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Seasonal changes in specific growth rates, production and biomass of a bacterial community in the water column above a Mediterranean seagrass system

Branko Velimirov, Martha Walenta-Simon*

Institut für Allgemeine Biologie, Abt. Mikrobiologie, Universität Wien, Schwarzspanierstraße 17, A-1090 Wien, Austria

ABSTRACT: Bacterial abundance, biomass and production rates were determined at 3 depths (5, 10 & 15 m) in the water column above a Mediterranean seagrass bed in the Gulf of Calvi (west coast of Corsica, France) from 1988 to 1990. We used dialysis bags for *in situ* incubation of 2 µm prefiltered seawater sampled from the respective depths to determine bacterial growth parameters and conducted light- and dark-bottle incubations to estimate planktonic primary production by O_2 measurements. Bacterial density and biomass was subject to marked seasonal changes. Bacterial density varied clearly over the seasons and between the 3 depths, with maximum values being recorded in Aug and Oct 1988 at the 10 and 15 m depths. Differences in bacterial biomass and density patterns were mainly attributed to changes of abundance and biovolume of rod-shaped bacteria. Highest carbon values were recorded during the summer months in 1989 and 1990 at the 3 depths and ranged from 32 to 65 µg C l^{-1} Bacterial growth rates were closely correlated to temperature, with highest specific growth rates (0.075 to 0.125 h^{-1}) found in summer, when chlorophyll *a* concentrations were at a minimum during this season. During Jan and Feb 1989 and 1990, when chl *a* concentrations were at a maximum, bacterial growth rates were below 0.001 h^{-1} Doubling times (*g*) ranged from 5.2 to 23 h in summer, being lowest at the 5 m depth. Highest *g* values were recorded in Jan 1989 at 10 m (259 h). During this period we observed an increase bacterial numbers within the dialysis bags, but a decrease in biovolume of the 4 morphotypes. We hypothesize that the observed growth strategy is necessary for bacteria to resist starvation and to obtain a competitive advantage for nutrient scavanging under oligotrophic conditions. In Jan, bacterial production corresponded to 7.6 % of gross primary production. In summer, bacterial production ranged from 18.5 to 48.4 % of gross primary production. Carbon requirements of the bacterial population in the water column were discussed in view of various carbon conversion efficiencies. The range of our bacterial production values is compared with values from other systems and seen in the context of the methodological approaches.

INTRODUCTION

It is established knowledge that in aquatic systems dominated by vascular plants, most of the primary production is not utilized directly by macroconsumers (Thayer et al. 1975, Ott & Maurer 1977, Zimmermann et al. 1979, Morgan 1980, Phillips & McRoy 1980, Traer 1980, Ott 1981, Velimirov 1986, Mann 1988). The bulk of plant material undergoes fragmentation and chemical modification (Velimirov et al. 1981, Morgan & Kitting 1984, Velimirov 1987) before entering the food chain, or is transferred to the higher trophic levels by first being changed into bacterial biomass which is subsequently consumed by bacterivores. Since bacteria are involved in both decomposition processes (Newell et al. 1983) and the transfer of energy to meio- and macrofauna (Newell et al. 1982), reliable data on biomass and growth rates of bacteria are needed to understand and quantify the carbon cycle in seagrass-dominated ecosystems. However, bacterial degradation in such systems is not restricted to seagrass-derived particles; the presence of phytoplanktonic particulate organic carbon (Murray & Wetzel 1987) and exudates in the water column (Chrost 1981, Chrost & Faust 1983, Münster & Chrost 1990) represents easily degradable organic matter compared to the structural

* Present address: Bundesanstalt für Wassergüte, A-1220 Wien, Austria

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carbohydrates from vascular plants (Benner et al. 1986, Moran & Hodson 1989) or their epiphytes. Therefore bacterial biomass and growth dynamics in the water column above the seagrass bed may be different from those within the meadow.

Most information on bacterial biomass and production in seagrass systems is available for *Zostera capricorni* beds (Moriarty & Pollard 1981, 1982) and a multi-species seagrass community (Moriarty et al. 1990) in Australia. In general, less information is available for temperate seagrass systems and more specifically, for those of the Mediterranean Sea. Density data relating to bacteria on seagrass debris and leaves of *Posidonia oceanica* (Velimirov et al. 1981, Novak 1984) as well as in the water column above and within a *Posidonia* bed (Velimirov 1986a, Velimirov 1987) have been published, but only limited data on bacterial growth rates from a site near the Gulf of Naples, Italy (Velimirov 1989) can be found.

In the following study we report on bacterial biomass as well as on growth rates and production obtained at a site in the Gulf of Calvi (west coast of Corsica, France) which is characterized by an extensive seagrass bed. We investigated seasonal variations of the bacteria populations in the water column above the seagrass bed and integrated estimations on chlorophyll *a* concentrations and phytoplanktonic primary production into the study. As an alternative to the methods of Fuhrman & Azam (1980), Moriarty & Pollard (1981) and Moriarty et al. (1990) using thymidine incorporation into DNA to estimate bacterial productivity, we chose to follow growth of microbial populations by direct observation using *in situ* incubations in dialysis bags (Lochte & Turley 1985, Turley & Lochte, 1985).

MATERIALS AND METHODS

The investigation site was located 300 m off the research station STARESO in the Gulf of Calvi. A dense *Posidonia oceanica* bed characterizes the shallow benthos of the gulf, extending from 4 to 35 m depth, and is adjacent to a deeper sand and mud bottom ecosystem. A detailed description of the site is given by Bay (1984). Data on wind, main current directions and speed are available from Djenedi (1985). Highest shoot density is found between depths of 10 and 20 m, with an average of 408 shoots m^{-2} (Bay 1984). All measurements, water sampling and *in situ* incubations took place at 3 depths (5, 10 & 15 m) at a permanent station marked by a surface buoy. Depth at this station was 20 m.

Temperature was measured at least twice a month at the 3 depths by SCUBA divers. Multiple water samples for the determination of bacterial density, incubation experiments and chlorophyll *a* measurements were collected at each of the 3 depths between 1988 and 1990 using 1.4 l IRO bottles. All containers were acid-washed and rinsed with distilled water prior to use. Glassware used for storage of pooled water samples was autoclaved after being cleaned as described above. Two 20 ml aliquots of each pooled sample per depth were preserved with 800 µl of 35 % formaldehyde for enumeration and sizing of bacterial cells.

To determine bacterial secondary production, each pooled water sample was taken to the laboratory and gravity-filtered through 2 µm pore size Nuclepore polycarbonate filters (45 mm diameter) to eliminate most bacterial predators. Each filtered water sample was split into two 1.2 l subsamples and poured into separate pretreated dialysis bags (Union Carbide, 65 mm inflated diameter, molecular weight cutoff 12000 to 14000 D), modifying the method of Turley & Lochte (1985). Pretreatment consisted of washing the strips of seamless regenerated cellulose tubing in boiling water for 2 h, rinsing in running tap water overnight, followed by washing for 1 h in boiling water and further rinsing in distilled water. Each end was sealed by 2 knots, 3 cm apart. The filtration and filling procedure took approximately 45 min per depth. During transport the bags were kept in a light-tight cooling box. One end was then connected with a polypropylene rope to a bottom weight, while the other end was connected to a small subsurface buoy which kept the bag in an upright position without exerting tension stress on it. SCUBA-divers positioned each pair of dialysis bags at 5, 10 and 15 m, respectively, by adjusting the length of the bottom rope. The lowest bag (at the 15 m depth) was located approximately 5 m above the seagrass meadow. Each pair of bags, situated 1 m apart, was incubated for 24 h.

All bags were collected 24 to 26 h after immersion (at 45 min intervals) by SCUBA divers and brought to the laboratory within 5 min. Three 20 ml aliquots were taken from each bag to conduct replicate bacterial counts. The acridine orange epifluorescence direct counting technique (Hobbie et al. 1977) was applied to estimate total bacterial number, using a Leitz Diaplan microscope fitted with a Leitz Orthomat E Photosystem (excitation wavelength 450 to 490 nm, cutoff filter 515 nm).

Bacteria were sized by eyepiece micrometer, classifying bacteria into cocci, rods, curved rods and spirillae. We counted all cells in a minimum of 30 eyefields per sample and measured between 100 and 180 cells per subsample. Cells were operationally defined as rods if their length and width differed by more than 0.1 µm. Volume estimations were based on the assumption that all bacteria are spheres or rods (i. e. cylinders with 2 hemispherical caps). The difficulties of obtaining

reliable size estimates during direct observation in the epifluorescence microscope are demonstrated by Krambeck & Krambeck (1984), Bratback (1985), Lee & Fuhrman (1987) and Krambeck et al. (1990). Fluorescent latex beads with diameters of 0.11, 0.22, 0.6 and 0.88 µm (Polyscience Lim.) were used for calibration of the sizing procedure. Our estimates by eye were controlled using both an automatic image analyzer (Leitz-ASBA III) and a semi-automatic image analyzer (Leitz-ASM 68 K) on magnifications of epifluorescence photomicrographs (Lee & Fuhrman 1987). We overestimated the diameter of spheres with 0.11 and 0.22 µm diameters by 16 %, 0.6 µm diameter by 11 % and 0.88 µm diameter by 6 %.

The frequency of dividing cells (FDC) was determined by the method of Hagström et al. (1979), and cellular carbon was calculated from the estimated total bacterial volume, using the conversion factor 380 fg C μm^{-3} cell volume after Lee & Fuhrman (1987). Bacterial growth rate was calculated by the equation for exponential growth: $\mu = (\ln N_2 - \ln N_1)/(t_2 - t_1)$ where N_1 and N_2 = bacterial abundance at the beginning and the end of an incubation interval; t_1 and t_2 = beginning and ending incubation times. The doubling time g was calculated by: $g = \ln 2/\mu$. Estimation of bacterial production was obtained by: (total bacterial carbon at t_2 − total bacterial carbon at t_1)/($t_2 - t_1$).

For chlorophyll measurements we filtered a minimum of 5 to 7 l water onto one or several Whatmann GF/F filters using low vacuum (<0.2 atm). The filters were stored at −18 °C in the dark until extraction in 90 % acetone and spectrophotometric determination according to Parsons et al. (1985). Estimates of primary production in the water column were obtained by monitoring the evolution of dissolved oxygen in capacity calibrated light and dark Winkler flasks according to the modified classical Winkler procedures (Parsons et al. 1985). Duplicate light and dark bottles were incubated for 4 h, usually between 10:00 and 14:00 h, at 1, 5, 10 and 15 m depth and always using the same set of bottles for the same depth. Although the incubations were started in August 1988 we only used data from experiments from July 1989 on, which were run at the same time or close to the 24 h incubation experiments of dialysis bags to determine bacterial growth rates. Temperature readings were performed at the beginning and the end of both types of incubation experiments. To convert O_2 values into carbon equivalents, a photosynthetic quotient of 1.36 (Williams & Robertson 1991) and a respiratory quotient of 1.0 (Holligan et al. 1984, Bender et al. 1987) were used. We used a Metrohm titration sytem (Oudet et al. 1988) consisting of a digital Titroprocessor 686 and a Multidosimat (Dosimat 665) with automatic burette and digital display combined with platinum electrode. Each titration was preceded by a control of the system, using water which was supersaturated with oxygen and water boiled for 40 min and subsequently flushed with nitrogen.

RESULTS

The bacterial density pattern from July 1988 to 1990 at 5 m (Fig. 1) varied substantially from density patterns at the 10 and 15 m deeper depths. This difference was due to high densities at the 10 m depth in Aug 1988 (11.5×10^5 cells ml^{-1}) and at the 15 m depth in Oct 1988 and Jul 1990 with 26×10^5 and 11.23×10^5 cells ml^{-1} respectively. In contrast, the 5 m depth showed a density peak in Jun and Jul 1989 (9.60 and 10.89×10^5 cells ml^{-1}) as well as in Apr 1990 (8.36×10^5 cells ml^{-1}). Although a smaller peak was also noticed from Jan to Jul 1989 for the 10 and 15 m depths, no such clear peak could be detected at 5 m.

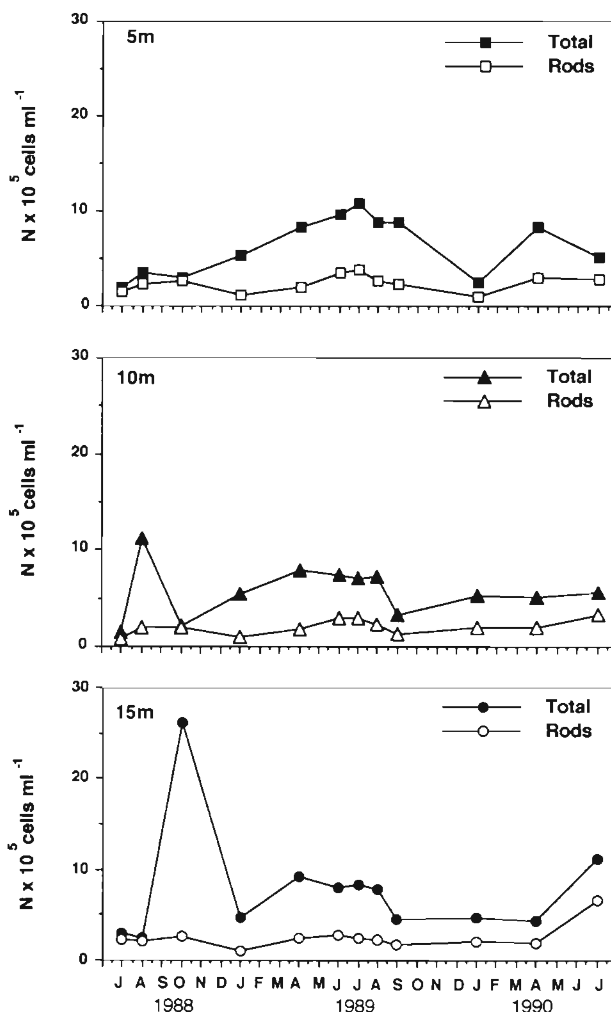

Fig. 1. Variations in total bacterial number and rod-shaped bacteria at 5, 10 and 15 m depths from 1988 to 1990

Total bacterial abundance and the number of rod-shaped bacteria showed similar variation patterns over the 2 years with the exception of Aug 1988 at 10 m and Oct 1988 at 15 m. However, for most of the samples from 1989 and 1990, cocci and curved rods were the dominant bacterial morphotype. At the 5 m depth, the numerical importance of rods was only noticed in samples from 1988 and for Jan 1990. The density peak at 10 m in Aug 1988 was due to the dominance of cocci, amounting to 89.2 % of the total cell number. Again, high number of rods were only noticed in Jul and Oct; during the remainder of the sampling period, their contribution was below 40 % of total cell number. The peak in Oct 1988 at 15 m was also due to a dominance of cocci (82.4 %), and with the exception of Jul and Aug 1988, the contribution of rods to the total cell number was comparable to that at 10 m.

Bacterial biomass estimates (Fig. 2) showed that variations of bacterial carbon over the investigated period were similar for the 5 m and 10 m depths while the pattern at the 15 m depth showed little similarity. Variations of rod biomass closely followed the variation pattern of the total bacterial biomass; in contrast to their relatively low numerical contribution to the total number (Fig. 1), the biomass contribution was generally above 50 % of the total bacterial biomass. Exceptions were observed in Jul 1989 and Apr 1990 at 5 m, in Jan, Jun and Sept 1989 at 10 m as well as in Jun and Apr 1989 at 15 m. Maximum biomass values were seen in summer 1989 and 1990 at 5 m and ranged from 32 to 43 $\mu g\ C\ l^{-1}$. At the 10 m depth 3 summer peaks were seen in the seasonal distribution pattern. The lowest peak value was found for August/October 1988, amounting to 19 $\mu g\ C\ l^{-1}$. Although the Aug/Oct peak in 1988 could also be found at 15 m, high carbon values for summer 1989 are missing and bacterial carbon only amounts to 18 $\mu g\ C\ l^{-1}$. In summer 1990, however, the highest biomass value of all depths 65 $\mu g\ C\ l^{-1}$, was recorded.

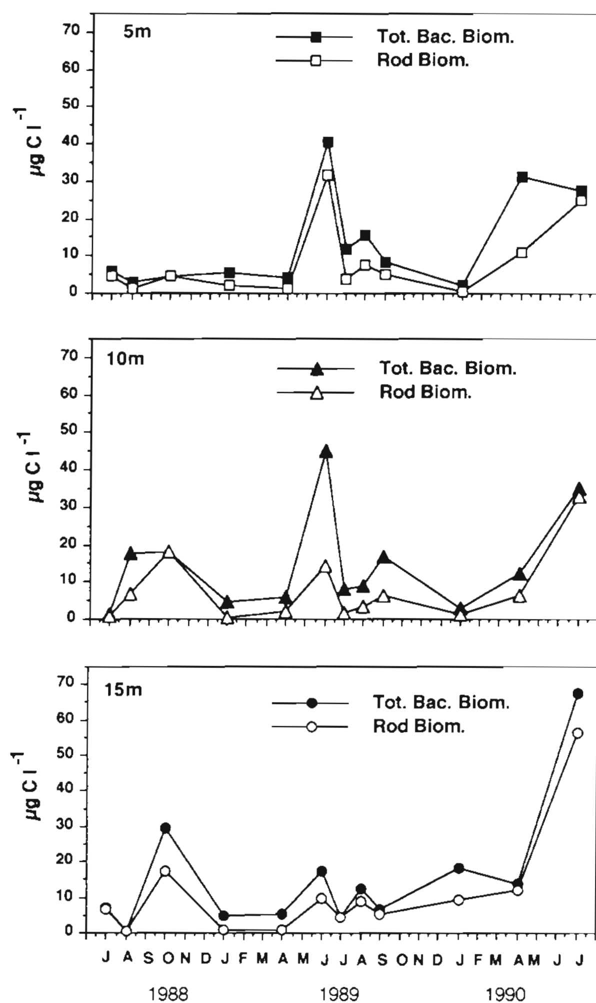

Fig. 2. Changes in bacterial biomass at 5, 10 and 15 m depths from 1988 to 1990

When comparing the curve of specific bacterial growth rates obtained from dialysis bag incubations for the 3 depths with the corresponding temperature curves (Fig. 3), it becomes evident that high growth rates occurred at high water temperatures, while chl *a* concentrations were at a minimum. During Jan and Feb 1989 and 1990, when maximum chl *a* concentrations were recorded for all stations, bacterial growth rates were at a minimum.

Table 1 presents our estimates of generation times, FDC and bacterial secondary production of the 2 µm filtered bacterial population from dialysis bag experiments. Generation times for the summer months (Jun to Sep) ranged from 5.2 to 53 h. Usually the doubling time was lowest at the shallow depth (5 m) with the exception of Jun 1989 where we calculated a generation time of 2.2 d. FDC values tended to increase with increasing bacterial production rates over the summer months. However, the statistical significance of this trend could only be confirmed at 5 m ($r = 0.79$, $p < 0.005$) by a regression analysis. Bacterial production rates in summer reached 9.8 $\mu g\ C\ l^{-1}\ h^{-1}$ with a mean value of 3.07 (SD = 2.28) and the lowest value being 0.41 at 10 m in Jul 1988. In Jan and Apr (both characterized by low bacterial production), the highest value was 1.67 $\mu g\ C\ l^{-1}\ h^{-1}$, average production being as low as 0.72 (SD = 0.52). In Jan 1989, despite an increase in cell number over 24 h, a decrease in bacterial carbon production due to changes of average cell volumes was noticed (see 'Discussion'). Our estimates of bacterial biomass ranged from 1.1 to 32.6 $\mu g\ C\ l^{-1}$ and represent the 2 µm filtered fraction of the population at the beginning of the experiments, providing a basis of comparison with the bacterial biomass from untreated samples shown in Fig. 2. It should be mentioned that in 1989 and 1990, we

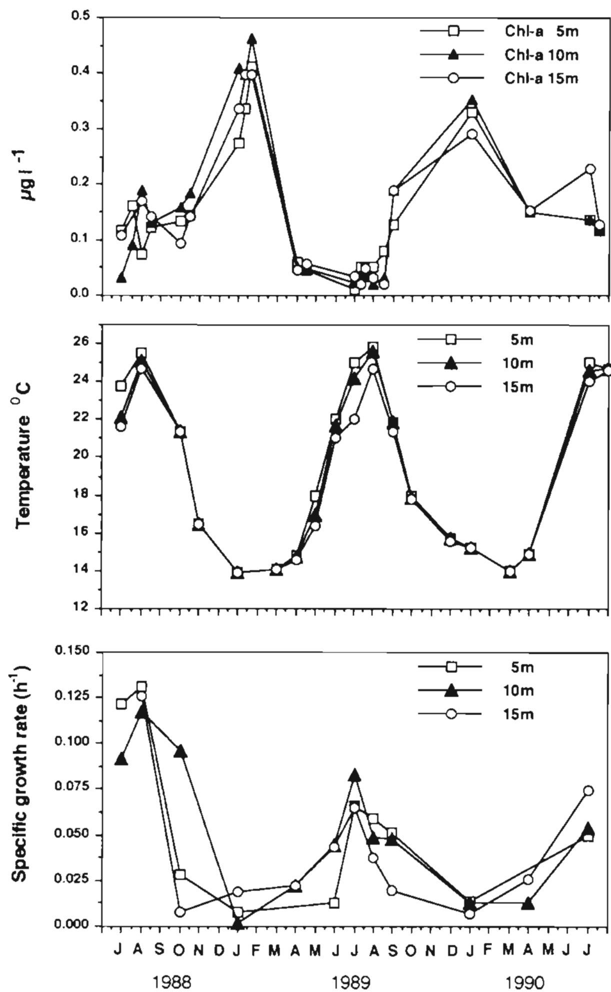

Fig. 3. Variations in chlorophyll a, temperature and specific growth rate (h^{-1}) of water column bacteria at 3 depths from 1988 to 1990

had time intervals of over 24 h between prefiltration of water for dialysis bag experiments and sampling for determination of seasonal bacteria biomass determination. Despite these time intervals, little difference was observed between bacterial biomass from filtered and untreated samples. A significant difference between filtered and unfiltered bacterial biomass variation over the seasons could only be detected for the 15 m depth ($F = 6.67$, $p < 0.01$), where higher values were noted for unfiltered samples in Jun 1989, Jan 1990 and Jul 1990. Although relatively high biomass values were also observed in Jan and Jun 1989 for the untreated samples at the other depths, no significant differences in seasonal biomass variations were detected for the 5 m depth ($F = 2.00$, $p > 0.01$), or the 10 m depth ($F = 2.49$, $p > 0.01$).

We also compared variations of the average cell volume over the seasons at all depths for prefiltered and unfiltered samples (Fig. 4). No significant difference in the variations of the mean cell volume could be detected at 5 m ($F = 1.12$, $p > 0.01$), 10 m ($F = 0.90$, $p > 0.01$) or 15 m ($F = 2.22$, $p > 0.01$).

Table 1. Generation time (*g*), frequency of dividing cells (FDC), standing stocks (biomass), and production of bacterial populations in 2 µm filtered water from 3 depths in the water column above a seagrass bed in Calvi (Corsica) from July 1988 to July 1990. Values are the mean of 2 experiments per month. NP = negative production after 24 h of incubation; nd = not determined

Month/ depth	*g* (h)	FDC (%)	Biomass (µg C l^{-1})	Production (µg C l^{-1} h^{-1})
Jul 1988				
5 m	5.69	2.24	5.93	3.07
10 m	8.87	4.94	1.10	0.41
15 m	nd	nd	7.13	nd
Aug 1988				
5 m	5.28	3.16	3.80	2.24
10 m	5.95	2.31	3.20	1.57
15 m	5.49	2.64	6.28	1.34
Oct 1988				
5 m	24.70	2.50	4.78	4.03
10 m	7.18	1.23	18.10	2.96
15 m	74.60	1.58	29.40	1.30
Jan 1989				
5 m	83.73	3.40	6.93	NP
10 m	259.06	1.86	32.62	NP
15 m	36.08	4.80	2.02	0.12
Apr 1989				
5 m	NP	3.21	4.05	NP
10 m	30.76	6.08	5.76	0.17
15 m	31.46	5.40	5.34	0.61
Jun 1989				
5 m	53.27	10.15	7.86	2.22
10 m	15.41	15.35	5.92	2.79
15 m	14.84	23.74	6.31	1.29
Jul 1989				
5 m	10.54	25.81	12.61	9.84
10 m	8.38	16.37	9.44	3.75
15 m	10.72	21.66	8.39	3.38
Aug 1989				
5 m	11.63	13.11	31.42	4.91
10 m	14.02	17.08	8.33	3.68
15 m	18.33	16.13	8.00	2.49
Sep 1989				
5 m	13.56	13.59	6.19	1.61
10 m	14.98	29.00	6.42	2.53
15 m	23.33	17.16	9.61	0.81
Jan 1990				
5 m	49.81	3.62	4.32	0.16
10 m	63.18	11.04	5.10	0.99
15 m	58.92	6.07	6.61	0.28
Apr 1990				
5 m	167.69	0.49	25.96	0.99
10 m	37.21	5.10	9.74	0.91
15 m	26.56	4.07	13.80	1.67
Jul 1990				
5 m	14.04	14.46	12.09	3.95
10 m	12.90	12.55	12.45	4.86
15 m	9.51	19.16	4.93	3.34

Measurements of O_2 production and consumption for the 3 depths in Fig. 5 revealed a similarity in production and respiration values over the 2 years for the 5 and 10 m depths. The average summer values for 1989 at the 5 and 10 m depths [33.2 (SD = 4.27) and 25.86 µg O_2 l^{-1} h^{-1} (SD = 6.89) respectively] were higher than those found in summer 1990 [21.25 (SD = 8.42) and 18.89 µg O_2 l^{-1} h^{-1} (SD = 11.46)]. The production values at 15 m ranged from 15 to 46 µg O_2 l^{-1} h^{-1}, the highest value being recorded in Apr 1990. The average production value for summer 1989 was 25.71 µg O_2 l^{-1} h^{-1} (SD = 7.32), comparable to the 10 m depth, while the mean summer value for 1990 was 11.60 µg O_2 l^{-1} h^{-1} (SD = 3.85), the lowest summer average of all stations.

To relate bacterial production to primary production in the water column, we expressed hourly production rates of bacteria as percentage of gross primary production from parallel incubation experiments with light and dark bottles (Table 2). In Jan and Apr bacterial production corresponded at most to 7.6 % of the gross primary production, with the lowest bacterial production representing only 1.3 %. A different situation was noticeable in summer; in Jul and Aug 1989 bacterial production ranged from 15.2 to 48.4 % of gross primary production. The highest bacterial production value for Jul 1990 was measured at the 10 m depth and corresponded to 36 % of the gross primary production.

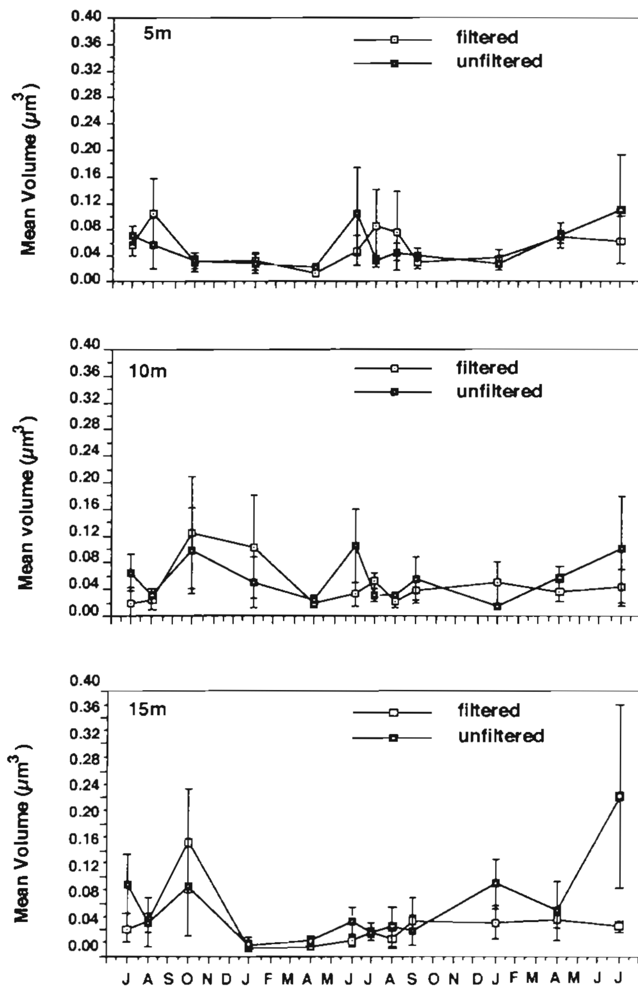

Fig. 4. Mean bacteria cell volume in 2 µm filtered and unfiltered water samples from the 5, 10 and 15 m depth (Mean ± SD) from 1988 to 1990

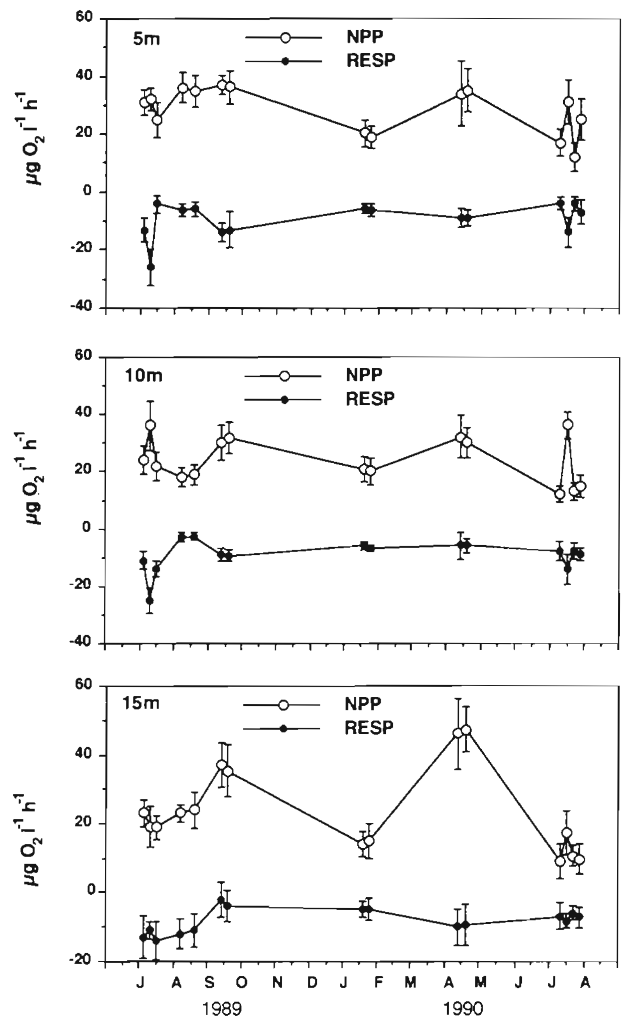

Fig. 5. Oxygen production and consumption in the water column at the 5 m, 10 m and 15 m depth station (Mean ± SD). NPP: Oxygen evolution in light bottle, RESP: Oxygen evolution in dark bottles

DISCUSSION

Comparison of seasonal bacterial growth rates (Fig. 3) with the temperature curve indicates that high growth rates mostly occur above 16 °C. At least on a seasonal basis, it seems that bacterial growth rates are

Table 2. Gross primary production (GPP) and bacterial secondary production (BP), expressed as percentage of GPP for the investigation periods between July 1989 and 1990. Data are mean values of all incubation experiments within the month of investigation as follows: GPP: 11, 13 and 17 Jul, 9 and 20 Aug, 25 and 26 Sep 1989; 29 and 30 Jan, 16 and 17 Apr, 14, 17, 21 and 27 Jul 1990. BPP: 7, 8, 15 and 16 Jul, 7, 8, 18 and 19 Aug, 23, 24, 26 and 27 Sep 1989; 29 and 30 Jan, 13, 14, 17 and 18 Apr, 14, 15, 19 and 20 Jul 1990

Month	Depth (m)	Gross primary production (GPP) ($\mu g\ C\ l^{-1}\ h^{-1}$)	Bacterial production (% of GPP)
Jul 1989	5 m	20.33	48.40
	10 m	20.18	18.53
	15 m	10.85	31.15
Aug 1989	5 m	20.16	24.35
	10 m	10.52	34.98
	15 m	16.29	15.28
Sep 1989	5 m	23.77	6.77
	10 m	19.27	13.12
	15 m	19.58	4.13
Jan 1990	5 m	12.20	1.31
	10 m	12.89	7.68
	15 m	9.25	3.02
Apr 1990	5 m	20.97	4.72
	10 m	18.06	5.03
	15 m	27.40	6.09
Jul 1990	5 m	13.55	29.15
	10 m	13.21	36.79
	15 m	8.59	38.88

not related to the phytoplankton biomass maxima, which occur when bacterial growth rates are lowest. Our data on chl *a* concentrations obtained during winter and spring are in agreement with those recorded by Brohee et al. (1989) in the Gulf of Calvi from Mar to Apr 1986. With the exception of 2 peaks of chl *a* amounting to 1.5 $\mu g\ l^{-1}$ (Brohee et al. 1989) and being recorded during a daily sampling program in Mar 1986, their values are in close agreement with our findings, showing a similar concentration decrease in chl *a* (0.15 $\mu g\ l^{-1}$) for April 1986 as we recorded in April 1989. A point deserving attention is that lowest rates of primary production (Table 2) were measured in Jan, when chl *a* values were at a maximum, while in summer, with the exception of Jul 1990, primary production rates were high. As mentioned by other authors (Larsson & Hagström 1982, Hagström & Larsson 1984, Lancelot & Billen 1984) phytoplanktonic exudate release occurs mainly in summer, thus stimulating bacterial growth but being generally lower in winter when phytoplanktonic biomass may be high but production rates are low. We speculate that the strong seasonal effect on bacterial growth is not mainly due to the effect of changing temperature but rather to seasonal peaks of phytoplankton exudation occurring in summer.

Changes of bacterial cell volumes under low temperature conditions

A contrasting situation with respect to growth rates and corresponding changes in bacterial carbon production was noted in Jan 1989. Despite an increase in cell number at all 3 depths we calculated a decrease of bacterial carbon production over the 24 h incubation period. Generation times in Jan were long (from 36 to

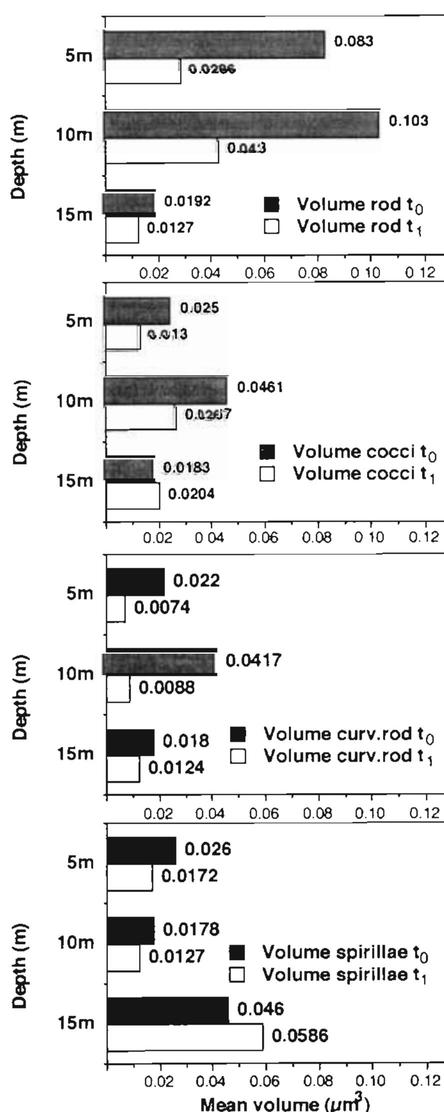

Fig. 6. Comparison of cell volumes for the bacteria morphotypes at beginning and at end of dialysis incubation experiments at 3 depths in January 1989. t_0: bacterial volume at beginning of incubation experiment; t_1: bacterial volume at end of incubation experiment; $t_1 - t_0$ = 24 h

259 h), FDC ranged from 1.8 % of 4.8 % but bacterial carbon production was negative. The analysis of bacterial cell volumes showed that the volumes of most morphotypes decreased over the incubation time (Fig. 6). The volume change was most pronounced for rods at the 5 m and 10 m depths with a decrease by more than one-half. A significant decrease in mean cell volume of rods was detected at 5 m ($F = 17.5$, $n = 200$, $p < 0.01$), at 10 m ($F = 3.25$, $n = 180$, $p < 0.01$) and at 15 m ($F = 6.00$, $n = 200$, $p < 0.01$). A similar situation was observed for curved rods, where mean cell volumes were significantly smaller after the incubation at all depths. For cocci, a significant decrease in mean cell volume was observed for the 5 and 10 m depths, but could not be confirmed for the 15 m depth ($F = 0.857$, $n = 190$, $p > 0.1$). Spirillae were shown to decrease significantly in volume at 5 m ($F = 10$, $n = 140$, $p < 0.01$) but at 10 m and 15 m station significant volume differences could not be confirmed. Such observations were never made for summer incubations, and in most experiments from Jun to Oct we recorded increasing mean cell volumes as well as increasing cell numbers. The tendency of decreasing cell volumes during the winter seasons is confirmed by the variation of the average bacterial cell volume over the seasons at the 5 m depth (Fig. 4) and at least partly supported by the volumes recorded in unfiltered water in Jan and Apr 1989 at the 15 m depth. This appearance of small cell volumes during winter incubations could indicate that bacteria display different growth strategies over the year. Previous to this study, only the increase of bacterial cell volumes under experimental conditions, where predation pressure is reduced by filtration of the water samples, was recorded on several occasions by various authors for dialysis experiments and seawater cultures (Turley & Lochte 1985, 1986, Herndl & Malacic 1987, Velimirov 1989). However, there is no indication that the bacterial volume decrease for the winter incubation experiments is related to higher grazing rates on bacteria compared to the other experiments. All water samples were treated with the same filtration procedure, and heterotrophic flagellates which passed the 2 μm pore size filter did not increase in abundance during the experimentation time. In unfiltered samples used for determination of bacterial abundance and biomass we found low densities of ciliates (4 to 10 ciliates ml^{-1}) and heterotrophic flagellates ranging from 70 to 100 individuals ml^{-1}. Filtration of these samples removed all ciliates and reduced the flagellates on average to 15 ml^{-1} In most samples taken in Jan, flagellate density after filtration was < 7 ml^{-1} without a noticeable increase in number after the incubation period. This observation was confirmed by our seawater culture experiments where an increase of flagellates could only be recorded after 52 h (Velimirov & Walenta-Simon unpubl.). The decrease of cell volume was not restricted to the winter period and also took place in Apr 1989 at the 10 and 15 m depths. We hypothezised that an increase in bacterial number together with a decrease in size may be an appropriate growth strategy under unfavorable environmental conditions. Despite an overall loss of carbon during the process of cell division, the favorable surface-to-volume ratio resulting from the decrease in size may be of advantage to harvest dissolved organic and inorganic nutrients under oligotrophic conditions. Furthermore, environmental events leading to an increase of exudates resulting from occasional bursts of phytoplankton production in winter due to input of inorganic nutrients by upwelled water (Brohee et al. 1989) or resuspension of sediments and pore water nutrients due to winter storms can be used efficiently by a population dominated by small bacteria. The phenomenon of non-growth (Kjelleberg et al. 1983, 1987, Güde 1990) or decreasing cell volume by marine bacteria was repeatedly observed in laboratory experiments as a response to starvation (Novitsky & Morita 1978, Amy & Morita, 1983) and could be triggered by reducing nutrient levels in culture media of various *Vibrio* species (Hood et al. 1986). Also, fast recovery from nutrient starvation was observed for marine psychrophilic *Vibrio* species, and a doubling of cell volume was recorded 8 h after nutrient addition (Amy et al. 1983). These experiments support our speculation based on observations from *in situ* experiments with dialysis bags that cell volume reduction of bacteria during periods of low temperature and low primary production in the water column may be a strategy enabling bacteria to resist starvation and increase their potential for a competitive advantage in nutrient scavenging.

Implications of incubation experiments with dialysis bags

Before attempting to use data from dialysis bag experiments for a more generalized view of the bacterial production in the water column, it was necessary to consider a number of methodological implications. We were able to record direct changes in cell number and biovolume by using dialysis bags because bags possess a combination of qualities necessary for bacterial incubation experiments *in situ* such as sterilizability, strength of the membranes and good diffusivity (for details see Turley & Lochte 1985). Possible disadvantages include the filtration process before incubation and the enclosure conditions of the bacterial population resulting from membrane characteristics of the bags.

Despite prefiltration of our samples we did not expect an important change in the bacterial population (above) and assumed that the enclosed bacteria represented the active fraction of free bacteria in the water column. This is in agreement with earlier studies (Ferguson & Rublee 1976, Watson et al 1977, Sieburth et al. 1978) on size distributions in microbial communities and activity studies (Hoppe 1983) which detected maximum enzyme activity in the 0.2 to 0.6 µm fraction. However, filtration removes most of the particulate organic matter above 2 µm diameter as well as the attached bacteria on these particles. Thus, our estimated bacterial production values are restricted to the free bacteria and bacteria attached to particles below 2 µm. The contribution of attached bacteria on the larger particle size classes to the total bacterial production of the water column is difficult to assess and may lead to an underestimation of the total production. However, it was found that larger seagrass and epiphyte-derived particles are only suspended during periods of strong water movement, have fast settling rates and were poorly colonized by bacteria (Velimirov 1987). Therefore we assumed that bacteria attached to larger particles do not contribute significantly to the total bacterial production in the water column.

A second disadvantage in using dialysis bags was the possibility of bacterial growth on the membranes, observed by several authors after 3 d of incubation (Sieburth 1976, 1979, Vargo et al. 1975), leading to a potential inhibition of diffusion by blocking the pores of the membrane. To avoid this situation, all of our incubation experiments were limited to 24 to 26 h. Furthermore, the connection between bacteria enclosed in the dialysis bag and the dissolved organic and inorganic matter of the surrounding water body is not established at the same rate as in the undisturbed water column. Although various authors have observed that growth is not restricted by diffusion or by a build up of toxic substances (Gerhardt & Gallup 1963, Schultz & Gerhardt 1969) and that growth in experimental bags is exponential, it should still be taken into consideration that the diffusion rate of low molecular weight DOC is expected to be reduced by 40 to 60 % as compared to the diffusion rate in water alone. Therefore the recorded growth rates from dialysis bags may tend to underestimate the potential bacterial growth, especially in experiments where organic nutrients may be a limiting factor.

Carbon requirements of the bacterial community in the water column

As mentioned earlier, bacterial carbon production values within a year may be grouped into 2 periods, characterized by temperature regimes below 16 °C (Nov to Apr) and above 16 °C (May to Oct). Table 3 allows a comparison of estimated mean biomass and production values for 1 l of seawater, assumed to be representative for each of the 3 depths, and provides a basis for speculations on the magnitude of carbon flow between the main compartments in the water column. It can be seen that the seasonal variations in bacterial productivity for the 2 temperature regimes within the year are more pronounced than that of primary productivity. This may be partly due to high primary production values in April, when temperature reaches late spring and summer values. Assuming a carbon conversion efficiency of 50 %, which is close to values obtained from studies using isotope-labeled low molecular weight substrates (Iturriaga & Hoppe 1977, Bell & Sakshaug 1980, Billen et al. 1980, Iturriaga & Zsolnay 1981), it is obvious that to allow a bacterial carbon production in summer ranging from 47.7 to 95.5 µg C l^{-1} d^{-1}, at least 96 to 191 µg C l^{-1} d^{-1} would be required. If we base our calculations on a conversion efficiency of 20 %, as recommended by researchers using direct methods and substrates as phytoplankton detritus (Newell et al. 1981 Bell & Kuparinen, Linley & Newell 1984, Bauernfeind 1985, Bjornsen 1986), some 238 to 477 µg C l^{-1} d^{-1} would be required. Such a carbon requirement could not be covered by phytoplankton production alone and would imply that a carbon input from the seagrass meadow into the water column takes place. In order to decide on the appropriate magnitude of a carbon conversion efficiency representative for the situation in our dialysis bags, we have to consider the fact that over 24 to 26 h incubation we measured primary production of water column bacteria, based on degradation and uptake of dissolved organic substances. Therefore it was appropriate to expect organic carbon conversion with an efficiency closer to 50 % than to 20 %, assuming that phytoplankton production can support all bacterial secondary production in the water column. A different situation is noted for the colder period of the year. To support the bacterial production between Nov and Apr (Table 3), 40.8 to 62.4 µg C l^{-1} d^{-1} are required when a factor of 50 % is used, while 82.8 to 156 µg C l^{-1} d^{-1} were estimated to be required for a 20 % carbon conversion efficiency. All estimated values are well within the range of primary production during this season.

It is obvious that our data, based on growth characteristics of confined bacterial populations, should be applied with caution to field conditions. Nonetheless, we believe that the average production rates for summer and winter reflect the production potential of the water column bacteria above our seagrass bed. Bacterial production rates from the water column above a shallow tropical seagrass bed and a reef flat colonized

Table 3. Comparison of averaged values for heterotrophic bacteria biomass (HBB), bacterial secondary production (BSP) and primary production for periods of high (> 16 °C) and low (< 16 °C) temperature regimes over a year at the 3 depths

Depth	HBB (µg C l^{-1})		BSP (µg C l^{-1} d^{-1})		PP* (µg C l^{-1} d^{-1})	
	Mean	Range	Mean	Range	Mean	Range
May to October (Temperature > 16 °C)						
5 m	14.47	3.08 – 40.54	95.52	38.64 – 236.16	229.48	94.76 – 324.31
10 m	13.72	1.10 – 45.17	67.69	9.84 – 116.64	192.07	113.45 – 345.02
15 m	13.55	0.59 – 67.55	47.76	19.44 – 81.12	164.08	94.60 – 222.88
November to April (Temperature < 16 °C)						
5 m	11.29	2.12 – 31.32	31.20	23.76 – 38.64	172.72	101.84 – 244.30
10 m	10.41	2.74 – 32.62	16.20	4.08 – 23.76	158.91	109.95 – 213.74
15 m	8.66	2.74 – 18.40	20.40	6.72 – 40.08	197.17	76.89 – 317.58

* Daily primary productivity was estimated assuming that mean rates measured over the incubation interval are representative for the photoperiod of the day (Murray & Wetzel 1987), which we defined as 90 % of daylight hours, ranging from 8.53 h in Jan to 12.44 h in Jul. Information on total daylight hours for the northwest coast of Corsica was obtained from the meteorological station-airport St. Cathrine/Calvi

by seagrass (Moriarty et al. 1990) ranged from 12 to 72 µg C l^{-1} day^{-1}, which is in agreement with averaged rates obtained from dialysis bag experiments, with the exception of the higher values at 5 m, monitored during the summer temperature regime. Also, the bacterial production range from a saltmarsh system dominated by *Spartina* was 36 to 242.4 µg C l^{-1} day^{-1} (Newell et al. 1983), similar to the production ranges from our summer experiments. A comparison of our data with bacterial production ranges obtained in other ecosystems shows that high rates were also reported by Vyshkvartsev (1980) who monitored the increase in biovolume, by Newell & Christian (1981) who used frequency of dividing cells to estimate production rates, and Sieburth et al. (1977) who recorded ATP increase in diffusion cultures. Preliminary results from our seawater culture experiments (unpubl. data) seem to confirm our production estimates for both the summer and winter season.

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