

## Abundance and production of pelagic bacteria in the southern Bay of Biscay during summer\*

SUSANA BARQUERO<sup>1</sup>, J. ALFONSO BOTAS<sup>2</sup> and ANTONIO BODE<sup>1</sup>

<sup>1</sup>Instituto Español de Oceanografía, Centro Costero, Apdo. 130, E-15080 La Coruña, Spain.

<sup>2</sup>Depto. Biología de Organismos y Sistemas, Área de Ecología, Universidad de Oviedo, E-33070 Oviedo, Spain.

**SUMMARY:** The first studies on bacterial abundance and production in representative areas of the shelf in the southern Bay of Biscay were carried out in coastal, shelf-break and off-shelf zones of the Central Cantabrian Sea in summer 1993 and 1994. In 1993 some coastal stations displayed the effects of an upwelling pulse. Thymidine uptake rates were minimal during upwelling conditions in coastal waters (range 0.4 - 4 pmol l<sup>-1</sup> h<sup>-1</sup>). In shelf-break and off-shelf waters, thymidine uptake profiles displayed surface and subsurface peaks (range 0.3 - 15.5 pmol l<sup>-1</sup> h<sup>-1</sup>). Vertical distribution of heterobacteria abundance varied from 0.28 to 2.27 x 10<sup>6</sup> cell ml<sup>-1</sup> in the whole area studied. Cyanobacteria varied from 0.04 x 10<sup>4</sup> to 1.04 x 10<sup>5</sup> cell ml<sup>-1</sup>. Heterobacteria accounted for 13 to 46% of total particulate carbon. In this study we concluded that during summer, pelagic heterobacteria can enhance high carbon turnover rates when upwelling relaxes and primary production rates increase, allowing the accumulation of phytoplankton. In turn, bacterial production rates decay abruptly during the upwelling process. Off-shore the system is typically oligotrophic, bacterioplankton balance the primary production rates and even bacteria seem to be food-limited. Our results on abundance and production of pelagic bacteria in the Central Cantabrian Sea are within the published range for the Galician upwelling areas.

**Keywords:** Bacteria, abundance, production, upwelling, Bay of Biscay.

**RESUMEN:** ABUNDANCIA Y PRODUCCIÓN DE LAS BACTERIAS PELÁGICAS EN LA REGIÓN SUR DEL GOLFO DE VIZCAYA DURANTE EL VERANO. – En este trabajo se estudian los primeros resultados sobre abundancia y producción bacteriana en regiones de la plataforma continental del Mar Cantábrico, durante el verano en 1993 y 1994. En 1993 se detectaron los efectos de un pulso de afloramiento en algunas estaciones costeras. Las tasas de incorporación de timidina fueron mínimas durante el afloramiento en las aguas costeras (rango 0.4 - 4 pmol l<sup>-1</sup> h<sup>-1</sup>). En la zona del talud continental y fuera de la plataforma, los perfiles de incorporación de timidina mostraron picos en superficie y también subsuperficiales (rango 0.3 - 15.5 pmol l<sup>-1</sup> h<sup>-1</sup>). La distribución vertical de la abundancia de bacterias heterotróficas varió entre 0.28 y 2.27 x 10<sup>6</sup> células ml<sup>-1</sup> en el área estudiada. La abundancia de cianobacterias varió entre 0.04 x 10<sup>4</sup> a 1.04 x 10<sup>5</sup> células ml<sup>-1</sup>. Las bacterias heterotróficas constituyeron del 13 al 46 % del carbono particulado total. En este estudio se concluye que en el verano las bacterias heterotróficas pelágicas pueden alcanzar elevadas tasas de crecimiento durante la fase de relajación del afloramiento, cuando aumentan las tasas de producción primaria que a su vez conducen a la acumulación de fitoplancton. Durante el proceso de afloramiento las tasas de producción bacteriana disminuyen abruptamente. Fuera de la plataforma el sistema es oligotrófico, las tasas de producción del bacterioplancton y del fitoplancton se hallan en equilibrio e incluso las bacterias parecen estar limitadas por la disponibilidad de alimento. Nuestros resultados sobre la abundancia y la producción de las bacterias pelágicas en la plataforma continental del Mar Cantábrico están dentro de los rangos publicados para las áreas del afloramiento de Galicia.

**Palabras clave:** Bacterias, abundancia, producción, afloramiento, Golfo de Vizcaya.

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## INTRODUCTION

In upwelling systems, bacterioplankton dynamics are closely related to the upwelling cycle and the dynamics of phytoplankton (Sorokin and Kogelschatz, 1979; Sorokin, 1981; Hanson *et al.*, 1986; Bak and Nieuwland, 1993; Tenore *et al.*, 1995). Bacterial biomass and activity are low during early phases of upwelling and become increasingly important in the cycling of carbon and nutrients as the upwelling intensity decays.

The northern and north-western Iberian coasts are characterised by upwelling, primarily wind-driven, occurring in the period from March to October (Dickson *et al.*, 1980; Fraga, 1981; Blanton *et al.*, 1982; Botas *et al.*, 1990). This upwelling system shows variations of phytoplankton abundance and primary production which are similar to the succession of phases of vertical mixing during winter, early spring and autumn and thermal stratification of the water column during summer (Fernández and Bode, 1991, 1994; Bode *et al.*, 1994 a; Casas *et al.*, 1997). Primary production maxima are often related to favourable upwelling conditions, especially during spring and summer (Fernández and Bode, 1991; Varela *et al.*, 1991; Bode *et al.*, 1994 a; Tenore *et al.*, 1995). In contrast with the Galician region (NW Spain), where there are upwelling events during the spring and near the shelf-break (Varela *et al.*, 1991; Tenore *et al.*, 1995), the upwelling in the southern Bay of Biscay is known to occur near the coast in the summer period, where it causes the disruption of the thermally stratified surface layer (Botas *et al.*, 1990; Fernández *et al.*, 1991; Marañón and Fernández, 1995) and produces significant changes in planktonic community structure, biomass and primary production (Fernández and Bode, 1991; Fernández *et al.*, 1991; Bode and Fernández, 1992 a; Fernández and Bode, 1994; Marañón and Fernández, 1995; Marañón *et al.* 1995). These events are particularly important in the pelagic ecosystem of the southern Bay of Biscay because the input of nutrients into the euphotic zone during summer allows for an increase in biological production when an oligotrophic situation is expected. Bode and Fernández (1992 b), analysing the biochemical composition and the size spectra of seston particles, concluded that this pelagic ecosystem would be based on a microbial food web for most of the year, but particularly during summer and in the off-shelf region where small flagellates and heterotrophic dinoflagellates dominate the microplankton community (Fernández and Bode, 1994).

There is limited information on bacterial abundance and activity during upwelling events on the Galician coast (Hanson *et al.*, 1986; Bode *et al.* 1994 b; Tenore *et al.*, 1995), despite their potential importance, bacteria were scarcely studied in the southern Bay of Biscay. The only available studies were carried out in a shallow environment in the eastern coast, (Iriberry *et al.*, 1987, 1990; Barcina *et al.*, 1992; Unanue *et al.*, 1992). The main pattern which emerged from these studies was the marked seasonal change between the low bacterial activity and biomass values during the cold period (winter-spring) and the maximum values measured during the warm period (summer-autumn). However, the place where these studies were made was not affected by the upwelling, which is restricted to the western coast of the Cantabrian Sea (Dickson *et al.*, 1980).

The present study describes cell abundance and production of bacterioplankton in three distinct zones (coastal, shelf-break and off-shelf zone) of the Central Cantabrian Sea (southern Bay of Biscay) during summer in relation to upwelling conditions. These are the first data on bacterioplankton for this coastal region.

## MATERIAL AND METHODS

Sampling was made during two cruises, ASTURIAS-0793 (July 1993) and ASTURIAS-0794 (July 1994), in the Central Cantabrian Sea (southern Bay of Biscay). Stations were arranged in a cross-shelf transect covering a bathymetric range from 30 to 900 m and some of them were sampled several times during the study (Fig. 1). We considered four types of stations according to the vertical distribution of temperature and distance from the coast: coastal stations displaying characteristics of an upwelling pulse (labelled U in the Fig. 1), coastal stations with weak-upwelling conditions (C), shelf-break stations (S), and off-shelf stations (O).

Vertical profiles of temperature and salinity were obtained with a CTD SBE-25. Irradiance (400 to 700 nm) was measured with a Li-COR radiometer equipped with a 4Π sensor. Water samples for the determination of chlorophyll-a, particulate organic carbon and bacterial abundance and production were collected with acid cleaned Niskin bottles from the surface to the bottom of the euphotic zone. The water was transferred to acid

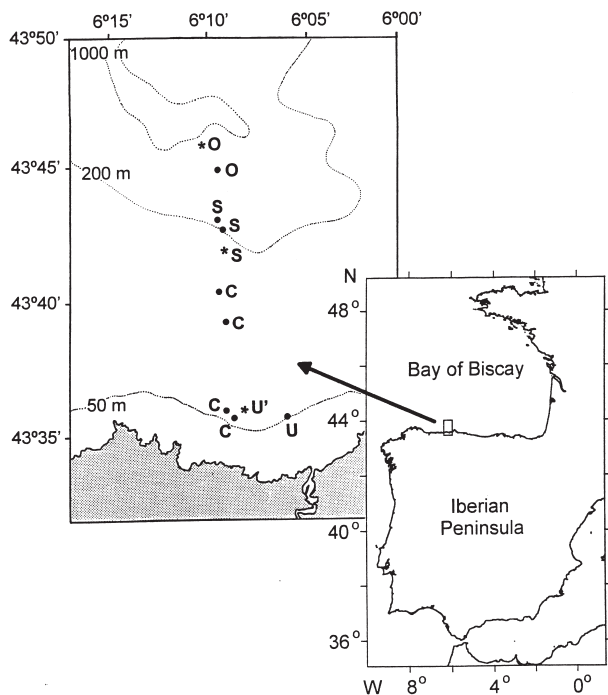


FIG. 1. – Location of sampling stations. Dots (●) indicate stations sampled only during summer 1993. Asterisks (\*) indicate stations sampled during summer 1993 and repeated in summer 1994. Labels refer to the type of hydrographic station: O, off-shelf station; S, shelf-break station; C, coastal station with weak-upwelling conditions; U, station with upwelling conditions. The station labelled as U' was found with upwelling conditions only during summer 1993, and was in weak-upwelling conditions in summer 1994.

cleaned carboys and transported to the laboratory within four hours of sampling in the field. Chlorophyll-a was determined in particles retained by Poretics 0.2  $\mu\text{m}$  polycarbonate filters (ASTURIAS-0793 cruise) or Whatman GF/F filters (ASTURIAS-0794). Chlorophyll-a concentration was analysed by the fluorometric procedure of Yentsch and Menzel (1963) and Parsons *et al.* (1984). Particulate carbon was analysed in material retained by Whatman GF/F filters using either a CHN Carlo-Erba 1500N (ASTURIAS-0793) or a Perkin-Elmer 2400 analyser (ASTURIAS-0794).

Samples for the enumeration of bacterial abundance (only available for ASTURIAS-0794 cruise) were preserved with glutaraldehyde (2% final concentration), stained with DAPI (4',6-diamidino-phenylindole, final concentration 2.5  $\mu\text{g ml}^{-1}$ ) and filtered (10 ml) through Poretics 0.2  $\mu\text{m}$  black-stained polycarbonate filters, following the procedure described in Porter and Feig (1980). Filters were examined with an epifluorescence microscope (OLYMPUS BH-2) under ultraviolet excita-

tion (OLYMPUS UG-1 filter combination) from a mercury short arc lamp (HBO 100 W/2). Cyanobacteria were distinguished from heterobacteria by the emission of red autofluorescence when using green excitation (OLYMPUS BP490 filter combination).

Bacterial production was estimated by measuring the incorporation of [ $^3\text{H}$ ] thymidine into the trichloroacetic acid (TCA) insoluble fraction, following the procedure of Fuhrman and Azam (1982). Three 10 ml replicates were drawn from each sample into centrifuge glass tubes, labelled with thymidine (5 nM final concentration) and incubated in the laboratory for 60 minutes. The thymidine concentration and incubation times were similar to those described by Iriberry *et al.* (1990), and adequate to saturate linear thymidine uptake. Temperature and irradiance conditions during the incubation were similar to those observed at the depth where samples were collected using laboratory incubators equipped with fluorescent lights. TCA-soluble pools of bacterial material were extracted on ice with TCA (5% final concentration) for 20 minutes. Particulate material was then filtered through 0.2  $\mu\text{m}$  Poretics polycarbonate filters, rinsed three times with 4 ml of 5% TCA and finally washed with filtered seawater. Ethanol was not used during extraction. Blank values were obtained from thymidine labelled samples, killed with TCA and filtered immediately.

Phytoplankton carbon biomass was calculated from chlorophyll-a equivalents (chlorophyll-a + 1.51 phaeophytin) and using a C:Chl-a ratio of 50. The factor 1.51 is the ratio of molar weights of chlorophyll-a to phaeophytin. Bacterial carbon was calculated assuming 11.35 fg C cell $^{-1}$ , computed for free-living bacteria from Table 1 in Iriberry *et al.* (1990). The conversion from thymidine uptake to bacterial carbon production was made applying the factor 1.276  $\times 10^{11}$   $\mu\text{g C (mol thymidine)}^{-1}$  in Iriberry *et al.* (1990). It was presumed no variation of bacterial production rates during the day (24 h).

## RESULTS AND DISCUSSION

A clear upwelling pulse was detected at two coastal stations in 1993, as surface temperature increased from approximately 15  $^{\circ}\text{C}$  near the coast (sta. U) to ca. 19  $^{\circ}\text{C}$  at the O stations (Fig. 2). In general there were no marked thermoclines although the temperature profiles for the O stations

TABLE 1. – Means ( $\pm$  sd) of carbon stock, carbon production and growth rates of bacteria in the main zones identified. All values integrated for 0-60 m depth interval, when possible.

	1993				1994		
	sta. type O	sta. type S	sta. type C	sta. type U	sta. type O	sta. type S	sta. type C
Chlorophyll-a (mg Chl-a m <sup>-2</sup> )	21.9 $\pm$ 8.5	25.6 $\pm$ 18.8	60.7 $\pm$ 25.3	6.0 $\pm$ 5.7	16.5 $\pm$ 3.4	18.4 $\pm$ 1.3	40.7 $\pm$ 14.9
Phytoplankton carbon (mg C m <sup>-2</sup> ) <sup>(1)</sup>	1618 $\pm$ 437	2086 $\pm$ 1463	5105 $\pm$ 2048	598 $\pm$ 518	1370 $\pm$ 408	1675 $\pm$ 172	2928 $\pm$ 1119
Total particulate carbon of seston (mg C m <sup>-2</sup> )	3938 $\pm$ 525	5225 $\pm$ 2878	6949 $\pm$ 3063	2558 $\pm$ 613	2378	2526	3754
Heterotrophic bacterial carbon (mg C m <sup>-2</sup> ) <sup>(2)</sup>	-	-	-	-	1103 $\pm$ 74	676 $\pm$ 33	481 $\pm$ 276
Bacterial production (mg C m <sup>-2</sup> d <sup>-1</sup> ) <sup>(3)</sup>	921 $\pm$ 143	771 $\pm$ 605	188 $\pm$ 71	93 $\pm$ 50	405 $\pm$ 448	886 $\pm$ 434	601
Bacterial growth rate (d <sup>-1</sup> ) <sup>(4)</sup>	-	-	-	-	0.37	1.31	1.20

<sup>(1)</sup> Calculated from chlorophyll-a equivalents and a C:Chl-a ratio of 50 g C (g Chl-a)<sup>-1</sup>. See methods. <sup>(2)</sup> Conversion factor: 11.35 fg C cell<sup>-1</sup> (Table 1, Iriberry *et al.*, 1990). <sup>(3)</sup> Conversion factor: 1.276 x 10<sup>11</sup>  $\mu$ g C (mol thymidine)<sup>-1</sup> (Iriberry *et al.*, 1990). Constant bacterial production daily rates are assumed. <sup>(4)</sup> Computed by dividing bacterial production by heterotrophic bacterial carbon.

displayed the highest gradients between 20 and 40 m. The conditions found in 1994 were similar to those of 1993, except that in coastal waters upwelling conditions were weaker, and temperature in the upper 10 m exceeded 16 °C in all stations. Mixing phenomena in the upper 50 m of the water column are relatively frequent in this area (Botas *et al.*, 1990) and they prevent the development of a well defined thermal stratification of the water column. Therefore, we realize that thermal distribution could be insufficient to justify our zonation into the four mentioned station types, if spatial location and chlorophyll profiles were not taken into account.

Chlorophyll-a concentration decreased, and their maxima were located deeper, from the coast towards the off-shelf, excepting the U stations in 1993 which showed the lowest chlorophyll concentrations through the water column (Fig. 3). Low phytoplankton biomass is expected in early upwelling stages (Botas *et al.*, 1990; Varela *et al.*, 1991). The upwelling situation observed in 1993 was described by Marañón and Fernández (1995): Cryptophyceae and other flagellates dominated through the studied transect, but diatoms increased their numbers near the coast. Upwelling dynamics caused the transport and accumulation of phytoplankton towards deep layers near the shelf-break (Fig. 3) driven by a mechanism similar to that described in the Galician upwelling (Castro *et al.*, 1994).

Bacterial thymidine uptake rates were low near the coast in 1993 because of the unfavourable upwelling conditions and ranged 0.4 - 4 pmol l<sup>-1</sup> h<sup>-1</sup>, whereas they increased towards deeper waters with a marked subsurface maximum at the O stations (Fig. 3). In contrast, in 1994 the highest production values were at C station with 15.8 pmol l<sup>-1</sup> h<sup>-1</sup>, and surface maxima were found in all cases. During summer 1993 and 1994, in shelf-break and off-shelf waters thymidine uptake profiles varied between 0.3 and 15.5 pmol l<sup>-1</sup> h<sup>-1</sup>. After upwelling events, when water column reach a relative stability, lower turbulence and reduced advective transport of the surface layer near the coast, would favour phytoplankton accumulation and therefore bacterial growth would be enhanced, as reported in other upwelling systems (Sorokin and Kogelschatz, 1979; Sorokin, 1981; Bak and Nieuwland, 1993). Although no clear relationship was found in our study between the depth of chlorophyll-a maxima and the peaks of bacterial production, integrated stocks of phytoplankton and heterotrophic bacterial carbon, and bacterial production rates exhibited a close relationship, as will be discussed below.

Heterotrophic bacteria resulted in general with lower abundances at S station than at C and O stations (Fig. 3). In all cases, one or several subsurface peaks occurred. The abundance maximum was coincident with that of chlorophyll-a at C station, but it

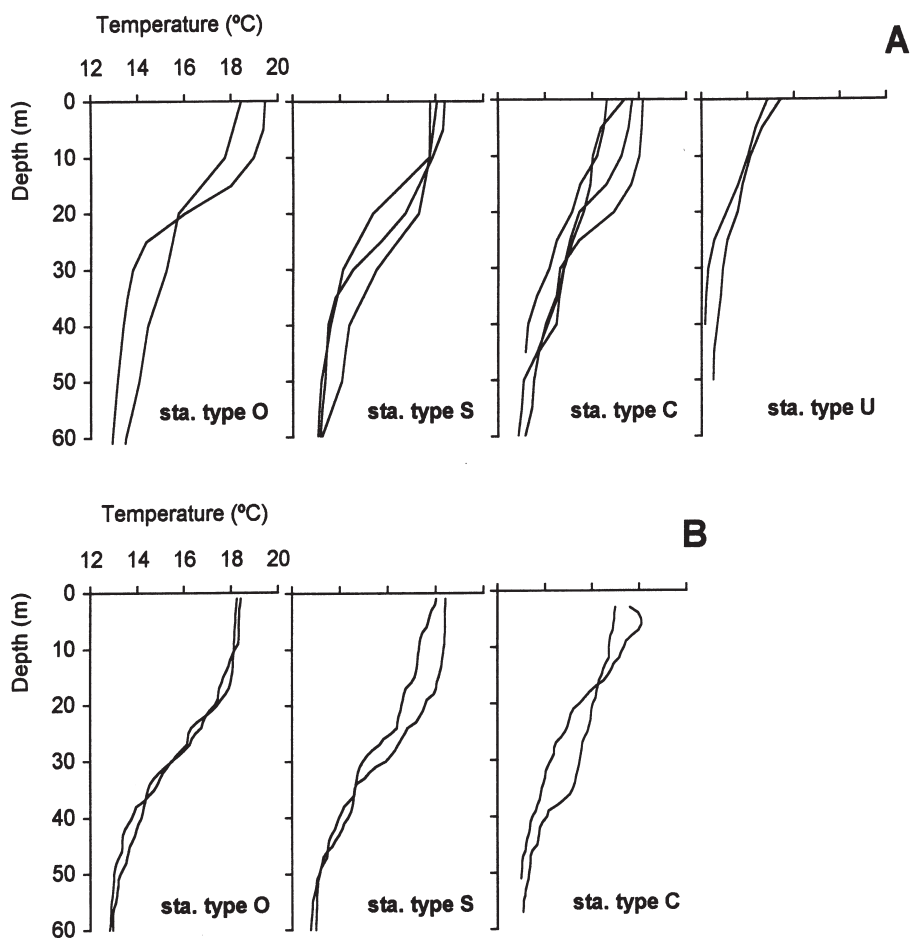


FIG. 2. – Vertical distribution of temperature (°C) in the upper 60 m during summer 1993 (A) and summer 1994 (B), from every station of type O, S, C and U as indicated in Fig. 1.

was above the chlorophyll maximum at S and O stations. Cyanobacteria increased from C to O station, and their abundances were similar to those found in some areas of the N Atlantic Ocean (Li *et al.*, 1993) but lower than those reported for estuarine areas (Kuosa, 1990; Caron *et al.*, 1991). Subsurface maxima of cyanobacteria occurred slightly deeper offshore, above the maxima of chlorophyll and heterotrophic bacteria, as it has been found in other areas (Olson *et al.*, 1990).

For comparison purposes, integrated values of phytoplankton and bacterial carbon stocks, bacterial production and growth rates were computed (Table 1). Heterotrophic bacterial carbon biomass was calculated using a factor of 11.35 fg C cell<sup>-1</sup> computed from Table 1 in Iriberry *et al.* (1990). Bacterial production was calculated using the same factor 1.276 x 10<sup>11</sup> µg C (mol thymidine)<sup>-1</sup> as in Iriberry *et al.* (1990). These authors provided data for free-living marine bacteria in the south-

eastern Bay of Biscay, and we decided to use their conversion factors as the best approach to our own study. We are aware that these carbon production/thymidine uptake and carbon biomass/bacterial cell factors may vary depending upon, e.g., bacteria biovolume (Bratbak, 1985) and environmental conditions (Simon and Azam, 1989; Li *et al.*, 1993). It will be necessary to obtain empirical conversion factor in further studies in this Cantabrian region.

The largest variations occurred in the coastal zone depending on the upwelling phase: total particulate carbon and phytoplankton biomass were very low during the upwelling event in summer 1993, but peaked during weak-upwelling condition (Table 1). In the C case, we estimated that phytoplankton was 73 and 78 % of total particulate carbon in summer 1993 and 1994 respectively, while heterobacteria only accounted for 13 % in summer 1994. In contrast, progressing from the coast, heterobacterial car-



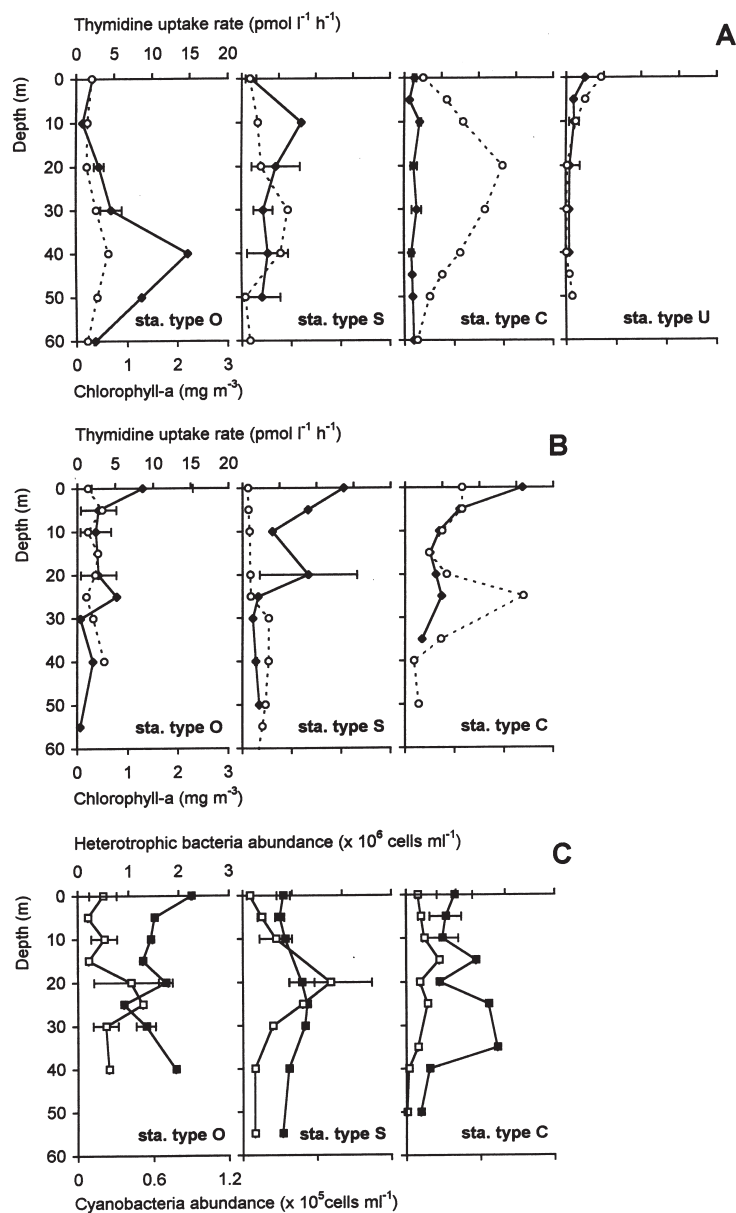


FIG. 3. – Average profiles of bacterial thymidine uptake rates ( $\text{pmol l}^{-1} \text{h}^{-1}$ ) (—◆—) and chlorophyll-a concentration ( $\text{mg m}^{-3}$ ) (---○---) in the upper 60 m during summer 1993 (A) and summer 1994 (B). Heterotrophic bacterial abundance ( $\pm$  sem,  $\times 10^6$  cells  $\text{ml}^{-1}$ ) (—■—) and cyanobacterial abundance ( $\pm$  sem,  $\times 10^5$  cells  $\text{ml}^{-1}$ ) (---□---) in 1994 cruise (C).

bon increased up to 46 % of total particulate carbon in O station. During 1994, along with a sharp increase in bacteria numbers from coast to off-shelf, production rates seemed lower in O station suggesting a great proportion of ‘dormant’ bacteria (Table 1). Therefore, lower average bacterial growth rates resulted in O station compared to S and C ones. In this sense Fuhrman *et al.* (1980) argued that bacterioplankton may be a significant fraction of seston, even in the euphotic zone, and that bacterial growth

rates are density independent. In this study, vertical profiles of carbon turnover rate of heterobacteria (not shown) were found quite similar to those of thymidine uptake rate (Fig. 3), in all cases showing two peaks: at surface and between 20 - 25 m depth, above the subsurface maxima of phytoplankton. In addition, constant and pronounced maxima of thymidine uptake rates appeared at the surface, where chlorophyll-a concentration was very low. This contrasts with the correlation commonly seen between the

TABLE 2. – Ranges of published values of bacterial abundance ( $\times 10^5$  cells ml<sup>-1</sup>), thymidine uptake (pmol l<sup>-1</sup> h<sup>-1</sup>) and bacterial growth rates (d<sup>-1</sup>) on the N-NW Iberian coast.

Zone	Abundance	Thymidine uptake	Growth rate	Reference
Ría de Arousa, Galicia. Spring upwelling (NW Spain)	2.5 - 12.0	0.0 - 8.0	< 0.10 - 1.28	Hanson <i>et al.</i> (1986)
Galician shelf. Summer upwelling (NW Spain)	1.0 - 10.2	0.1 - 10.10	-	Tenore <i>et al.</i> (1995)
Galician shelf. Autumn upwelling (NW Spain)	-	-	< 0.24 - 3.36	Tenore <i>et al.</i> (1995)
Galician shelf. Spring downwelling (NW Spain)	5.1 - 14.5	0.84 - 59.82	-	Tenore <i>et al.</i> (1995)
Coastal station, Bilbao, País Vasco (N Spain)	3.2 - 12.8 <sup>(1)</sup>	-	-	Iriberry <i>et al.</i> (1987)
La Salvaje Beach, País Vasco (N Spain)	5.2 - 34.5 <sup>(1)</sup>	-	0.70 - 3.48	Iriberry <i>et al.</i> (1990)
La Salvaje Beach, País Vasco (N Spain)	5.4 - 23.7 <sup>(1)</sup>	-	-	Barcina <i>et al.</i> (1992)
La Salvaje Beach, País Vasco (N Spain)	8.4 - 21.8 <sup>(2)</sup>	4.4 - 15.4 <sup>(2)</sup>	0.50 - 4.50 <sup>(1)</sup>	Unanue <i>et al.</i> (1992)
Asturias coast (N Spain)	2.8 - 22.6	0.4 - 15.8	0.37 - 1.31 <sup>(3)</sup>	This study

<sup>(1)</sup> Range of individual values from samples of different seasons. <sup>(2)</sup> Range of mean values from the cold (winter-spring) and warm (summer-autumn) seasons. <sup>(3)</sup> Range of mean values from the different shelf zones.

location of maxima of phytoplankton biomass and heterobacterial rates (Fuhrman *et al.*, 1980; Fuhrman and Azam, 1982), and suggests the presence of other food sources for heterobacteria (perhaps dissolved organic matter).

Even when no primary production measurements are available for either 1993 and 1994 cruises, we compared bacterial production rates with the published primary production values for the Cantabrian Sea, as a first approach in order to evaluate the importance of bacteria for this pelagic ecosystem. Using values given by Botas *et al.* (1989) and Anadón *et al.* (1991), and extrapolating hourly rates to daily values assuming a 12:12 h photoperiod, the average values of primary production were: 1533, 921 and 744 mg C m<sup>-2</sup> d<sup>-1</sup> for the coastal, shelf-break and off-shelf zones respectively. Despite the acknowledged variability of primary production rates from year to year even in the same region, these averages are representative of the pelagic system in the Central Cantabrian Sea (Bode *et al.*, 1996). According to this, our estimations of bacterial production would represent from 54 to 124% of primary production in O stations, 84 - 96% in S stations and 12 - 39% in C stations. These results are indicative of an oligotrophic system off-shelf, as reported in other areas where microbial heterotrophic processes are in balance with primary production (Linley *et al.*, 1983; Cho and Azam, 1990). Altogether, much lower turnover rates for bacteria (0.37 d<sup>-1</sup>) than on-shelf, along with relatively low phytoplanktonic and total particulate carbon biomass were supporting this suggestion of an oligotrophic system in off-shelf waters, where heterotrophic bacteria would be well limited by food supply.

In this work we provide the first data on abundance and production of pelagic bacteria in representative areas of the continental shelf of the Bay of Biscay. Our results are within the range of values available for nearby areas in the northern and north-western Iberian Peninsula, especially with those from the Galician upwelling (Table 2). The large range of values reported for the País Vasco Coast (south-eastern Bay of Biscay) may be due to the fact that those are samples from a shallow and relatively eutrophic coastal environment which is not affected by the upwelling. In our study, average bacterial growth rates exhibited a quite narrow range, close to the lower limit of the values available for the S Bay of Biscay (Table 2), implying doubling times of the bacterial carbon from 0.8 to 2.7 days. However, these are preliminary estimates and more measurements are required to determine bacterial importance in various upwelling stages of this ecosystem.

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## REFERENCES

- Anadón R., E. Fernández, A. Botas, A. Bode, P. Serret, J.L. Acuña, J. Cabal, J. Sostres and F. Alvarez-Marqués. – 1991. Datos básicos de la campaña 'ASFLOR I'. *BIOBAS Rev. Biol. Univ. Oviedo*, 5: 1-36.
- Bak R.P.M. and G. Nieuwland. – 1993. Patterns in pelagic and benthic nanoflagellate densities in the coastal upwelling system along the Banc d'Arguin, Mauritania. *Hydrobiol.*, 258: 119-131.
- Barcina Y., B. Ayo, M. Unanue, L. Egea and J. Iriberry. – 1992. Comparison of rates of flagellate bacterivory and bacterial production in a marine coastal system. *Appl. Environ. Microbiol.*, 58: 3850-3856.
- Blanton J.O., F.F. Atkinson, F.F. Castillejo and A. Lavín. – 1982. Coastal upwelling off the Rías Bajas, Galicia, NW Spain. I. Hydrographic studies. Rapports et Process-verbaux Réunion Conseil International pour l'Exploration de la Mer, 183: 79-90.
- Bode A. and E. Fernández. – 1992 a. Influence of water-column stability on phytoplankton size and biomass succession patterns in the central Cantabrian Sea (Bay of Biscay). *J. Plankton Res.*, 14: 885-902.
- Bode A. and E. Fernández. – 1992 b. Variability of biochemical composition and size distributions of seston in the euphotic zone of the Bay of Biscay: implications for microplankton trophic structure. *Mar. Biol.*, 114: 147-155.
- Bode A., B. Casas and M. Varela. – 1994 a. Size-fractionated primary productivity and biomass in the Galician shelf (NW Spain): Netplankton versus nanoplankton dominance. *Sci. Mar.*, 58: 131-141.
- Bode A., B. Casas, E. Fernández, E. Marañón, P. Serret and M. Varela. – 1996. Phytoplankton biomass and production in shelf waters off NW Spain: spatial and seasonal variability in relation to upwelling. *Hydrobiol.*, 341: 225-234.
- Bode, A., M. Varela, E. Fernández, B. Arbones, N. González, R. Carballo, M.T. Alvarez-Ossorio, R. Anadón and S. Barquero. – 1994 b. Biological characteristics of the plankton associated to a shelf-break front off the Galician Coast. *Gaia*, 8: 9-18.
- Botas J.A., E. Fernández, A. Bode and R. Anadón. – 1990. A persistent upwelling off the Central Cantabrian Coast (Bay of Biscay). *Estuar. Coast. Shelf Sci.*, 30: 185-199.
- Botas J.A., E. Fernández, A. Bode, R. Anadón and E. Anadón. – 1989. Datos básicos de campañas COFACE. I. Hidrografía, nutrientes, fitoplancton y seston en el Cantábrico Central. *BIOBAS Rev. Biol. Univ. Oviedo*, 1: 1-80.
- Bratbak, G. – 1985. Bacterial biovolume and biomass estimations. *Appl. Environ. Microbiol.*, 1488-1493.
- Caron D.A., E.L. Lim, G. Miceli, J.B. Waterbury and F.W. Valois. – 1991. Grazing and utilization of chroococoid cyanobacteria and heterotrophic bacteria by protozoa in laboratory cultures and a coastal plankton community. *Mar. Ecol. Prog. Ser.*, 76: 205-217.
- Casas B., M. Varela, M. Canle, N. González and A. Bode. – 1997. Seasonal variations of nutrients, seston and phytoplankton, and upwelling intensity off La Coruña (NW Spain). *Estuar. Coast. Shelf Sci.*, 44.
- Castro C.G., F.F. Pérez, X.A. Álvarez-Salgado, G. Rosón and A.F. Ríos. – 1994. Hydrographic conditions associated with the relaxation of an upwelling event off the Galician coast (NW Spain). *J. Geophys. Res.*, 99: 5135-5147.
- Cho B.C. and F. Azam. – 1990. Biogeochemical significance of bacterial biomass in the oceanic euphotic zone. *Mar. Ecol. Prog. Ser.*, 63: 253-259.
- Dickson R.R., P.A. Gurbutt and V.N. Pillai. – 1980. Satellite evidence of enhanced upwelling along the European continental slope. *J. Phys. Oceanogr.*, 10: 813-819.
- Fernández E. and A. Bode. – 1991. Seasonal patterns of primary production in the Central Cantabrian Sea (Bay of Biscay). *Sci. Mar.*, 55: 629-636.
- Fernández E. and A. Bode. – 1994. Succession of phytoplankton assemblages in relation to the hydrography in the southern Bay of Biscay: a multivariate approach. *Sci. Mar.*, 58: 191-205.
- Fernández E., Madariaga Y. and P. Serret. – 1991. Photosynthate partitioning by natural phytoplankton populations in a shallow coastal front. *Sci. Mar.*, 55: 599-604.
- Fraga F. – 1981. *Upwelling off the Galician coast, Northwest Spain*. In: F.A. Richards (ed.): Coastal Upwelling, Coastal Estuarine Sci., 1, pp. 176-182. AGU, Washington, D. C.
- Fuhrman J. and F. Azam. – 1982. Thymidine incorporation as a measure of heterotrophic bacterioplankton production in marine surface waters: evaluation and field results. *Mar. Biol.*, 66: 109-120.
- Fuhrman, J.A., J.W. Ammerman and F. Azam. – 1980. Bacterioplankton in the coastal euphotic zone: distribution, activity and possible relationships with phytoplankton. *Mar. Biol.*, 60: 201-207.
- Hanson R.B., M.T. Álvarez-Ossorio, R. Cal, M.J. Campos, M. Roman, G. Santiago, M. Varela and J.A. Yoder. – 1986. Plankton response following a spring upwelling event in the Ría de Arosa, Spain. *Mar. Ecol. Prog. Ser.*, 32: 101-113.
- Iriberry J., M. Unanue, B. Ayo, I. Barcina and L. Egea. – 1990. Bacterial production and growth rate estimation from [3H] thymidine incorporation for attached and free-living bacteria in aquatic systems. *Appl. Environ. Microbiol.*, 56: 483-487.
- Iriberry J., M. Unanue, I. Barcina and L. Egea. – 1987. Seasonal variation in population density and heterotrophic activity of attached and free-living bacteria in coastal waters. *Appl. Environ. Microbiol.*, 53: 2308-2314.
- Kuosa H. – 1990. Protozoan grazing on pico- and nanophytoplankton in the northern Baltic Sea: direct evidence from epifluorescence microscopy. *Arch. Hydrobiol.*, 119: 257-265.
- Li W.K.W., P.M. Dickie, W.G. Harrison and B.D. Irwin. – 1993. Biomass and production of bacteria and phytoplankton during the spring bloom in the western North Atlantic Ocean. *Deep-Sea Res.*, 40: 307-327.
- Linley E.A.S., R.C. Newell and M.Y. Lucas. – 1983. Quantitative relationships between phytoplankton, bacteria and heterotrophic microflagellates in shelf waters. *Mar. Ecol. Prog. Ser.*, 12: 77-89.
- Marañón E. and E. Fernández. – 1995. Changes in phytoplankton ecophysiology across a coastal upwelling front. *J. Plankton Res.*, 17: 1999-2008.
- Marañón E., E. Fernández and R. Anadón. – 1995. Patterns of macromolecular synthesis by natural phytoplankton assemblages under changing upwelling regimes: in situ observations and microcosm experiments. *J. Exp. Mar. Biol. Ecol.*, 188: 1-28.
- Olson R.J., S.W. Chisholm, E.R. Zettler and E. Virginia Armbrust. – 1990. Pigments, size, and distribution of *Synechococcus* in the North Atlantic and Pacific Oceans. *Limnol. Oceanogr.*, 35: 45-58.
- Parsons T.R., Y. Maita and C.M. Lalli (eds.). – 1984. *A manual of chemical and biological methods for seawater analysis*, 173 pp. Pergamon Press, Oxford.
- Porter K.G. and Y.S. Feig. – 1980. The use of DAPI for identifying and counting aquatic microflora. *Limnol. Oceanogr.*, 25: 943-948.
- Simon, M and F. Azam. – 1989. Protein content and protein synthesis rates of planktonic marine bacteria. *Mar. Ecol. Prog. Ser.*, 51: 201-213.
- Sorokin Y.I. – 1981. Microheterotrophic organisms in marine ecosystems. In: A.R. Longhurst (ed.): Analysis of marine ecosystems, pp. 293-342. Academic Press, London.
- Sorokin Y.I. and J.E. Kogelschatz. – 1979. Analysis of heterotrophic microplankton in an upwelling area. *Hydrobiol.*, 66: 195-209.
- Tenore K.R., M. Alonso-Noval, M. Álvarez-Ossorio, L.P. Atkinson, J.M. Cabanas, R.M. Cal, H.J. Campos, F. Castillejo, E.J. Chesney, R.B. González, R.B. Hanson, C.R. McClain, A. Miranda, M.R. Roman, J. Sánchez, G. Santiago, L. Valdés, M. Varela and J. Yoder. – 1995. Fisheries and oceanography off Galicia, NW Spain: mesoscale spatial and temporal changes in physical processes and resultant patterns of biological productivity. *J. Geophys. Res.*, 100: 10943-10966.
- Unanue M., B. Ayo, I. Az a, I. Barcina and J. Iriberry. – 1992. Temporal variability of attached and free-living bacteria in coastal waters. *Microb. Ecol.*, 23: 27-39.
- Varela M., G. Díaz del Río, M.T. Álvarez-Ossorio and E. Costas. – 1991. Factors controlling phytoplankton size class distribution in the upwelling area of the Galician continental shelf (NW Spain). *Sci. Mar.*, 55: 505-518.
- Yentsch C.S. and D.W. Menzel. – 1963. A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. *Deep-Sea Res.*, 10: 221-231.

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