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Pelagic bacteria and phytoplankton in oceanic waters near the Canary Islands in summer

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ABSTRACT: Bacterial abundance, biomass and heterotrophic activity along with hydrographic and phytoplankton variables were measured in waters surrounding the Canary Islands during Cruise BIOCAN-98 in September 1998. Three distinct oceanographic zones, defined using temperature and phytoplankton biomass concentrations, were studied. Zone A, located NW of La Palma Island, was characterized by the presence of alternating cold and warm eddies, and generally low phytoplankton biomass. Zone B was located beween La Palma and Tenerife islands and showed a predominance of cold-core eddies and higher phytoplankton concentrations than Zone A. All stations occupied in the eastern part of the Canary Islands were grouped in Zone C and were characterized by relatively low surface temperature (<22°C) and high phytoplankton biomass. The vertical structure of the upper water column in these zones was indicative of relatively low mixing in stations of Zones A and B, while stations of Zone C displayed characteristics of frequent mixing events. Phytoplankton biomass showed deep relative maxima between 40 and 100 m at all stations. These maxima were shallower and more marked at stations with colder waters near the surface. Coccoid cyanobacteria were significantly correlated with chlorophyll *a* and reached abundances of up to 10^4 cells ml^{-1} in subsurface maxima. Heterotrophic bacteria were generally more abundant near the surface, and varied between 1.1 and 5.9×10^5 cells ml^{-1} in the upper 100 m. Bacterial abundance between 100 and 300 m was approximately constant. Bacterial production, estimated by leucine incorporation, was not correlated with bacterial abundance or chlorophyll *a*, and displayed relative maxima between 80 and 90 m depth but also near the surface. There were no significant differences in mean values of abundance of cyanobacteria and heterotrophic bacteria between the oceanographic zones considered, but bacterial production and growth rates were significantly higher in Zone B. Using empirical conversion factors determined during the study, we estimated bacterial production values integrated in the upper 100 m that varied between 15 and 289 mg C m^{-2} d^{-1}, with population generation times between 2 and 25 d. Taking into account phytoplankton biomass and primary production values, our results suggest that pelagic bacteria are able to consume dissolved organic carbon in excess of the amount produced *in situ* by phytoplankton in the upper surface waters of this region.

KEY WORDS: Bacterial production · Bacterial abundance · Phytoplankton biomass · Primary production · Central Eastern Atlantic

INTRODUCTION

Pelagic bacteria are a major component of biomass in oceanic oligotrophic systems (Cho & Azam 1990, Binder et al. 1996, Carlson et al. 1996). Heterotrophic bacteria represent a major pathway for the flux of dissolved organic matter (Cho & Azam 1988, Cole et al. 1988, Simon et al. 1992, Ducklow 1993, Carlson et al. 1996), while coccoid cyanobacteria may account for an important fraction of nanophytoplankton biomass (Li 1995, Binder et al. 1996). The production of heterotrophic bacteria in aquatic systems is related generally to

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phytoplankton biomass and primary production (Cole et al. 1988, White et al. 1991). Earlier studies suggested that roughly half of particulate primary production was processed by bacteria (e.g. Cole et al. 1988), but now the large variability in the degree of coupling between bacterial and phytoplankton productivity in different oceanic systems is well documented (Simon et al. 1992, Ducklow 1993, Li et al. 1993, Carlson et al. 1996, Head et al. 1996, Jones et al. 1996, Barquero et al. 1998, Gasol et al. 1998). Bacteria take up dissolved organic substrates that are known to form a substantial fraction of dissolved carbon in the ocean surface waters, and are thereby expected to play a major role in the biogeochemistry of the upper ocean (Toggweiler 1989). Recent studies indicate that bacteria of oligotrophic ocean areas may consume dissolved organic carbon in excess of primary production, producing imbalances in the carbon budgets of these areas (del Giorgio et al. 1997, Duarte & Agustí 1998). Bacteria from oligotrophic regions (Carlson & Ducklow 1996, Gasol et al. 1998) display lower conversion efficiencies of the consumed dissolved carbon than bacteria from coastal and eutrophic regions (Kroer 1993, Gasol et al. 1998), suggesting major losses of organic carbon through bacterial respiration in oligotrophic areas. However, whether there are extra sources of the required dissolved organic matter to fuel bacterial metabolism or simply periods when primary production and respiration are uncoupled in open-ocean waters is still a matter of debate (Kirchman 1997, Williams 1998).

The eastern Atlantic waters around the Canary Islands display characteristics of oligotrophic systems. A seasonal thermocline at depths from 50 to 120 m separates low-nutrient low-chlorophyll surface waters from deep nutrient-rich waters for most of the year (de León & Braun 1973, Braun et al. 1976, 1990, Braun 1980, Braun & Real 1984, 1986). Consequently, phytoplankton biomass and primary production are low except for a short bloom after winter mixing (de León & Braun 1973, Braun 1980). Local examples of relatively productive areas near the islands have been reported (Real et al. 1981, Braun & Real 1984, Arístegui et al. 1989, Fernández de Puelles & Braun 1989, Arístegui 1990, Ojeda 1996). In addition, several types of mesoscale eddies have been related to nutrient enrichment in the surface layer or to the transport of phytoplankton-rich patches from the nearby upwelling in the African shelf, causing local accumulations of phytoplankton (Arístegui et al. 1997). Wind stress and flow perturbations of the Canary current caused by the islands are the main mechanisms involved in the formation of these eddies (Arístegui et al. 1989, 1994, 1997).

Phytoplankton biomass was not related to zooplankton abundance or biomass during the relatively short productive periods in these waters (Fernández de Puelles & Braun 1989), although significant positive correlations between chlorophyll and zooplankton biomass suggested an effective grazing control for most of the stratified period (Arístegui 1990). Estimations of zooplankton grazing rates suggested that zooplankton could account for more than 90% of daily particulate primary production (Braun 1974, 1981, Fernández de Puelles & Braun 1996). Also, Hernández-León (1986) and Hernández-León & Torres (1997) reported a significant role of zooplankton in the remineralization of particulate organic matter in Canarian waters. On the other hand, there are indications that bacteria and microheterotrophs may be significant contributors to carbon fluxes in this region. Ballesteros (1994) showed than mean bacterial abundances varied seasonally between 2.4 and 7.7×10^5 cells ml^{-1}, while bacterial biomass greatly exceeded phytoplankton biomass during summer. As in other oceanic environments, small phytoplankton cells (<10 µm) account for a large fraction of phytoplankton biomass and production (Braun & Real 1981, Braun et al. 1985), but there are few measurements of picophytoplankton biomass in this area (Li 1995, Head et al. 1996, Zubkov et al. 1998). The relatively high zooplankton grazing rates may be associated with the release of dissolved organic matter from phytoplankton (Jumars et al. 1989). Such dissolved materials may be taken up by bacteria and other microheterotrophs. Arístegui & Montero (1995) measured relatively high respiration rates in planktonic microbial communities compared to those of zooplankton of the region (Hernández-León 1987, 1988, Hernández-León & Miranda-Rodal 1987), which suggests that bacteria may account for a significant fraction of the total oxygen consumption and carbon flow. As far as we know, there are no available measurements of bacterial production in oceanic waters around the Canary Islands to test this hypothesis, since there is but limited information on pelagic bacteria in the region (Ballesteros 1994, Li 1995, Head et al. 1996).

In this study we describe bacterioplankton abundance, biomass and production values measured in different oceanographic zones around the Canary Islands in September 1998. These measurements are related to phytoplankton composition, biomass and primary production values to obtain estimates of the importance of bacterioplankton in carbon cycling in the upper layer of this region of the Atlantic Ocean.

MATERIALS AND METHODS

Water-column temperature, salinity and fluorescence were recorded at 156 stations around the Canary Islands during the BIOCAN-98 cruise in September 1998 (Fig. 1). A CTD Mark-III probe with fluo-

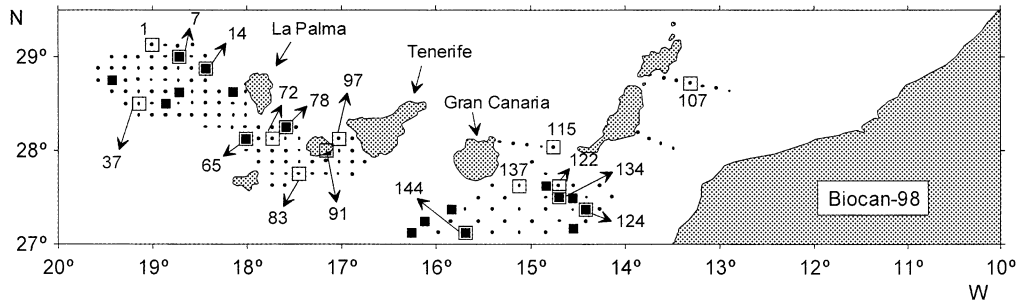

Fig. 1. Map of sampling stations during BIOCAN-98 cruise. Dots: CTD stations; numbered open squares: stations where bacterial samples were collected; black squares: stations were phytoplankton samples were collected and primary production was measured

rometer attached to a 12 l Niskin-bottle rosette was employed. Water, phytoplankton and bacteria samples were collected at 5 to 9 depths between the surface and 300 m depth at 17 stations (Fig. 1). Water-column stratification for each plankton station was determined using the depths of the main discontinuities of σ_t profiles in the upper 100 m. Three water layers (p1, p2 and p3) were revealed, corresponding to differences in σ_t values >0.02 at 1 m depth intervals.

Chlorophyll *a* concentration (chl *a*) was determined by the spectrophotometric method (Parsons et al. 1984) in acetone extracts of phytoplankton collected after filtration of up to 4 l of water onto Whatman GF/F filters at selected stations (Fig. 1). The measured chlorophyll values were used to calibrate the fluorescence measured by the fluorometer of the CTD (Fig. 2). Primary production rates (PP) were measured in 125 ml of water from 5 depths at selected stations which were inoculated with 4 µCi (148 kBq) $NaH^{14}CO_3$ and incubated on board at surface-water temperature for up to 4 h at midday. The irradiance equivalent to the original depth of the samples was simulated using a neutral density screen. Two light bottles and one dark bottle from each depth were incubated. Incubations were terminated by filtration onto Whatman GF/F filters. The filters were then treated with 5% HCl, scintillation cocktail was added, and radioactivity was then counted using a liquid scintillation counter.

Eukaryotic phytoplankton species (>8 µm) were identified in Lugol-preserved samples under an inverted microscope. The abundance of coccoid cyanobacteria (CB) and heterotrophic bacteria (HB) was determined in samples preserved with glutaraldehyde (5% final concentration) using the method of Porter & Feig (1980). Ten millilitres of each sample were filtered on board ship onto 0.2 µm black, polycarbonate, membrane filters and stained with DAPI (4′-6-diamidino-2-phenylindole) for 5 min. The filters were mounted with low-fluorescence oil on microscope slides and stored frozen. Bacteria were counted using ultraviolet light in an epifluorescence microscope (Olympus BH-2). Cyanobacteria were counted in the same slides observed under blue light and were distinguished from heterotrophic bacteria by their emission of yellow-orange autofluorescence. Bacterial cellular carbon was estimated from biovolumes using the empirical equation of Norland et al. (1987) for bacteria ranging from 0.001 to 0.5 µm^3:

$$C = 0.09\ BV^{0.9}$$

where C is the carbon content (pg C cell^{-1}) and BV is the bacterial biovolume (µm^3 cell^{-1}). Bacterial biovolumes were computed from measurements of bacterial dimensions using a graduated bar coupled to the microscope eyepiece. Cocci were considered as spheres and rods as cylinders. The mean biovolume of bacteria in this study was 0.16 (±0.25 SD) µm^3 cell^{-1} (n = 587), and the resulting carbon content was 17 (±26 SD) fg C cell^{-1}.

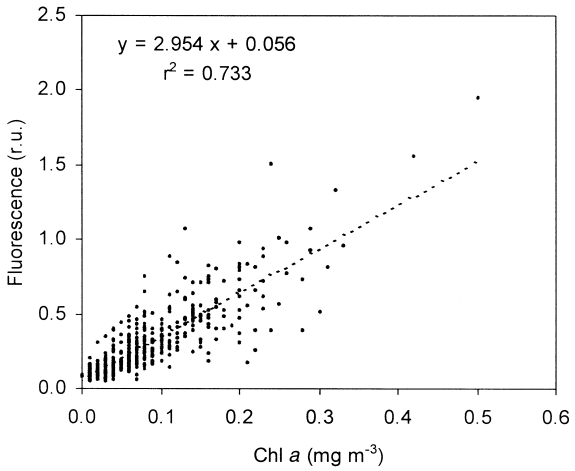

Fig. 2. Relationship between *in situ* fluorescence (r.u. = relative units) measured with fluorometer attached to the rosette and chl *a* concentration determined in acetone extracts. Coefficients of the regression line and determination coefficient (r^2) are indicated

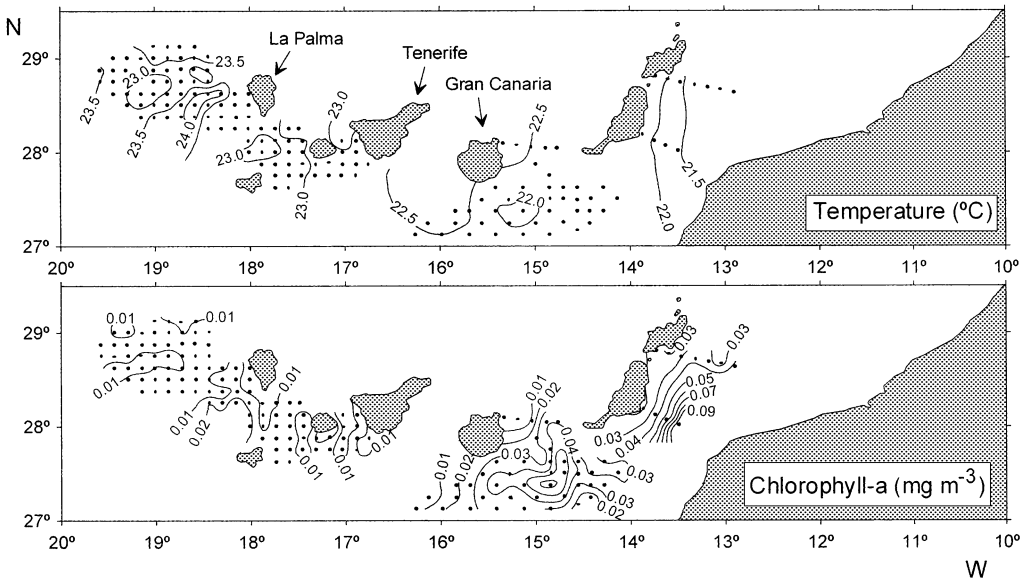

Fig. 3. Distribution of surface temperature and chl *a* concentration in the study area

Production of heterotrophic bacteria (PBact) was estimated by ^{3}H-leucine incorporation, using the method described by Kirchman (1993), substituting the final filtration of bacteria by centrifugation (Smith & Azam 1992). Four 1 ml aliquots of water samples from each depth were inoculated with ^{3}H-leucine to a final concentration of 150 nM and incubated for 30 min on board ship in 1.5 ml Eppendorf vials at a temperature equivalent to that of the surface water temperature (mean ± SD = 23.8 ± 3.3°C, n = 15). In addition, two 1 ml controls killed with trichloroacetic acid (TCA, 5% w/v final concentration) were incubated for each depth. Incubations were terminated by the addition of 5% TCA to the incubation vials. Dissolved leucine was removed from the incubation vials by repeated washing with 5% TCA and successive centrifugation (12 000 rpm, 10 min). Scintillation cocktail (Ultima X-Gold, Packard) was added to the vials and radioactivity was measured in a liquid scintillation counter. The mean (± SD) coefficient of variation of the radioactivity measurements between the 4 replicates for each sample was 16 ± 7% (n = 76 samples). The conversion factors between leucine incorporation and cell growth or carbon production were determined experimentally on board at 5 stations by the procedures indicated in Bjørnsen & Kuparinen (1991) and Kirchman & Ducklow (1993). For each experiment, 200 ml of surface water were diluted in 1000 ml of 0.2 µm filtered seawater and incubated at room temperature for 32 h. Every 4 h, aliquots of this culture were removed for the determination of bacterial abundance and leucine incorporation rates by the described procedures.

RESULTS

Oceanographic zones and phytoplankton

Surface temperature and chlorophyll *a* concentrations allowed the distinction of 3 main zones in the study area (Fig. 3). Zone A, located to the west of La Palma Island in the NW part of the Canarian Archipel-

Table 1. Mean (±SD) surface chlorophyll *a* concentration (chl *a*, mg m^{-3}), depth-integrated chl *a* (0 to 100 m and 0 to 150 m depth, mg m^{-2}) and primary production (0 to 100 m depth, PP, mg m^{-2} h^{-1}). n: number of samples. SNK: means with different letters are significantly different at $p < 0.05$ level (Student-Newman-Keuls test)

Zone	Surface chl *a*			100 m-integrated chl *a*			150 m-integrated chl *a*			100 m-integrated PP		
	Mean ± SD	(n)	SNK	Mean ± SD	n	SNK	Mean ± SD	n	SNK	Mean ± SD	n	SNK
A	0.02 ± 0.01	(20)	a	6.1 ± 1.2	(20)	a	7.9 ± 1.7	(20)	a	26.2 ± 34.2	(6)	a
B	0.04 ± 0.01	(9)	b	7.8 ± 1.4	(9)	a	9.8 ± 1.4	(9)	b	17.8 ± 3.0	(3)	a
C	0.05 ± 0.02	(36)	b	10.4 ± 3.1	(36)	b	11.3 ± 2.7	(36)	b	28.2 ± 11.2	(9)	b
Total	0.04 ± 0.02	(65)		8.7 ± 3.1	(64)		10.0 ± 2.7	(65)		25.8 ± 20.4	(18)	

ago, was characterised by the presence of mesoscale eddies of alternating cold and warm cores. Chlorophyll concentrations at the surface were patchy but never reached 0.02 mg m^{-3}. Zone B was located between La Palma and Tenerife islands and also contained cold-core eddies, but surface chlorophyll values were generally higher than in Zone A. Finally, all stations sampled in the eastern part of the archipelago were grouped in Zone C, characterised by cold surface waters and chlorophyll concentrations generally exceeding 0.02 mg m^{-3} (Fig. 3). These characteristics of the surface waters were indicative of differences in water-column properties between zones. Surface chlorophyll was significantly correlated with water-column integrated chlorophyll, either in the upper 100 m layer ($r = 0.605$, $n = 65$, $p < 0.01$) or in the 0 to 150 m layer ($r = 0.472$, $n = 65$, $p < 0.01$). Significant differences also existed in water-column-integrated chl *a* and PP values between zones (Table 1). Zones A and B had equivalent mean values of either chl *a* or PP for the upper 100 m layer, whereas zones B and C had non-significant differences in the values of either chl *a* at the surface or integrated in the 0 to 150 m layer.

Vertical profiles of temperature and chl *a*, the latter estimated by conversion of the measurements of the CTD fluorometer, also showed differences between zones (Fig. 4). A well-mixed surface layer reaching to ca 40 m depth was well developed in the stations of Zone A, as evidenced by temperature profiles. A seasonal thermocline was marked at some stations (e.g. Stn 37) but was less so at others (e.g. Stn 1), indicating frequent mixing events in the upper 100 m at the latter stations. The variability in the temperature profiles of the stations in Zone A was also reflected by the differences in values measured at either the surface or 100 m depth of the end-member stations (e.g. Stns 1 & 37). Deep chlorophyll maxima of similar magnitude developed at all stations in this zone between 60 and 100 m depth, and their position in the water-column was closer to the surface at stations with colder temperatures (Fig. 4). Temperature profiles for the stations of Zone B were more homogeneous than for Zone A; however, no clear signal of the seasonal thermocline was found, except for Stn 72, which

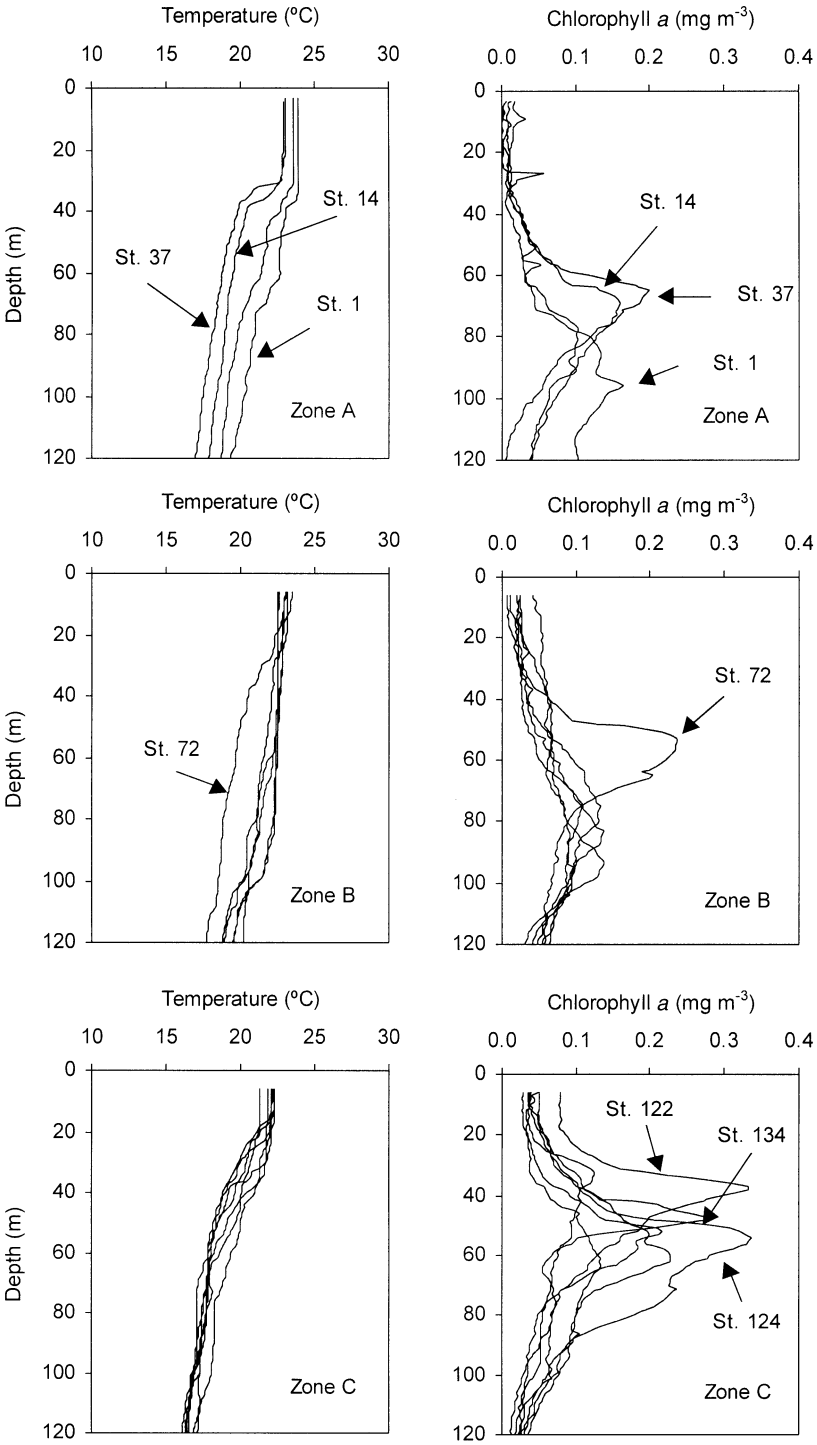

Fig. 4. Vertical profiles of temperature and chl *a* at stations where bacterial samples were collected grouped by characteristic oceanographic zones (see 'Results' for description)

showed the lowest subsurface temperature values. As in Zone A, the largest and shallowest deep chlorophyll maximum was related to the coldest temperatures (Stn 72). In contrast, stations in Zone C showed less extreme variations in temperature profiles, being characterised by a shallow upper mixing layer and a subsurface layer with weak thermoclines. The deep chlorophyll maxima, located between 35 and 60 m depth, were well marked in this zone, reaching the maximum absolute values of all stations studied.

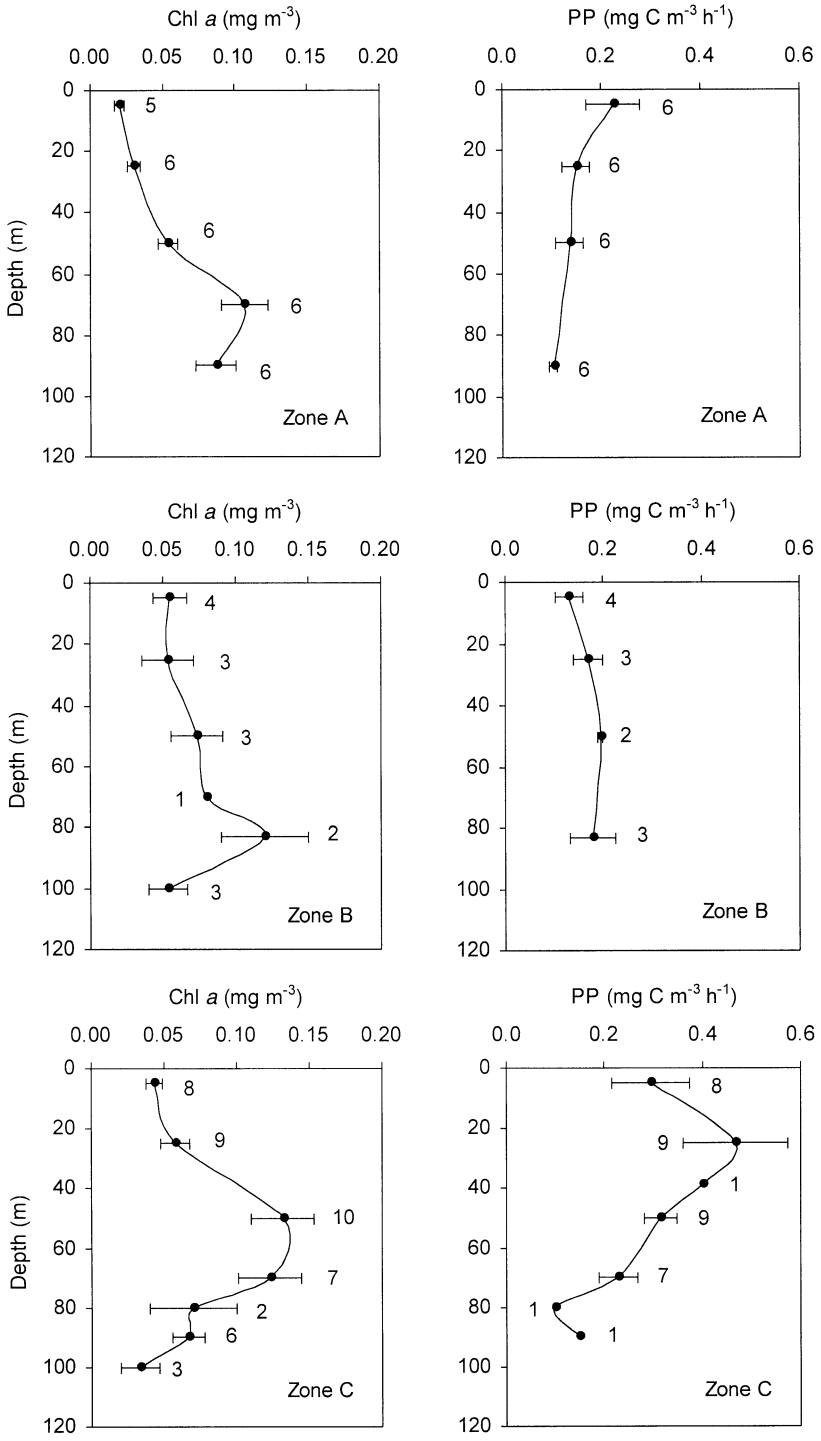

Fig. 5. Vertical profiles (means ±SE) of chl *a* concentration, measured from acetone extracts, and primary production (PP) in the selected oceanographic zones. Number of samples averaged for each depth is indicated

Despite the deep maximum concentration of chl *a* in all zones, primary production was generally higher at the surface (Zone A) or above the chlorophyll maximum (Fig. 5). The average depth of the production maximum was 50 m in Zone B and 25 m in Zone C. Mean maximum values were higher in Zone C, where they almost doubled those of Zones A and B. Production rates measured below the deep chlorophyll maximum were >0.2 mg C m^{-3} h^{-1}.

The dominant phytoplankton species determined in all zones were dinoflagellates, particularly small forms (Table 2), which attained densities of up to 73 cells ml^{-1}. In contrast, diatoms rarely exceeded 1 cell ml^{-1} in the samples studied, they reached maximum abundances in Zone C (9 cells ml^{-1}). Abundance of large and medium-sized flagellates (8 to 10 µm) were generally >5 cells ml^{-1} throughout the area.

Pelagic bacteria

Coccoid cyanobacteria ranged from ca. 0.1 to 9.4×10^3 cells ml^{-1}. Their vertical distribution displayed maximum values in subsurface layers: at 50 and 90 m in Zone A, at 70 m in Zone B, and between 40 and 60 m in Zone C (Fig. 6). Abundance values of heterotrophic bacteria ranged from 1 to 5.9×10^5 cells ml^{-1} in the upper 100 m, and mean abundance decreased with increasing depth. Zone C displayed higher mean values of HB in the upper 60 m compared to stations in other zones. Bacterial production (not measured in Zone A) showed similar vertical profiles to those of HB; maximum values generally occurred at depth (90 m in Zone B and between 60 and 80 m in Zone C), although a

Table 2. Mean (±SD) abundance (cells ml^{-1}) of the main phytoplankton species and groups in a total of 33 samples examined. %: percent of samples in which the species or group appeared. –: absent

Species or group	%	Zone A		Zone B		Zone C	
		Mean	SD	Mean	SD	Mean	SD
Dinophyceae	91	3.1	11.4	2.3	7.8	3.8	20.6
Pronoctiluca acuta (Lohmann) Schiller	15	0.3	–	0.1	–	0.2	0.0
Oxytoxum cf. *longiceps* Schiller	21	–	–	0.2	0.1	0.4	0.1
Oxytoxum sp.	21	0.6	0.1	0.8	0.6	1.5	0.7
Torodinium robustum Kofoid & Swezy	24	0.3	0.2	0.2	0.0	0.2	0.0
Gyrodinium glaucum (Lebour) Kofoid & Swezy	27	0.6	0.4	0.3	0.0	0.2	0.1
Oxytoxum gracile Schiller	30	1.0	0.5	0.9	0.2	1.0	0.6
Cachonina hallii Freudentahl & Lee	45	4.3	3.1	2.8	–	4.1	3.4
Gyrodinium spirale (Bergh) Kofoid & Swezy	58	0.3	0.1	0.4	0.4	0.3	0.2
Dinoflagellates >30 µm	73	0.3	0.2	0.4	0.1	0.3	0.1
Dinoflagellates <30 µm	100	22.2	10.9	19.3	7.7	32.9	20.3
Other dinoflagellates	100	1.0	1.0	0.5	0.7	0.6	0.8
Diatomophyceae	100	0.4	0.7	0.3	0.4	0.7	1.8
Leptocylindrus danicus Cleve	515	0.4	–	–	–	1.1	0.8
Rhizosolenia setigera Brightwell	15	–	–	–	–	0.2	0.0
Pseudonitzschia subcurvata (Hasle) Fryxell	18	0.2	–	0.2	–	0.3	0.2
Rhizosolenia fragilissima Bergon	18	0.4	–	–	–	1.1	0.8
Pennate diatoms <30 µm	21	0.4	0.3	0.4	0.2	0.2	–
Nitzschia longissima (Brébisson) Grunow	24	–	–	0.2	–	0.8	0.9
Pennate diatoms >30 µm	36	0.5	0.3	0.2	0.0	0.5	0.4
Pseudonitzschia sp.	42	0.4	0.3	0.4	0.2	1.2	0.8
Other diatoms	100	0.5	0.6	0.3	0.3	0.6	0.6
Cryptophyceae	67	3.5	2.4	1.8	1.2	5.6	6.1
Other groups	100	0.8	1.5	0.2	0.5	0.7	1.6
Unidentified flagellates (8–10 µm)	88	6.5	3.6	5.5	3.2	9.5	7.4

secondary maximum also appeared at the surface (Fig. 6). However, it is difficult to determine a consistent pattern of variation with depth in our observations because of the small number of samples available for some depths.

No significant differences were found between mean values of either CB, HB or PBact in each zone (Kruskal-Wallis test, $p > 0.05$, n = 57 for CB, n = 82 for HB, n = 63 for PBact). However, mean values of bacterial production normalized to bacterial abundance in Zones B ($12.9 \pm 12.1 \times 10^{-2}$ amol leu $cell^{-1}$ h^{-1}, mean ± SD, n = 37) and C ($7.5 \pm 8.6 \times 10^{-2}$ amol leu $cell^{-1}$ h^{-1}, mean ± SD, n = 26) were significantly different (Mann-Whitney *U*-test, $p < 0.01$, n = 63). Bacterial abundance decreased below 100 m, with little variation down to 300 m (Fig. 7). Values were generally near 10^5 cells ml^{-1}, except for Stn 83, where concentrations near 3×10^5 were found between 100 and 300 m. Bacterial production also decreased below 100 m at most of the studied stations. The exception was again Stn 83, in which production values increased from ca 10 pmol leu l^{-1} h^{-1} at 100 m to 50 pmol leu l^{-1} h^{-1} at 300 m (Fig. 7).

Considering all observations, CB was significantly correlated to chl *a* ($r = 0.677$, n = 64, $p < 0.001$) and to HB ($r = 0.328$, n = 58, $p < 0.05$) but not to temperature. However, these correlations accounted for less than 50% of the variance of CB. In contrast, HB was not significantly correlated to either chl *a*, Pbact or temperature. The mean depth of maximum values in the vertical profiles of bacterial and phytoplankton variables was related to water-column stratification (Fig. 8). All biological maxima considered were significantly above the seasonal pycnocline near 95 m (Table 3). Maximum values of CB appeared significantly below maximum HB and the limit of the upper mixing layer. The HB maximum occurred significantly above maximum chl *a* and the intermediate pycnocline. Other significant differences between the mean depth of maximum values displayed in Fig. 8 were those for chl *a* and PP, the former occurring significantly below the upper mixing layer and maximum PP.

Carbon budgets

Leucine incorporation by bacteria was converted to carbon production using the empirical conversion factors measured at some stations (Table 4). The conversion factors computed by the procedure described in Kirchman & Ducklow (1993) were not significantly different (Wilcoxon test, $p > 0.05$, n = 5) from those com-

puted by the procedure of Bjørnsen & Kuparinen (1991). Leucine-to-carbon conversion factors computed for stations in Zone B were significantly higher than those for stations in Zone C (Wilcoxon test, $p > 0.05$, $n = 5$); therefore, the mean value of the carbon conversion factor estimated by the method of Bjørnsen & Kuparinen (1991) for each zone was employed to obtain bacterial carbon production estimates.

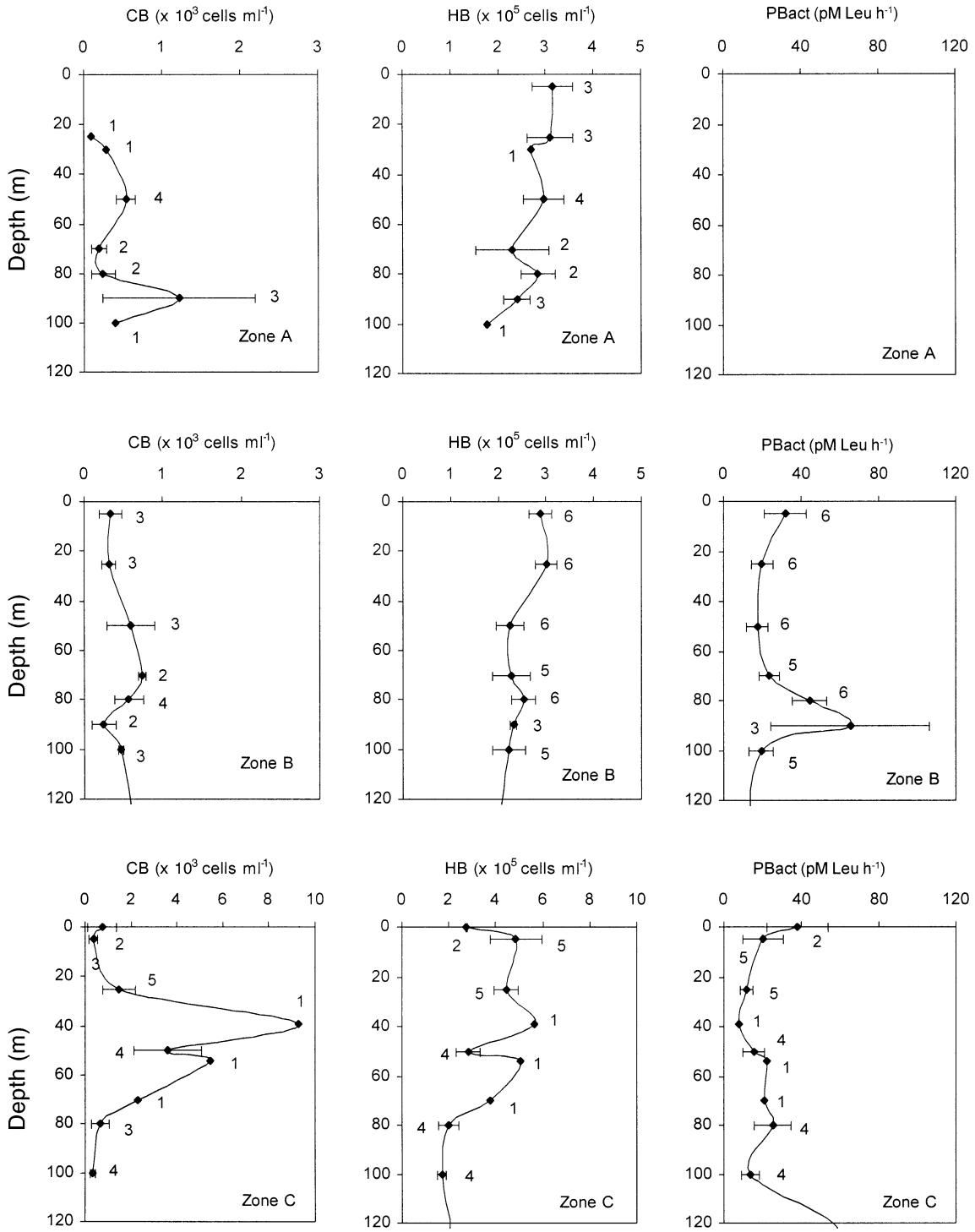

Fig. 6. Vertical profiles (means ±SE) of abundance of cyanobacteria (CB) and heterotrophic bacteria (HB), and of leucine incorporation (PBact, pM leu) in the upper 100 m of the selected oceanographic zones. Number of samples averaged for each depth is indicated. PBact was not determined in Zone A

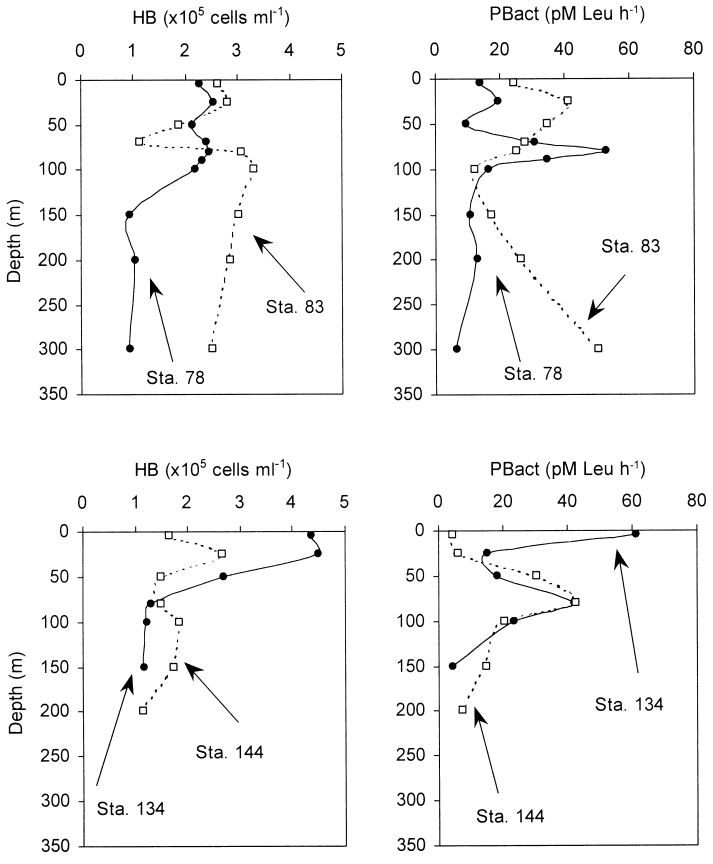

Fig. 7. Examples of vertical distribution of heterotrophic bacteria (HB) and leucine incorporation (PBact, pM leu) between the surface and 300 m depth at selected stations

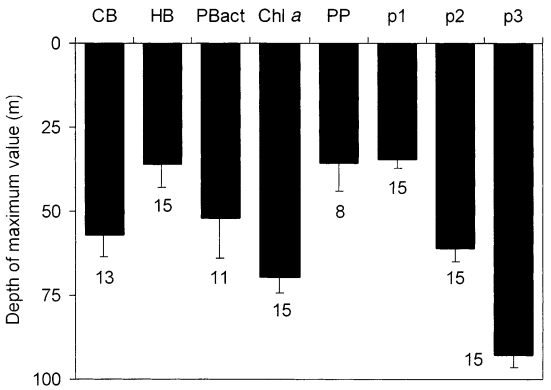

Fig. 8. Mean depth (±SE) of the maximum value of bacterial, phytoplankton and water-column stratification variables (see 'Results') in the 0 to 100 m layer. p1, p2 and p3: depths of surface upper mixing layers (see 'Materials and methods'). Number of samples averaged is indicated below each bar

Water-column integrated bacterial biomass ranged from 291 to 731 mg C m^{-2} (Table 5). No significant differences between mean values of integrated bacterial biomass for each zone were found (Kruskal-Wallis test, $p > 0.05$, $n = 15$), but maximum and minimum values occurred in stations of Zone C. Integrated bacterial carbon production varied between 0.6 and 12 mg C m^{-2} h^{-1} (15 and 289 mg C m^{-2} d^{-1}). In this case, mean values of bacterial production in Zones B and C were significantly different (Mann-Whitney *U*-test, $p < 0.01$, $n = 11$). Bacterial growth rates, estimated from integrated values of carbon production and biomass, ranged from 0.028 to 0.437 d^{-1} and corresponded to generation times from ca 2 to more than 25 d, with the largest range of values in Zone C. Growth rates in Zone B were significantly higher (and generation times lower) than those in Zone C (Mann-Whitney *U*-test, $p < 0.01$, $n = 11$).

Using stations where simultaneous measurements of bacterial and phytoplankton variables were made, we computed daily carbon budgets in the upper 100 m for Zones B and C (Table 6). Despite equivalent biomass values of bacteria or phytoplankton in both zones, the mean primary production of Zone C was more than twice the value computed for Zone B, while mean bacterial production was only slightly higher in the latter zone. Bacterial biomass exceeded phytoplankton bio-

Table 3. Probability of significance of paired comparisons (Wilcoxon test) between depth of maximum value of selected bacterial and environmental variables. Upper half of the matrix shows probability of significance (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, ns: not significant), lower half of the matrix shows number of data pairs compared. Variable names are explained in Methods. CB: cyanobacteria; HB heterotrophic bacteria; PBact: production of heterotrophic bacteria; PP: primary production; p1–p3: depths of surface upper mixing layers

	CB	HB	PBact	Chl *a*	PP	p1	p2	p3
CB	–	*	ns	ns	*	*	ns	**
HB	13	–	ns	**	ns	ns	*	**
PBact	9	11	–	ns	ns	ns	ns	**
Chl *a*	13	15	11	–	*	**	ns	**
PP	8	8	6	8	–	ns	*	*
p1	13	15	11	15	8	–	***	***
p2	13	15	11	15	8	15	–	***
p3	13	15	11	15	8	15	15	–

Table 4. Empirical conversion factors between leucine and cell growth or carbon uptake. $FCell_{KD}$: leucine to cell conversion factor ($\times 10^{17}$ cells [mol leu]$^{-1}$) computed by procedure of Kirchman & Ducklow (1993); $FCell_{BK}$: leucine to cell conversion factor ($\times 10^{17}$ cells [mol leu]$^{-1}$) computed by procedure of Bjørnsen & Kuparinen (1991); FC_{KD}: leucine to carbon conversion factor (kg C [mol leu]$^{-1}$) computed by procedure of Kirchman & Ducklow (1993). FC_{BK}: leucine to carbon conversion factor (kg C [mol leu]$^{-1}$) computed by procedure of Bjørnsen & Kuparinen (1991). Cell to carbon conversion was made using the estimated empirical factor of 17 fg C cell^{-1} (see 'Materials and methods')

Station	$FCell_{KD}$	$FCell_{BK}$	FC_{KD}	FC_{BK}
Zone B				
65	1.83	1.26	3.11	2.14
91	2.51	2.25	4.27	3.83
Mean (SD	2.17 (0.48)	1.76 (0.70)	3.69 (0.82)	2.98 (1.20)
Zone C				
107	0.74	0.96	1.26	1.63
115	0.39	0.71	0.66	1.21
134	0.21	0.55	0.36	0.41
Mean (SD)	0.45 (0.27)	0.74 (0.21)	0.76 (0.45)	1.08 (0.61)
Total				
Mean (SD)	1.14 (0.99)	1.15 (0.67)	1.93 (1.69)	1.84 (1.28)

mass in all cases by approximately 30%. In contrast, bacterial production was equivalent to a small fraction of both phytoplankton biomass or production, except at Stn 65, where both production rates were nearly equivalent. Stations in Zone C showed the lowest ratios of bacterial production relative to either phytoplankton biomass or production in the upper surface layer.

DISCUSSION

Mesoscale eddies are a major characteristic of the upper waters in the Canary region and greatly influence plankton distribution and productivity (Arístegui et al. 1994, 1997). The oceanographic situation found during the BIOCAN-98 cruise can be considered typical of late summer in this region, characterized by coexisting cold- and warm-core eddies and the marked influence of the NW African upwelling in the eastern islands of the archipelago. Cold-core cyclonic eddies generally have surface waters with low chlorophyll inside the eddy, while relatively high chlorophyll concentrations can be found at the surface near the eddy limits. Local upwelling may enhance phytoplankton productivity in subsurface layers near the center of the eddy and at its borders (Arístegui et al. 1997). Warm-core anticyclonic eddies were usually associated with relatively high chlorophyll concentrations inside the eddy, probably due to transport and concentration of phytoplankton patches. Trade winds, which interact with island topography and the Canary current in driving and maintaining these eddies (Arístegui et al. 1994, 1997), reach their maximum intensity during the summer months, resulting in maximum development of the NW African upwelling. Our observations of relatively cold and phytoplankton-rich surface waters in the eastern part of the archipelago (Zone C), along with greatly modified thermoclines and shallower subsurface chlorophyll maxima, confirm the importance of the upwelling in this region. In contrast, the productivity of the relatively low-phytoplankton waters in the western islands (Zones A and B) may depend to a large extent on local enrichments caused by eddy-induced up-

Table 5. Integrated biomass and production values of heterotrophic bacteria in a 100 m deep water-column. Cell abundances were converted to carbon biomass (HB_C, mg C m^{-2}) using the factor: 17 fg C cell^{-1} (see 'Materials and methods'). Bacterial leucine incorporation was converted to carbon uptake ($Pbact_C$, mg C m^{-2} h^{-1}) using the average empirical factor determined for each zone (Table 4). Daily bacterial production ($Pbact_C^d$, mg C m^{-2} d^{-1}) was computed by multiplying hourly values by 24. Bacterial growth rate (μ, d^{-1}) was computed as $\ln(1 + Pbact_C^d/HB_C)$. Generation time of the bacterial population (GT, days) was computed as $\ln 2/\mu$. –: no data

Station	HB_C	$Pbact_C$	$Pbact_C^d$	μ	GT
Zone A					
1	391.4	–	–	–	–
7	442.9	–	–	–	–
14	489.5	–	–	–	–
37	507.6	–	–	–	–
Mean (SD)	457.8 (52.0)	– (–)	– (–)	– (–)	– (–)
Zone B					
65	526.7	12.0	289.0	0.437	1.6
72	357.6	8.0	192.7	0.431	1.6
78	374.8	6.5	155.6	0.347	2.0
83	383.8	8.5	203.8	0.426	1.6
91	381.5	5.2	126.0	0.285	2.4
97	445.8	7.4	177.9	0.336	2.1
Mean (SD)	441.7 (63.8)	8.0 (2.3)	190.8 (55.5)	0.377 (0.063)	1.9 (0.3)
Zone C					
122	705.7	1.3	32.2	0.045	15.5
124	730.5	2.0	48.3	0.064	10.8
134	444.0	2.7	64.5	0.136	5.1
137	527.1	0.6	14.8	0.028	25.1
144	290.6	2.4	57.7	0.181	3.8
Mean (SD)	539.6 (183.9)	1.8 (0.8)	43.5 (20.1)	0.091 (0.065)	12.1 (8.6)

Table 6. Carbon budget of heterotrophic bacteria and phytoplankton for selected stations. Biomass values in mg C m^{-2} and production in mg C m^{-2} d^{-1}. Bacterial biomass (HB_C) and production ($Pbact^d_C$) as in Table 5, P_C: phytoplankton carbon computed from chl *a* using the conversion 50 g C (g chl *a*)$^{-1}$. PP^d: daily primary production computed for a 12 h light period. Percent ratios of bacterial biomass and production relative to phytoplankton are also given

Station	HB_C	$Pbact^d_C$	P_C	PP^d	$\%HB_C:P_C$	$\%Pbact^d_C:P_C$	$\%Pbact^d_C:PP^d$
Zone B							
65	526.7	289.0	440.0	172.8	120	66	167
78	374.8	155.6	245.0	243.6	153	64	64
Mean (SD)	450.8 (107.4)	222.3 (94.3)	342.5 (137.9)	208.2 (50.1)	136 (24)	65 (2)	116 (73)
Zone C							
124	730.5	48.3	495.0	603.6	148	10	8
144	290.6	57.7	280.0	432.0	104	21	13
Mean (SD)	510.6 (311.1)	53.0 (6.6)	387.5 (152.0)	517.8 (121.3)	126 (31)	15 (8)	11 (4)

welling, as suggested by the association between larger subsurface chlorophyll maxima and shallower and eroded thermoclines at some stations. The significantly higher water-column-integrated (0 to 150 m) chlorophyll concentration of stations in Zone B compared to Zone A may be a consequence of the presence of islands that favour eddy develoment and plankton transport from the coast (Arístegui et al. 1989, 1994, 1997). Phytoplankton species composition reflects the general oligotrophy of these waters. Small dinoflagellates were always the most abundant cells for the 5 to 30 µm phytoplankton size group, but total phytoplankton abundance was generally lower than 50 cells ml^{-1}. However, the influence of the African upwelling was indicated by the greater species diversity and an increase in the abundance of diatoms in Zone C compared to the other zones.

Our results of bacterial abundance agree with those of Ballesteros (1994) for the Canary Islands region in June 1990, and they are also within the range reported for other studies in oligotrophic oceanic waters (Campbell et al. 1994, Ducklow et al. 1995, Pomeroy et al. 1995, Binder et al. 1996, Carlson et al. 1996). The maximum values observed in this study are lower than those observed in oceanic stations of oligotrophic waters near the Iberian peninsula, either in the NW Mediterranean (1.6×10^6 cells ml^{-1}; Gasol et al. 1998) or in the S Bay of Biscay, in the NE Atlantic (1.9×10^6 cells ml^{-1}; Barquero et al. 1998). Similarly, our measured abundances of coccoid cyanobacteria are within the range of reported values in oceanic waters (McManus & Dawson 1994, Li 1995, Binder et al. 1996) and in the Canary Islands (Ballesteros 1994). Recent studies of pico- and nanoplankton in oceanic waters using flow cytometry report large abundances of prochlorophytes (Campbell et al. 1994, Li 1995, Binder et al. 1996, Zubkov et al. 1998) that may be difficult to distinguish from small heterotrophic bacteria using epifluorescence microscopy (Sieracki et al. 1995), thus overestimating bacterial numbers and underestimating primary producers. However, Campell et al. (1994) and Binder et al. (1996) report that prochlorophyte abundance was <45% of the abundance of heterotrophic bacteria in the vicinity of the subsurface chlorophyll maximum, and <5% in the surface. In the same way, Li (1995) concluded that, even when prochlorophytes comprised on average 78% of the cell numbers of ultraphytoplankton (<5 µm in size) in the central Atlantic (including samples from the Canary region), their contribution did not exceed 10% of carbon biomass, and 20% of primary production. More recently, Buck et al. (1996) and Zubkov et al. (1998) found that the biomass of heterotrophic bacteria was >50% of total picoplankton biomass in the subtropical north Atlantic. In our study, the relatively low abundances of heterotrophic bacteria compared to similar studies in oceanic waters, and the absence of a significant correlation between bacterial abundance and chlorophyll, suggests that prochlorophytes did not greatly affect our estimations.

Estimations of bacterial carbon biomass in oligotrophic environments are largely dependent on the conversion factors between abundance, cell biovolume and carbon employed. We computed a mean carbon content of 17 fg C $cell^{-1}$ that is close to the 20 fg C $cell^{-1}$ (Simon & Azam 1989) used in other oceanic studies (eg. Ducklow 1993: Li et al. 1993) and included in the range determined for marine bacteria (5.9 to 23.5 fg C $cell^{-1}$; Fukuda et al. 1998). Although our estimates of bacterial size by visual observation under the microscope were higher when compared with other studies in which bacteria were measured with more precise techniques (Carlson et al. 1996, Gasol et al. 1998), our computations of bacterial biomass yielded an average value of ca 10 mg C m^{-2} in the upper mixing layer, within the range reported for some studies (Campbell et al. 1994, Barquero et al. 1998), but relatively high compared to values reported for others (Pomeroy et al. 1995, Carlson et al. 1996). Nevertheless, minimum values in our study were lower than those reported for the

nearby African upwelling (Head et al. 1996) and than those observed during phytoplankton blooms in oceanic regions (Ducklow et al. 1993, Li et al. 1993). The same is true for the computed bacterial carbon production values. The large range of values reported for oligotrophic regions: 0.2 to >30 mg C m^{-2} d^{-1} (Ducklow 1993, Pomeroy et al. 1995, Carlson et al. 1996, Jones et al. 1996, Gasol et al. 1998) includes our values, which are low compared to those of productive regions (Ducklow et al. 1993, Li et al. 1993, Head et al. 1996). In addition to these comparisons, there are several methodological considerations that support the reliability of our results on bacterial biomass and production in Canarian waters.

First, we used additions of leucine which were relatively high compared to the 10 to 50 nmol l^{-1} used in other studies (Simon & Azam 1989, Li et al. 1993, Carlson et al. 1996, Gasol et al. 1998). Large additions of leucine ensure that bacteria use mainly the labelled amino acid in protein synthesis and not unlabelled extra- or intracellular pools of leucine (Simon & Azam 1989), since the goal is to obtain rates of protein synthesis and not amino acid turnover at *in situ* concentrations (Kirchman 1993). Preliminary experiments with bacteria from coastal and oceanic stations in the upwelling area of NW Spain showed that leucine incorporation reached complete saturation at concentrations ranging from 42 to >100 nM even in oligotrophic stations (A. Bode, A. Cid & J. Valencia, unpubl. results). Using these data, the estimated effect of additions of leucine of up to 150 nM would have multiplied the incorporation rates expected at 50 nM by 1.2 to 2.1 times (mean 1.7, n = 8). However, in the absence of specific experiments to measure the saturation of leucine incorporation by bacteria of Canarian waters it is difficult to demonstrate a stimulating effect of the leucine additions employed. Comparison between our measured rates and those in the literature suggests that in our study leucine incorporation was not enhanced because of large initial additions.

Second, although our incubations were not made at in situ temperatures, we can discount any significant effect of temperature on the estimated bacterial production rates since other studies in temperate waters during summer have found no significant correlations between these 2 variables (Shiah & Ducklow 1994), with other factors such as the availability of dissolved organic substrates probably controlling bacterial production. Similarly, the average conversion factor between leucine and carbon uptake determined in our study is within the range of empirical factors employed in other studies (Kirchman 1992, Li et al. 1993, Carlson et al. 1996) and is lower than the maximum theoretical value of 3.1 kg C (mol leucine)$^{-1}$, assuming that incorporated leucine is diluted by a factor of 2 in the intracellular pool (Kirchman 1993). Our estimates of hourly bacterial carbon-production rates can be considered as potential rates, but at the same time our results are within the published ranges of bacterial production and agree with the measured microbial respiration in Canarian waters (Aristegui & Montero 1995) (see later discussion on carbon budgets).

Finally, there are reports of diurnal changes in leucine incorporation in oligotrophic environments (e.g. Gasol et al. 1998), with maximum rates occurring around noon. These changes are related to variations in dissolved organic carbon concentrations and imply a close coupling between bacterial activity and substrate availability in surface waters. Extrapolation of short-term rates measured around noon to daily incorporation may be overestimated if significant changes in short-term rates occur during the day. In our study, all incubation experiments were made around noon and dissolved organic carbon was not measured. However, we can estimate the potential effect of daily changes in bacterial production rates similar to those reported by Gasol et al. (1998), assuming that the value of hourly production at noon is 220% of daily mean rate and that rates decay to 80% of this mean value in an interval of 6 h around noon. In such case, our daily values of bacterial carbon production assuming constant rates would have overestimated actual values by up to 40%; however, comparisons of our results with literature values and primary production rates (see below) do not suggest severe overestimations.

The abundance of heterotrophic bacteria was not significantly correlated to either temperature or chlorophyll concentration in our study. However, significant correlations between these variables were found at seasonal scales and during comparisons across systems (Cole et al. 1988, White et al. 1991, Shiah & Ducklow 1994). Maximum abundance of heterotrophic bacteria was not directly related to phytoplankton vertical distribution in our samples. The observed distributions generally showed higher abundance of bacteria near the surface, but sometimes also near the subsurface chlorophyll maximum, the latter associated with the seasonal pycnocline displaying a 'typical subtropical structure' (sensu Cullen 1982). This subsurface chlorophyll maximum was repeatedly reported in Canarian waters (de León & Braun 1973, Braun 1980, Real et al. 1981, Braun & Real 1984, 1986, Arístegui et al. 1989, 1997, Fernández de Puelles & Braun 1989, Arístegui 1990, Ojeda 1996). In contrast, maximum cyanobacterial abundances were related to the chlorophyll maximum, as in other studies of oceanic waters (Li et al. 1993, McManus & Dawson 1994, Binder et al. 1996). Surface maximum abundances of heterotrophic bacteria have been reported in most studies (Li et al. 1993, Binder et al. 1996, Carlson et al. 1996, Jones et al.

1996). Indeed, some studies (e.g. Ducklow 1993) also noted the presence of relative maxima in the vertical distribution of bacteria near the surface and near the chlorophyll maximum, as in our study. The maximum near the surface occurred at depths equivalent to those of the highest rates of PP and PBact, which were located significantly above the chlorophyll maximum. It can be hypothesized that bacteria in the subsurface maximum efficiently utilize released organic matter from recent photosynthates and produce noticeable increases in their population numbers.

The integrated biomass and production rates of heterotrophic bacteria suggest that these organisms are important components of the carbon flux of the Canary region. The estimated growth rates and generation times indicate that bacteria were growing relatively fast compared to other oligotrophic regions (e.g. Carlson et al. 1996). The slower growth rates in Zone C were an additional indication of the influence of the African upwelling, as specific bacterial activity is generally reduced near active upwelling areas (Watson 1978, Hanson et al. 1986, Tenore et al. 1995, Barquero et al. 1998). Direct comparison of bacteria and phytoplankton at the same stations (Table 6) indicates that bacterial biomass exceeded phytoplankton carbon in the upper 100 m, while bacterial production comprised from 10 to 66% of primary production. These values may be considered low compared to the average value of 190% reported by Ballesteros (1994) in waters around the Canary Islands in June 1990, but are within the range of 18 to 130% reported by Carlson et al. (1996) in the oligotrophic Sargasso Sea. Cyanobacteria would be comparatively less important, since their biomass would be less than half the estimated biomass of heterotrophic bacteria and less than 20% of phytoplankton carbon, assuming a cyanobacterial carbon content of 250 fg C cell^{-1} (Campbell et al. 1994). Ballesteros (1994) estimated that cyanobacteria contributed up to 32% of phytoplankton carbon biomass in Canarian waters during spring but only 12% during summer. In contrast, bacterial production constituted a very variable fraction of particulate primary production in the upper mixing layer (from 14 to 108%, according to values in Table 6), while literature values ranged from 2 to 92% in both oligotrophic (Ducklow 1993, Carlson et al. 1996, Jones et al. 1996) and eutrophic (Li et al. 1993, Head et al. 1996) ocean areas. Taking into account that the excretion of recent photosynthates by phytoplankton can account for up to 10% of particulate primary production (e.g. Wood et al. 1992), the ratio between bacterial and primary production could be reduced by ca 10%. However, the existence of a close coupling between heterotrophic bacteria and phytoplankton may not require high ratios of bacterial to primary production. High bacterial growth rates can be sustained by phytoplankton populations growing faster than bacteria. Using the results in Table 6, we estimated phytoplankton growth rates of between 0.331 and 0.933 d^{-1}, i.e. from 0.8 to 12.5 times the bacterial growth rates at the same stations. This suggests that primary production was high enough to support bacteria in the upper mixing layer even when the biomass of the latter generally exceeded phytoplankton biomass.

Gasol et al. (1998) compared leucine incorporation rates of bacteria in oligotrophic waters of the Western Mediterranean with daily changes in the concentration of dissolved organic carbon and concluded that the bacterial production of protein did not account for the observed disappearance of organic dissolved carbon. Low carbon conversion efficiencies, implying high bacterial respiration rates, may explain the use of relatively large amounts of dissolved substrates and increase the participation of bacteria in the carbon fluxes in oligotrophic marine areas (del Giorgio et al. 1997, Duarte & Agustí 1998). We can examine further the implications of the measured bacterial biomass and production values in the pelagic ecosystem around the Canary Islands using the available information on biomass and carbon fluxes in this region (Table 7). Bacterial biomass and production were on average 24% of phytoplankton biomass or primary production per volume. Taking into account that phytoplankton were restricted mostly to the upper 100 m and that bacteria are distributed throughout the whole water column with no clear reduction in abundance or production, at least in the upper 300 m, the integrated values suggest that bacterial production would account for ca 50% of primary production in the upper 200 m. Even considering a reduction of bacterial production values below 100 m to 10% of the average values in the upper 100 m, and an increase of 10% in primary production values to account for the excretion of recent photosynthates, integrated bacterial production would be still more than 50% of primary production in the upper 500 m. Also, bacterial biomass and production exceeded the average values of micro- or mesozooplankton biomass and carbon ingestion, even when considering values integrated in a 500 m depth water column, thus indicating that bacteria are the main contributors to heterotrophic carbon in these waters. The values obtained in these comparisons do not vary greatly, even when one recalculates bacterial production at 50 nM of leucine by dividing bacterial production by the empirical factor of 1.7 as discussed earlier. Reported carbon conversion efficiencies for aquatic bacteria ranged from <10 to >50% of consumed carbon (Carlson & Ducklow 1996, del Giorgio et al. 1997, Gasol et al. 1998). According to these values and those in Table 7, bacteria in the euphotic zone (0 to 200 m)

Table 7. Preliminary carbon budget of the pelagic ecosystem in Canarian waters. Phytoplankton and bacterial biomass and production are averages for the upper 200 m of the water-column. Microzooplankton (100 to 250 µm) and mesozooplankton (>200 µm) values are averages for the 0 to 200 m and 0 to 500 m layers, respectively. Microplankton respiration includes organisms smaller than 225 µm, i.e. mostly phytoplankton, bacteria and microheterotrophs. Biomass values in mg C m^{-3} and fluxes in mg C m^{-3} d^{-1}

Component	Mean ± SD	Observations	Source
Phytoplankton biomass[a]	11.4 ± 19.0	All periods, all islands, (n = 362)	Arístegui (1990) Arístegui et al. (1989, 1997) Fernández de Puelles & Braun (1989, 1996) Ojeda (1996)
Primary production	4.2 ± 5.8	All periods, Gran Canaria and Tenerife islands, (n = 37)	de León & Braun (1973) Braun (1980) Arístegui et al. (1989) Fernández de Puelles & Braun (1989, 1996)
Microzooplankton biomass[b]	2.7 ± 0.2	All periods, Tenerife Island, (n = 25)	Fernández de Puelles (1987) Fernández de Puelles & Braun (1996)
Mesozooplankton biomass[b]	1.3 ± 0.8	All periods, Gran Canaria and Tenerife islands, (n = 33)	Hernández-León et al. (1984) Fernández de Puelles (1987) Fernández de Puelles & Braun (1996)
Microzooplankton ingestion[c]	0.4	All periods, Tenerife island	Fernández de Puelles & Braun (1996)
Mesozooplankton ingestion[d]	0.4	All periods, Tenerife island	Braun (1981) Fernández de Puelles & Braun (1996)
Microplankton respiration[e]	17.7 ± 6.6	Canarian waters, (n = 14)	Arístegui & Montero (1995)
Mesozooplankton respiration[f]	0.1 ± 0.1	All periods, Tenerife island, (n = 26)	Hernández-León (1986)
Bacterial biomass	4.8 ± 2.0	Summer, all islands, (n = 15)	This study
Bacterial production	1.2 ± 0.9	Summer, all islands, (n = 11)	This study

[a]A ratio of 50 g C (g chl *a*)$^{-1}$ is assumed
[b]Carbon biomass (C) computed from dry weight (DW) using equation of Wiebe (1988): log(DW) = 0.499 + 0.991log(C)
[c]Estimated annual average
[d]Mean of reported annual average values: 0.3 and 0.5 mg C m^{-3} d^{-1}
[e]Computed from oxygen consumption values assuming a respiratory quotient of 1.25 mol O_2 (mol CO_2)$^{-1}$
[f]Computed using a mean respiration rate of 159 µl O_2 (mg DW)$^{-1}$ (Hernández-León 1986) and a respiratory quotient of 1.25 mol O_2 (mol CO_2)$^{-1}$

would consume daily an amount of dissolved carbon equivalent to 1 (50% efficiency) or ca 5 times the average value of primary production (10% efficiency). The high respiration rates required to explain these estimated consumption values are supported by the results of Arístegui & Montero (1995), who reported average respiration rates of 18 mg C m^{-3} d^{-1} for microplankton in Canarian waters (Table 7). Using again extreme efficiency values of 10 and 50% for bacterial production, the average bacterial carbon production measured in our study would require the respiration of 2 to 11 mg C m^{-3} d^{-1}, that is from 11 to 60% the average respiration rate of microplankton. Since bacteria are the main components of microplanktonic biomass, it is likely that they are also the main contributors to microplanktonic respiration, assuming that phytoplankton respiration is equivalent to 15% of particulate primary production (Setchell & Packard 1979). Therefore, bacterial carbon-conversion efficiencies in Canarian waters must be ca 5% to account for the measured respiration rates. This low efficiency value concurs with recent estimates explaining bacterial respiration in unproductive ocean waters (del Giorgio et al. 1997, Gasol et al. 1998). However, further studies of carbon fluxes in the Canary Islands region must also include measurements of biomass, production and respiration of heterotrophic flagellates, all of which are important contributors to carbon fluxes and display significant abundances in these waters (Ballesteros 1994).

Another implication of these results is that external sources of dissolved carbon are required to sustain the estimated heterotrophic consumption rates. One of the most immediate sources may be the productive upwelling on the African coast, since there are reports of lateral exports of phytoplankton biomass over large distances (Head et al. 1996, Arístegui et al. 1997). Nevertheless, the importance of bacteria in the carbon budget of oceanic waters around the Canary Islands must be appropriately weighted to the main time

scales affecting the pelagic ecosystem, since short-term fluxes may be not balanced as reported in other studies (Pomeroy & Wiebe 1993). Our preliminary estimations of a carbon budget for the Canarian waters must be confirmed by a seasonal study of planktonic biomass and carbon fluxes, particularly taking into account bacteria and heterotrophic flagellates, and including productive phytoplankton blooms such as those observed during the spring (de León & Braun 1973, Braun 1980, Real et al. 1981, Braun & Real 1984, Arístegui et al. 1989, Fernández de Puelles & Braun 1989, Arístegui 1990) and near cyclonic eddies or coastal sites (Arístegui et al. 1989, 1997).

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