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Structure and functioning of the anthropogenically transformed Comacchio lagoonal ecosystem (Ferrara, Italy)

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ABSTRACT: Since 1985, the lagoons of Comacchio, in the coastal area of the NW Adriatic Sea, have been experiencing an ecological catastrophe caused by an extremely dense bloom of picocyanobacteria. The bloom has resulted in a drastic depletion of all kinds of zooplankton, including protozoa. It has caused mass mortality of benthic fauna and the collapse of valuable eel and mullet fisheries. The ecosystem of these lagoons, being thus completely transformed and deprived of animal components of its food web, appears to be remarkably stable on annual and seasonal scales. Its main functional component is the phytoplankton community dominated by several species of picocyanobacteria of the genera *Coelosphaerium*, *Aphanothece* and *Synechococcus*. In this paper quantifications of the main components of the plankton are presented together with data on standing stocks of organic matter and its cycling, and on the cycling of phosphorus and sulfur. The energy balances of the ecosystem are calculated and energy flow schemes derived. The mechanism of the extreme stability of this new kind of aquatic ecosystem and a probable scenario of its origin are discussed.

KEY WORDS: Lagoonal ecology · Aquaculture · Cyanobacteria · Eutrophication · Microplankton

INTRODUCTION

The Comacchio lagoonal system is situated in the coastal zone of the Northwestern Adriatic Sea 25 km north of Ravenna. It is separated from the sea by the 2.5 km wide Spina spit (Fig. 1) and includes the Magnavacca lagoon, 8 km in diameter, and the Campo lagoon, 2 km in diameter. The lagoons are connected with the Adriatic Sea by 2 marine channels (Fig. 1). They have a salinity of 30 to 38‰ and depth range of 0.8 to 1.5 m. For centuries they were among the most valuable fishing grounds in Italy, being rich in eels, mullets, clams, shrimps and other animals. However, during the last decade they have been experiencing an ecological catastrophe caused by an extremely dense chronic bloom of picocyanobacteria. The bloom began in 1985 and resulted in depletion of zooplankton and of zoo- and macro-phytobenthos. Finally it also caused fish mortality. These developments led to a drastic collapse of all kinds of fishery.

Initial studies on the environmental situation in the lagoons in August 1993 revealed a previously unknown kind of ecological collapse. A formerly productive and healthy lagoonal ecosystem degenerated into one practically devoid of a food web or animal grazers and producing chiefly cyanobacterial biomass in the water column and hydrogen sulfide in bottom sediments, both toxic for aquatic fauna. The processes leading to the build-up of cyanobacterial biomass and hydrogen sulfide production are interconnected thus providing a stability in time over seasons and years unusual for any temperate natural aquatic system. This transformed ecosystem has not shown any signs of seasonal succession since 1985. This phenomenon deserved careful study. The present research was carried out during summer (August to September) and November 1993.

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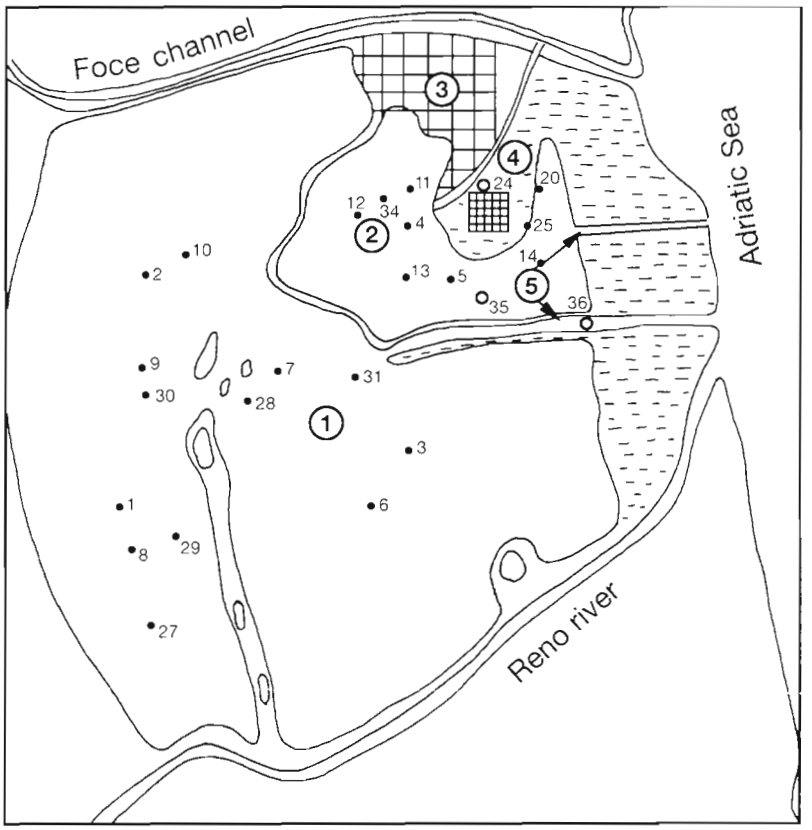

Fig. 1. Schematic map of the Comacchio lagoons and positions of stations. Encircled numbers: 1, lagoon of Magnavacca; 2, lagoon of Campo; 3, lagoons of Salina; 4, intensive fish culture plant of SIVALCO and Laboratory; 5, marine channels

MATERIALS AND METHODS

Samples of water and bottom sediments were taken in the main Comacchio lagoons in August at Stns 1 to 5, in September at Stns 6 to 14 and in November at Stns 27 to 31 and 33. For positions of stations, see Fig. 1. Stns 24 to 26 were situated around the fish culture plant: Stn 24 in front of the entrance, Stn 25 in the exit channel pond, and Stn 26 in the exit intermedial pond. Stn 36 was situated in the Bellocchio marine channel through which Adriatic water enters the lagoons.

Phytoplankton numbers and average sizes of cells within size groups were estimated after Caron (1983) by epifluorescence microscopy on black Nuclepore filters stained with the primuline fluorochrome. Bacterioplankton was likewise quantified after Hobbie et al. (1977). Zooflagellates were counted on the same filters prepared for counts of phytoplankton. Viable ciliates were quantified by counting in chambers 4 mm deep and 15 ml in volume after Sorokin (1980). The same chamber was used to count rotifers if any were present in the sample. Mesozooplankton was collected by passing 80 l of water through a 40 µm mesh plankton net.

The primary production of phytoplankton was estimated a using modified radiocarbon method (Sorokin 1960, 1987). Samples for measuring the photosynthetic rate in the surface layer (C_{ps}) were exposed to natural illumination *in situ* for 2 h during the second half of the light day. For the calculation of primary production per whole day we used empirical curves of its diurnal course (Fig. 2). To estimate the primary production per m^2 in the water column empirically estimated K_t curves were used (see Fig. 3). These curves describe the dependence of the relative photosynthesis rate along a vertical profile in the water column upon the light attenuation within the depth (Sorokin 1960). They were estimated experimentally by exposure of bottles containing identical water samples at different depths *in situ*. We did not correct for its dependence also upon the vertical distribution of active phytoplankton (K_p-curves), because the latter appeared to be quite even in these shallow lagoons.

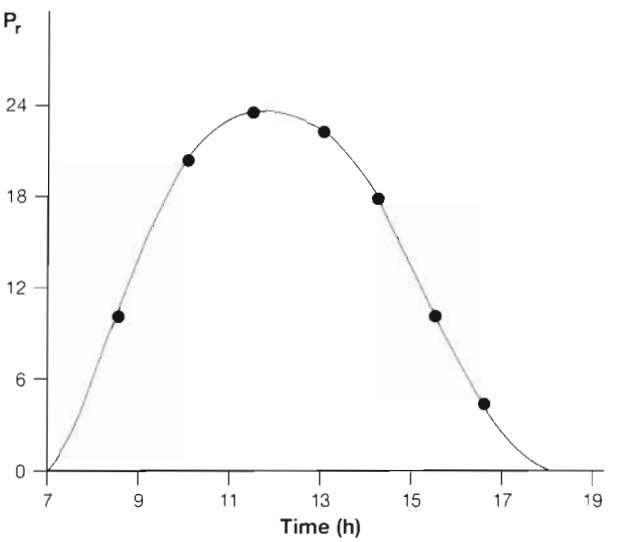

Fig. 2. Diurnal course of photosynthesis rate in water sample from the Magnavacca lagoon in September; P_r: relative rate of photosynthesis

The production of bacterioplankton was measured by the dark ^{14}C uptake method of Romanenko modified by Sorokin (1990). The total plankton respiration (decomposition, M_1) was estimated as dissolved oxygen uptake rate in water samples contained in 250 ml bottles by their exposure (in triplicate) for 6 h at the *in situ* temperature. The oxygen content in these experiments was measured by Winkler titration. Uptake rates (A_1) and turnover time (TP) were estimated with the aid of $^{32}PO_4$-P as label (Sorokin 1985). The stock of labile organic matter (LOM) in water was estimated with the use of the BOD-30 method after Sorokin & Mamaeva (1980). The original water samples for this analysis were diluted 1:20 with double distilled water. The BOD-30 in the distilled water used was accounted for during the calculations. The value of LOM stock (SL) was calculated in units of carbon as: SL = 0.55 BOD – 30 mg l^{-1}. The suspended organic matter content in water was analysed by wet chromic combustion on glass fiber filters, using chromic acid solution in concentrated (95%) H_2SO_4 containing a trace of $AgSO_4$. The samples were combusted at 135°C for 30min, and titrated iodometrically after cooling. The content of organic matter in bottom sediments was measured by the same method after previous exposure of the dried samples to concentrated phosphoric acid for 1 d to dissipate chlorides. The stock of acid-soluble sulfides in sediments was measured in samples of mud in which the sulfides were previously fixed with a mixture of $ZnSO_4$ + Na_2CO_3. The hydrogen sulfide was distilled out from the acidified sediments and trapped with Cd-acetate + Na_2CO_3 solution after Sorokin (1975). Then the sulfide in this mixture was estimated by iodometric titration. The rate of H_2S production in sediments due to the microbial sulfate reduction was estimated with the use of labeled sulfate, $^{35}SO_4$, after Sorokin (1982).

All estimations of C, P and S uptake or turnover rates were made in duplicate. In the tables mean values are given to an accuracy of ±5 to 8% SD. The stations represented in the tables were selected to cover the ranges of parameters measured in the lagoons.

RESULTS

Phytoplankton and primary production

The data on phytoplankton density and composition (Table 1) show in both main lagoons, in both summer and late autumn, a highly dense bloom of picocyanobacteria without substantial differences except for a decrease in density from 140 to 300 g m^{-3} in late summer to 50 to 140 g m^{-3} in late autumn. However even the latter lower level of phytoplankton density is at least 3 to 5 times more than that found during an ordinary seasonal bloom or even in 'red tide' blooms in eutrophic coastal marine waters or in upwelling areas. The density of phytoplankton in August–September was above any previously recorded numbers in natural marine lagoonal or coastal waters. At most stations it was over 100 g m^{-3}, while at some of them it was over 200 g m^{-2}. The numbers of picocyanobacteria in August were over 100 × 10^6 cells ml^{-1}, and in September–November over 30 × 10^6 ml^{-1}.

Table 1. Number (N) and biomass (B, g m^{-3}) of the main phytoplankton groups in the Comacchio lagoons

Month	Lagoon	Stn no.	Cyanobacteria				Eucaryotic algae				Total biomass (g m^{-3})
			Pico		Nano		Pico		Nano + Micro		
			N (10^6 ml^{-1})	B	N (10^6 ml^{-1})	B	N (10^6 l^{-1})	B	N (10^6 l^{-1})	B	
August	Magnavacca	1	139	262	2.4	30	140	0.9	3.17	0.7	293.6
		2	143	333	1.7	23	128	0.8	3.40	0.6	358.2
		3	144	226	1.2	16	133	0.8	3.32	0.7	243.5
	Campo	4	69	169	0.9	11	117	0.6	3.51	0.7	181.3
		5	66	130	0.6	7	165	2.2	3.80	0.8	140.0
September	Magnavacca	7	53	91	1.1	28	293	8.2	5.70	1.3	128.5
		8	96	164	2.3	46	550	11.0	6.33	1.1	222.1
		10	46	78	0.6	11	455	8.0	3.80	0.8	97.8
	Campo	12	53	100	0.1	1	120	1.4	9.50	1.9	104.3
		14	24	45	0.4	7	710	12.8	7.20	1.4	66.2
	Marine channel	36	0.02	0.04	0	0	0.32	0.03	0.36	1.3	1.37
November	Magnavacca	27	76	132	0.3	5	124	2.2	3.40	0.8	140.0
		29	30	62	0.2	3	350	6.3	6.75	1.5	72.8
		30	18	35	0.2	4	620	12.3	2.60	0.6	51.9
	Campo	34	33	67	0.2	3	330	7.2	1.46	3.1	79.3
		35	34	68	0.1	2	260	5.7	3.54	0.8	76.5

Over 97% of total phytoplankton biomass was formed by picocyanobacteria in August, and over 80% in September and November. The cyanobacteria, which had cells of 1 to 3 µm size, were randomly distributed within their mucous colonies. Their populations were dominated by 2 species of *Coelosphaerium* with small cells, *C. kutzengianum* (a potentially toxic species) and *C. minutissimum*, and by *Synechococcus* sp. Their nano-fraction was represented mostly by *Aphanothece salina*, which also forms mucous colonies. A minor eucaryotic fraction of phytocoenosis was represented by *Chlorella marina*, nanophytoflagellates and rare gymnodiid dinoflagellates. In November the composition of phytocoene did not significantly change in comparison with that observed in August–September.

Primary production in the upper water layer (0 to 5 cm) in the lagoons was extremely high, within the range 0.7 to 3.5 mg C l^{-1} both in summer and in late autumn (see Table 4). At most stations it exceeded 1.5 mg C l^{-1} d^{-1} — the highest ever recorded rates in the upper layer of coastal eutrophic marine basins or in upwelling areas. But in the latter such high levels of primary production were achieved by phytoplankton populations 10 to 20 times less dense than those observed in the Comacchio lagoons, e.g. by a phytoplankton biomass of 5 to 20 g m^{-3}. In fact, the specific photosynthetic production coefficients (P/B) calculated for upper water layers of the lagoons appeared to be very low even at the surface under optimal illumination. In summer these coefficients were only 0.06 to 0.15 d^{-1} (average 0.09 d^{-1}; Table 5). In autumn they were higher — about 0.3 d^{-1}. Calculated for the total phytoplankton population in the water column they were only half as much, due to self-shading: 0.05 in summer and 0.14 in autumn.

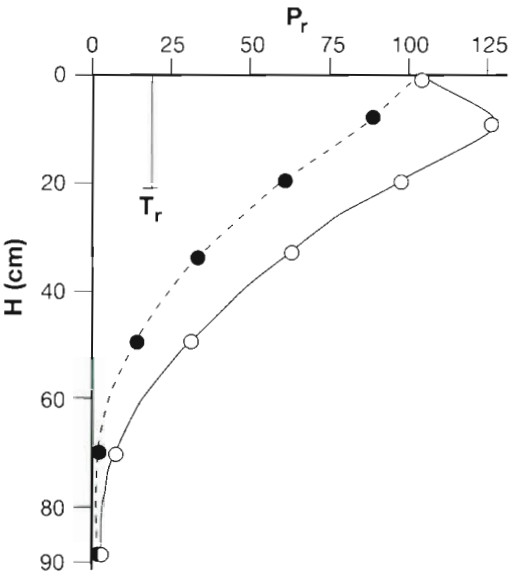

Fig. 3. Dependence of photosynthesis rate (P_r, relative values) in water column of the Campo lagoon upon light attenuation with depth (K_p curve) on a dull (●) and a bright day (○); T_r: Secchi disk depth

Because of the extreme density of phytoplankton the Secchi disk depth was only 20 to 30 cm. Thus the depth of the euphotic zone in the lagoons was only 70 to 80 cm, and not down to the bottom as is usual in shallow lagoons. The K_t curves measured on a bright day had a maximum at 10 cm, showing a definite light inhibition near the surface, which was absent on a dull day.

Table 2. Numerical abundance (N) and wet biomass (B, g m^{-3}) of heterotrophic plankton in the major Comacchio lagoons

Season	Lagoon	Stn no.	Bacteria		Microplankton: Nanoheterotrophs		Microplankton: Ciliates + rotifers		Mesozooplankton	
			N (10^6 ml^{-1})	B	N (10^6 l^{-1})	B	N (10^3 l^{-1})	B	N (10^3 m^{-3})	B
August	Magnavacca	1	83	16.6	76	0.64	0.95	0.01	23.1	0.37
		2	86	25.3	48	0.37	0.85	0.02	19.7	0.32
		3	76	14.7	33	0.50	2.50	0.03	63.3	0.96
	Campo	4	63	13.0	133	0.84	13.65	0.46	46.1	0.54
		5	52	9.1	144	0.99	17.68	0.67	2.6	0.03
September	Magnavacca	6	83	16.9	350	2.62	0.88	0.08	4.5	0.19
		8	52	9.7	222	1.66	3.15	0.04	15.2	0.35
		10	71	10.7	280	1.82	1.75	0.02	10.9	0.24
	Campo	11	70	11.8	220	1.44	1.75	0.02	10.9	0.29
		12	97	17.3	240	1.40	5.83	0.04	4.6	0.07
		14	73	11.9	158	2.11	15.65	0.18	0.2	0.004
November	Magnavacca	27	28	4.0	62	0.47	0.90	0.02	0.8	0.01
		28	18	2.2	51	0.55	0.20	0.05	1.3	0.02
		30	11	1.4	34	0.36	0.30	0.01	2.0	0.03
	Campo	34	14	1.7	38	0.36	3.6	0.04	2.6	0.03
		35	16	1.5	66	0.69	5.4	0.07	2.4	0.02
	Marine channel	36	3.5	0.4	82	0.94	22.6	1.15	68.1	1.47

Table 3. Mesozooplankton in experimental ponds receiving water from the Campo lagoon, sampled by day (14:00 h) and at night (22:00 h); N: number ($\times 10^3$ m^{-3}); B: biomass (mg m^{-3})

Sampling time	Stn no.	Nauplii		Copepods		Small mysids		Total biomass (mg m^{-3})
		N	B	N	B	N	B	
14:00 h	24	0.5	0.1	0.20	3	0	0	3
	25	0.5	0.1	0.10	1	0	0	1
	26	0.9	0.2	0.06	3	0.03	8	11
22:00 h	24	0.5	0.1	1.30	21	0	0	21
	25	0.5	0.1	0.40	11	0	0	11
	26	0.5	0.1	2.60	34	0.15	39	74

Density and production of bacterioplankton

The corresponding data are presented in Tables 2 and 3. In the summer the density of bacterioplankton was extremely high in both lagoons. The total number of bacteria attained a level never recorded before in any natural water body — 50 to 97 $\times 10^6$ ml^{-1}, which is 20 to 30 times more than is usual in eutrophic coastal marine waters. Bacterial biomass was correspondingly high, 10 to 25 g m^{-3}; moreover, the average volume of bacterial cells was 1.5 to 2 times greater than in an ordinary basin, being 0.14 to 0.25 µm^3. Of total bacterioplankton 5 to 10% was represented by yeast-like eucaryotic microbial cells with clearly visible nuclei when stained with acridine orange. Bacterial production (B_p, Table 4) was most intensive in August, when it reached 380 to 605 mg C m^{-3} d^{-1} or 2 to 3.5 g m^{-3} d^{-1} of wet biomass. This represents 5 to 10 times more than ordinarily found in marine eutrophic waters. In November the bacterioplankton density and especially its production decreased several times probably because of the low autumn water temperature (9 to 11°C). But even then the total number of bacterioplankton remained at 11 to 28 $\times 10^6$ ml^{-1}, which has rarely been recorded even in polluted estuarine waters. The specific growth rate of bacterioplankton was low both in summer (average 0.12 d^{-1}) and in autumn (average 0.04 d^{-1}).

Zooplankton

The data on density and composition of zooplankton are given in Table 2. The microzooplankton was represented in the lagoons mainly by nanoheterotrophs and ciliates. Copepod nauplii were very rare (biomass less than 2 mg m^{-3}). Rotifers were found only once at 2 stations in the Campo lagoon (biomass 0.3 g m^{-3}). In all other samples they were curiously absent both in summer and in autumn. Within the group of nano-

Table 4. Parameters of organic matter production, decomposition and standing stock. PP: primary production; BP: bacterial production; TPM: decomposition rate (total plankton respiration); LOM and SOM: stocks of labile and suspended organic matter

Season	Lagoon	Stn no.	Depth (m)	PP (mg C l^{-1} d^{-1})	PP (g C m^{-2} d^{-1})	BP (mg C m^{-3} d^{-1})	TPM (mg O_2 l^{-1})	LOM (mg C l^{-1})	SOM (mg C l^{-1})
August	Magnavacca	1	1.1	3.05	1.37	385	3.96	19.0	24.3
		2	1.2	1.76	0.80	410	4.15	21.9	30.3
		3	0.9	3.19	1.43	370	3.80	29.1	23.9
	Campo	4	0.9	1.71	0.76	665	5.03	17.8	25.7
		5	0.4	1.49	0.67	642	5.15	24.3	23.7
September	Magnavacca	6	1.2	1.25	0.56	240	6.10	26.9	39.3
		8	0.9	1.23	0.56	112	4.82	25.8	32.4
		10	0.8	0.81	0.45	90	4.10	28.6	38.6
	Campo	12	1.1	0.74	0.26	180	6.41	30.1	21.3
		13	0.9	0.84	0.29	122	6.33	29.6	24.0
		14	0.3	0.93	0.20	52	6.10	32.6	22.6
November	Magnavacca	28	1.3	1.81	0.72	24	1.85	29.0	25.5
		29	1.1	1.56	0.62	22	1.94	22.3	20.4
		30	0.9	2.46	0.91	32	2.29	18.4	16.0
	Campo	34	0.9	1.90	0.76	14	1.54	13.3	18.6
		35	0.8	0.90	0.36	16	1.28	12.9	20.3
	Marine channel	36	1.5	0.07	0.08	12	0.66	1.5	1.0

heterotrophs the most numerous were zooflagellates of 3 to 5 µm size. The nanoheterotrophs were the only zooplankton group which attained a significant density. In September at some stations it was over 1 g m^{-3}, and up to 2.6 g m^{-3} at Stn 6. In August and November their biomass was 0.2 to 0.6 g m^{-3} (Table 2). In September their number was as much as 200 to 350 × 10^6 l^{-1}, and in August and November 30 to 70 × 10^6 l^{-1}. The ciliate population in the lagoons were very small. Only in summer in the Campo lagoon did it reach a moderate density of 5 to 10 × 10^3 l^{-1} (biomass 0.1 to 0.3 g m^{-3}) at some stations. At other stations the biomass was less than 30 to 40 mg m^{-3}. In most samples ciliates were represented by a medium size (30 to 60 µm) *Strombidium* sp. In samples from the Campo lagoon *Triarina fusus* was also present. No tintinnids were recorded.

Net mesozooplankton also appeared to be surprisingly scarce in the lagoons (Table 2). The marine waters entering the lagoons via the channels contained a rich copepod population with biomass over 1 g m^{-3} (Table 2, Stn 36). Thus the largest mesozooplankton biomass was recorded at sites in both lagoons adjacent to the channels (Stn 3 and 4, Table 2). Probably the mesozooplankton in samples collected at more distant stations had the same origin. The copepods in these samples had the same taxonomic composition with predomination of *Acartia* sp. Most of them had a degenerated appearance, some with broken antennae, and having a blackish color or apparently dead. A scarcity of nauplii (Table 3) also indicated that the copepods did not breed in the lagoons. Larger numbers of nauplii were also recorded at Stns 31 and 34 near the marine channels. At other stations they were rare — less than 1 l^{-1}. In September at some stations early decapod larvae (zoea) were also recorded, numbering 30 to 100 per m^3 (biomass 70 to 150 mg m^{-3}). Other representatives of mesozooplankton such as veligers or trocophores were absent in samples taken with a plankton net of 40 µm mesh, which should catch them if present. The demersal zooplankton appeared to be surprisingly poor. Zooplankton in nocturnal catches in the experimental ponds adjacent to the lagoon of Campo were found to be as scarce as in diurnal ones (Table 3), except for the presence of some small mysids at 1 station out of 3 thus sampled.

Stock of organic matter and its decomposition rates

The stock of labile organic matter (LOM) in the lagoons was found to be very high: 20 to 30 mg C l^{-1} in summer and 12 to 22 mg C l^{-1} in late autumn, i.e. 10 to 20 times more than is usual in coastal eutrophic waters. At Stn 27, where wind driven phytoplankton accumulated in November, it was even 29 mg C l^{-1} (Table 4) The corresponding BOD-30 values were about 50 to 60 mg O_2 l^{-1} in comparison with 3 to 5 mg O_2 l^{-1} in ordinary eutrophic coastal waters (Zsolnay 1975, Sorokin et al. 1983, Tchebotarev & Sorokin 1983).

The stock of suspended organic matter varied in the lagoons within the range 12 to 30 mg C l^{-1} (Table 4). A reduced content was recorded in November, when the phytoplankton density decreased. Thus the content of suspended organic matter was 30 to 50 times more than it was in ordinary eutrophic marine waters (Romankevich 1977; see Table 4, Stn 36) such as the Magnavacca lagoon in August. The ratio of total plankton biomass to suspended organic matter (both expressed in carbon units) reached 75 to 90% in the Magnavacca lagoon in August. This shows that the larger part of suspended organic matter was comprised by the living plankton biomass, dominated by the picocyanobacteria. In September and November the living biomass comprised 25 to 50% of suspended organic carbon. On average its value was about 40% — also a very high value (Table 5).

Total plankton respiration (TPM) as a measure of the decomposition rate in summer ranged from 4 to 6 mg O_2 l^{-1} at different stations, which corresponded to between 60 and 80% of oxygen saturation in saline

Table 5. Basic ratios characterizing structure and functioning of the Comacchio lagoonal ecosystem calculated as averages for stations

Ratios			Summer	Late autumn
Contribution of zooplankton to total plankton biomass (%)			1.2	0 7
Contribution of microzooplankton to total zooplankton biomass (%)			84	96
Contribution of living biomass to suspended organic matter			42	40
Ratio of primary production to decomposition (TPM) in water column			0.4	1.3
Specific production coefficients (P/B) per day	of phytoplankton	at the surface	0.09	0.3
		in the water column	0.05	0.14
	of bacterioplankton		0.12	0.04
Turnover time	of labile organic matter (LOM/TPM) (d)		13	25
	of labile sulfides in bottom sediments (d)		–	95
	of inorganic phosphate (min)		–	2.4

water at 26°C (Table 4). In September at Stns 11 and 12 in the Campo lagoon, which receive waste waters from the fish culture plant, it reached 10.5 to 11.5 mg O_2 l^{-1} d^{-1}, or about 150% of the oxygen saturation value. Calculated per m^2 the decomposition rate was 3 to 10 g O_2 d^{-1} or 1 to 4 g C d^{-1} in the water column only. However, a significant oxygen consumption should also be expected by the bottom sediments of the lagoons which are enriched with organic matter and with labile sulfides (see Table 10). Therefore, for estimation of total oxygen uptake rates the contribution of bottom sediments also needs to be be estimated. To measure it we sampled undisturbed sediment cores 8 cm in diameter with a column of water. The cores, with capped bottoms were brought to the laboratory. The upper water was siphoned out and then replaced, being careful that no air bubbles remained. One empty bottle was also filled in the same way as a control without mud. Following incubation for several hours the decrease of oxygen in the bottles was estimated by Winkler titration in subsamples siphoned out from them. Results showed that the oxygen consumption by the bottom surface varied at stations within the narrow range of 1.3 to 1.8 g O_2 m^{-2} d^{-1} in comparison with that in the water column of 3.8 to 10.2 g O_2 m^{-2} d^{-1}. This indicates that the contribution to oxygen uptake by bottom sediments varied at different stations from 11 to 48% (Table 6). During the core-sampling we were surprised by the discovery of algo-bacterial mats on the surface of black bottom muds in deeper parts of lagoons at depths of 1.1 to 1.4 m, which had appeared even in conditions of frequent and strong wave turbulence. The mats appeared as a quite structured black-greenish cover about 0.7 to 0.8 cm thick. They consisted of filamentous cyanobacteria, sulfur bacteria and diatoms, and were populated by small nematodes.

The high rates of respiratory oxygen consumption against the background of a high photosynthetic oxygen production of some 1 to 2 g O_2 m^{-2} d^{-1} resulted in drastic diurnal fluctuations of dissolved oxygen content in the water column of the lagoons. In the Magnavacca lagoon, with a more intensive photosynthesis in the evening at the surface, the oxygen content was 8.4 to 9.3 mg O_2 l^{-1} or some 110 to 120% of saturation in the whole water column down to the bottom, while in the morning it dropped to between 1.2 and 3.6 mg O_2 l^{-1}, also in the whole water column, despite quite intensive wind mixing during the observations. In the lagoon of Campo where the water column oxygen consumption was about double that in Magnavacca, the nocturnal depletion was even more – down to 0.5 mg O_2 l^{-1} near the bottom (Tables 4 & 7) This means that in calm weather, at least in the bottom layer in summer, complete anoxia could be expected as a common phenomenon in large areas of the Comacchio lagoons. It is no wonder therefore that the benthic fauna was drastically depleted during the period of the catastrophical cyanobacterial bloom. With the high rate of decomposition in the Campo lagoon the deep nocturnal oxygen depletion was not compensated even by the daytime photosynthetic production. Thus the oxygen content there, even in windy weather in the evening, hardly reached 100% of saturation even at the surface and remained at 3 to 5 mg O_2 l^{-1} near the bottom.

The decomposition rate in the water column in summer, not even taking into account the bottom oxygen consumption, was 1.5 to 4 times more than the primary production. The former ratio applies to the Magnavacca lagoon, with a lesser anthropogenic impact, and the latter to the Campo lagoon, which receives waste waters from the fish culture plant. An average ratio of primary production to decomposition calculated per station in both lagoons was 0.4 in summer. By late autumn it was 1.3, since at that time decomposition processes were inhibited in both lagoons by the low

Table 6. Oxygen uptake by bottom surface; surface area of cores 50 cm^2; volumes of NaCl solution over the cores: 0.8 l; exposure time: 5 h 30 min; initial O_2 content: 7.92 mg O_2 l^{-1}; temperature: 22°C. SM: O_2 consumed per volume of water with controls subtracted (mg O_2); TBM: O_2 consumed by bottom surface, g O_2 m^{-2} d^{-1}; TPM: total oxygen uptake (decomposition rate) by plankton (g O_2 m^{-2} d^{-1}) units; TCM: total community respiration (TBM + TPM)

Lagoon	Stn no.	SM	TBM	TPM	TCM	TBM/TCM (%)
Magnavacca	8	2.11	1.84	3.84	5.68	32
	10	1.81	1.58	5.04	6.62	24
Campo	12	1.49	1.38	10.26	11.64	12
	13	1.77	1.54	5.86	7.40	21

Table 7. Diurnal changes in oxygen concentration in lagoon waters in mid September

Lagoon	Stn no.	Time of day	O_2 contents in water (mg l^{-1}) Surface	5 cm above bottom
Magnavacca	8	19:40 h	8.65	8.55
		07:40 h	2.79	1.23
	10	20:00 h	9.33	8.42
		07:50 h	3.62	2.79
Campo	11	20:10 h	6.67	3.04
		07:00 h	2.12	0.46
	13	20:20 h	7.67	5.39
		07:05 h	3.96	0.58

November temperatures, while primary production remained high (Table 4). The rate of decomposition in autumn was 2 to 3 times less in comparison with summer, being between 1.3 and 1.9 mg O_2 l^{-1}.

Inorganic phosphorus dynamics

A very specific feature of the lagoonal ecosystem during the picocyanobacterial bloom was its phosphorus metabolism. The standing stock of phosphorus was kept by the planktonic communities in its organic form. The content of organic phosphorus in lagoonal waters was quite large in conjunction with the high biomass of phytoplankton and bacteria. The total content of organic phosphorus was 8 to 9 µg-at. P l^{-1}, and 60 to 80% of this was found in the particulate fraction, e.g. in plankton (Table 8). The inorganic phosphorus content in water in November was negligible. In most samples it was close to the analytical zero. Only in rare cases was it more than 0.1 µmol l^{-1}, i.e. the PO_4-P concentration limited phytoplankton growth (Thomas & Dodson 1969). The high phototrophic and microbial production in the lagoonal waters inevitably required a correspondingly high flow of phosphorus. Under the above conditions of a low ambient PO_4-P stock this could be provided only by high turnover rates. In fact experiments done with ^{32}P-label revealed that, within the range of concentration close to ambient (0.02 to 0.15 µmol l^{-1}), even in the low temperatures in November (11 to 12°C), the turnover time of PO_4-P was only 2 to 3 min, while in a normally structured pelagic community in water of the marine channel at Stn 36 it was over 40 h (Table 8). The labeled PO_4-^{32}P added to the sample was 90 to 95% consumed within only 5 to 10 min (Fig. 4). The uptake rate (A_t) of PO_4-P within the range of ambient concentrations estimated by exposure times less than 1 min (linear uptake part of the curve, Fig. 4) varied from 0.3 to 1 µg P min^{-1} (Table 8).

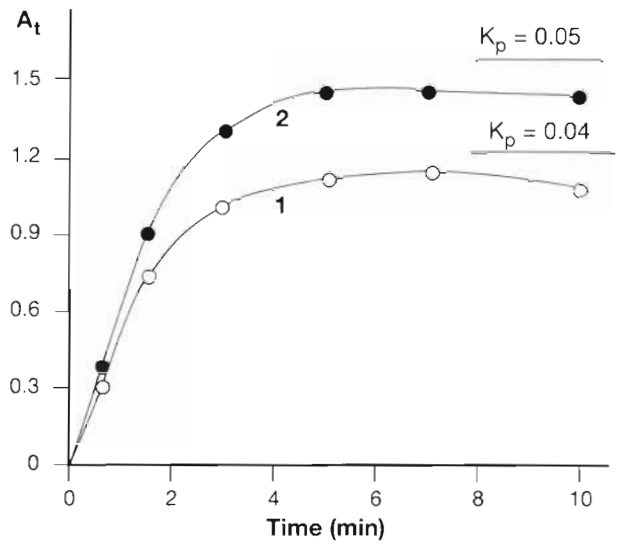

Fig. 4. Time course curves of PO_4-P uptake (A_t; µg P l^{-1}) in water samples taken at Stns 24 (1) and 26 (2): K_p: ambient initial PO_4-P content in the sample (µmol l^{-1})

Uptake rates in water samples with artificially elevated initial PO_4-P content (up to above-natural levels of 10 to 30 µmol l^{-1}) were also estimated in order to evaluate the potential capacity of microplankton communities in the blooming lagoons to take up and retain inorganic phosphate. Results showed that a maximum uptake rate, attained when its content in water was 8 to 10 µmol l^{-1}, was close to 3 to 4 µg P l^{-1}. This implies a turnover time of even this large stock of PO_4-P of about 1 h (Table 9). At such a speed of uptake, which was some 2 orders more than that in a normal coastal waters, the initial content of PO_4-P added of 4 to 8 µmol l^{-1} was depleted in samples of blooming water down to analytical zero in some 3 to 8 h (Fig. 5). With initial PO_4-P contents over 30 µmol l^{-1} it was depleted by about 25 µmol and then reached a plateau. Thus the latter amount characterized the potential capacity of the microplankton community to take up and retain phos-

Table 8. Uptake rates (A_t) turnover time of inorganic phosphate (TP) and stock of organic phosphorus in waters of Comacchio lagoons in November at water temperature 10.5 to 11°C. K_p: content of PO_4P in water after addition of 'working' solution of labeled phosphate

Lagoon	Stn no.	K_p (µmol l^{-1})	A_t (µg P l^{-1} min^{-1})	TP (min)	Stock of organic phosphorus (µg-at. P l^{-1}) in intact samples	in filtered samples
Experimental ponds	24	0.02	0.39	1.6	8.5	3.0
	25	0.06	0.81	2.3	7.9	3.2
Magnavacca	27	0.07	0.74	2.9	9.3	1.4
	28	0.02	0.30	2.1	8.0	1.6
	29	0.06	1.03	1.8	7.8	2.6
	30	0.04	0.48	2.6	7.5	3.0
Campo	34	0.07	0.73	2.6	8.5	1.5
	35	0.02	0.36	1.7	8.1	2.9

Table 9. Time course of PO_4-P uptake (A_t) and its turnover time (TP) in water taken at Stn 24 and enriched with phosphate. K_p: initial PO_4-P content in water

K_p (µmol l^{-1})	Exposure time (min)	A_t (µg P l^{-1} min^{-1})	TP (min)
4.0	3	2.63	48
	10	2.72	47
	30	2.31	54
8.0	3	4.24	59
	23	4.14	60
	40	3.50	70

phate. The uptake of such an amount of PO_4-P should entail a rise of organic phosphorus content in plankton (and also the C:P ratio in its substance) by 3 to 5 times.

Organic matter and sulfides in bottom sediments

The content of organic matter in bottom sediments of the lagoons was found to be extremely high, especially in deeper areas where the bottom was covered by black mud with signs of algo-bacterial mats forming (Table 10). In upper layers it attained 17 to 23%, i.e. close to that in lake sapropels and 10 to 20 times more than usual in estuarine sediments (Romankevich 1977). Even in shallow lagoonal sediments containing a significant shell fraction it was still high — over 7 to 10% of dry weight. In the underlying sediments at core depths >5 to 7 cm the content of organic matter was found to be only 0.6 to 4%, which was close to a normal level in coastal marine sediments.

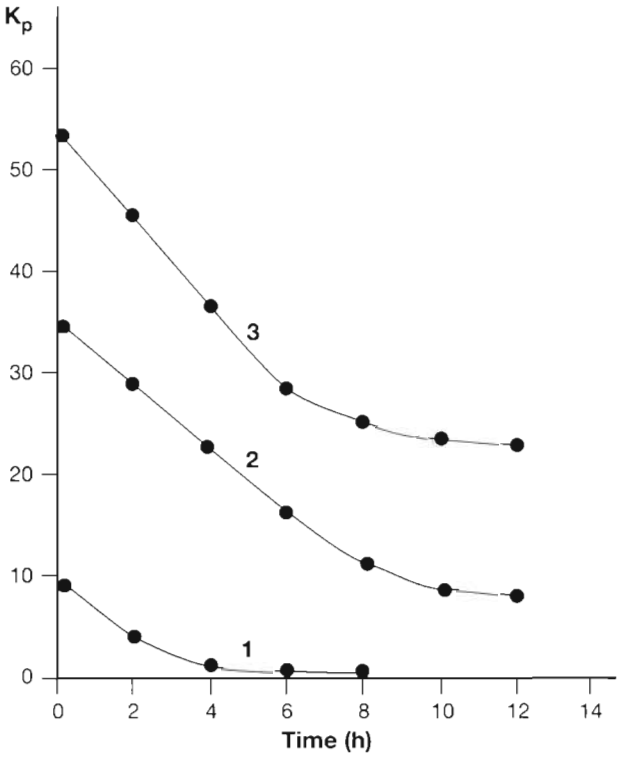

Fig. 5. Time course of depletion of absolute PO_4-P concentration in water samples (K_p) taken at Stn 24 and enriched with phosphate up to levels of: 9.7 µmol l^{-1} (1), 34 µmol l^{-1} (2) and 53 µmol l^{-1} (3)

Table 10. Contents of organic matter and labile sulfides in bottom sediments of the Comacchio lagoons. K_{org}: percentage of organic matter in dry sediment; KS: contents of labile sulfides (mg S^{2-} dm^{-3} wet silt); RS: rate of sulfide production in sediments (mg S^{2-} dm^{-3} wet silt d^{-1}); TS: turnover time of labile sulfide stock in sediments (d)

Lagoon	Stn no.	Depth layer in the core (cm)	K_{org}	KS	RS	TS
Magnavacca	28	0–2	17.2	495	17.20	29
	29	0–2	19.0	420	19.00	22
	30	0–2	7.3	894	7.26	123
	30b	5–7	4.0	1060	4.04	260
		0–2	24.0	715	23.90	30
	31	0–2	8.9	1218	8.90	136
		5–7	1.9	315	1.93	163
		10–12	0.9	518	0.90	645
	31a	0–2	4.2	861	4.20	205
Campo	34	0–2	17.9	990	17.86	55
	34a	0–2	11.4	1216	11.42	106
		5–7	0.6	946	0.62	1520
	35	0–2	12.8	1590	12.8	124

The stock of labile acid-soluble sulfides in the upper layer of bottom sediments was about 1 g S^{2-} dm^{-3} of wet silt. At some stations it reached 1.2 to 1.6 g S^{2-} dm^{-3} (Table 10). Such a high level of sulfide content could be readed only in anthropogenically stressed marine basins (Sorokin 1975, 1982). At 2 out of 3 stations, the sulfide content decreased further down in the sediment column, instead of the usual increase within the core because of oxidation. This is evidence that the build-up of sulfide in the upper layer of sediments in the lagoons is a recent phenomenon connected with the acceleration of sulfide production during the bloom. The latter was proved by direct estimation of its rate in the sediments using the radiolabeled sulfate $^{35}SO_4$. The rate of sulfide production due to microbial reduction of sulfate in the upper layer of sediments was at many stations over 10 mg S^{2-} dm^{-3} of wet silt per day (Table 10). At Stn 30b it even attained 24 mg S^{2-}, which is a record value in

marine basins including the meromictic ones (Degens et al. 1992). Further down in the core the rate decreased 3 to 10 times. This indicates that the process of sulfide formation was fuelled in the lagoons by the freshly sedimenting organic matter, consisting mainly of the cyanobacterial biomass (see Table 4).

DISCUSSION

The data presented above confirm that the lagoons of Comacchio are experiencing an ecological catastrophe caused by an unusually dense picocyanobacterial bloom which has been proceeding there since 1985 (F. Gelli pers. comm.; the bloom continued with the same force in 1995). It has resulted in the formation a new kind of coastal marine ecosystem, which produces mainly the potentially toxic biomass of the invading cyanobacteria, and hydrogen sulfide. A drastic difference in basic characteristics from those of a normal eutrophic lagoonal ecosystem with an ordinary food web is quite obvious (Table 11). This kind of ecosystem seems to be a new one not only for natural, but also perhaps for anthropogenically stressed estuarine environments. Periodical cyanobacterial blooms, stimulated by eutrophication (de Kloet et al. 1984), are usually caused by a larger colonial or coenobial species such as *Aphanisomenon* or *Microcystis*, and are rather temporal phenomena. They do not substantially change the biological regime. We had previously observed a similar kind of ecosystem, absolutely dominated by a quasipermanent picocyanobacterial bloom with a biomass over 30 g m^{-3}, but in an extreme sulfide environment in the crater lake Green. This lake is situated in the caldera of an active volcano on Raoul Island (Kermadek Islands, SW Pacific). The lake had a water temperature of about 35°C, and received hot sulfide-containing water from surrounding thermal vents (Sorokin et al. 1994). This kind of ecosystem does not show any significant successional changes. Its main characteristics, such as the composition and density of bloom, a negligible density of zooplankton, and extremely high rates of metabolism by depleted inorganic nutrients, appeared to be practically the same in summer and in late autumn.

We had an opportunity to investigate the microplankton and the microbial sulfate reduction in the Comacchio lagoons in 1979, before the cyanobacterial bloom started (Sorokin & Bilio 1981). At that time definite signs of hyper-eutrophication also appeared in these lagoons due to the influence of intensive fish culture discharges. The changes were especially evident in the lagoon of Campo into which they flow. In this lagoon the phytoplankton was practically absent, having been replaced by several species of *Euglena*, reflecting a high level of eutrophication. Water of this lagoon contained an abundant population of ciliates with a biomass up to 2.7 g m^{-3} and moderately abundant bacterioplankton (Table 12). In the Magnavacca lagoon a very dense bloom of chrysomonadic phytoflagellates proceeded with a biomass about 20 g m^{-3}. The bottom vegetation was still intact here, as well as the zoobenthos (*Cerastoderma*), but sulfate reduction had also started and the sulfides in the sediments had begun to incease. In the fish culture ponds their contents had also reached a critical level of 2 to 3 g S^{2-}

Table 11. Comparison of basic characteristics of the Comacchio lagoon ecosystem during the catastrophic cyanobacterial bloom with those of a 'healthy' eutrophic lagoon with normal biological regime, given as ranges of values during summer

Parameter	Comacchio lagoons	Lagoon with normal regime
No. of dominating phytoplankton species	2–3	5–10
Biomass of phytoplankton (g m^{-3})	60–300	1–10
Biomass of bacterioplankton (g m^{-3})	5–25	0.5–2
Biomass of rotifers (g m^{-3})	0–0.1	0.5–1
Biomass of ciliates (mg m^{-3})	20–100	200–800
Biomass of holoplanktonic mesozooplankton (mg m^{-3})	30–100	500–1500
Biomass of demersal meroplankton (g m^{-3})	0–0.05	2–20
Biomass of zoobenthos (g m^{-3})	2–6	50–300
Biomass of macrophytes and seagrasses (g m^{-2})	0	300–3000
Stock of labile organic matter in water (mg C l^{-1})	20–30	1.5–2
Stock of organic carbon in the sediments (% of dry weight)	8–15	0.5–2
Stock of suspended organic matter in water column (mg C l^{-1})	20–30	0.3–1
Stock of acid-soluble sulfides in bottom sediments (mg S dm^{-3} of wet silt)	800–1500	50–200
Primary production by phytoplankton in upper layer (mg C m^{-3} d^{-1})	800–3000	50–200
Specific production of phytoplankton in water column (d^{-1})	0.03–0.06	0.5–0.8
Share of zooplanktonic total plankton biomass (%)	0.8–1.5	20–50
Direct grazing of primary production by phytoplankton (%)	0.1–0.3	20–50
Turnover time of phosphate in water column	2–3 min	20–60 h

Table 12. Data on microplankton and sulfate reduction in the Comacchio lagoon in May 1979 (Sorokin & Bilio 1981). B: biomass (mg m^{-3} wet biomass); CS: content of labile sulfides in upper layer of bottom sediments (mg S dm^{-3} of wet silt); RS: rate of their formation due to microbial sulfate reduction (mg S^{2-} dm^{-3} d^{-1}); ranges of values observed at stations are given

Site	Sulfate reduction and sulfides in sediments		Phytoplankton		Bacterio-plankton	Ciliates
	CS	RS	Dominating groups	B	B	B
Eel culture pond	1700–3000	6–23	*Euglena* sp.	300–500	2000–10000	40–1200
Lagoon of Campo	600–950	5–13	Euglenoids	1000–4500	1000–1400	360–2750
Lagoon of Magnavacca	270–1250	3–13	Chrysomonadic phytoflagellates	22000	970–2500	20–560

dm^{-3}. Thus the environments in the lagoonal area in 1979 also displayed definite signs of destabilization.

The cyanobacterial bloom, which started in the lagoons in 1985, rapidly transformed the ecosystem. The most profound changes were experienced by the zooplankton. All its components, especially those breeding in the lagoon (rotifers, demersal forms of crustaceans) and also the meroplanktonic larvae, which are usually very abundant in lagoons, have been drastically depleted. The obliteration of the 2 latter components of zooplankton was definitely connected with the disappearance of bottom vegetation weeds and grasses, and with the build-up of sulfides in the bottom sediments. The depletion of the benthic fauna was caused by the accumulation of sulfides, by nocturnal anoxia near the bottom in summer and also, probably, by the potential toxicity or poor food quality of the cyanobacterial biomass as a dominating component of particulate food produced in the water column during the bloom (Ayles et al. 1976). The phytoplankton community of the blooming lagoons included one definitely toxic species, *Coelosphaerium kützengianum* (Elenkin 1938). The food quality of mucous colonial cyanobacteria like *Aphanothece* or *Microcystis* is also known to be poor (Sorokin 1968, De Bernardi & Giussani 1990).

To investigate the possibility of filtering fauna using phytoplankton from the blooming lagoons as food, we measured the rate of its consumption and assimilation in short-term (1 h) experiments with ^{14}C-labeled phytoplankton of water samples taken at Stn 24, using the methodology described by Sorokin (1968). The results, shown in Table 13, proved poor food quality in comparison with other algae, like diatoms of *Chlorella*. Even with an optimal concentration 6 g m^{-3} wet biomass its assimilation by the bivalve *Tapes philippinarum* did not cover the energy expenditure for respiration (the value of *G* was negative). Moreover a significant portion of the assimilated substance of natural phytoplankton in the sample was probably represented by *Chlorella* and phytoflagellates present in small amounts (see Table 1).

The success of the strategy of the key blooming algae (the picocyanobacteria), a surprisingly time-stable survival and domination, could be seen in their ability to accumulate and reproduce an enormously high biomass through prevention of grazing and by successfully opposing competition from any other plants. This goal was achieved by drastic depletion of animal filtering fauna, both planktonic and benthic. The zooflagellates, which were present in some summer samples in significant amounts, being 2 to 4 µm in size, could graze mostly on the bacterioplankton but not on the cyanobacterial cells of about their own size.

Evidence for the apparent inhibiting effect of the picocyanobacteria blooming in the lagoons upon the ciliates was provided by the unusual stability of their populations in bottled water samples. The samples were kept for over a month in natural light without visible changes in density of cyanobacteria in them, while normally the phytoplankton in water sample would be cleared by ciliates within a couple of days. But these water samples behaved like sterile algal cultures.

The competing macro- and microalgae were overwhelmed by the cyanobacteria due to the light attenuation by the latter's huge biomass, by a permanent depletion of nutrients, and by the fuelling of sulfide production with their non-grazed biomass. An excess of sulfides and the free H_2S thus produced migrate up the water column and there create a specific sulfur environment which is welcomed by the cyanobacteria (Elorenta 1972, Oren & Shilo 1979, Cohen et al. 1986), but which inhibits all other eucaryotic competitors or grazers due to the cytochrome poison.

Table 13. *Tapes philippinarum*. Elements of food balance for different kinds of food. FR: food ration; A: assimilated food; G: use of assimilated food for growth; all numbers are given as mg C per g of clam meat for 24 h; food concentration in experiments: 6 mg l^{-1} (wet biomass)

Kinds of food	FR	A	G
Nitzschia	66.8	46.1	32.8
Chlorella	44.0	25.5	12.2
Phytoplankton from Stn 24 dominated by picocyanobacteria	10.4	4.2	−9.1

An enormous biomass of picocyanobacteria was built up and supported by rather low specific production rates of some 0.08 to 0.12 d^{-1} in the water column (Table 5). This phenomenon is usual for pelagic communities with a low grazing pressure (Sorokin 1981). The above values were calculated as the ratio of primary production to biomass. But in fact a significant part of the latter will be produced heterotrophically, if we take into account the ability of cyanobacteria for heterotrophy (Rippka 1972, Ohki & Katon 1975, Whitton & Sinclair 1975, Oren & Shilo 1979, Kuzmenko 1981), and the light deficiency in the water column of the lagoons (cf. Fig. 3). Despite a low specific production, the absolute rates of primary production and decomposition in the lagoons appeared to be at the highest level ever recorded in natural marine basins, even coastal, because of the enormous biomass of phytoplankton and bacterioplankton which this curiously transformed ecosystem managed to support.

The nutrient depletion observed during all periods of the bloom occurred because all the available nutrient stock, which itself was high (8 to 9 µg-at. P l^{-1}, see Table 8), was kept tightly inside the biomass (Riegman 1985). It was recycled within semiclosed microcosms of the cyanobacterial mucous colonies (Khoja & Whitton 1971, Whitton & Sinclair 1975, Kuzmenko 1981). The cyanobacteria also easily shift from phototrophy to heterotrophy, and thus are themselves able to recycle the nutrients (Karnaukhov et al. 1980, Carr & Whitton 1982).

In order to investigate further how the Comacchio lagoonal ecosystem functions we calculated tentative energy balances and composed energy flow schemes. The balances were calculated for summer and late autumn situations at most typical stations in the Magnavacca lagoon, and also for the summer period at stations in the Campo lagoon, which received a large load of external organic matter. For their calculation specific production coefficients (P/B), growth efficiency coefficients (K_2) and assimilability coefficients (I) known from the literature were used (Sorokin 1968, Zaika 1973, Grese 1979, Vinogradov & Shushkina 1987; Table 14). The production of that part of cyanobacteria fed chemoorganotrophically (P_c) was calculated via the probable value of their respiration (M_c): $P_c = M_c\ [K_2/(1 - K_2)]$, assuming a value of K_2 equal to that in bacteria (0.32, see below). The value of M_c itself was calculated as the difference between the total plankton respiration (M_t) measured by the dark bottle oxygen method (see Table 3) and the joint respiration of bacterioplankton (M_b) plus the autotrophic part of phytoplankton (M_p): $M_c = [M_t - (M_b + M_p)]$. The value of M_b was found using the values of measured bacterioplankton production (P_b): $M_b = P_b\ [(1 - K_2)/K_2]$, where $K_2 = 0.32$ (Sorokin 1981).

Table 14. Coefficients used for the energy balance calculations. KB: caloric equivalent of wet biomass (cal mg^{-1}); I: assimilability (A/B); P/B: specific production; K_2: secondary growth efficiency (P/A), where A = assimilation, B = biomass, and P = production

Components of ecosystem	KB	I	P/B	K_2
Phytoplankton	0.7	–	–	–
Bacterioplankton	0.8	–	–	0.3
Microzooplankton	0.75	0.6	0.8	0.4
Mesozooplankton	0.9	0.4	0.05	0.5
Benthic bacteria	1.8	–	0.05	0.3
Zoobenthos	0.5	0.5	0.015	0.3

The value of M_p was assumed to be 10% of primary production by phototrophs. The use by the lagoonal ecosystem of external allochthonous organic matter entering the lagoons from the land and from the fish culture ponds was also taken into account. Its values were calculated as the difference between local primary production and the total energy demand of the whole ecosystem (Sorokin 1972).

The results of the balance calculations are given in Table 15 and in Figs. 6 to 8. They show that the blooming picocyanobacteria represented in the ecosystem the main productive and metabolic component. In the lagoon of Campo in summer and in the Magnavacca lagoon in autumn their share even in total plankton respiration was about 70%, while the total share of animal heterotrophs including zoobenthos was only 3 to 5%. The combined food ration of animals was several times less than the combined production of particulate food by microplankton. But, in spite of this obvious discrepancy between the production of particulate food and animal grazing, the ecosystem appeared to be extremely stable and self-sufficient, producing conditions convenient for the dominating picocyanobacteria. A major portion of primary production and of allochthonous organic matter used by microplankton was respired by the heterotrophic part of the picocyanobacterial population and by the bacterioplankton. Between 80 and 90% of all microbial production must remain unused by the depleted animal grazers. In part it was respired by the microplankton community itself, but a large portion settled to the bottom and was used by microflora in sediments for H_2S production. The allochthonous organic matter in the Magnavacca lagoon in summer and autumn provided only 6 to 10% of the needed energy. But in the Campo lagoon in summer the ambient population of cyanobacteria existed mostly heterotrophically using basically the allochthonous organic matter from the fish culture plant. The water turbidity there was extremely high, and the photosynthetic production in the water column

Table 15. Elements of energy balance in main components of the Comacchio lagoonal ecosystem. B: biomass; FR: food ration; A: assimilated food; P: production; M: respiration (i.e. metabolism); F: non-assimilated food; M_t: integral respiration of all biological community, calculated as ΣM; TPM: total respiration of plankton, measured experimentally; all numbers are given in cal m^{-2} d^{-1}

Lagoon, Stn no., month, TPM	Components of ecosystem	B	FR	A	P	M	F	M/M_t (%)
Magnavacca, Stn 3, End of August, TPM = 13000	Phytoplankton	170000	–	14300	13000	1300	–	9
	Heterotrophic cyanobacteria	17000	–	6200	2000	4250	–	29
	Bacterioplankton	27000	–	10400	3400	7000	–	49
	Microzooplankton	500	1300	800	400	400	500	3
	Mesozooplankton	900	200	80	30	50	120	0.3
	Benthic bacteria	15000	–	1900	600	1300	–	9
	Zoobenthos	2000	200	100	30	70	100	0.7
Campo, Stn 12, Mid-September, M_t = 22000	Phytoplankton	16000	–	2600	2400	200	17600	1
	Heterotrophic cyanobacteria	52000	–	25800	8200	17600	–	72
	Bacterioplankton	32000	–	5000	1600	3400	–	14
	Microzooplankton	1100	2600	1600	800	800	1000	3
	Mesozooplankton	70	20	10	4	5	10	0.02
	Benthic bacteria	30000	–	3100	1000	2100	–	7.80
	Zoobenthos	4000	600	280	80	200	320	1.30
Magnavacca, Stn 30, Mid-November, M_t = 7930	Phytoplankton	33000	–	9000	8000	1000	–	12
	Heterotrophic cyanobacteria	8000	–	8800	2800	6000	–	69
	Bacterioplankton	2600	–	900	300	600	–	7
	Microzooplankton	350	1250	550	250	290	700	3.6
	Mesozooplankton	30	17	7	3	4	10	0.004
	Benthic bacteria	6000	–	900	300	600	–	11.4
	Zoobenthos	2000	200	100	30	70	100	1

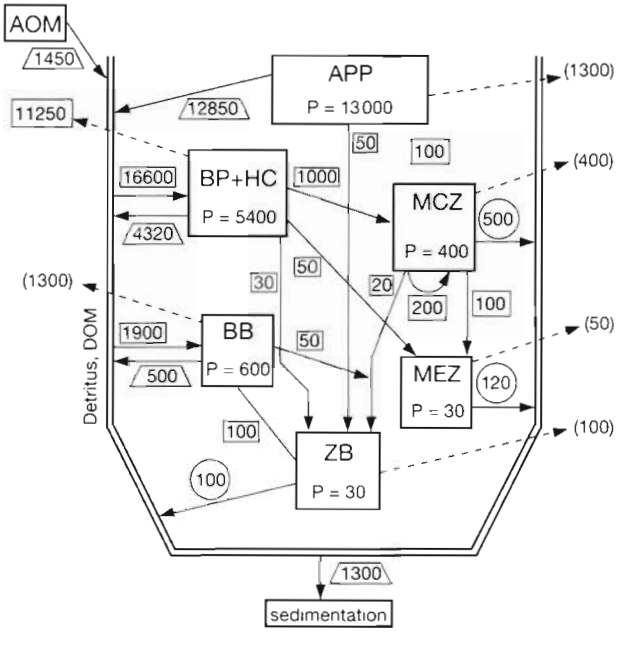

Fig. 6. Scheme of energy flow in the ecosystem of Magnavacca lagoon (Stn 3) in August. P: production; DOM: dissolved organic matter; numbers in squares: food ration of subsequent component of food web; numbers in trapezia: non-grazed production; numbers in circles: non-assimilated part of food ration; numbers in brackets: respiratory losses of assimilated food. All numbers are given as cal m^{-2} d^{-1} Food web components: APP, phototrophic phytoplankton; BP, bacterioplankton; HC, chemoorganotrophic part of picocyanobacteria; MSZ, microzooplankton; MEZ, mesozooplankton; BB, benthic bacteria; ZB, zoobenthos; AOM, allochthonous organic matter

was relatively low with a very high rate of total planktonic respiration, over 70% of which was contributed by heterotrophic cyanobacteria.

A high production rate of the non-grazed excess organic matter in the lagoons during the bloom significantly changed the bottom life and its chemistry. The bottom vegetation died out, the zoobenthos was

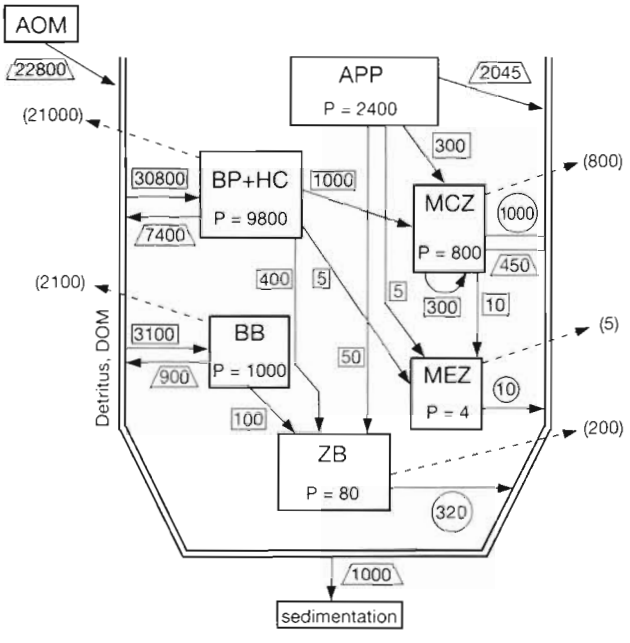

Fig. 7. Scheme of energy flow in the ecosystem of the Campo lagoon (Stn 12) in September; for designations, see Fig. 6

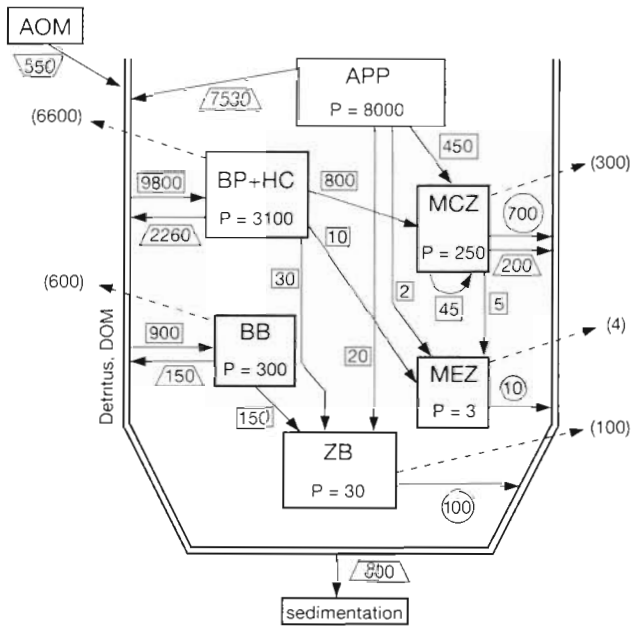

Fig. 8. Scheme of energy flow in the ecosystem of the Magnavacca lagoon (Stn 30) in November, for designations, see Fig. 6

depleted to a negligible amount of a few polychaetes and nematodes. Over the sediment surface the formation of algo-bacterial mats began, which is a feature of suboxic sulfide basins (Cohen & Rosenberg 1989). An intensive accumulation of organic matter proceeded in the upper 0 to 5 cm layer of sediments formed during the bloom period (Table 10). It increased the sulfate reduction rate which finally caused a mass mortality of zoobenthos.

A scenario of how the above described man-made ecological catastrophe developed could be as follows. Since ancient times the lagoons have been an area of intensive economic activity, being the location of productive eel, clam and shrimp fisheries and having very limited water exchange with the sea. A complicated system of channels and dikes was constructed in them to regulate the hydrological regime and fish migrations for the benefit of the fisheries. By the early 1970s the experimental plant for intensive eel aquaculture had been established in the Comacchio lagoonal area with the use of the larger lagoons as receipt and self-purification basins for waste waters. The aquaculture of eels produced large amounts of waste, because there fishes do not take pellets and were fed with fish paste. A large part of it remained uneaten by fish, dissolved in the water, and was discharged into the lagoons with the waste waters. The input of large loads of organic matter into already eutrophic lagoons, which also experienced eutrophication impacts from intensive agricultural activity and had restricted water exchange with the sea, resulted in the build-up of large stocks of nutrients, of labile organic matter and of microbial biomass which could not be consumed and digested by local planktonic and benthic communities aerobically. Thus anaerobic sulfate reduction was triggered in the bottom sediments. A rapid accumulation of labile sulfides and free H_2S in sediments began. These developments have been recorded in the lagoons since 1979 (Table 12). Especially high loads of sulfides were recorded in the fish culture ponds. Its oxidation induced formation of anoxic zones and resulted in the disappearance of normal phytoplankton and its zooplankton grazers. Their place was taken by the cyanobacteria, which are resistant to anoxia and sulfides (Carr & Whitton 1982, Cohen 1984, Schmidt 1988). Their biomass was then pumped out into the Campo lagoon, which also had been destabilized by the waters discharged from the plants (Table 12). Thus the cyanobacterial bloom was started there too, and spread to the large Magnavacca lagoon.

The bloom has been proceeding in these lagoons for about a decade without a visible decrease, and could be assumed to proceed for another decade with a consequent complete collapse of the fisheries and danger of similar catastrophic events in adjacent lagoonal and coastal basins of the western Adriatic, many of which are also now at the threshold of hypereutrophication due to wastes from numerous aquaculture and other enterprises (UNESCO 1988). Only radical measures could stop the bloom in the Comacchio lagoons. At this point we would recommend the complete draining of the lagoons and the weathering of their bottoms for a couple of years. During this time the remaining eel population could be maintained in the lagoons of Salina if previously prepared for this purpose.

After weathering, the lagoons should be refilled twice with Adriatic water to remove the stock of extra nutrients from the sediments.

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