

# Hydrological complexity supports high phytoplankton richness in the Doñana marshland (SW Spain)

I. Reyes · M. A. Casco · J. Toja · L. Serrano

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**Abstract** Two hundred and twenty-four phytoplanktonic taxa were recorded in a riverine floodplain on the NE side of the Doñana marshland from September 2002 to 2004. This collection of 11 samples included 80 Bacillariophyceae (Diatoms), 71 Chlorophyta, 39 Cyanophyta, 19 Euglenophyta, 6 Chrysophyceae, 5 Cryptophyta, and 4 Dinophyceae. Fifty-five percent of the total taxa had a very low frequency of appearance (<5%), while only three species appeared with a frequency >90% (*Monoraphidium contortum* Komárková-Legnevorá, *Cyclotella atomus* Hustedt, and *Nitzschia palea* W. Smith). According to multivariate analyses, both temporal and spatial factors produced a pattern in the phytoplankton assemblages dominated by freshwater inputs during winter flooding, tidal inputs in summer, and transitional stages during the rest of the year. Spatial segregation of phytoplankton was likely due to differences in retention time and distance to water input. The main taxa involved in this

segregation were *Chrysidalis* sp. 1 (June 2003 and 2004), *Chlamydomonas* sp. 4 (September 2003), *C. atomus* (December 2003), and *Tetradesmus* aff. *crocini* (February 2004). The hydrologic complexity of the study area could account for this high taxa richness by promoting replacement and colonization episodes following seasonal changes in water source (freshwater versus tidal inputs).

**Keywords** Mediterranean coastal wetlands · Rice-pads · Guadiamar River

## Introduction

Coastal wetlands under Mediterranean climate are largely influenced by hydrologic features, nutrient availability, and seasonality (Comín & Valiela, 1993; Quintana & Moreno-Amich, 2002; Nuccio et al., 2003). This kind of systems is difficult to study because they are very dynamic and subject to variable stages (Comín et al., 1999). Consequently, few publications on phytoplankton composition are available (Sabater & Muñoz, 1990; Romo & Miracle, 1994; Gilabert, 2001; Rodrigo et al., 2001; Puigserver et al., 2002; Villena & Romo, 2003; López-Flores et al., 2006).

Changes in phytoplankton composition of Mediterranean coastal wetlands are often related to salinity (Puigserver et al., 2002), eutrophication (Sorokin

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I. Reyes · J. Toja · L. Serrano  
Plant Biology and Ecology Department, University  
of Sevilla, Sevilla, Spain

M. A. Casco (✉)  
División Científica Ficología, Facultad de Ciencias  
Naturales y Museo, UNLP, CONICET, La Plata,  
Argentina  
e-mail: casco@fcnym.unlp.edu.ar

et al., 1996; Villena & Romo, 2003), and seasonality of temperature and light conditions (Romo & Miracle, 1994). An annual seasonal pattern driven by marine and freshwater fluxes, often due to anthropic control, has been generally observed in Mediterranean coastal wetlands (Rojo & Miracle, 1989; Comín & Valiela, 1993; Puigserver et al., 2002). Stagnation versus flushing cycles due to drainage of rice pads has also been reported to account for seasonal changes in phytoplankton assemblages (Romo & Miracle, 1995). In other cases, the phytoplankton community of coastal wetlands with permanent confinement has been driven by hydrologic disturbances with no fix pattern (López-Flores et al., 2006). The influence of allochthonous flora is commonly overlooked in wetland studies (Romo, 1997) despite different water inputs that allow the colonization of organisms from different origins (Comín et al., 1999).

The present study was carried out in the NE Doñana marshland, located at the final stretch of the Guadiamar River. This site is subject to tidal flow from the Guadalquivir River estuary. Therefore, the hydrology of the study site is complex due to both natural and artificial water bodies receiving water inputs from different origins depending on the season (Serrano et al., 2006; Reyes et al., 2007). The objectives of this

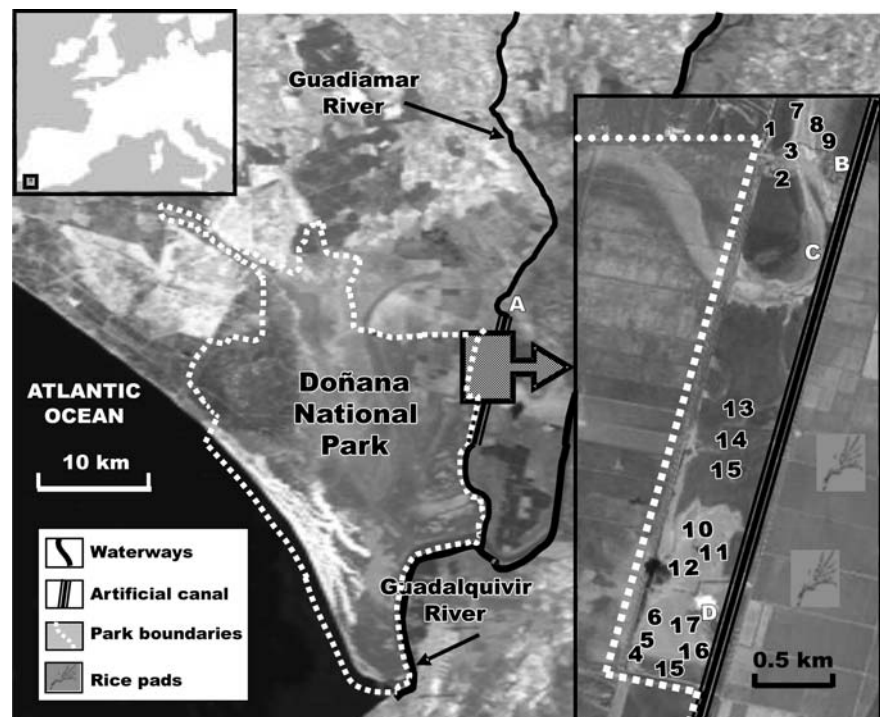
study are: (1) to relate hydrologic heterogeneity to phytoplankton richness, composition, and abundance; (2) to test whether phytoplankton assemblages follow spatial and/or temporal patterns by means of multivariate analysis; (3) to study the influence of colonization events on phytoplankton composition.

#### Study area

Doñana has a Mediterranean climate with Atlantic influence, generally classified as dry subhumid. Rainfall is quite variable, both within a year and over the years. About 80% of the rainfall yearly average (580 mm) falls between the end of September and the beginning of April. Summers are very dry and hot, while winters are short and mild. Water balance is generally deficient as rainfall exceeds evapotranspiration only during 3 to 4 months of the year.

About 23,000 ha of the Doñana marshland are preserved within the Doñana National Park and the Natural Park. The study site covers 250 ha of the final stretch of the Guadiamar River encroached by two parallel levees built in 1956 (Fig. 1). It includes natural and man-made waterways, isolated waterbodies, and playa-floodplains (locally named as

**Fig. 1** Map of the Doñana National Park and location of the study site



lucios), which give name to the whole site (“Lucio El Cangrejo Grande”). Most of the Guadiamar River water flow is diverted toward the Guadalquivir River estuary through an artificial canal, which is permanently connected to the study area by two inlets (Fig. 1: sites B and C), seasonally by a floodgate (Fig. 1: site D), and occasionally during floods by the outflow of the Guadiamar River (Fig. 1: site A). Water in the study area is generally temporary and shallow except at the floodgate where water can reach up to 2 m in high-tide. Water temperature ranged from 8 to 30°C, conductivity (at 25°C) from 0.5 to 15.7 mS cm<sup>-1</sup>, Na<sup>+</sup> was the dominant cation in the floodplains, while Ca<sup>2+</sup> dominated in some waterways (Reyes et al., 2007). Water flowing through the artificial canal was usually turbid due to a high load of inorganic suspended matter largely composed of CaCO<sub>3</sub> particles associated to P (Serrano et al., 2006). Vegetation of elevated areas was dominated by *Sarcocornia fruticosa* (L.) A.J. Scott, and *Hordium marinum* Hudson, while aquatic emergent macrophytes (*Phragmites australis* (Cav.) Trin. ex Steudel, *Scirpus maritimus* L., *Juncus subulatus* Forsskall), and submerged macrophytes (*Chara galioides* DC, *Callitriche truncata* subsp. *occidentalis* (Rouy) Schotsman, *Ranunculus peltatus* subsp. *fucoides* (Frey) Muñoz Garmendia, *Ruppia drepanensis* Tineo ex Guss) grew in flooded areas.

## Material and methods

Twenty-one sampling sites were located within the study area and were sampled 11 times bimonthly during two consecutive hydrologic cycles: 2002/2003 and 2003/2004 (Fig. 1). Four sites corresponded to inlets, of which only three acted as outlets during floods or tidal flow (sites B, C and D), as site A was located upstream. Water samples of 125 ml were preserved in situ with Lugol's iodine solution, and the determination of phytoplankton composition and abundance was performed in duplicates on fixed samples. Phytoplankton taxa were identified with an optical microscope. Abundance of phytoplankton cells was estimated with an inverted microscope following Utermöhl's method. Statistical analyses for community analyses (MDS, ANOSIM, SIMPER) were performed with PRIMER v5 based on quantitative samplings (three samplings

in 2002/2003 and five in 2003/2004). An analog of the univariate ANOVA called ANOSIM was used to test for differences between multivariate samples from different sites or from different samplings. Similarity matrices of the multivariate samples were calculated using the Bray-Curtis coefficient after log-transformation [ $\log(x + 1)$ ] of the original taxa abundance to perform a non-metric multidimensional scaling (MDS). A SIMPER test was used to identify the taxa primarily providing the discrimination between samplings. Duplicates were averaged before calculations except to record cumulative richness. Rainfall data were obtained from the meteorological station of Palacio de Doñana (RBD-CSIC).

## Results

Phytoplankton cumulative richness (or total number of taxa) recorded in the study area was 224 taxa: 80 Bacillariophyceae (Diatoms), 71 Chlorophyta, 39 Cyanophyta, 19 Euglenophyta, 6 Chrysophyceae, 5 Cryptophyta, and 4 Dinophyceae. That is, 85% of the total taxa belonged to the sum of Bacillariophyceae (Diatoms), Chlorophyta, Cyanophyta, while each of the rest of groups amounted for less than 3% of the total taxa. Phytoplankton cumulative richness was significantly correlated with the number of samplings at each site ( $r = 0.765$ ,  $P < 0.05$ ). The number of samplings was constrained by the availability of water at each site during the study. Therefore, the inlet sites, being permanent, accumulated the highest richness (115 taxa at site A).

Fifty-five percent of total taxa had a very low frequency of appearance (<5%). Eighteen taxa appeared in at least 40% of total samplings (Table 1). Only three species (*Monoraphidium contortum* Komárková-Legnevorá, *Nitzschia palea* W. Smith, and *Cyclotella atomus* Hustedt) had a frequency of appearance  $\geq 90\%$ , being also relatively abundant species. Consequently, frequency of appearance and average abundance were positively correlated ( $r = 0.789$ ,  $P < 0.01$ ).

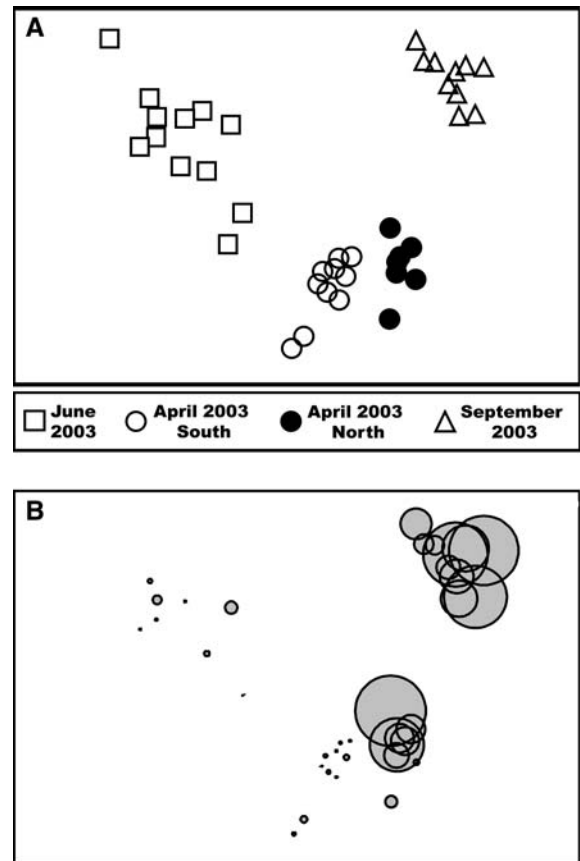
An ordination in MDS showed that phytoplankton assemblages were segregated into groups according to the number of samplings carried out during each cycle (Fig. 2A). This temporal segregation was stronger in 2002/2003 (ANOSIM test,  $R = 0.968$ ,

**Table 1** List of phytoplankton taxa with a frequency of appearance  $\geq 40\%$  showing average abundance (cell  $\text{ml}^{-1}$ )

Taxa	Frequency (%)	Average abundance (cell $\text{ml}^{-1}$ )
<i>Nitzschia palea</i> W. Smith	99	$4.0 \times 10^3$
<i>Monoraphidium contortum</i> Komárková-Legnevorá	96	$4.0 \times 10^3$
<i>Cyclotella atomus</i> Hustedt	90	$3.0 \times 10^3$
<i>Schroederia</i> sp.	80	$1.0 \times 10^3$
<i>Nitzschia longissima</i> Ralfs	75	$4.0 \times 10^2$
<i>Euglena variabilis</i> Klebs	72	$2.0 \times 10^2$
<i>Monoraphidium circinale</i> Nygaard	70	$3.0 \times 10^2$
<i>Navicula radiosa</i> Kützing	70	$1.0 \times 10^2$
<i>Nitzschia acicularis</i> W. Smith	67	$6.0 \times 10^2$
<i>Monoraphidium</i> sp.	59	$3.0 \times 10^2$
<i>Scenedesmus tenuispina</i> Chodat	53	$1.0 \times 10^2$
<i>Cryptomonas ovata</i> Ehrenberg	53	$4.0 \times 10^2$
<i>Chlorococcum</i> sp.	52	$2.0 \times 10^2$
<i>Chlamydomonas</i> sp. 3	49	$3.0 \times 10^2$
<i>Scenedesmus ecornis</i> Chodat	49	$2.0 \times 10^2$
<i>Synechocystis</i> sp.	47	$1.0 \times 10^3$
<i>Entomoneis alata</i> Ehrenberg	46	10
<i>Chlorella minutissima</i> Fott & Novak	41	$2.0 \times 10^2$

$P < 0.01$ ) than in 2003/2004 when five samplings were carried out ( $R = 0.718$ ,  $P < 0.01$ ). In 2002/2003, phytoplankton assemblages showed a weak segregation within the April sampling between sites located in the northern and southern end of the study area ( $R = 0.617$ ,  $P < 0.01$ ). Therefore, phytoplankton assemblages were basically arranged following temporal changes, while segregation according to spatial differences was evident only on certain occasions and occurred at the same time as temporal segregation (Fig. 2A). For example, the abundance of *C. atomus* was larger during September compared to June 2003, and in the northern rather than southern part of the study area during April 2003 (Fig. 2B). It is likely that *C. atomus* derived from the downstream drift of the Guadiamar River, which enters the study area from its northern end.

Few taxa contributed to the temporal segregation of each cycle according to a SIMPER test, which indicated that most taxa provided a very small contribution to the segregation among samplings (Table 2). Only eight taxa were involved in the characterization of each sampling with a contribution higher than 10%:



**Fig. 2** (A) Ordination in MDS of phytoplankton assemblages of each site according to sampling during 2002/2003. North and South sites are distinguished in April 2003; (B) Size of bubbles represents relative abundance of *Cyclotella atomus* Hustedt at each site during 2002/2003

*Chrysidalis* sp. 1, *C. atomus*, *Tetradesmus* aff. *crocini*, *Monoraphidium* sp., *M. contortum*, *Chroococcus* aff. *minutus*, *N. palea*, and *Chlamydomonas* sp. 4. Only four taxa accounted for the dissimilarity among groups with a contribution of at least 10%. The presence and abundance of *Chrysidalis* sp. 1 and *Chlamydomonas* sp. 4 differentiated the phytoplankton assemblages of June and September 2003, respectively, from the rest of samplings within 2002/2003, while *C. atomus*, *T. aff. crocini*, and *Chrysidalis* sp. 1 were responsible for the differences in December 2003, February 2004, and June 2004, respectively, within 2003/2004 (Table 2).

Abundance of main phytoplankton taxa ranged widely (Table 1). Some taxa maintained a relatively high abundance ( $1.4 \times 10^4$  cells  $\text{ml}^{-1}$ ) throughout the study period (e.g., *M. contortum*), while others were more

**Table 2** List of phytoplankton taxa with a contribution above 10% to similarity within each sampling and dissimilarity among samplings

Sampling	Similarity within sampling	Dissimilarity among samplings
April 2003	<i>Chroococcus</i> aff. <i>minutus</i> <i>Nitzschia palea</i> W. Smith <i>Monoraphidium contortum</i> Komárková-Legnevorá	None
June 2003	<i>Chrysidalis</i> sp. 1 <i>Monoraphidium contortum</i> Komárková-Legnevorá <i>Chroococcus</i> aff. <i>minutus</i>	<i>Chrysidalis</i> sp. 1
September 2003	<i>Chlamydomonas</i> sp. 4 <i>Nitzschia palea</i> W. Smith <i>Cyclotella atomus</i> Hustedt	<i>Chlamydomonas</i> sp. 4
December 2003	<i>Cyclotella atomus</i> Hustedt <i>Nitzschia palea</i> W. Smith	<i>Cyclotella atomus</i> Hustedt
February 2004	<i>Monoraphidium contortum</i> Komárková-Legnevorá <i>Tetradesmus</i> aff. <i>crocini</i> <i>Nitzschia palea</i> W. Smith	<i>Tetradesmus</i> aff. <i>crocini</i>
April 2004	<i>Monoraphidium contortum</i> Komárková-Legnevorá <i>Monoraphidium</i> sp. <i>Nitzschia palea</i> W. Smith	None
June 2004	<i>Chrysidalis</i> sp. 1 <i>Nitzschia palea</i> W. Smith	<i>Chrysidalis</i> sp. 1
September 2004	<i>Nitzschia palea</i> W. Smith <i>Cyclotella atomus</i> Hustedt	None

abundant at certain samplings: *Chrysidalis* sp. 1 reached  $8.4 \times 10^5$  cells  $\text{ml}^{-1}$  in June 2003. On some occasions, high taxa abundance was preceded and/or followed by a negligible number of cells. Average abundance of 18 taxa, which appeared at both the inlet and the inner sites at the same time, fluctuated widely along successive samplings, suggesting that they were likely the result of colonization events (Table 3). Maximum abundance of *Chrysidalis* sp. 1 ( $8.4 \times 10^5$  cell  $\text{ml}^{-1}$ ), *Chlamydomonas* sp. 4 ( $3.1 \times 10^5$  cell  $\text{ml}^{-1}$ ), and *T. aff. crocini*. ( $8.3 \times 10^4$  cell  $\text{ml}^{-1}$ ) occurred in June 2003 and 2004, September 2003, and February 2004, respectively. This high abundance contributed to the segregation of each of these samplings.

## Discussion

Primary producers of coastal wetlands are expected to cope with wide variation in salinity, turbidity, and nutrient concentrations (Odum, 1988). Most

phytoplankton taxa had a low frequency within the study area (<5%), suggesting a rapid replacement of species. Only *M. contortum*, *C. atomus*, and *N. palea* had a frequency of appearance higher than 90%. The first two species are typical of estuaries (Trigueros & Orive, 2001) and *N. palea* has been recorded in the Guadiamar River (Toja et al., 2004). Most abundant taxa in the study period corresponded to the functional groups of Reynold's (Reynolds et al., 2002) classification D, J, and X1, which are indicative of shallow systems rich in nutrients.

The positive correlation between cumulative richness and number of samplings indicated that a longer study period and/or a higher frequency of samplings would be required to reach a more conclusive result on the total number of taxa and the rate of species replacement. Despite this limitation, cumulative richness per surface area was higher than in nearby waterways (Guadiamar River and Guadalquivir River estuary) and reached similar values to other Mediterranean wetlands (Reyes et al., 2007). The study



**Table 3** Average abundance of phytoplankton taxa appearing simultaneously at inlet and inner sites during each sampling

Taxa	April 2003	June 2003	September 2003	December 2003	February 2004	August 2004	June 2004	September 2004
<i>Aphanocapsa elachista</i> W. & G. S. West	NG	NG	$1.0 \times 10^3$	NG	NG	NG	NG	NG
<i>Aphanothece nidulans</i> Richter	NG	NG	$1.7 \times 10^3$	NG	NG	NG	NG	NG
<i>Anabaena torulosa</i> Lagerheim	NG	NG	$1.0 \times 10^2$	NG	NG	NG	NG	NG
<i>Merismopedia warmingiana</i> Lagerheim	NG	NG	NG	NG	NG	NG	$3.0 \times 10^3$	$1.0 \times 10^3$
<i>Limnothrix</i> aff. <i>planctonica</i>	NG	$1.0 \times 10^2$	$2.2 \times 10^3$	NG	30	NG	NG	NG
<i>Oscillatoria</i> aff. <i>rosea</i>	20	20	60	NG	NG	NG	$3.0 \times 10^2$	$5.7 \times 10^3$
<i>Synechococcus linearis</i> Kómarek	80	NG	NG	NG	NG	NG	$10^2$	NG
<i>Synechococcus vantiagemii</i> Bourelly	NG	NG	40	NG	NG	40	$3.3 \times 10^3$	40
<i>Chlamydomonas</i> sp. 3	$6.0 \times 10^2$	NG	NG	NG	$1.0 \times 10^3$	$3.0 \times 10^2$	NG	$1.0 \times 10^2$
<i>Chlamydomonas</i> sp. 4	NG	NG	$1.2 \times 10^4$	NG	30	NG	NG	$5.0 \times 10^2$
<i>Coelastrum microporum</i> Nägeli	$3.4 \times 10^3$	$3.0 \times 10^2$	NG	NG	$3.0 \times 10^2$	NG	40	NG
<i>Pyramimonas</i> sp.	NG	NG	NG	NG	NG	$1.0 \times 10^3$	40	NG
<i>Tetradismus</i> aff. <i>crocini</i>	$4.0 \times 10^3$	NG	NG	$2.0 \times 10^2$	$2.5 \times 10^4$	70	NG	NG
<i>Rhodomonas minuta</i> Skuja	NG	NG	NG	$3.3 \times 10^2$	$1.0 \times 10^2$	NG	$1.0 \times 10^2$	NG
<i>Chrysidalis</i> sp. 1	NG	$1.5 \times 10^5$	NG	NG	NG	30	$7.6 \times 10^4$	NG
<i>Fallacia pygmaea</i> Stickle & Mann	30	$2.0 \times 10^2$	$1.5 \times 10^3$	NG	NG	30	$3.0 \times 10^2$	$3.0 \times 10^2$
<i>Nitzschia longissima</i> Ralfs	$1.0 \times 10^2$	$1.5 \times 10^3$	$4.0 \times 10^2$	$1.0 \times 10^2$	$1.0 \times 10^3$	50	40	20
<i>Nitzschia sigma</i> W. Smith	NG	NG	$1.3 \times 10^3$	NG	NG	NG	NG	60

NG, negligible

area included a large diversity of water bodies with different water duration that could provide a wide range of aquatic conditions for phytoplankton development. There were lotic and lentic systems of both artificial and natural origins: trenches, canals, drainage channels, floodplains, and ponds. They received water from different sources following seasonal and yearly changes. When rainfall is heavy, the overflow of the Guadamar River floods most part of the study area during winter–spring. As freshwater flow decreases during spring–summer, tidal water from the estuary of the Guadalquivir River becomes the only source of water until rice pads are drained in September–October (Serrano et al., 2006).

This hydrologic complexity could support high phytoplankton richness by enhancing species replacement through colonization processes. Infrequent taxa generally appeared with low average abundances

probably due to drifting, but some taxa showed intermittent peaks of large abundance, simultaneously at inner and inlet sites, which could account for diverse episodes of colonization. Some of these taxa were also responsible for segregation among samplings: *Chrysidalis* sp. 1 (June 2003 and 2004), *Chlamydomonas* sp. 4 (September 2003), and *T.* aff. *crocini*. (February 2004). It is likely that *Chrysidalis* sp. 1 arrived to the study area with the tidal flow. Chrysophyceans are a significant fraction of marine phytoplankton and can also reach high abundance in brackish Mediterranean wetlands (Sorokin et al., 1996; Cruz-Pizarro et al., 2003). *T.* aff. *crocini* has already been recorded in the Guadamar River (Marín & García-Novo, 2006), and so it may have arrived to the study area in large numbers through the overflow of the Guadamar River during winter flooding.

In the present study, the composition and abundance of phytoplankton assemblages were segregated basically following temporal changes (samplings). Occasionally, some taxa showed spatial changes (e.g., North-South distribution of *C. atomus* in April 2003), probably due to the direction of the overflow of the Guadiamar River during spring. The influence of temporal, rather than spatial variation, was also more relevant for the composition of phytoplankton in the Albufera of Valencia (Romo, 1991). In the present study, spatial distributions were likely caused by differences in distance to the water input and/or retention time. Similarly, Romo (1997) found that the phytoplankton composition of inlet channels draining the rice pads was different from the composition at the inner sites of the Albufera of Valencia. Moreover, phytoplankton composition at inlet sites can be expected to change more than at inner sites. When phytoplankton assemblages from inlet and inner sites were analyzed separately in a previous work, highest average diversity occurred at the inlet sites (Reyes et al., 2007).

Taken into account the colonization processes, we conclude that phytoplankton assemblages were largely influenced by seasonal changes due to the arrival of water from different sources to the study area: freshwater input in winter (from the Guadiamar River) versus tidal water in summer (from the estuary of the Guadalquivir River). Transient stages occurred when no particular taxa contributed significantly to segregation (April 2003 and 2004, and September 2004). The fact that the freshwater influence was only evident in the segregation observed in 2003/2004 could be due to the higher amount of rainfall collected during that cycle (755 mm), which brought about a larger increase of river overflow, compared to the previous cycle (510 mm). Phytoplankton cumulative richness was relatively high despite poorer water quality than in other areas of the Doñana marshland (Serrano et al., 2006), and despite hydrologic variability being partly caused by anthropic control (rice pads, diversion of the overflow of the Guadiamar River through canals, floodgates, etc).

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