $m^{-2}$ $d^{-1}$) (Table 3). At the offshore stations the daily average PP was 1034 ± 897 mg C $m^{-2}$ $d^{-1}$ (n = 2, range 399 to 1668 mg C $m^{-2}$ $d^{-1}$). During the winter cruises the BSP also reached its lowest values in the Coquimbo area, both inshore (77 ± 56 mg C $m^{-2}$ $d^{-1}$, n = 5, range 34 to 173 mg C $m^{-2}$ $d^{-1}$) and offshore (109 ± 39 mg C $m^{-2}$ $d^{-1}$, n = 3, range 66 to 144 mg C $m^{-2}$ $d^{-1}$). The average BSP/PP measured at the inshore stations was 16 ± 18 % (n = 2, range 3 to 29 %) while at the offshore stations it was 19 ± 15 % (n = 2, range 9 to 29 %).

### Concepción upwelling ecosystem

#### Spring (non-El Niño)

The Concepción upwelling ecosystem comprises the widest continental shelf (40 km) in the HCS off Chile, and is an area known for its high productivity. This area was visited during a 2 wk long cruise in October 1998 (austral spring) under intense, wind-driven upwelling conditions. The daily average PP measured at the inshore stations in the Concepción upwelling ecosystem during this study was 4540 ± 2531 mg C $m^{-2}$ $d^{-1}$ (n = 6, range 1200 to 8740 mg C $m^{-2}$ $d^{-1}$), while offshore it decreased by an order of magnitude (430 ± 156 mg C $m^{-2}$ $d^{-1}$, n = 2, range 320 to 540 mg C $m^{-2}$ $d^{-1}$) (Table 3). The daily average BSP measured at the inshore stations was 421 ± 196 mg C $m^{-2}$ $d^{-1}$ (n = 7, range 239 to 760 mg C $m^{-2}$ $d^{-1}$), while offshore the average BSP decreased by a factor of 4 (97 ± 8 mg C $m^{-2}$ $d^{-1}$, n = 2, range 93 to 102 mg C $m^{-2}$ $d^{-1}$). Inshore, the average BA was 22.7 ± 16.2 × $10^9$ cells $m^{-2}$ (n = 7, range 12.7 to 58.8 × $10^9$ cells $m^{-2}$), while offshore it was 20.9 ± 2.4 × $10^9$ cells $m^{-2}$ (n = 2, range 19.2 to 22.6 × $10^9$ cells $m^{-2}$). BOC inshore averaged 621 ± 444 mg C $m^{-2}$ $d^{-1}$ (n = 7, range 348 to 1612 mg C $m^{-2}$ $d^{-1}$), while offshore the average BOC was 573 ± 65 mg C $m^{-2}$ $d^{-1}$ (n = 2, range 527 to 618 mg C $m^{-2}$ $d^{-1}$) (Table 3). Inshore the average BSP/PP was 11 ± 7 % (n = 6, range 4 to 22 %) while offshore it was 24 ± 7 % (n = 2, range 19 to 29 %).

#### Winter (non-El Niño)

During the winter, upwelling favourable wind events in the Concepción area show a marked decline. This, coupled with a reduction in the light field, results in a seasonal drop in the productivity of the area. This condition was reflected in the average PP at the inshore stations which, during the winter cruise, showed a 5-fold drop (874 ± 477 mg C $m^{-2}$ $d^{-1}$, n = 6, range 481 to 1710 mg C $m^{-2}$ $d^{-1}$) compared to the values measured in October (Table 3). Offshore, however, the average PP values were similar (573 ± 253 mg C $m^{-2}$ $d^{-1}$, n = 3, range 415 to 865 mg C $m^{-2}$ $d^{-1}$) to those measured during the October cruise. The seasonal drop in the productivity of the system was also reflected in the BSP values, which inshore showed a 6-fold decrease (70 ± 8 mg C $m^{-2}$ $d^{-1}$, n = 6, range 63 to 80 mg C $m^{-2}$ $d^{-1}$). Offshore, the average BSP was similar to the BSP measured during the spring season (97 ± 19 mg C $m^{-2}$ $d^{-1}$,

Table 4. Bacterial secondary production (mg C $m^{-2}$ $d^{-1}$). Kruskal-Wallis ANOVA by rank ($H$) comparing latitudinal (Antofagasta, Coquimbo and Concepción upwelling ecosystems), seasonal (spring/summer upwelling and winter non-upwelling) and coast-offshore differences. *Significant difference, n = no. of samples

| Parameter | $H$ | n | df | p |
|---|---|---|---|---|
| Latitude | 26.8 | 96 | 2 | <0.001* |
| Antofagasta | | | | |
| Season | 21.5 | 55 | 1 | <0.001* |
| Summer: inshore-offshore | 0.5 | 26 | 1 | >0.1 |
| Winter: distance-offshore | 3.8 | 29 | 1 | <0.05* |
| Coquimbo | | | | |
| Season | 11.3 | 23 | 1 | <0.001* |
| Summer: inshore-offshore | 0.06 | 17 | 1 | >0.1 |
| Winter: inshore-offshore | 1.9 | 6 | 1 | >0.1 |
| Concepción | | | | |
| Season | 10.4 | 18 | 1 | <0.001* |
| Summer: inshore-offshore | 4.2 | 9 | 1 | <0.05* |
| Winter: inshore-offshore | 3.3 | 9 | 1 | >0.05 |

n = 3, range 75 to 111 mg C $m^{-2}$ $d^{-1}$). Inshore, the average BA was 57.7 ± 9.6 × $10^9$ cells $m^{-2}$ (n = 6, range 48.3 to 71.4 × $10^9$ cells $m^{-2}$), while offshore it was 44.7 ± 14.2 × $10^9$ cells $m^{-2}$ (n = 3, range 35.9 to 61.1 × $10^9$ cells $m^{-2}$). Inshore, the average BOC was 1274 ± 211 mg C $m^{-2}$ $d^{-1}$ (n = 6, range 1067 to 1579 mg C $m^{-2}$ $d^{-1}$) while offshore it was 733 ± 233 mg C $m^{-2}$ $d^{-1}$ (n = 3, range 589 to 1002 mg C $m^{-2}$ $d^{-1}$). The average BSP/PP inshore

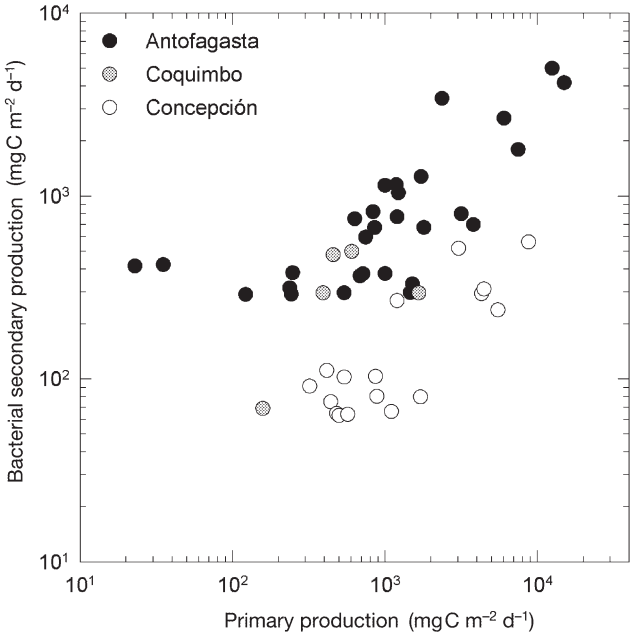


Fig. 2. Primary production versus bacterial secondary production. Integrated data from Antofagasta, Coquimbo and Concepción upwelling systems and adjacent oceanic areas (log-log scale)

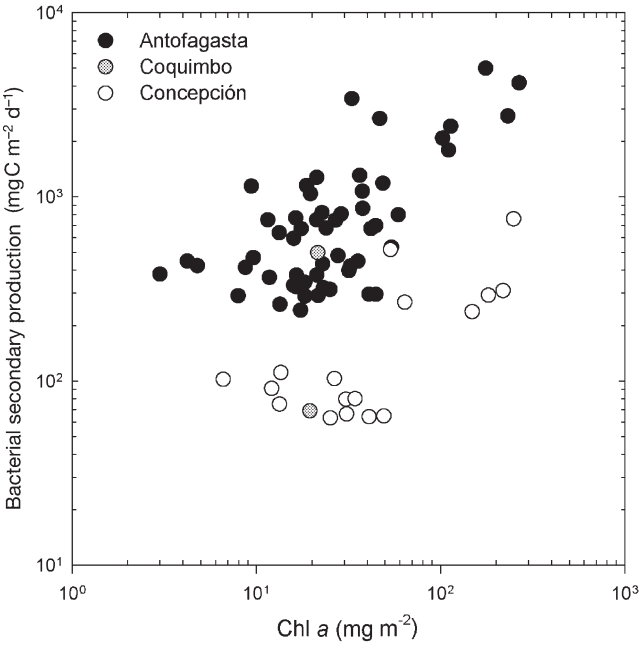


Fig. 3. Chl *a* versus bacterial secondary production. Integrated data from Antofagasta, Coquimbo and Concepción upwelling systems and adjacent oceanic areas (log-log scale)

was 10 ± 4% (n = 6, range 5 to 14%), while offshore it was 19 ± 8% (n = 3, range 12 to 27%).

Results of a Kruskal-Wallis ANOVA by ranks ($H$) comparing latitudinal (Antofagasta, Coquimbo and Concepción upwelling ecosystems), seasonal (spring/summer upwelling and winter non-upwelling) and coast-offshore differences in BSP are shown in Table 4. Significant differences in BSP were found between the 3 study areas ($H$ = 26.8, $p < 0.001$). Within the Antofagasta data set there was a significant difference ($H$ = 21.5, $p < 0.001$) between the summer and winter cruises, but significant difference between inshore and offshore stations were only found during the winter (summer: $H$ = 0.5, $p > 0.1$; winter: $H$ = 3.8, $p < 0.05$). In Coquimbo, the BSP also showed significant seasonal differences ($H$ = 11.3, $p < 0.001$), but no significant differences were detected between inshore and offshore stations (summer: $H$ = 0.06, $p > 0.1$; winter: $H$ = 1.9, $p > 0.1$). In Concepción there were significant differences between the spring and winter cruises ($H$ = 10.4, $p < 0.001$). Significant differences between inshore and offshore stations were detected during the spring ($H$ = 4.2, $p < 0.05$), but not in winter ($H$ = 3.3, $p > 0.05$).

### PP, BSP, BOC, and chl *a*

Integrated water-column BSP values from Antofagasta, Coquimbo and Concepción, were correlated

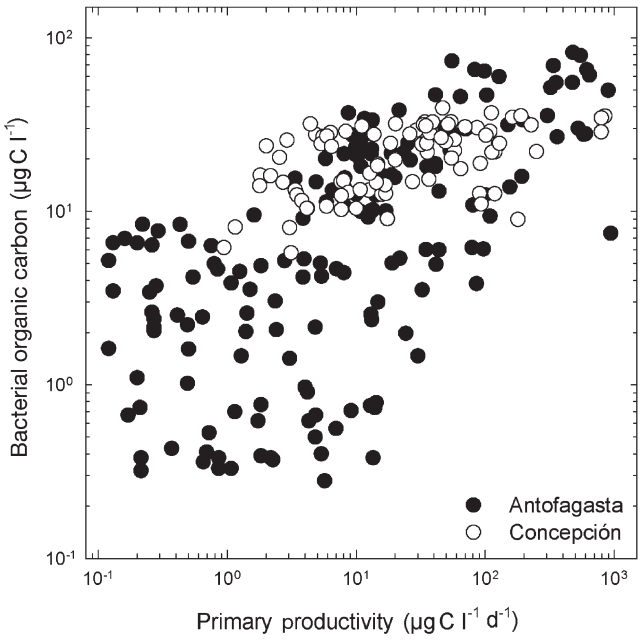


Fig. 4. Primary production versus bacterial organic carbon. Discrete data from Antofagasta and Concepción upwelling systems and adjacent oceanic areas (log-log scale)

with integrated water-column PP and chl *a*. A significant positive relationship was found between integrated PP and integrated BSP ($r^2 = 0.57$, $p < 0.05$, n = 51, $y = 0.25x + 186.26$) (Fig. 2). The correlation between integrated chl *a* and integrated BSP was lower, but still significant ($r^2 = 0.28$, $p < 0.05$, n = 74, $y = 8.29x + 374.6$) (Fig. 3). The correlation between discrete PP and BOC and between discrete chl *a* and BOC values was also significant ($r^2 = 0.25$, $p < 0.05$, n = 270, $y = 0.05x + 13.89$) and ($r^2 = 0.19$, $p < 0.05$, n = 427, $y = 1.63x + 13.18$), respectively (Figs. 4 & 5). The correlation between discrete temperature and both discrete BSP and discrete BOC values was not significant ($r^2 = 0.0$, $p > 0.05$, n = 420 and $r^2 = 0.04$, $p > 0.05$, n = 420), respectively (Figs. 6 & 7).

## DISCUSSION

The data show that bacteria are an important component of the pelagic planktonic community in upwelling ecosystems in the HCS off Chile. With the exception of the values measured in the Coquimbo upwelling system, the upper values of BSP reported in this study are higher than any reported in the literature for a variety of marine environments (Brown et al. 1991, Kirchman et al. 1995, Lochte et al. 1997, Wiebinga et al. 1997, Pomroy & Joint 1999, Shiah et al. 2000). This was also apparent in the case of discrete values of BSP (data not shown in this study) (Fuhrman et al. 1980, Coffin & Sharp 1987, McManus & Peterson 1988, Sherry et al. 1999). The highest value of 4999 mg C $m^{-2}$ $d^{-1}$ measured in Antofagasta is possibly the highest value of BSP ever reported in the literature. This result was not unexpected, as the HCS constitutes

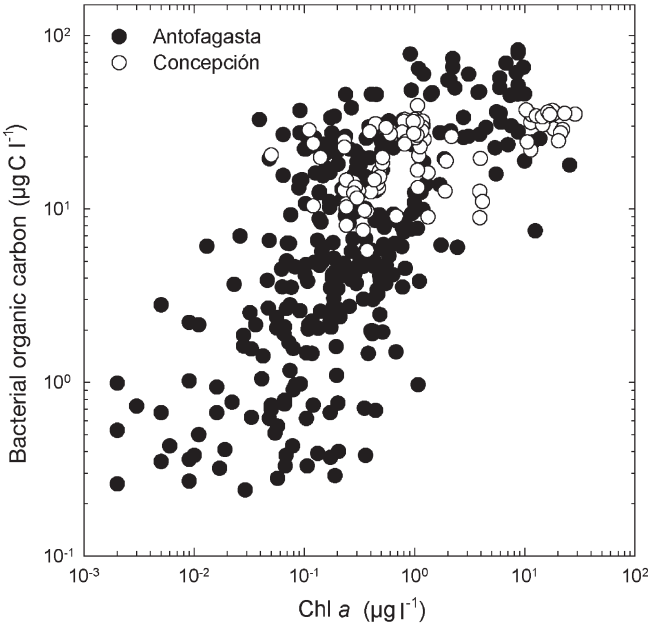


Fig. 5. Chl *a* versus bacterial organic carbon. Discrete data from Antofagasta and Concepción upwelling systems and adjacent oceanic areas (log-log scale)

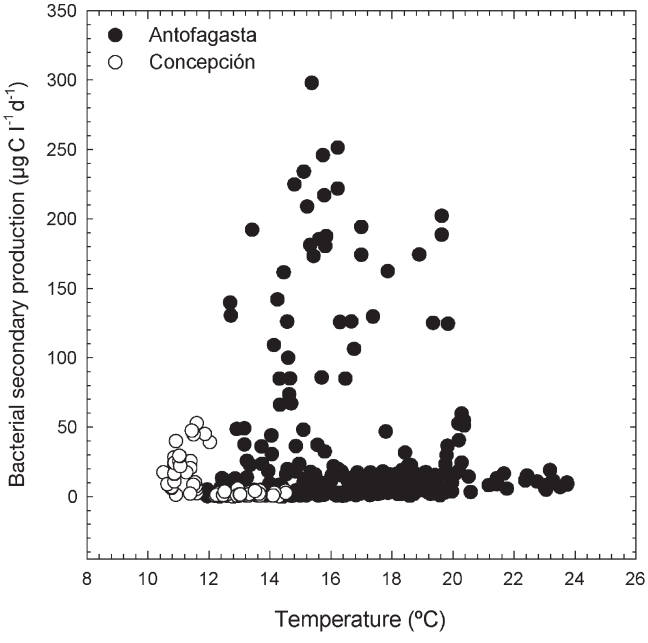


Fig. 6. Temperature versus bacterial secondary production. Discrete data from Antofagasta and Concepción upwelling systems and adjacent oceanic areas

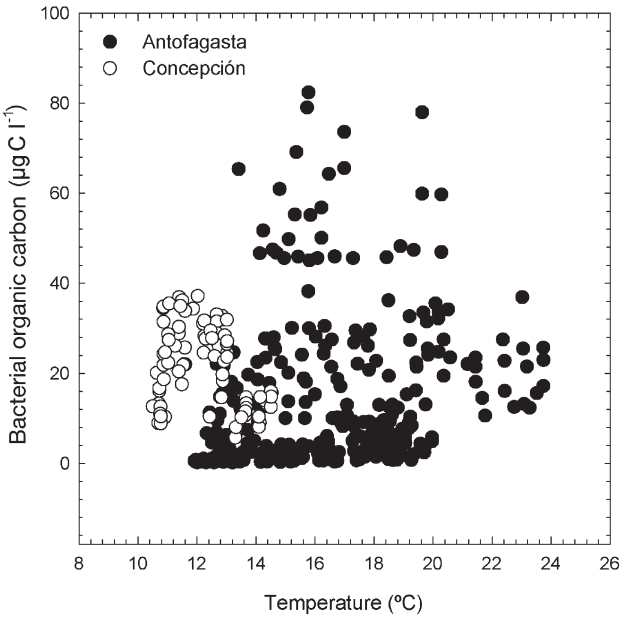


Fig. 7. Temperature versus bacterial organic carbon. Discrete data from Antofagasta and Concepción upwelling systems and adjacent oceanic areas

one of the most productive large marine ecosystems, and is consistent with the fact that the highest values of PP have been reported in the area (Daneri et al. 2000).

The data also showed significant latitudinal differences in the levels of bacterial activity. Highest BSP values were measured in the Antofagasta upwelling area during the January 1997 cruise, while the lowest BSP values were recorded in the Coquimbo upwelling area. During January 1997 the Antofagasta upwelling area suffered an anomalous decrease in winds, favouring upwelling, which almost certainly prevented the area from attaining its full productivity potential. It is possible therefore that bacterial activity in the Antofagasta area could potentially be higher. However, it is also possible that the more quiescent upwelling conditions that characterised the pre-El Niño period stimulated higher levels of bacteria activity than usual. The pre-El Niño (low upwelling activity) conditions found in Antofagasta contrast with the situation observed during the summer cruise to the Concepción upwelling area which was subjected to active upwelling and wind-stress conditions that were 2 standard deviations greater than the climatological mean (D. Figueroa pers. comm.). High wind stress induces mixing in the water column which, to a certain extent, restricts biological productivity. It is thus possible that bacteria can reach higher levels of activity in the Concepción upwelling area. The only published BSP data reported for the Concepción upwelling area, and indeed, for the whole HCS, indicates that the highest levels of BSP are attained in the area during periods of calm post-upwelling conditions (McManus & Peterson 1988). Our discrete BSP values measured in Concepción were a factor of 2 higher than the values reported by McManus & Peterson (1988). A possible explanation for this difference may be related to our use of an empirical bacterial cellular carbon average of 27.4 fgC for the Concepción upwelling while McManus & Peterson (1988) relied on a fixed, literature-based value of 20 fgC. Of the 3 upwelling areas sampled, Coquimbo showed a consistently lower bacterial activity despite the fact that the area was only visited during years considered oceanographically as 'normal' that is non-El-Niño or La Niña years. This low bacterial activity in the Coquimbo area is in agreement with observations that Coquimbo has been oceanographically described as an oligotrophic permanent upwelling area with productivity values that are consistently lower than PP values observed in other upwelling centres within the HCS off Chile (Daneri et al. 2000).

Important seasonal differences in bacterial activity were also observed in the 3 sites visited. Highest levels of BSP were measured during the spring and summer cruises. Wind-driven upwelling events in the HCS are more prominent during the spring, summer and early austral fall months. During the winter, a weakening of the Pacific anticyclone coupled with a reduced light field results in a decrease in the productivity of the system. This was reflected in lower overall PP values, which showed a 2- to 5-fold decrease during the winter at the 3 study sites. This seasonal drop in the observed PP was also reflected in the BSP values which, in the case of Antofagasta and Coquimbo at the inshore stations, showed a near 4-fold decrease, while in the Concepción samples an almost 6-fold decrease was noted. This more pronounced decrease in BSP in Concepción may reflect the more marked seasonality in the productivity cycles in this upwelling area (Daneri et al. 2000). A strict seasonal comparison with the Antofagasta upwelling is, however, not possible since the Antofagasta upwelling area was visited during July 1998 when the region was under the influence of the particularly strong 1997-98 El-Niño event.

Although the dynamic nature of the HCS makes the setting of ecosystem boundaries difficult, important inshore-offshore differences were found during this study, in agreement with similar differences reported by Fuhrman et al. (1980) for the Southern California Bight. The main inshore-offshore differences were found in the Antofagasta and Concepción upwelling areas during the summer and spring cruises, respectively. This is consistent with inshore-offshore differences found in the levels of PP, although the decrease in BSP was not as pronounced as the decrease in PP.

The average PP measured inshore in the Antofagasta upwelling area was 5 times greater than the offshore PP, while for Concepción comparable offshore values were an order of magnitude lower than inshore PP values. The BSP values on the other hand showed a 2-fold drop at the inshore stations, while offshore they fell by a factor of 4 in the Antofagasta and Concepción upwelling ecosystems. In general, under more oligotrophic conditions such as those encountered during the winter cruises or during the cruises to the Coquimbo upwelling area, the coast-to-offshore gradient was less pronounced. As expected, the variance of the BSP data was greater inshore while the more oceanic stations showed lower variance. The less variable BSP values measured for the offshore stations reflect more homogeneous oceanographic conditions and probably represent accurate estimates of overall levels of bacterial activity within the more oceanic realm of the HCS off Chile.

The close coupling observed between PP levels and BSP during this study resulted in highly significant correlations between PP and BSP. The correlation of integrated PP and BSP was higher than the correlation of discrete PP and BSP values (data not presented in this study), thus supporting the view that a tighter coupling between bacteria activity and PP is obtained when analysing integrated data (Williams 1998). The strong correlation between PP and BSP reflects a tight coupling between carbon synthesis and bacterial consumption, confirming a very dynamic relationship between algal production and bacterial activity in the HCS. The correlation between chl *a* and BOC was significant, but not as high as that reported in a number of studies which have a shown strong correlation between bacterial abundance and chlorophyll in coastal environments (Fuhrman et al. 1980), including upwelling regions (Linley et al. 1983). Interestingly, the correlation between PP and BOC (a flux and a standing stock measurement) was better than the correlation between BOC and chl *a* (both standing stock measurements). During this study no significant correlation between BSP and BOC and temperature was found. This finding contradicts the data of Coffin & Sharp (1987), who found a significant correlation between bacterial abundance and temperature, and of other studies that have shown temperature to be a more critical factor than substrate availability in controlling bacterial activity (Vootamen 1980, Wilson & Stevenson 1980, Wright & Coffin 1983, Coffin 1986). The high correlation between PP and BSP, coupled with the lack of correlation between temperature and BSP, would indicate that, in the HCS, substrate availability seems to be more important than temperature in limiting bacterial activity and abundance.

The results of this study indicate that an important fraction of the organic matter produced by phytoplankton activity is being channelled through the bacteria in the HCS off Chile. Taken as a percentage of PP, the data from the 3 upwelling areas sampled during this study showed that a significant proportion of PP was utilised by bacteria (ca. 63 to 96% in Antofagasta, 16 to 34% in Coquimbo and 10 to 24% in Concepción). Assuming a conservative bacterial growth yield of 0.25 (Daneri et al. 1994), the overall carbon utilisation by bacteria seems to be around or in excess of the *in situ* PP. These results are in agreement with data reported for other upwelling systems (Brown et al.1991, Ducklow 1993, Wiebinga et al. 1997) and for the Concepción shelf upwelling area (McManus & Peterson 1988), and confirm the view that bacteria are an important component of upwelling ecosystems, and are capable of processing an important fraction of the organic carbon fixed by algal activity.

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