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CONTRIBUTION OF PHYTOPLANKTON AND PERIPHYTON TO THE PRODUCTION IN A RESERVOIR OF S.W. SPAIN

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SUMMARY

The phytoplanktonic and periphytic communities of La Minilla reservoir were studied from September 1987 to August 1988. The aim of the present paper is to assess their contribution to total primary production.

The sampling station for phytoplankton was situated in the middle of the reservoir, 500 m from the dam, above the deepest point. The periphyton was studied in a closed bay using slates as experimental substrata. Two kinds of samplers were used with these experimental substrata: potential production samplers (PPS) that always had the same position with respect to the water top, and real production samplers (RPS) that always had the same position with respect to the bottom.

The dominant species in both communities were small and unicellular: *Cyclotella ocellata*, *Rhodomonas minuta* and *Chrysidalis peritaphrena* in phytoplankton, and *Achnanthes minutissima*, *A. linearis* and *Geitleribactron periphyticum* in periphyton.

The production of both communities was estimated by the amounts of chlorophyll *a*. In order to compare the contribution of each community to the total production, the volume of water in the reservoir was estimated and the surface able to be colonized was determined by echosounding.

The annual mean of potential production of the periphytic community was the 5% of the total production (maximum 16% in spring) and the annual mean of real production was 2.44% of the total production (maximum 6% in spring). The differences between potential and real periphytic production were due to the water level fluctuations in autumn and winter and because of grazing in spring and summer.

KEY WORDS: Phytoplankton, periphyton, reservoirs, production

INTRODUCTION

In spite of the numerous studies that have been carried out in the last 20 years in Spanish reservoirs, only occasionally has anything been done on benthic microalgae, such as the work of ALVAREZ COBELAS (1982) on the floristic composition of El Vellón reservoir. The high fluctuations of water level that occur in most of the Spanish reservoirs are considered to be unfavourable for the development of well-structured benthic communities and so their contribution to the total production is of little importance. As yet, though, there are not sufficient studies about this subject. The situation of the studies on benthos in reservoirs and their relation to plankton in the rest of the world also leaves much to be desired.

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Considering the water level fluctuation and the input of nutrients as related factors and limiting to both benthic and planktonic production, we find a series of situations in which water fluctuation affects the benthic organisms negatively, by preventing the settlement of mature communities as they undergo changes in their environment. And it affects the plankton positively since floods mean an input of nutrients and elements that these organisms use more rapidly than the benthic ones. Plankton is then more ready to reproduce and it grows in a way that shades and limits the algae on the bottom surface.

Our studies were centered on La Minilla reservoir (Fig. 1) since its general limnology is well known (TOJA, 1980a, 1980b, 1983, 1984, 1990; TOJA *et al.*, 1983; SANCHO & GRANADO, 1988; GABELLONE & GUISANDE, 1989). Several parameters have been characterized as high constraints for the development of periphyton: 1) the great water level fluctuation (12,4 m during the period of study) that prevents the settlement of macrophytes; 2) the scarcity of nutrients; 3) low water transparency due to inorganic seston; 4) the instability of the substratum and steep slopes.

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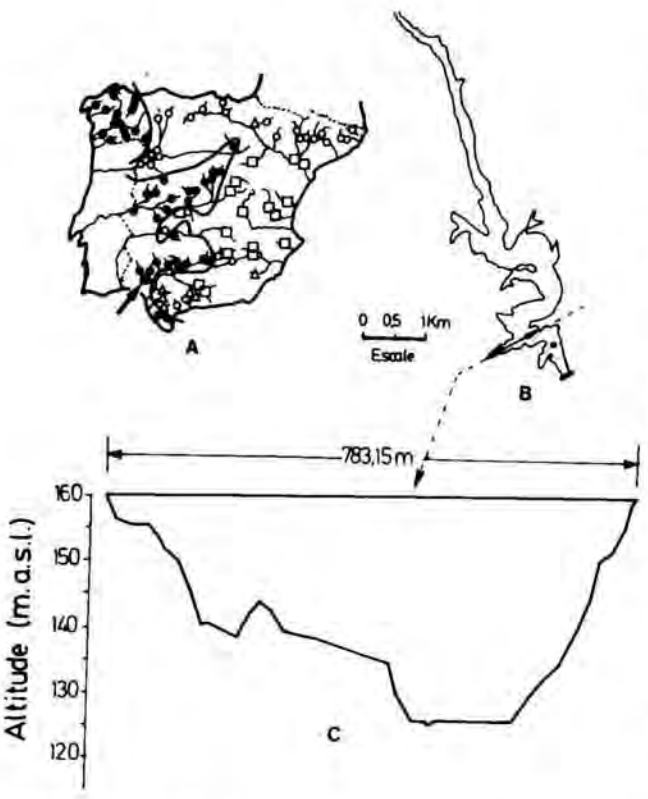

FIGURE 1. A) Location of La Minilla reservoir and its situation in the typology of Spanish reservoirs according to the total dissolved salts (TDS) (ARMENGOL *et al.*, 1991). Full dots, low TDS with high silicate concentrations; open dots, Bicarbonate waters with intermediate TDS; squares, Sulfate waters with high TDS, and triangles, very high TDS with dominance of chloride. B) Location in La Minilla reservoir of the phytoplankton sampling point (dot) and the transect (arrow) for the study of periphyton. C) Section of the transect measured by echosounding.

GEOGRAPHY AND MORPHOMETRY

La Minilla reservoir is located in the Rivera de Huelva river, a tributary of the Guadalquivir river, at 37°43'58''N and 6°9'56''W. It holds a maximum capacity of 60 Hm^3, has a maximum depth of 37 m and a mean depth of 20.83 m. The perimeter at full capacity is 14.5 km. This reservoir is used for the water supply of Seville.

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MATERIALS AND METHODS

Samples were collected monthly from September 1987 to August 1988. A Van Dorn sampler of 6 l of capacity was employed to collect the samples for chemical and phytoplanktonic analysis. The phytoplanktonic study was carried out in the deepest area, at 500 m from the dam and at several depths from 0 m to 35 m. This was the only vertical profile used to characterize the reservoir and it was based on the work by TOJA (1990) who from an extensive sampling concluded that the most prominent differences took place seasonally and not spatially.

The benthic studies were developed at the bay crossed by the transect designed from an extensive benthic sampling (CASCO & TOJA, 1991; Fig. 1). Three samples were collected for the analysis of nutrients: one was obtained at the mean depth of the potential production sampler (PPS) (at 2 m depth) and the other two were obtained from the real production samplers (RPS) at 1,5 and 3 m depth.

Temperature was measured *in situ* with a mercury thermometer; conductivity with a portable YSI conductivimeter and light extinction was compared using a 30 cm diameter Secchi disc; the extinction light coefficient was calculated using k=1.7/Dm (MARGALEF, 1983) and k=2.5/Dm (MARGALEF *et al.*, 1976) equations. The samples for chemical analysis were stored in a refrigerator at 4°C . All analyses were made before 72 hours. Alkalinity was measured by titration using H_2SO_4 with mixed methyl red bromocresol green indicator (APHA, 1971). Soluble phosphate was determined according to the ascorbic acid method (MURPHY & RILEY, 1963). Nitrate was measured by reduction to nitrite through a Cd-Cu column (MORRIS & RILEY, 1963) and nitrite by the colorimetric method of SHINN (1941), all of them from STRICKLAND & PARSONS (1965). Ammonium was determined using Nessler reactive after precipitation with $ZnSO_4$ and OHNa (APHA, 1971).

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Enough substrata were placed at each depth to produce two replicates of the analysis, both for the identification and

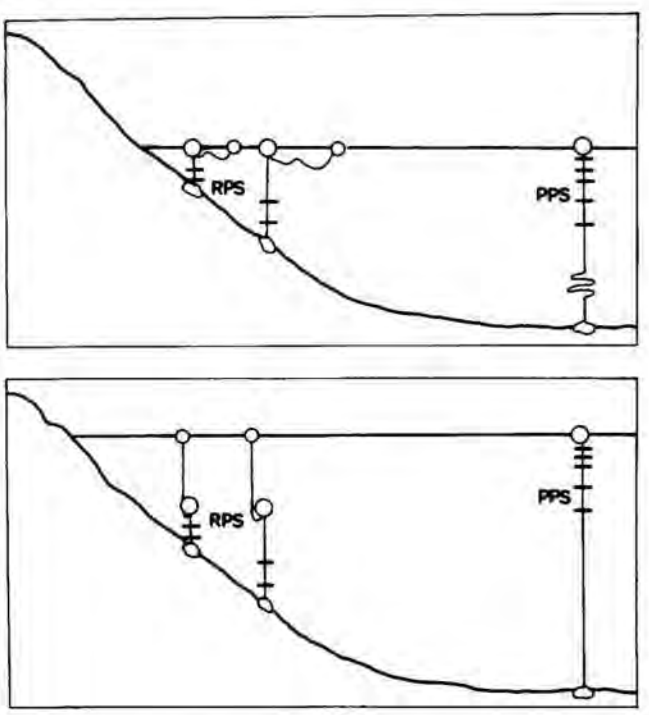

FIGURE 2. Diagrammatic representation of the experimental sampling substrata. The water level fluctuations modified the position of the real production samplers (RPS) with respect to the water surface and the position of potential production samplers (PPS) with respect to the bottom.

counting of species and for the photosynthetic pigment determination.

In order to foresee the situation in which the RPS were dried or below the photic zone, stones or sediment were collected using a dredge or a core sampler respectively on each sampling day at different depths (up to 30 m). The amount of photosynthetic pigments were determined in the same way as for the experimental surfaces.

Phytoplankton was fixed with Lugol and the number of cells were counted following UTERMÖHL's (1958) method. A volume of 25 or 50 ml of each sample was sedimented and the fields were counted at random under a 400x magnification. To determine the floristic composition of the periphyton, samples were fixed with a formalin solution of 4%. On each stone an area was scratched whose surface had been calculated by wrapping it in aluminium foil and its weight compared with the weight of a known area of the same kind of foil. The use of this method allowed the inclusion of every crack on the stone in the determination of the surface for colonization. The solution obtained was homogenized and then aliquots of 50fl were taken and fields were counted at random at 400x under the optical microscope. Colonies, coenobies and filaments in both plankton and benthos have been considered as individuals.

In the photosynthetic pigment determination, 1 litre was filtered for the phytoplankton at each depth through a Whatman GF/C filter. Two pieces of rock of a known area were scratched for the benthos determination. Methanol was used in both analyses as solvent. The methanolic extracts were preserved in a freezer for less than 10 days. Then they were filtered through Whatman GF/C filters and their absorbance was read on a Perkin Elmer 550 SE UV/VIS spectrophotometer. After acidification with HCl 0.4 N the absorbance at 750 and 665 nm was read again in each sample for the correction of the phaeopigments (LORENZEN, 1967; VARELA, 1981).

The surface and volume available for benthic and planktonic colonization respectively, were determined from the bathimetric data obtained by echosounding (50 KHz, 12° transducer, pulse length: high 1.1 msec, low 0.3 msec) along the transect chosen (Fig. 1; HAKANSON, 1981). Four sounding tracks were performed and the perimeter of the bottom was estimated as the mean value obtained from the 4 echoprofiles with respect to the maximum height of 160 m asl. A strip of one meter in width was used to calculate the surface and volume to be colonized according to the water level and the depth of light penetration.

The total amount of planktonic chlorophyll in this strip was calculated by multiplying the chlorophyll *a* concentration of each sampling depth by the water volume of the corresponding strip. The results of each strip were all added up to the limit of the euphotic zone. The benthos was obtained in a similar way, by calculating the total surface to be colonized at each sampling depth and by multiplying it by the corresponding chlorophyll concentration. If the photic zone were wider than the sampling depth, the chlorophyll obtained from the natural substratum was then employed, since, as previous studies had shown (Casco, unpublished data), substrata acquired their stability of colonization before one month of exposure.

RESULTS

Physico-chemical data obtained in the photic zone from the open water and from the bay where the samplers had been placed are shown on Table I.

The temperature of the open water photic zone ranged from 11.80 °C in February 1988 to 27.10 °C in July 1988. Thermal stratification started in March and

TABLE I. Data of some physico-chemical parameters obtained from the water taken in the sampling point of plankton (at a depth of 2 m), and from the potential samplers (PPS, at 2 m of depth) and from the real samplers (RPS1 at 1.5 m and RPS2 at 2.5 m of depth). T: temperature (°C). C: Conductivity (µS cm^{-1}). A: Alkalinity (meq l^{-1}). No: nitrate (µg-at N l^{-1}). Ni: Nitrite (µg-at N l^{-1}). A: Ammonia (µg-at N l^{-1}). P: Phosphate (µg-at P l^{-1}).

Date	T	C	A	No	Ni	A	P	Date	T	C	A	No	Ni	A	P
Open Water								RPS1							
22-09-87	23.5	276	1.87	0.97	0.12	63.26	0.46	22-09-87	26.0		2.46	0.03	0.03	1.43	0.18
28-10-87	19.5	260	1.88	0.39	0.36	1.07	0.50	28-10-87	15.7		1.55	0.00	0.00	4.84	0.00
27-11-87	13.9	256	1.83	9.32	0.13	24.33	0.07	27-11-87	13.2	118	1.00	0.48	0.48		0.00
08-01-88	12.0	160	0.93	28.03	0.64	5.10	1.33	08-01-88	11.0	118	0.71	0.63	0.63	3.11	1.08
08-02-88	11.8	173	1.15	28.63	0.24	6.20	1.80	08-02-88	10.0	120	1.19	0.33	0.33	7.31	0.85
16-03-88	13.9	182	1.26	22.29	0.10	1.30	0.00	16-03-88	18.0	151	1.35	0.30	0.30	2.98	0.00
16-04-88	17.8	215	1.57	8.25	0.38	5.26	0.00	16-04-88	17.5	228	1.30	0.75	0.75		2.00
20-05-88	21.6	218	1.65	5.25	0.38	6.76	0.00	20-05-88	16.0	190	1.64	0.21	0.21	5.71	0.07
24-06-88	24.3	216	1.68	1.50	0.04	5.06	0.00	24-06-88	24.0	210	1.69	0.12	0.12	6.04	0.27
27-07-88	27.1	218	1.83	4.58	0.06	3.35	0.20	27-07-88	28.0	258	1.83	0.12	0.12	6.18	0.00
27-08-88	26.2	250	1.96	0.95	0.09	4.82	0.00	27-08-88	26.0	180	1.62	0.27	0.27	1.12	4.52
PPS								RPS2							
22-09-87	26.0		2.08	0.00	01.00	0.71	1.88	22-09-87	25.2		2.36	0.00	0.00	1.78	0.18
28-10.87	17.5		1.64	9.69	9.69	15.31	0.00	28-10-87	17.5		1.57	0.00	0.00	4.60	0.00
27-11-87	13.0	11.8		0.56	0.56		0.00	27-11-87	13.2	118	1.00	0.48	0.48		0.00
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08-02-88	10.0	120	1.10	0.41	0.41	6.64	1.02	08-02-88	10.0	120	1.14	0.36	0.36	11.29	0.73
16-03-88	13.0	148	1.33	0.19	0.19	2.98	0.00	16-03-88	15.0	153	1.33	0.25	0.25	2.98	0.00
16-04-88	15.0	228	1.55	0.76	0.76	6.43	0.22	16-04-88	14.5	228	1.30	0.46	0.46	1.90	0.16
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27.08-88	26.0	2770	1.95	0.27	0.27	0.67	3.68	27-08-88	15.0	180	1.62	0.27	0.27	1.12	4.52

the thermocline was established at a depth of between 5 and 10 m in April. The maximum gradient was produced in July with a decrease of 1.96 °C per meter.

Conductivity ranged from 160 to 276 µS cm^{-1} in the open water. However, the bay showed a rather different pattern. Conductivity here is slightly below that of the open water during rainy periods due to the direct effect of run-off inputs and to a delay in the mixing with the water that arrives from the rest of the drainage basin. The values were the same only in July, then the conductivity in the bay started to increase at a proportional rate as a result of evaporation and resuspension of the sediment when the water level fell.

Nitrogen and phosphorus were similarly concentrated in the open water and the littoral and their variation with time followed a similar pattern. However, there were differences at certain moments which are mostly due to the removal of sediments from the shore caused by the water level fluctuations. These fluctuations can be observed in figure 3, where the water level variation of the reservoir is indicated for the study period, as well as the location of the RPS (from their emplacement to their removal) with respect to the water surface and the limit of the euphotic zone. The heavy rainfall during the autumn-winter period of 1987-88 determined that the reservoir was practically full during the rest of the study. The water level started to fall only during July and August, but it was always higher than in the summer of 1987 when the width of the fluctuation reached 17 m.

This heavy rainfall also provoked a high increase in suspended inorganic seston during December, January and February, limiting the width of the photic zone to a maximum of 2.5 m. During this period the

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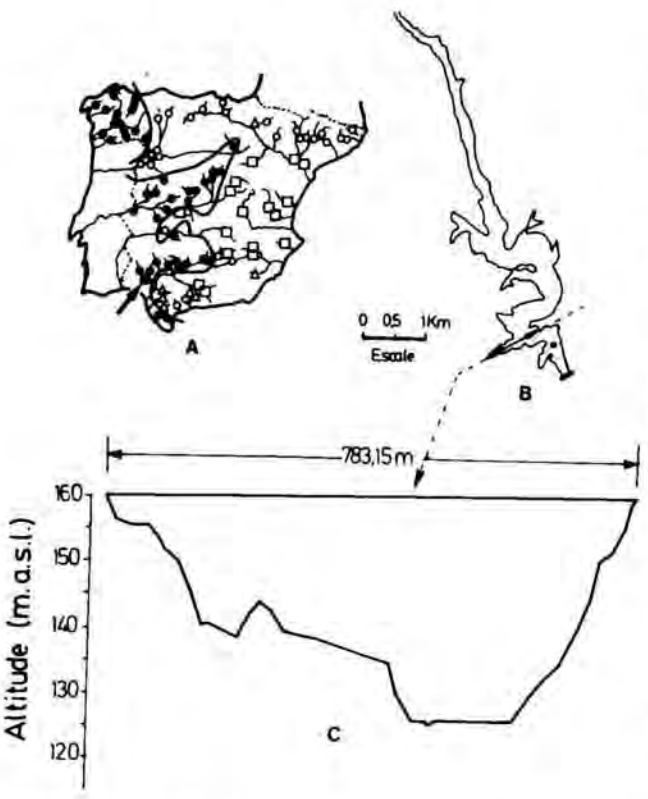

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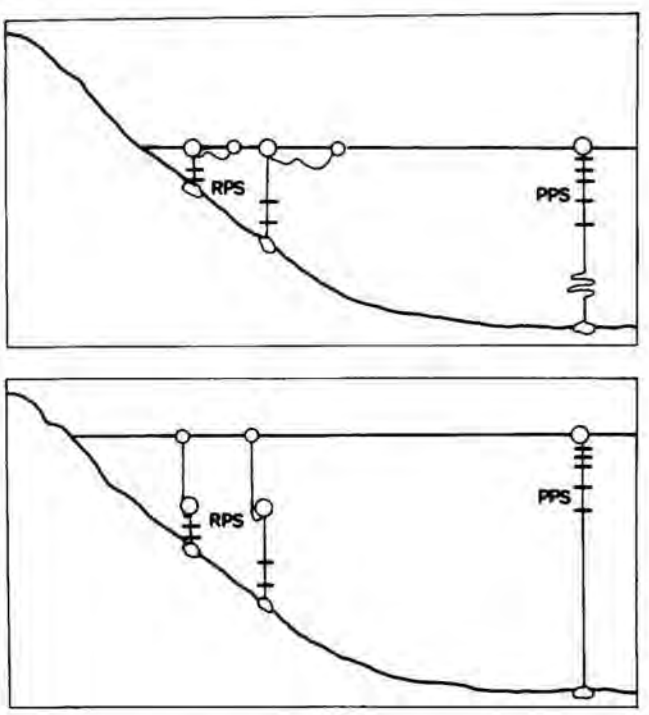

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In order to foresee the situation in which the RPS were dried or below the photic zone, stones or sediment were collected using a dredge or a core sampler respectively on each sampling day at different depths (up to 30 m). The amount of photosynthetic pigments were determined in the same way as for the experimental surfaces.

Phytoplankton was fixed with Lugol and the number of cells were counted following UTERMÖHL's (1958) method. A volume of 25 or 50 ml of each sample was sedimented and the fields were counted at random under a 400x magnification. To determine the floristic composition of the periphyton, samples were fixed with a formalin solution of 4%. On each stone an area was scratched whose surface had been calculated by wrapping it in aluminium foil and its weight compared with the weight of a known area of the same kind of foil. The use of this method allowed the inclusion of every crack on the stone in the determination of the surface for colonization. The solution obtained was homogenized and then aliquots of 50fl were taken and fields were counted at random at 400x under the optical microscope. Colonies, coenobies and filaments in both plankton and benthos have been considered as individuals.

In the photosynthetic pigment determination, 1 litre was filtered for the phytoplankton at each depth through a Whatman GF/C filter. Two pieces of rock of a known area were scratched for the benthos determination. Methanol was used in both analyses as solvent. The methanolic extracts were preserved in a freezer for less than 10 days. Then they were filtered through Whatman GF/C filters and their absorbance was read on a Perkin Elmer 550 SE UV/VIS spectrophotometer. After acidification with HCl 0.4 N the absorbance at 750 and 665 nm was read again in each sample for the correction of the phaeopigments (LORENZEN, 1967; VARELA, 1981).

The surface and volume available for benthic and planktonic colonization respectively, were determined from the bathimetric data obtained by echosounding (50 KHz, 12° transducer, pulse length: high 1.1 msec, low 0.3 msec) along the transect chosen (Fig. 1; HAKANSON, 1981). Four sounding tracks were performed and the perimeter of the bottom was estimated as the mean value obtained from the 4 echoprofiles with respect to the maximum height of 160 m asl. A strip of one meter in width was used to calculate the surface and volume to be colonized according to the water level and the depth of light penetration.

The total amount of planktonic chlorophyll in this strip was calculated by multiplying the chlorophyll *a* concentration of each sampling depth by the water volume of the corresponding strip. The results of each strip were all added up to the limit of the euphotic zone. The benthos was obtained in a similar way, by calculating the total surface to be colonized at each sampling depth and by multiplying it by the corresponding chlorophyll concentration. If the photic zone were wider than the sampling depth, the chlorophyll obtained from the natural substratum was then employed, since, as previous studies had shown (Casco, unpublished data), substrata acquired their stability of colonization before one month of exposure.

RESULTS

Physico-chemical data obtained in the photic zone from the open water and from the bay where the samplers had been placed are shown on Table I.

The temperature of the open water photic zone ranged from 11.80 °C in February 1988 to 27.10 °C in July 1988. Thermal stratification started in March and

TABLE I. Data of some physico-chemical parameters obtained from the water taken in the sampling point of plankton (at a depth of 2 m), and from the potential samplers (PPS, at 2 m of depth) and from the real samplers (RPS1 at 1.5 m and RPS2 at 2.5 m of depth). T: temperature (°C). C: Conductivity (µS cm^{-1}). A: Alkalinity (meq l^{-1}). No: nitrate (µg-at N l^{-1}). Ni: Nitrite (µg-at N l^{-1}). A: Ammonia (µg-at N l^{-1}). P: Phosphate (µg-at P l^{-1}).

Date	T	C	A	No	Ni	A	P	Date	T	C	A	No	Ni	A	P
Open Water								RPS1							
22-09-87	23.5	276	1.87	0.97	0.12	63.26	0.46	22-09-87	26.0		2.46	0.03	0.03	1.43	0.18
28-10-87	19.5	260	1.88	0.39	0.36	1.07	0.50	28-10-87	15.7		1.55	0.00	0.00	4.84	0.00
27-11-87	13.9	256	1.83	9.32	0.13	24.33	0.07	27-11-87	13.2	118	1.00	0.48	0.48		0.00
08-01-88	12.0	160	0.93	28.03	0.64	5.10	1.33	08-01-88	11.0	118	0.71	0.63	0.63	3.11	1.08
08-02-88	11.8	173	1.15	28.63	0.24	6.20	1.80	08-02-88	10.0	120	1.19	0.33	0.33	7.31	0.85
16-03-88	13.9	182	1.26	22.29	0.10	1.30	0.00	16-03-88	18.0	151	1.35	0.30	0.30	2.98	0.00
16-04-88	17.8	215	1.57	8.25	0.38	5.26	0.00	16-04-88	17.5	228	1.30	0.75	0.75		2.00
20-05-88	21.6	218	1.65	5.25	0.38	6.76	0.00	20-05-88	16.0	190	1.64	0.21	0.21	5.71	0.07
24-06-88	24.3	216	1.68	1.50	0.04	5.06	0.00	24-06-88	24.0	210	1.69	0.12	0.12	6.04	0.27
27-07-88	27.1	218	1.83	4.58	0.06	3.35	0.20	27-07-88	28.0	258	1.83	0.12	0.12	6.18	0.00
27-08-88	26.2	250	1.96	0.95	0.09	4.82	0.00	27-08-88	26.0	180	1.62	0.27	0.27	1.12	4.52
PPS								RPS2							
22-09-87	26.0		2.08	0.00	01.00	0.71	1.88	22-09-87	25.2		2.36	0.00	0.00	1.78	0.18
28-10.87	17.5		1.64	9.69	9.69	15.31	0.00	28-10-87	17.5		1.57	0.00	0.00	4.60	0.00
27-11-87	13.0	11.8		0.56	0.56		0.00	27-11-87	13.2	118	1.00	0.48	0.48		0.00
08-01-88	10.8	11.8	0.71	0.63	0.63	2.83	1.09	08-01-88	10.5	118	0.71	0.63	0.63	2.83	1.09
08-02-88	10.0	120	1.10	0.41	0.41	6.64	1.02	08-02-88	10.0	120	1.14	0.36	0.36	11.29	0.73
16-03-88	13.0	148	1.33	0.19	0.19	2.98	0.00	16-03-88	15.0	153	1.33	0.25	0.25	2.98	0.00
16-04-88	15.0	228	1.55	0.76	0.76	6.43	0.22	16-04-88	14.5	228	1.30	0.46	0.46	1.90	0.16
20-05-88	16.0	190	1.66	0.23	0.23	3.93	0.07	20-05-88	16.0	190	1.64	0.21	0.21	5.71	0.07
24-06-88	23.0	218	1.69	0.13	0.13	7.97	0.11	24-06-88	23-7	210	1.71	0.09	0.09	3.30	1.10
27-07-88	28.0	272	1.81	0.15	0.15	7.89	0.34	27-07-88	28.0	258	1.81	0.10	0.10	13.43	1.46
27.08-88	26.0	2770	1.95	0.27	0.27	0.67	3.68	27-08-88	15.0	180	1.62	0.27	0.27	1.12	4.52

the thermocline was established at a depth of between 5 and 10 m in April. The maximum gradient was produced in July with a decrease of 1.96 °C per meter.

Conductivity ranged from 160 to 276 µS cm^{-1} in the open water. However, the bay showed a rather different pattern. Conductivity here is slightly below that of the open water during rainy periods due to the direct effect of run-off inputs and to a delay in the mixing with the water that arrives from the rest of the drainage basin. The values were the same only in July, then the conductivity in the bay started to increase at a proportional rate as a result of evaporation and resuspension of the sediment when the water level fell.

Nitrogen and phosphorus were similarly concentrated in the open water and the littoral and their variation with time followed a similar pattern. However, there were differences at certain moments which are mostly due to the removal of sediments from the shore caused by the water level fluctuations. These fluctuations can be observed in figure 3, where the water level variation of the reservoir is indicated for the study period, as well as the location of the RPS (from their emplacement to their removal) with respect to the water surface and the limit of the euphotic zone. The heavy rainfall during the autumn-winter period of 1987-88 determined that the reservoir was practically full during the rest of the study. The water level started to fall only during July and August, but it was always higher than in the summer of 1987 when the width of the fluctuation reached 17 m.

This heavy rainfall also provoked a high increase in suspended inorganic seston during December, January and February, limiting the width of the photic zone to a maximum of 2.5 m. During this period the

turnover rate of water in the epilimnion was also very high: the water in the photic zone was renewed 4.77 times in January and 3.64 times in February. Thus, plankton was negatively affected in such a way that in January the amount of chlorophyll was very low (0.5 mg m^{-3}) and in February only 1.25 mg m^{-3} of chlorophyll were detected.

Table II shows the dominant species in both plankton and the littoral areas of the reservoir for every sampling date. It also indicates the number of individuals per millilitre in each area and the total number of ind. ml^{-1} in the community. The plankton community was represented by an integrated sample of the whole photic zone, whereas the benthos was represented by the average result from the samplers. The maximum density in the plankton was 4239 indiv ml^{-1} in October 1987 and the minimum was 123 ind. ml^{-1} in February 1988 (with a chlorophyll concentration of 7.42 and 1.25 mg m^{-3} respectively). There is a seasonal tendency to establish the maximum values on the surface as a result of a lower light intensity in winter and, particularly during this winter, when the turbidity constrained the development of organisms to the upper layers, *Cyclotella ocellata* was the dominant species during almost the whole sampling period, although its dominance was substituted by *Rhodomonas minuta* during the winter of 1987-88. The motility of this last species enables it to migrate to the upper layers where light intensity is less limiting. This situation has already been verified (TOJA, 1984). However, light intensity is not the only cause of this shift in the dominance of species: alkalinity seems to be of greater importance (Table I). MARGALEF *et al.* (1976) mentioned that *Cyclotella ocellata* is a better competitor in calcium-enriched waters.

Aphanocapsa elachista is present almost all the year and it is generally limited to the hypolimnion. In October it extended to the whole profile and co-dominated with

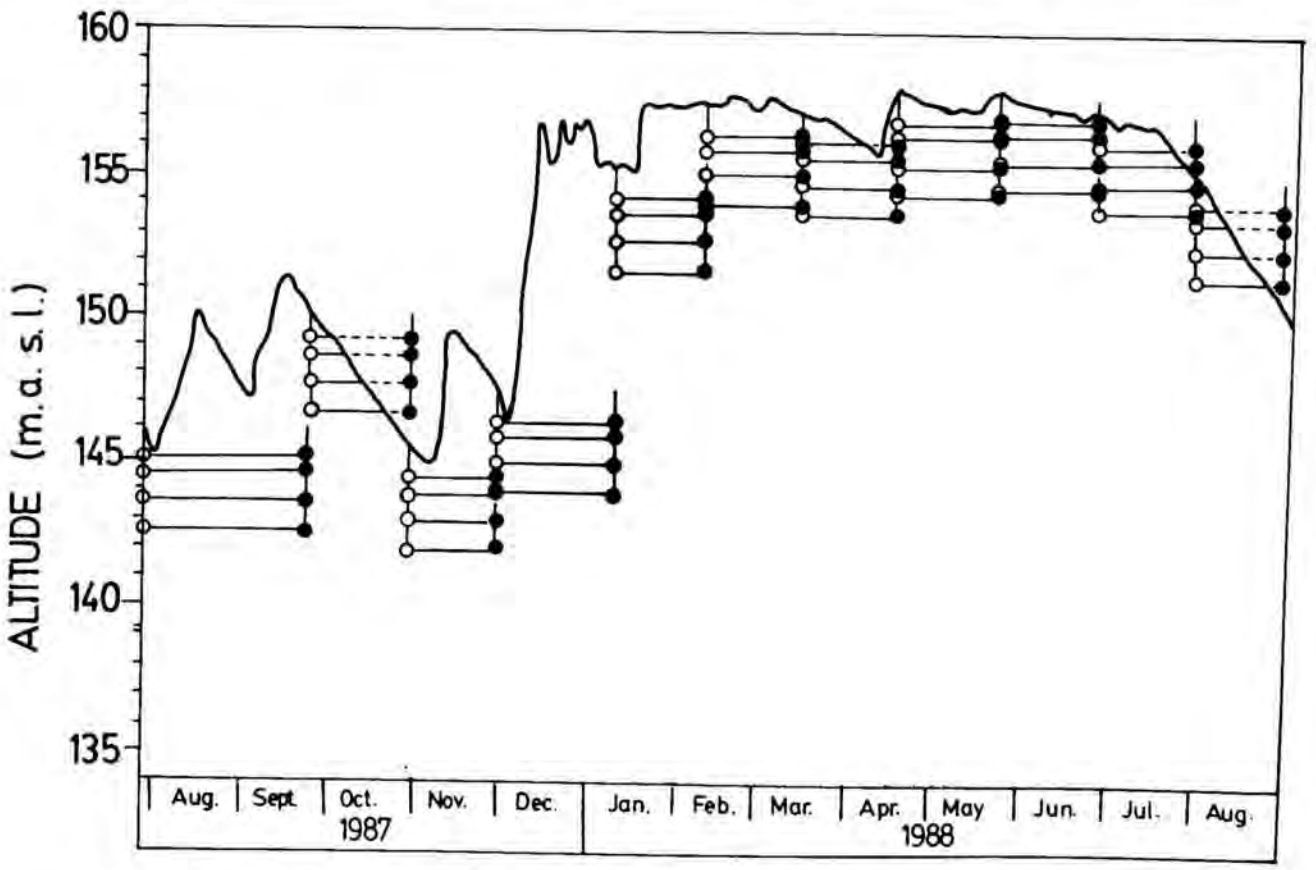

FIGURE 3. Variation of the water level during the study period. The location of the periphyton real production samplers (RPS) at the moment of their installation (open dots) and removal (full dots) have been marked with respect to their distance to the water surface. The depths without light have been shadowed.

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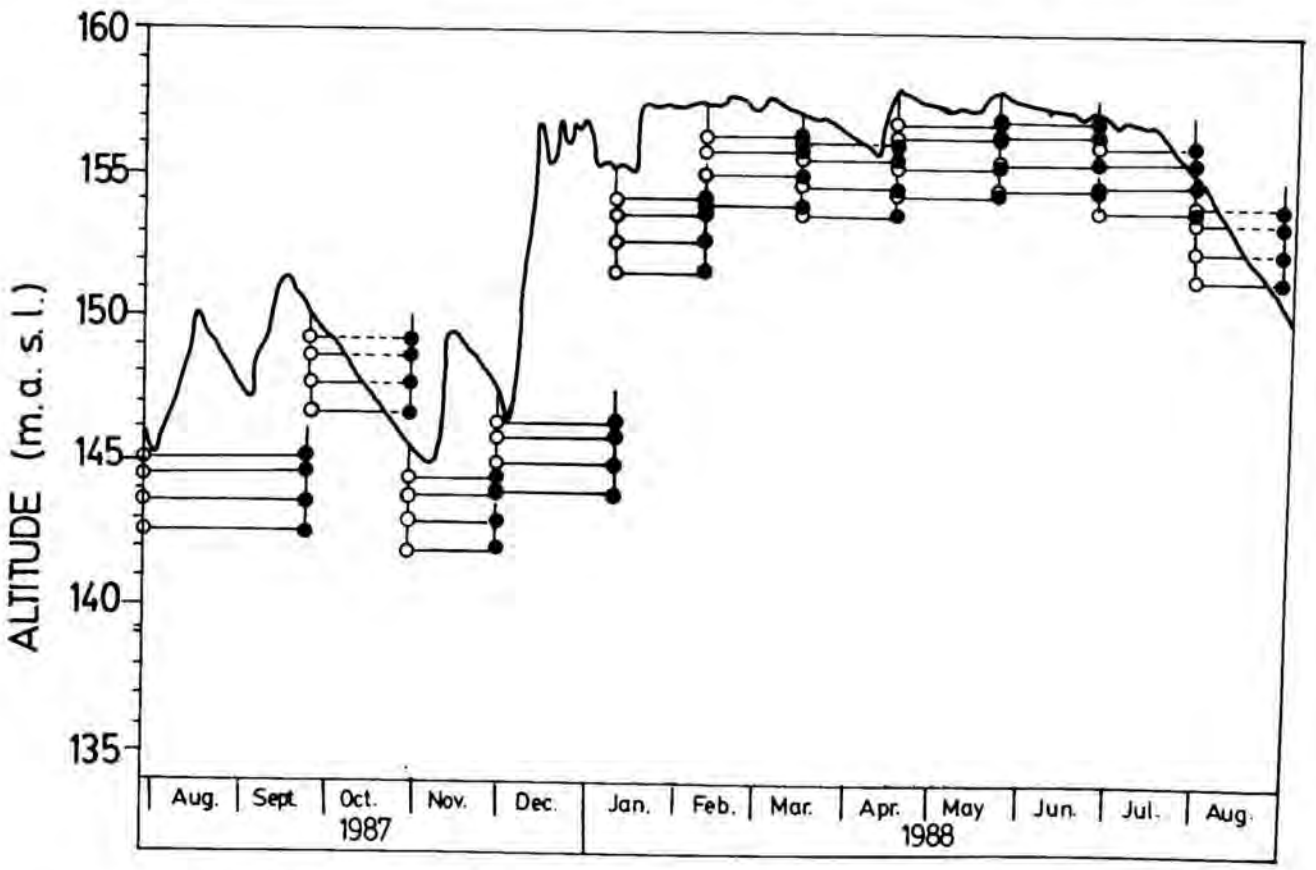

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TABLE II. Dominant species and total number of individuals per millilitre on each sampling date. For the phytoplankton community the mean value of ind ml^{-1} from the photic zone has been used. For potential and real production benthos samplers the mean value of ind cm^{-2} in all samplers has been used. The coenobia and colonies have been counted as one individual. Only live individuals have been considered.

SEPTEMBER 1987					
Cyclotella ocellata	1410	Lyngbya sp.	1061148	G. periphyticum	313544
Chrysidalis peritaphrena	1063	Lyngbya perelegans	244156	Achnanthes linearis	135112
Oocystis marssoni	294	Achnanthes linearis	186516	Achnanthes minutissima	6499
		G. periphyticum	138800	Lyngbya perelegans	5914
Total	3491	Total	1845294	Total	488576
OCTOBER 1987					
Lyngbia limnetica	1137	Achnanthes minutissima	172645	G. periphyticum	15658
Aphanocapsa elachista	991	G. periphyticum	142100	Achnanthes linearis	2315
Cyclotella ocellata	810	Achnanthes linearis	86165	Lyngbia perelegans	1795
Total	4239	Total	451680	Total	28174
NOVEMBER 1987					
Rhodomonas minuta	1097	A. minutissima	244742	A. minutissima	174497
Cyclotella ocellata	466	Achnanthes linearis	117480	Achnanthes linearis	127653
Lyngbia limnetica	190	Synedra acus	57943	G. peryphyticum	127628
Total	2422	Total	492595	Total	4300927
JANUARY 1988					
Rhodomonas minuta	374	A. minutissima	1994200	A. minutissima	249
Cyclotella ocellata	14	Navicula placentula	30027	A. linearis	61
		Achnanthes linearis	7629	Navicula placentula	37
Total	401	Total	2082615	Total	710
FEBRUARY 1988					
Cryptomonas ovata	28	A. minutissima	1319276	Navicula placentula	54
Rhodomonas minuta	22	Achnanthes plinensis	42082	A. minutissima	21
Trachelomonas intermedia	11	Gomphonema herculeana	41150	Achnanthes linearis	17
Total	123	Total	1465647	Total	143
MARCH 1988					
Chrisidalis peritaphrena	299	A. minutissima	4650476	A. minutissima	156799
Cyclotella ocellata	259	Chloroccocal sp. 1	127710	Cymbella laevis	74975
Navicula sp. 3	149	Achnanthes lanceolata	28725	Amphora veneta	61142
Total	1446	Total	4897814	Total	838927
APRIL 1988					
Cyclotella ocellata	792	A. minutissima	4650476	A. minutissima	6330098
Rhodomonas minuta	734	Achnanthes linearis	636944	Achnanthes linearis	366695
Oocystis parva	112				
Total	2858	Total	4186725	Total	1071124
MAY 1988					
Mycrocystis minutissima	486	A. minutissima	7668923	A. minutissima	7872246
Rhodomonas minuta	233	Achnanthes linearis	280588	Achnanthes linearis	94018
Cyclotella ocellata	180				
Total	1115	Total	7975112	Total	7975100
JUNE 1988					
Aphanocapsa elachista	725	A. minutissima	5250513	A. minutissima	1680203
Rhodomonas minuta	576	Achnanthes linearis	280588	Achnanthes linearis	1538127
Chrysidalis peritaphrena	313				
Cyclotella ocellata	180				
Total	2294	Total	7325441	Total	3256618
JULY 1988					
Cyclotella ocellata	723	A. minutissima	1421200	A. minutissima	1093640
Rhodomonas minuta	347	Achnanthes linearis	1476822	Achnanthes linearis	1025433
Chrysidalis peritaphrena	108				
M. tennuissima	99				
Total	2872	Total	2986417	Total	2243158
AUGUST 1988					
Chrysidalis peritaphrena	723	A. minutissima	1436783		
Cyclotella ocellata	276	Achnanthes linearis	303244	DRY	
M. tennuissima	245				
Total	1421	Total	2234315		

Lyngbya limnetica. The presence of this species decreased during the mixing period and was constrained to the hypolimnon until June when it co-dominated again, this time with *Rhodomonas minuta*.

With respect to the benthos, in general, it was noted that the number of species of diatoms without mucilaginous stalks predominated and that there was little representation of filamentous chlorophytes. In most cases, the resulting physiognomy was of a community developed in only one stratum.

Species of *Achnanthes* (especially *A. minutissima*) were present in great numbers during all the sampling period both in the potential and in the real samplers. Even after April 1988, *A. minutissima* and *A. linearis* composed almost the total community (Table II). Diversity reached a maximum in March but decreased after May. A conspicuous population of *Chlorohydra* sp. was established in the potential samplers during July (Table III). This allowed the chlorophyll level to be maintained though the number of individuals in the periphyton decreased. *Geitleribactron periphyticum* is another important species in this community, but it shows a greater relative abundance in the real samplers, where it grew in a layer.

The major qualitative difference between both experimental substrata was observed during April, and this was also the only time in which large green algae (*Pseudoulvella americana, Coleochaete scutata, C. soluta* and *Stigeoclonium* sp.) were present.

Generally in plankton, the maximum amount of chlorophyll during winter corresponded to the surface (Fig. 4) especially between January and April as a result of the lower light intensity and the turbidity of the water and of the output of water between 2 and 4 m in depth (154-156 m asl) in this particular winter. This brought about the exploitation of these levels (TOJA, 1982). When, in summer, the photic zone increased to an average of 10 m, the maximum amount of chlorophyll was obtained at a depth of between 5 and 10 m, which showed a certain relation to the depth of the thermocline.

The experimental surfaces were at a constant distance from the surface (Fig. 2). Thus, potential production of benthos was not affected by fluctuations in the water level, but rather by the turbidity and the availability of nutrients (Table I). In figure 4 chlorophyll *a* values are shown.

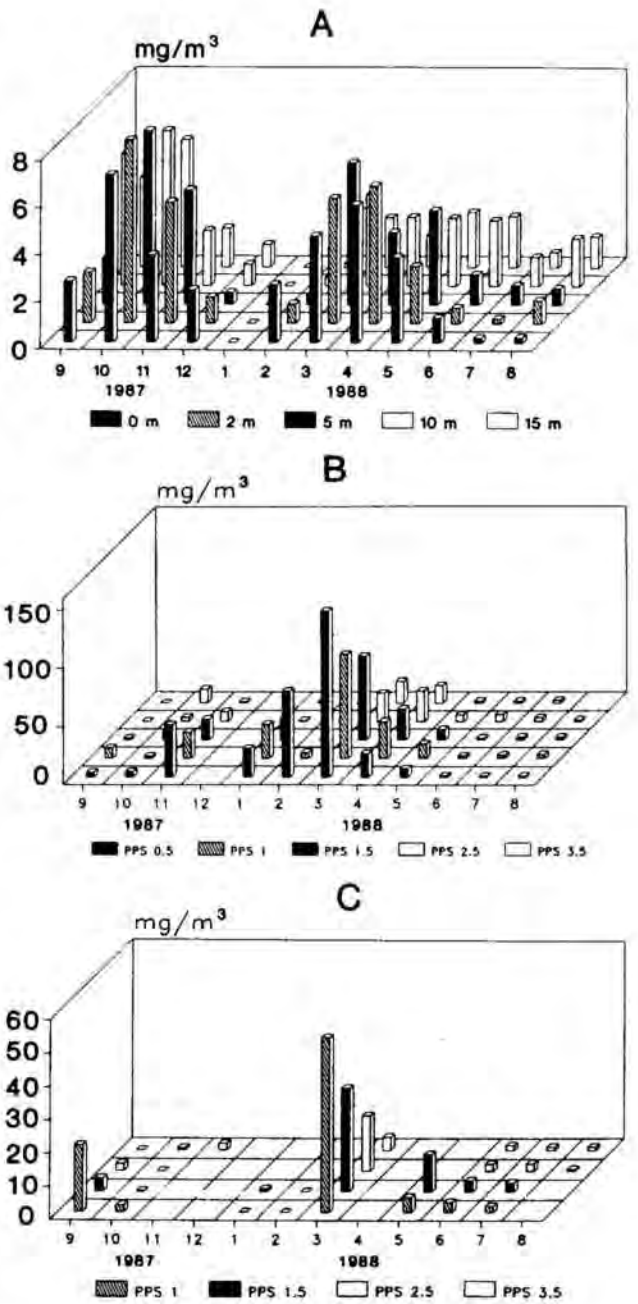

FIGURE 4. Variation of the chlorophyll concentrations in the plankton samples (A) and the potential production (B) and real production (C) benthos samplers.

TABLE III. Fauna associated with the potential and real production samplers of periphyton. 3: abundant; 2: frequent; 1: scarce.

	PPS 1987-88												RPS 1987-88											
	S	O	N	J	F	M	A	M	J	J	A		S	O	N	J	F	M	A	M	J	J	A	
Rhizopoda																								
Diflugia sp.	.	1	.	.	.	.	.	.	.	1	.		.	.	.	.	.	.	.	.	.	1	.	
Amoeba sp.	.	.	2	.	.	.	1	.	.	.	1		.	.	.	.	.	.	1	1	.	.	.	
Pseudoheliozoa																								
Vampyrella sp.	.	.	.	.	.	2	.	.	.	.	.		.	.	.	.	.	3	.	.	.	.	.	
Ciliophora																								
Vorticella sp.	3	2	.	1	1	.	.	.	.	1	.		3	2	2	1	.	1	.	.	.	.	.	
Codonella sp.													.	1	.	.	.	.	.	.	.	.	.	
Coelenterata																								
Chlorohydra sp.	.	.	.	.	.	1	.	.	3	1	.		.	.	.	.	.	.	.	.	.	.	.	
Nematoda	.	.	.	.	.	.	.	.	.	.	.		.	.	.	.	.	.	.	.	.	2	2	
Mollusca																								
Cl. Gasteropoda	.	.	.	.	.	.	1	.	.	.	.		.	.	.	.	.	.	.	.	.	.	.	
	.	.	.	.	.	1	2	2	.	.	.		.	.	.	.	.	.	.	.	.	.	.	
Ephemeroptera																								
Caenis luctuosa	2	2	2	.	.	.	.	.	.	.	.		.	.	.	.	.	.	.	.	.	.	.	
Diptera																								
F. Chironomidae	1	1	.	.	.	.	1	1	1	.	.		.	.	.	.	.	.	.	.	.	3	2	

Chlorophyll increased from August to November 1987 and reached a value of 50 mg m^{-2} at a depth of 0.5 m possibly because of an increase in nutrients due to the water input of the first rainfalls. Then, the massive rainwater discharge in winter produced a decrease, although much less marked than that of the plankton since the benthic community was not washed along by the water input. Nevertheless, the diminished photic zone limited the production to the upper layers, as can be proved by the great difference in chlorophyll concentration from the substratum at 0.5 m with respect to the rest of surfaces during February. The maximum concentrations were detected in March and April (up to 130 mg m^{-2} of chlorophyll) and were linked to the availability of nutrients and the increase of the photic zone. A much steeper decline than in the plankton can be observed after May. This may be produced by a lesser availability of nutrients or by a negative effect of light on the epiphytic community. Productivity was kept relatively low during the rest of the summer and values similar to the previous year were only attained in August.

The RPS, however, were subjected to the water level fluctuations in such a way that they were above the water surface for certain periods of time (October-November 1987; July-August 1988) or else they were so deep that they were found below the photic zone (December 1987, January-February 1988).

Although the real production samplers always showed lower values of chlorophyll (maximum of 70 mg m^{-2}), they evolved in a similar way to the potential production ones (Fig. 4). However it has to be noted that the surfaces at 1-1.5 and 2.5 m were lost in November 1987.

From March to July 1987 (Fig. 3) both PPS and RPS were subject to the same conditions of water level, light and

TABLE IV. Volume and surface that can be colonized by the phytoplankton and periphyton communities in a section of 1 m of width of the transect considered. Data of total amounts of chlorophyll *a* of phytoplankton and periphyton in the photic zone at each sampling date and both potential and real percentage of the total chlorophyll at each sampling date. The altitude of the water level (m asl) and the depth of the photic zone (z) are also given.

Date	Volume m^3	Area m^2	Plankton mg Cla m^{-3}	PPB mg Cla m^{-2}	PPB %	RPB mg Cla m^{-2}	RPB %	level m asl	Z m
22-09-88	4532	80	14401.44	282.02	1.92	363.84	2.46	152.00	8.12
27-10-87	3238	43	3237.95	90.72	0.37			146.50	5.56
21-11-87	8288	131	32768.39	541.79	1.62	189.78	0.57	149.20	10.83
08-01-88	1275	68	510.19	1746.40	77.39	65.58	11.38	156.35	1.81
08-02-88	1671	32	1986.12	400.24	16.77	33.17	1.64	158.38	2.30
16-03-88	3548	102	19541.81	3167.63	13.94	1259.01	6.05	158.60	5.09
16-04-88	7257	200	30267.04	1808.88	5.63	1296.72	4.10	158.80	14.08
20-05-88	8045	191	24112.99	407.47	1.66	293.21	0.98	158.90	12.20
24-06-88	6528	158	11942.42	219.17	2.38	203.92	1.67	158.16	9.75
29-07-88	6199	103	5216.11	215.51	3.96	173.71	3.22	155.50	9.71
29-08-88	4295	61	4945.25	107.13	2.12	51.13	1.02	150.86	7.31
Annual mean	4995	106	15448.43	823.54	5.06	387.60	2.44		

nutrients. Yet, the real production was lower than the potential production. This can only be explained by selective predation. The real production samplers always showed a greater colonization by animals (Table III), possibly due to a higher accessibility for the benthic fauna, than the potential production samplers, which were suspended at a medium depth.

Although real and potential benthic productivity per m^2 was higher than planktonic productivity per m^3, especially in spring, the volume available for planktonic colonization is much greater than the benthic surface available during the different seasons. Thus, the total amount of planktonic chlorophyll in absolute terms is much higher than the total benthic chlorophyll (Table IV).

The benthic percentage contribution to the total production is especially high in spring, reaching 16% for the PPS. However, the maximum value for the RPS is 6% (except during the unusual situation of winter time, when only the benthos is productive as the plankton is strongly affected).

The mean surface to be colonized by the benthos during the year was approximately 2% of the volume to be colonized by the plankton. On calculating the mean annual amount of chlorophyll both in the plankton and benthos from the RPS, it can be observed that the benthic chlorophyll represented 2.44% of the total chlorophyll, that is, the benthic production per m^2 is approximately equal to the planktonic one per m^3 of volume. These results are in accordance with those obtained by KAIRESALO (1980) in the oligotrophic lake Pääjärvi (Finland). KAIRESALO (1980) also found that the benthic share to the total production is 6%, 75% being from plankton and the rest from macrophytes. The latter component does not exist in La Minilla and it is rare in the rest of Spanish reservoirs.

DISCUSSION

Most of the work on algae living on the bottom surface, attached or not, has been developed in lakes and rivers. Descriptive studies have been carried out both at the community and species levels (MARGALEF, 1947a; DOUGLAS, 1958; CASTENHOLZ, 1960; TELL, 1972, 1979; ETTL, 1973; ROSENMARIN & GELIN, 1978; SULLIVAN, 1979; KOUWETS,

1980; HUDON & BOURGET, 1981; MUNTEANU & MALY, 1981; ROUNIK & GREGORY, 1981; BLUM, 1982; ANTONIETTI, 1983; KAIRESALO, 1984; MEULEMANS & ROSS, 1985; MEULEMANS, 1988). However, in spite of this wealth of descriptive data, there is little research work into the causes that determine the presence, attachment and growth of periphyton (HILLBRICHT-ILKOWSKA *et al.*, 1972; MARCUS, 1980; ROOS, 1983; AUSTIN & DENISEGER, 1985; KAIRESALO *et al.*, 1985; KAIRESALO & KOSKIMIES, 1987) as well as few *in situ* studies on primary production (WETZEL, 1963; HILLBRICHT-ILKOWSKA *et al.*, 1972; DAVIS BROWN, 1976; CATTANEO & KALFF, 1979; AIZAKI, 1979; APESTEGUIA & MARTA, 1979; ROGERS & BREEM, 1981; CARIGNAN & KALFF, 1982; FONTAINE & NIGH, 1983; KAIRESALO, 1983; DELBECQUE, 1983; BUTTON, 1986; ANTONIETTI *et al.*, 1987) or on the role of the periphyton in the functioning of the system analyzing the energetic metabolism of the littoral communities (WETZEL, 1960; CONFER, 1971; ALLEN, 1971; KAIRESALO, 1977; CATTANEO & KALFF, 1980; KAIRESALO, 1980).

It is widely known that research into the periphytic communities is very difficult. There is a great spatial heterogeneity in the microdistribution of organisms and in the different habitats from lotic and lentic environments. The methodology to deal with each piece of research is also highly diverse and has been the subject of numerous studies (MARGALEF, 1947b, 1949; KEVERN *et al.*, 1960; CASTENHOLZ, 1961; WETZEL, 1965; WETZEL & WESTLAKE, 1969; DUMONT, 1969; HICKMAN, 1969; BOTT & BROCK, 1970; HANSMANN *et al.*, 1971; JONES, 1974; GITTINS, 1976; VARELA, 1981; ELORANTA, 1983; DUFF *et al.*, 1984; ANTONIETTI & FERRINI, 1986; CASCO & D'AMELIO, 1987). Yet it is still necessary to formulate new methods and to adapt those already existing, mainly to explain their functioning.

The study of periphyton started long ago, but its advances have been slow and fragmented. Slow, because much of the work was devoted to interpreting the communities by describing and systematizing them, and fragmented because of the multiplicity of ways to deal with this work, chiefly due to the difficulty in applying proper methodologies. This brings about great trouble when it comes to comparing studies from different authors, as the aim of each of them needs to be explained.

When comparing the photosynthetic activities of different communities either absolute or relative production rates have been used (ELSTER, 1965). Relative production rates can be defined using various biomass parameters of which total cell volume and chlorophyll *a* concentration are the most common (MUNAWAR & MUNAWAR, 1975; KAIRESALO, 1980). In our case, the similar size of dominant species in both plankton and benthos permitted the use of chlorophyll *a* concentrations of each subsystem for this comparison.

Few data existing in the bibliography can be compared with the results from this work. All of them refer to periphyton in lakes but not in reservoirs. However, as has already been mentioned, some similarity with KAIRESALO's (1980) results exist both in the productivity per unit of volume and surface and in the percentage of benthic algae to the total production. MEULEMANS (1988) cited FLICK & KEINER's (1981) work about the contribution of epiphytes attached to *Phragmites communis* in Lake Maarsseveen, where it was estimated to represent 1% of total production. Chlorophyll values from this community range from 10 to 200 mg m^{-2} of substratum, which is in a similar order of

magnitude to the values found in this study. MARGALEF (1983) cited Moss's results in some epilithic communities: 127-1200 mg m^{-2}; Szczepanska's results in the periphyton of lakes of Masuria: 300 mg m^{-2}; Moss and Feljöldy's chlorophyll values from several periphytic communities: 110-2350 mg m^{-2}, and Moss's results in communities from mud and sand substrata: 281-286 mg m^{-2}. The chlorophyll concentration of samples from soft sediment found in this study ranged from 0.53 to 85.13 mg m^{-2}, varying according to each season and the depth of the sample.

The chlorophyll values obtained in this work from the samplers are always bordering on the lower limits of the data previously mentioned in the literature, possibly because of the lack of nutrients in the PPS and the effect of the water level fluctuation in the RPS. More similar to our data are TUITE's (1981) results found in a chain of lakes in Kenya and Tanzania, where he found average values of 45 mg m^{-2} in the photic zone.

The results found in this study indicate that the total planktonic production is much higher than the real benthic production. This could be chiefly due to the great difference existing between the volume and the surface to be colonized (which is very small because of the steep slopes of the basin) since both productivities per surface and volume units are similar. Therefore it is expected that in reservoirs with other morphology, that is, with a smaller mean depth, the share of benthos can be much higher. The water level fluctuation in La Minilla also contributes to a considerable decrease in production.

At first, the depth of the photic zone was calculated using k=2.5/Dm as the light extinction coefficient, suggested by MARGALEF *et al.* (1976) as the most suitable way to calculate it for reservoirs. However, the chlorohyll data obtained here both from RPS and PPS indicated that, in fact, below this limit there was enough light to support the development of periphyton so we adopted the equation k=1.7/Dm (MARGALEF, 1983) to fix a limit that is now adjusted to the results obtained, and is also confirmed by the results of RULL *et al.* (1984).

If the water level did not fall (as in a lake of similar morphology) the contribution of benthos would duplicate PPS. However, it would always be small and similar to the data found in oligotrophic lakes (KAIRESALO, 1980; MARGALEF, 1983). Not all of the Spanish reservoirs suffer the wide level fluctuations like those located in the Mediterranean area and devoted to water supply and irrigation. Therefore, the share of the benthos may be somewhat higher than that reported here.

Logically, the higher relative importance of plankton makes the physico-chemical characteristics of the water vary according to the planktonic activity and not the benthic activity. But, from a production point of view, the benthos also plays its role, especially in the littoral area where this production can be considerable for the associated fauna. When considering only the littoral area (up to the limit of the photic zone), the relationship surface/ volume increases and, then, so does also the relative benthic contribution. The annual mean of real production is aproximately 22% of the total in this area of La Minilla.

The effect of fauna on the samplers had been clearly observed when it was proved that real production is approximately half the potential production in the seasons favourable to snails (spring) and nematodes (summer), the rest of the factors being equal for both samplers. Table III shows that the abundance of these organisms is always higher in the RPS than in the PPS, except in the case of *Caenis luctuosa* which was only recorded in winter at a depth of 0.5 m in the PPS. However, this can easily be explained by the increase of water level in the reservoir in this season. Then, the RPS remained too deep to be colonized.

The effect of nematodes was very clear since an inverse relationship between their number (greater in the deepest sustrata) and the number of algae cells existed. The higher relative abundance of *Gleitleribactron periphyticum* in the RPS was probably a result of lower grazing than that suffered by diatoms, which would allow greater proliferation.

It is notable that in July 1988 the number of cells in the PPS was much lower than that of other samples collected near them (Table II), though chlorophyll concentration was similar (Fig. 4). This may be explained by a large population of *Chlorohydra* sp. that proliferated during this month. Then, the chlorophyll concentration could be overestimated in relation to May, June and August when fewer *Chlorohydra* sp. were observed.

It can be concluded from these results that benthic production is impeded more by a rise in water level than by a fall, especially if it is a sudden change. When the water rises the recently flooded areas must be colonized again because either they do not present algae or the algae are in resistant forms. However, previous data from the same reservoir (CASCO & TOJA, 1991) and from direct samples from benthos collected during the study period show that below the photic zone (even down to a depth of 30 m) a considerable amount of living algae can be found. They are rapidly activated at the moment in which the water level falls and they begin to receive light. SUNDBACK & GRANELI (1988) demonstrated that algae can survive for several weeks in the dark and can be rapidly activated when they are exposed to light. MOSS (1977) reported that epipelic algae can tolerate darkness for 3 weeks if they can find aerobic conditions (which is the normal situation in the hypolimnion of La Minilla) and, though their survival is reduced in anaerobic conditions, they can maintain a photosynthetic potential for several days in the absolute absence of oxygen. With relation to the specific composition it is noteworthy that there was a higher number of *Lyngbya perelegans*, *Lyngbya* sp. and *Geitleribactron periphyticum* in deeper samplers than in surface ones.

Finally, though our studies were carried out in one place in the reservoir it is very likely that the benthic production calculated for this section was very similar to the one that would be obtained when considering the total reservoir. Previous studies indicate that there are no significant differences in quantity or composition of phytoplankton (TOJA, 1989) or periphyton (CASCO & TOJA, 1991) along the longitudinal axis of the reservoir. Also, several echosounding tracks performed in 1981 (GUILLÉN & TOJA, unpublished data) show that, generally, the different sections of the reservoir have a similar morphology to the transect designed for this study, except in the tail of the reservoir. which is in fact, the old river bed.

The results of this study show that even in a reservoir where there are such unfavourable conditions for the benthos as in La Minilla, the benthic contribution to the total production is, at least in spring, noticeable. Reservoirs with fewer fluctuations in water level or with a lower mean depth might present a much more considerable benthic production; thus we claim that this subsystem should be paid more attention than to date.

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