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Authors: Quintana, Xavier D., and Moreno-Amich, Ramon

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Phytoplankton composition of Empordà salt marshes, Spain and its response to freshwater flux regulation

Xavier D. Quintana and Ramon Moreno-Amich

Institute of Aquatic Ecology and Department of Environmental Sciences,
University of Girona, Facultat de Ciències,
Campus de Montilivi, 17071 Girona,
Spain

ABSTRACT

A description is given of the response of phytoplankton composition to eutrophication caused by an increase in fresh water flux in four Empordà salt marsh basins. Cyanobacteria and mixotrophic phytoplankters (especially haptophytes and dinoflagellates) are the most abundant organisms in these basins. Under stable conditions, cyanobacteria take competitive advantage of the lack of inorganic nitrogen caused by confinement. Mixotrophs dominate coinciding with water inputs. The importance of the allochthonous supply probably favours mixotrophs, which may also take nitrogen heterotrophically. The phytoplankton-invertebrate biomass ratio (P/I) and the chlorophyll-phytoplankton biovolume ratio (Chl/BV) respond differently to stabilisation of freshwater input, depending on the degree of eutrophy of the basins. Thus, in more eutrophic basins flux regulation causes an increase in P/I and a decrease in Chl/BV, indicating higher density of mixotrophs and lesser density of invertebrates. Less eutrophic basins respond in the opposite fashion.

ADDITIONALINDEXWORDS: *Mediterranean wetlands, temporary marshes, mixotrophic behaviour, phytoplankton / invertebrate ratio, chlorophyll / biovolume ratio.*

INTRODUCTION

Negative effects caused by human alteration of the hydrological regime are the main environmental problem in coastal lagoons and marshes. The tendency to eutrophication in most Mediterranean marshes caused by anthropogenic changes in water circulation is well known. Opening or closing communication channels also caused substantial changes in the structuring and function of these ecosystems (AGUESSE and MARAZANOF, 1965; LASSERRE, 1989; LÓPEZ and TOMÁS, 1989; COMÍN and VALIELA, 1993; HERTEAUX, 1992). In contrast, the management of several Mediterranean coastal lagoons often have to modify hydrological regime of these ecosystems, but sometimes with undesirable results. This is the case of the Empordà salt marshes, where the installation of a sluice gate has favoured the eutrophication of its waters (QUINTANA *et al*., 1998a and 1998b).

Empordà salt marshes are a group of coastal lagoons and marshes characterised by a typically Mediterranean hydrology, with sudden and irregular flooding followed by long periods of confinement. During confinement the concentrations of dissolved inorganic nitrogen (DIN) are very low, favouring the presence of nitrogen-fixing planktonic cyanobacteria (QUINTANA *et al*., 1998a). Mixotrophic species are also abundant among phytoplankton here (QUINTANA, 1995).

The costs and benefits of phytoplankton's mixotrophic strategy are a current research topic in plankton ecology (THINGSTAD *et al*., 1996; JONES, 2000; ROTHHAUPT, 2000). Several mixotrophic strategies have been described and their activity has been reported to be relevant in planktonic food web dynamics, especially in humic lakes and in oligotrophic conditions (JONES, 1997; RAVEN, 1997; ISAKSSON, 1998; STOECKER, 1998). In eutrophic conditions mixotrophy has not been described so frequently, but mixotrophic phytoplankton may also be seasonally abundant in these waters (SANDERS *et al*., 1989; BENNETT *et al*., 1990; BERNINGER *et al*., 1992).

In this paper, phytoplankton composition in four basins of Empordà salt marshes is described and the responses of the most abundant phytoplankton groups (cyanobacteria and mixotrophs) to eutrophication caused by freshwater flux regulation are emphasised. Additionally, the effects of flux regulation on phytoplankton and zooplankton biomass ratios are discussed; these exhibit opposing responses to eutrophication depending on the initial trophic state of the basins.

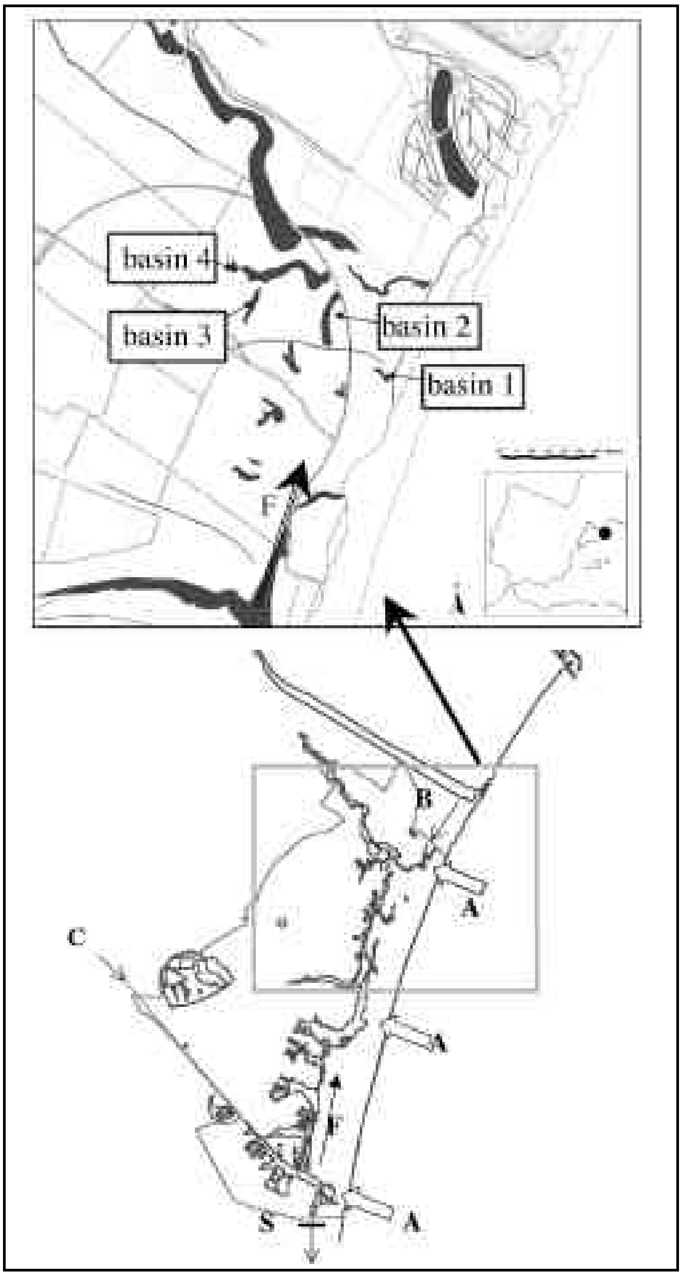

Figure 1. Sketch map of the study area, indicating basins and main routes of surface water circulation. (A) Entry of sea water during storms; (B) occasional entries proceeding from the Muga River; (C) permanent freshwater circulation; (S) sluice gate; (F) preferential freshwater flux deviated by the sluice gate.

STUDYAREA

The study was undertaken in a group of temporary basins in the most coastal area of the Empordà wetlands (Figure 1) from April 1989 to March 1991. These wetlands are made up of a group of coastal lagoons and Mediterranean salt marshes free from tidal influence. The hydrology of the area is dominated by sudden marine intrusions during sea storms that occur very irregularly, although relatively frequently. After sea storms or intense rainfall the marshes remain confined for a long time and tend towards desiccation.

Four basins lined up perpendicular to the coast were chosen and numbered 1-4 by proximity to the sea. In order to avoid the direct effects of freshwater inputs the basins chosen are far away from the freshwater channel (Figure 1). They are small depressions of the salt marsh (maximum lengths between 84 and 181 m) where flood water accumulates, situated between old sand barriers. They are isolated from the group of permanent lagoons, although during periods of maximal floods the whole area is submerged. The average depth of water is between 43 and 60 cm, with higher levels (up to 1 m) recorded rarely, during storms. In the summer all basins dry out and in some years they remain dry for periods in winter. Further details of the hydrology, the physical and chemical characteristics and the zooplankton species composition of the basins can be found elsewhere (QUINTANA, in press; QUINTANA *et al*., 1998a and 1998b). These same references describe two more-eutrophic basins (basins 1 and 2) and two less-eutrophic basins (basins 3 and 4) with differences in nutrient and species composition.

Just one surface fresh water channel from the cultivated plain supplies the lagoon system, before acting as an escape to the sea for excess water. In January 1990, during our period of observation, a sluice gate was installed in this drainage channel. Although first attempts at flux regulation began in January 1990, when a provisional sluice gate was installed in the drainage channel of the salt marshes, fresh water flooding of the salt marshes during the first months of 1990 was very variable. Flux regulation did not stabilize until autumn 1990, after the installation of a definitive sluice gate (March 1990). The effects of the sluice gate on species composition were not visible in the salt marshes until October, due to the lack of flow in the drainage channel in spring and summer. Thus, two autumn-winter periods can be compared before (1989-1990) and after (1990-1991) the consolidation of the flux regulation, whilst the spring periods (1989 and 1990) cannot be compared due to the high variability of the fresh water flow in spring 1990.

METHODS

Samples were taken from each one of the basins from one point close to the centre during the periods of inundation, with a frequency varying from weekly to monthly. A pump submerged 10 – 15 cm from the surface was used to collect water samples. Chlorophyll-a was extracted using 90% methanol as a solvent and samples were immediately submerged in solvent and refrigerated. The chlorophyll-a was measured after 20-24 hours using TALLING and DRIVER's expressions (1963). Physical and chemical variables, especially inorganic dissolved nutrients, were also analysed in these basins (see QUINTANA *et al*., 1998a).

Phytoplankton and free living invertebrates (the latter after filtering with nets of 50 µm) were counted and measured using an inverted microscope. Although most of the invertebrate species were zooplankters, we have used the term invertebrates due to the presence of benthic species, such as amphipods and insects. The estimations of the biomass (dry weight) were obtained, in most of the invertebrate species, from the allometric correlation

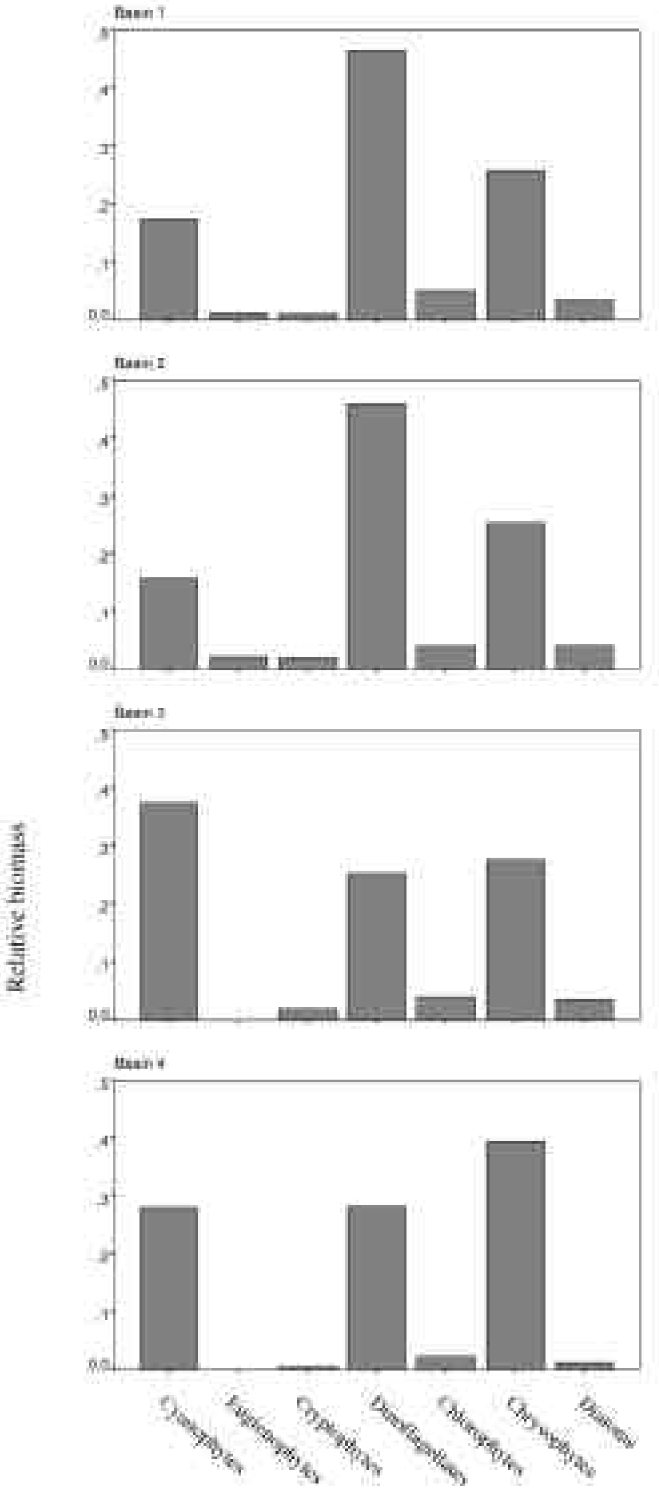

Figure 2. Mean values over the whole study of the relative abundance of the total biomass of the different phytoplankton groups found in the four basins.

between the weight and the length of the body -see QUINTANA *et al.* (1998b) for more details of biomass estimations and of invertebrate community composition. Phytoplankton biovolume was measured by adjusting the volume of the cells to a geometric figure as proposed in HILLEBRAND *et al*. (1999). Dry weight biomass was calculated by converting volume (V) into dry weight (W) using REYNOLDS' (1984) equation: $W = 0.47 \cdot V0.99$. Statistical analyses were carried out using SPSS statistical package. Scheffé tests were used for *post hoc* comparisons.

RESULTS

Phytoplankton composition

Phytoplankton composition of the basins (measured in biovolume units) was mainly dominated by dinoflagellates, haptophytes and cyanobacteria (Figure 2). Cyanobacteria were almost exclusively represented by *Synechococcus*-like organisms, which were the most abundant taxa (measured in number of individuals), with densities of over 106 cellsml-1 frequently recorded. Cyanobacteria peaked in stable conditions, coinciding with low DIN/SRP ratios due to the lack of dissolved inorganic nitrogen (Table 2). Amongst the haptophytes, several *Pavlova*-like species were present

Table 1. Mean and range of variation (in brackets) of physical and chemical variables of the basins before and after the installation of the sluice gate. Level in m; EC25 in $mScm^{-1}$; alkalinity in $meql^{-1}$, NH4+, NO2-, NO3- and SRP, µM; chlorophyll a and zooplankton biomass (dry weight) in mgl^{-1}, phytoplankton biovolume in $mm^{3}l^{-1}$. The value of p is indicated in those variables which exhibit significant differences (p<0.05). Data from all basins are included.

	BEFORE		AFTER		p
Water level	0.47	(0;1.11)	0.50	(0;0.82)	n.s.
Conductivity	40.14	(22.90;60.30)	26.94	(6.28;48.70)	<0.0001
pH	7.48	(5.42;8.66)	7.95	(6.80;8.87)	<0.0001
Alkalinity	5.21	(1.91;12.54)	6.50	(1.31;12.22)	0.002
NH4+	3.73	(0;29.73)	4.52	(0;31.96)	n.s.
NO2-	0.24	(0;2.06)	0.13	(0;3.64)	n.s.
NO3-	1.91	(0;12.17)	0.64	(0;9.80)	<0.0001
SRP	4.22	(0.48;42.22)	5.02	(0;47.00)	n.s.
DIN/SRP	3.58	(0.05;20.35)	7.16	(0;63.00)	n.s.
Chlorophyll a	9.48	(0.25;61.99)	23.84	(0.56;317.48)	0.020
Phytoplankton biovolume	5.55	(0.62;55.12)	23.02	(0.10;146)	0.006
Zooplankton biomass	603.3	(0.03;5065)	248.3	(0.01;2617)	0.016

Table 2. Pearson correlation coefficients (p values in brackets) between the percentage of the phytoplankton groups and the concentration of inorganic nutrients (at logarithmic scale). Only correlations with p values < 0.05 are displayed. N = 105. No significant correlations with other phytoplankton groups were observed. Data from all basins are included.

	DIN		SRP		DIN/SRP ratio	
% cyanophytes	-0.308	(0.001)		n.s.	-0.228	(0.020)
% dinoflagellates	0.192	(0.049)	0.339	(<0.001)	0.321	(0.001)
% haptophytes		n.s.	-0.283	(0.003)	-0.202	(0.040)
% cryptophytes		n.s.	-0.295	(0.002)		n.s.

throughout the year. *Oxyrrhis marina* and *Glenodinium* sp. were the most abundant dinoflagellates. They were present all year, especially in waters with high content of organic matter (great organic floccules surrounded with dinoflagellates were visible by microscope), normally coinciding with fresh water inputs. In some samples, *Katodinium rotundatum*, *Prorocentrum minimum* and *Diplopsalis* sp. were also abundant. Euglenophytes, cryptophytes, chlorophytes and diatoms were poorly represented, although they sporadically reached high densities, normally coinciding with low zooplankton biomass.

Mixotrophic activity of the most abundant haptophytes and dinoflagellates was observed under an inverted microscope. Morphological changes were apparent in *Oxyrrhis marina* and *Glenodinium* sp. In some specimens plastes were present, while in the interior of others phagocitate organisms were visible. This was also observable in some large haptophytes. Mixotrophy has also been reported in the other dinoflagellates and haptophytes present (STROM, 1991; LI *et al*., 1996; STOECKER *et al*., 1997; STOECKER, 1999), although there was no evidence in this case. The relative abundance of haptophytes and dinoflagellates was higher in the more eutrophic basins, whereas cyanobacteria were more abundant in less eutrophic ones, especially in basin 3 (Figure 2).

Correlations between percentages of the whole biomass of phytoplankton groups and the composition of inorganic nutrients (Table 2) suggest a dominance of cyanobacteria when DIN is low and a dominance of dinoflagellates under high DIN and SRP concentrations, which coincide with external water supplies. Relative abundance of haptophytes and cryptophytes is higher under low SRP. No correlations are found between inorganic nutrients and the biomass of other phytoplankton groups.

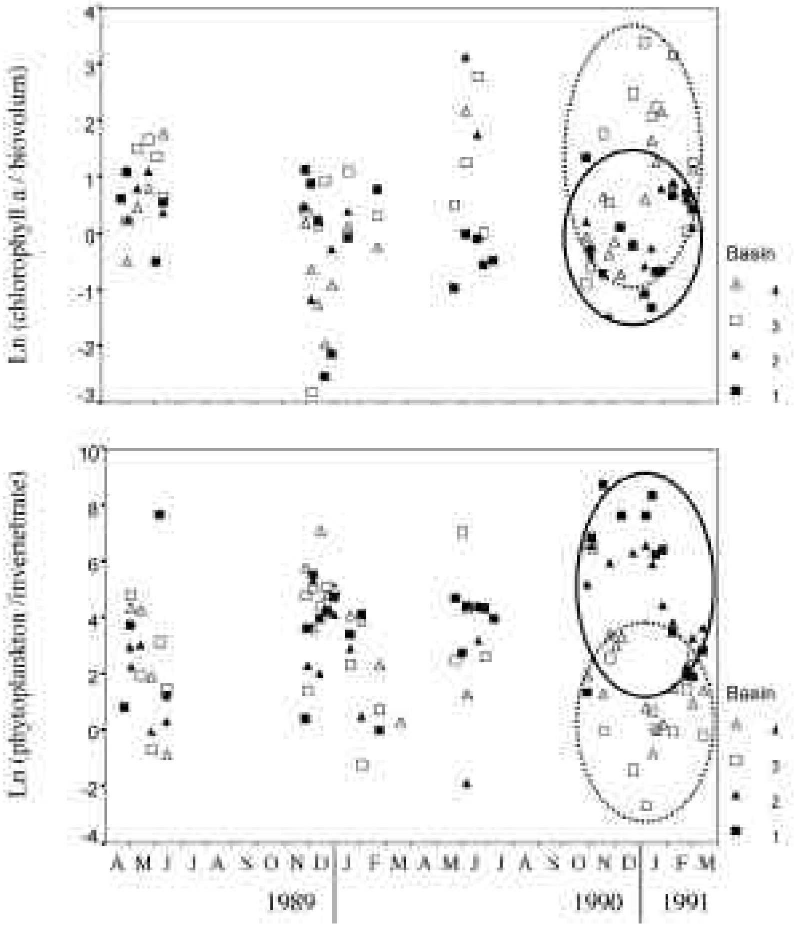

Figure 3. Variation over time of chlorophyll-a / biovolume and phytoplankton / invertebrate ratios in the four basins. Dark marks, more eutrophic basins; white marks, less eutrophic ones. Continuous line circles at least 90% of points in more eutrophic basins during the period autumn-winter 1990/91 and dashed line circles those in less eutrophic basins.

Effect of flux regulation

Freshwater flooding due to flux regulation increased pH, alkalinity, chlorophyll a and phytoplankton biomass and decreased conductivity, nitrate and zooplankton biomass (Table 1). Flux regulation also caused spatial variability of some variables related to phytoplankton and zooplankton biomass (Tables 3 and 4): no significant differences were observed between basins during autumn-winter 1989/90 (Table 3) nor during the spring periods. However, differences were significant during the autumn-winter period of 1990/91, when flux regulation was stabilised (Table 4). Differences were significant only between more eutrophic basins (basins 1 and 2) and less eutrophic ones (basins 3 and 4). Chlorophyll-a values, phytoplankton biovolume, the percentage of mixotrophic phytoplankton and the biomass ratio phytoplankton/invertebrates (P/I) were higher in the more eutrophic basins. Increases in biovolume values were especially high. However, the chlorophyll/biovolume (Chl/BV) ratio was lower in these basins than in less eutrophic ones as was the invertebrate biomass.

The variability over time of the Chl/BV ratio was very high (Figure 3), oscillating between 0.06 and 29.63 µgmm-3. Especially frequent were the values below 1µgmm-3, whereas values over 2 µgmm-3 were rarely recorded. Linear regression between chlorophyll-a and biovolume showed lower correlation (r = 0.74) than was observed by other authors in lakes and lagoons (MARGALEF, 1983; REYNOLDS, 1984; MIRACLE *et al*., 1984). The Chl/BV ratio varied very irregularly throughout the study, except during autumn-winter 1990/91, when it tended to be lower in more eutrophic basins (see also Table 4). The P/I ratio showed the opposite tendency during autumn-winter 1990/91, with an increase in more eutrophic basins and a decrease in less eutrophic ones (Figure 3 and Table 4). During the rest of the year, the P/I ratio oscillated between a wide range of values (between 0.29 and 1134).

Table 3. Mean, standard deviation and range of variation of chlorophyll-a and biomass values of phytoplankton and aquatic invertebrates for each basin during the period autumn-winter 1989/90, before consolidation of flux regulation. No significant differences ($p<0.05$) were observed within basins in any variable. Chlorophyll-a in $\mu g \cdot l^{-1}$. Phytoplankton biovolume in $mm^3 l^{-1}$. Biomass of invertebrates (>50 µm) and ciliates in $\mu g l^{-1}$ dry weight. Percentage of mixotrophic phytoplankton, in biovolume. Phytoplankton/invertebrate ratio measured using dry weight units.

Basin		**1**	**2**	**3**	**4**
Number of samples		9	7	8	10
Chlorophyll-a	mean (std)	9.76 (14.3)	19.17 (43.3)	3.38 (2.23)	8.72 (8.11)
	range	<0.01; 45.7	1.67; 126.2	<0.01; 7.37	<0.01; 20.02
Phytoplankton biovolume	mean (std)	10.72 (14.9)	6.04 (7.61)	11.61 (23.7)	20.89 (23.1)
	range	0.79; 44.9	1.04; 21.05	0.77; 65.29	2.10; 72.36
Chlorophyll-a /biovolume ratio	mean (std)	1.25 (1.18)	1.14 (0.52)	1.38 (1.14)	0.55 (0.43)
	range	<0.01; 3.08	0.30; 1.61	<0.01; 3.03	<0.01; 1.19
% of mixotrophic phytoplankton	mean (std)	0.72 (0.36)	0.66 (0.30)	0.72 (0.25)	0.78 (0.31)
	range	0.07; >0.99	0.22; >0.99	0.29; >0.99	0.02; >0.99
Invertebrate (>50mm) biomass	mean (std)	83.95 (183)	45.15 (68.9)	74.53 (128)	234.5 (512)
	range	0.01; 566.8	0.08; 165.2	0.55; 339.5	0.62; 1584
Phytoplankton/invertebrate ratio	mean (std)	67.70 (75.9)	46.85 (68.3)	66.69 (70.7)	207.0 (360)
	range	0.99; 248.2	1.55; 194.6	0.29; 159.8	1.28; 1134

Table 4. Mean, standard deviation and range of variation of chlorophyll-a and biomass values of phytoplankton and aquatic invertebrates in each basin during the period autumn-winter 1990/91, after consolidation of flux regulation. Numbers in square brackets indicate the basin number with which they are significant differences ($p<0.05$); differences between more and less eutrophic basins can be appreciated. Chlorophyll-a in $\mu g l^{-1}$. Phytoplankton biovolume in $mm^{3} l^{-1}$. Biomass of invertebrates (>50 µm) and ciliates in $\mu g l^{-1}$ dry weight. Percentage of mixotrophic phytoplankton, in biovolume. Phytoplankton/invertebrate ratio measured using dry weight units.

Basin		**1**	**2**	**3**	**4**
Number of samples		13	11	12	13
Chlorophyll-a	mean (std)	21.57 (19.9)	36.25 (27.7) [3, 4]	6.61 (8.30) [2]	5.18 (4.61) [2]
	range	1.11; 68.4	2.50; 80.3	1.39; 34.7	0.56; 16.7
Phytoplankton biovolume	mean (std)	38.59 (36.1) [3]	49.53 (46.1) [3 ,4]	8.01 (19.2) [1, 2]	4.06 (4.97) [2]
	range	1.64; 101	5.37; 146	0.10; 64.2	0.22; 14.3
Chlorophyll-a /biovolume ratio	mean (std)	1.18 (1.02) [3]	1.16 (0.72) [3]	8.73 (9.79) [1, 2]	2.57 (2.26)
	range	0.27; 3.81	0.23; 2.39	0.41; 29.6	0.47; 8.41
% of mixotrophic phytoplankton	mean (std)	0.73 (0.34) [3]	0.86 (0.12) [3]	0.43 (0.26) [1, 2]	0.69 (0.19)
	range	0.02; 0.99	0.64; 0.99	0.03; 0.85	0.33; 0.94
Invertebrate (>50mm) biomass	mean (std)	45.56 (62.3) [4]	50.15 (44.6)	187.83 (222)	197.79 (83.3) [1]
	range	0.13; 220	1.66; 133	1.75; 710	68.6; 318
Phytoplankton/invertebrate ratio	mean (std)	1364 (1940) [3, 4]	266 (258)	115.9 (263) [1]	8.27 (10.0) [1]
	range	3.8; 6040	9.67; 660	0.07; 716	0.41; 30.0

DISCUSSION

Phytoplankton composition and biomass in Empordà salt marsh basins are dominated by cyanobacteria, favoured by the low N/Pratio, and mixotrophic phytoplankton, probably related to the high proportion of allochthonous organic matter supply, characteristic of wetland ecosystems (Wetzel, 1992). Low N/P ratios, most probably caused by denitrification, are observed during confinement conditions, favouring the dominance of *Synechococcus*-like cells due to its capacity for fixing atmospheric nitrogen (MITSUI *et al*., 1986; PHLIPS *et al*., 1989; WEHR, 1989). In these conditions, a relative oligotrophy is reached, due to the loss of nitrogen, and plankton is dominated by calanoid copepods (QUINTANA *et al*., 1998b). Additionally, *Synechococcus* sp. might resist the predation preassure of zooplankton better than other phytoplankters (FAHNENSTIEL *et al*., 1991; STOCKNER, 1991), whilst mixotrophs are largely removed by grazing (ISAKSSON, 1998).

Eutrophication after flux regulation in the Empordà salt marshes has been seen to be due to nitrogen inputs from external water supply (QUINTANA *et a*l., in press). However, these nutrient inputs do not result in a significant increase in DIN and SRP concentrations, but in an increase of phytoplankton biomass, which probably exhausts inorganic nutrients, and an increase in alkalinity, attributable to higher respiration. Greater eutrophy also favours the development of mixotrophic species in the basins and results in low chlorophyll / biomass ratios. Mixotrophic activity has been widely reported in aquatic ecosystems, especially in oligotrophic and dystrophic conditions, in response to light and nutrient requirements (see ISAKSSON, 1998 for references). Phagotrophic activity on bacteria allows mixotrophs to obtain an additional source of P during P scarcity in oligotrophic conditions, by making use of the lower C/Pratios in bacteria (CURRIE and KALFF, 1984; SANDERS and PORTER, 1988; GAEDKE, 1998; NYGAARD and TOBIESEN, 1993). ISAKSSON (1998) also notes the advantage of a mixotrophic strategy in dystrophic lakes, where the lack of light and nutrients limits photosynthesis. However, their dominance in eutrophic conditions is not so frequent (SANDERS *et al*., 1989; BENNETT *et al*., 1990; BERNINGER *et al*., 1992).

The fluctuating conditions of source availability and the importance of the allochthonous supply may favour the abundance of mixotrophic species in Empordà wetlands. ISAKSSON (1998) affirms that a high allochthonous supply and a low P/R ratio due to a high decomposition rate benefit mixotrophs. The abundance of mixotrophic phytoplankton has been shown to be favoured by a high organic carbon / nutrients ratio (JONES, 2000). Organic carbon concentrations are not available in this study, but the increase in alkalinity and phytoplankton biomass without significant changes in nutrient concentrations suggests an increase in the organic C/nutrients ratio. In addition, surface allochthonous inputs are abundant in Empordà wetlands, especially after flux regulation.

It is debatable whether mixotrophy is a competitive method of obtaining P for phytoplankton in Empordà wetlands, because the availability of inorganic Pis normally very high (QUINTANA *et al*., 1998a). Nevertheless, it probably supplies an additional source of N in an environment especially poor in inorganic N, although heterotrophic incorporation of N by mixotrophs has been seen to be less efficient than Pincorporation (SANDERS *et al*., 1990; CARON *et al*., 1990; JANSSON *et al*., 1996). Amongst the mixotrophs, cryptophytes are less efficient at incorporating organic N (VIEIRA and KLAVENESS, 1986). Phagotrophy as an additional source of P could explain the negative correlation of cryptophyte biomass with SRP (Table 2) and the low biomass of cryptophytes compared with other mixotrophs, which would be more efficient in the heterotrophic incorporation of organic N.

Mixotrophic activity results in high variability of the Chl/BV ratio. Values of this ratio obtained by other authors oscillate between 0.56 and 19.7 and the more frequent values range between 1 and 8 µgmm-3 (MARGALEF, 1983; REYNOLDS, 1984; GARCIA-JIMÉNEZ, 1991; NIXDORF and HOEG, 1993). The P/I biomass ratio also oscillates over a wide range, indicating that zooplankters do not depend exclusively on phytoplankton for subsistence, but use other food such as bacteria or organic matter obtained from sediment.

It is remarkable how the different tendencies observed in these ratios after stabilising flux regulation depend on the degree of eutrophy of the basins. In less eutrophic basins, a decrease in P/I ratio and an increase in the Chl/BVratio may be explained by a general increase of the level of eutrophy caused by freshwater input. This would result in more photosynthetic activity as a result of nutrient supply, and in biomass accumulation in the highest trophic levels, as a consequence of top-down control. Invertebrates represent these highest trophic levels in the absence of fish in these temporary marshes.

More eutrophic basins behave in the opposite way, also responding to an increase in the level of eutrophy. We hypothesise that this is related to the high level of variability of oxygen concentration in these basins, caused by the accumulation of organic matter, leading to a situation of hypertrophy. The supply of organic matter (and its variability) would favour the presence of mixotrophs, whilst the lack of oxygen (and its diel variability) would retard the development of invertebrates. Although data on diel oxygen dynamics during the period of study are not available, nocturnal anoxias are frequent in the more eutrophic basins (pers. observation) and the percentage increase of mixotrophic species indicates an increase in concentration of organic matter. Additionally, some organisms able to withstand prolonged periods of anoxia, such as Brachionus plicatilis, are dominant in these periods (QUINTANA *et. al*., 1998b). Differences between basins were not observed before stabilising of flux regulation, suggesting that in natural conditions, when water inputs are basically pulses, temporal fluctuation within basins is more important than spatial variability between basins.

The negative effects of flux regulation appear to be as relevant to phytoplankton composition as they are in nutrient dynamics (QUINTANA *et al*., in press), since they cause general eutrophication and an increase in the frequency of hypertrophic events. Due to differences depending on the trophic state of the basin, the use of simple variables such as inorganic nutrient, chlorophyll concentration or zooplankton biomass, is not appropriate for evaluating the degree of eutrophy in this case, where a more general approach, such as understanding the behaviour of the P/I and Chl/BV ratios, is necessary.

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