

## Spatial and temporal variations of hydrological conditions, nutrients and chlorophyll *a* in a Mediterranean coastal lagoon (Mar Menor, Spain)

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**Key words:** eutrophication models, ecosystem responses, top-down control, coastal lagoons, chlorophyll, ichthyoplankton

### Abstract

The Mar Menor is a sheltered and hypersaline lagoon, with salinity ranges between 38 and 51 psu. The lagoon is threatened by several pressures and in the last decades detrimental impact on the natural community structure and dynamics have increased. In the watershed, agricultural practices are rapidly evolving from extensive dry crop farming to intensively irrigated crops, with increasing loads of nutrient and pollutants to the lagoon. Hydrological conditions, nutrients and chlorophyll *a* concentrations were analysed in 1997 and 2002–2003 in a grid of 20 stations in the lagoon. Different time scales, from daily to inter-annual, were considered. In the considered periods, the dissolved inorganic nitrogen (DIN) increased whilst phosphate decreased significantly. These contrasting patterns depended upon the increased agricultural loading for DIN and were due to the implementation of the wastewater works for phosphates. In 1997 and 2002, the highest nitrate concentrations were usually found on the west coast of the lagoon, close to the mouths of the main watercourses. In parallel, the lowest concentrations were detected at the inner coastline along “La Manga” sandy bar and “El Estacio” channel. Based on weekly data, correlations between chlorophyll *a* concentrations and environmental variables disagreed with traditional eutrophication models. Relationships between chlorophyll *a* and nutrients were negative, suggesting that in the short term phytoplankton controlled nutrient concentrations. Moreover, nitrate and phosphorous seemed to alternate as limiting factors. The relationships between chlorophyll *a* became positive when considering time lags and analysed at longer time scales (monthly or seasonal means), thus suggesting a very rapid response of primary producers to nutrient enrichment. A significant correlation between chlorophyll *a* concentration and fish larvae density was also found at all time scales analysed, suggesting a top-down control of the trophic web.

### Introduction

Coastal lagoons are naturally stressed systems with frequent environmental disturbances and fluctuations (Barnes, 1980; UNESCO, 1980, 1981; Kjerfve, 1994) and they are usually considered as physically controlled ecosystems *sensu* Sanders (1968). The high biological productivity relates to

their geomorphological characteristics. Coastal lagoons are characterized by shallow depths and they are partially isolated from the open sea by coastal barriers that maintain some communication channels or inlets. Due to shallowness, light penetration at the sediment-water interface is usually high. Hydrodynamics is closely conditioned by bottom topography and wind affects the

entire water column promoting the resuspension of materials, nutrients and small organisms from the sediment surface layer. Overall, coastal lagoons are composed by a high number of physical and ecological boundaries and gradients – between water and sediment, pelagic and benthic assemblages, lagoon-marine-freshwater and terrestrial systems as well as with the atmosphere. Moreover, the strong dependence of lagoon ecosystems from their watershed makes them especially vulnerable to human impact and terrestrial and freshwater input.

Hypersaline coastal lagoons are confined systems with a negative water balance when evaporation exceeds both rainfall and freshwater run-off, and the water balance is compensated by marine exchange. Under these conditions, and with moderate or low nutrient input, pelagic primary production tends to be low meanwhile benthic production based on macrophytes (phanerogams and macroalgae) and microphytobenthos supports the whole trophic webs (Canfield et al., 1984; Pérez-Ruzafa et al., 1987, 1989; Pérez-Ruzafa, 1989; Terrados & Ros, 1991; Knoppers, 1994; Scheffer, 1998; Souza et al., 2003) and usually important fisheries (Pérez-Ruzafa et al., 1987; Pauly & Yáñez-Arancibia, 1994).

In recent years, nutrient delivery to coastal areas has increased as a consequence of human activity, mainly agricultural practices and sewage discharges particularly affecting enclosed bays and lagoons (Kormas et al., 2001; Hung & Kuo, 2002; Muslim & Jones, 2003; Newton et al., 2003; Zaldivar et al., 2003).

While eutrophication related processes have been studied in freshwater systems for more than 40 years, in coastal waters this is a more recent concern and its scientific understanding is still in progress. Cloern (2001) found fundamental differences in the system-level responses to nutrient enrichment in lakes compared to estuarine and coastal ecosystems, suggesting that the old models and assumptions on system response to nutrient inputs must be reviewed. Some questions are still open, such as how do system-specific attributes constrain or amplify the responses of coastal ecosystems to nutrient enrichment? Or, how does nutrient enrichment interact with other stressors (including non-indigenous species, hydrological manipulation) in changing coastal ecosystems? (Cloern, 2001). The

central question is how does greater delivery of N and P change the functions and community structure in estuarine and coastal waters?

Limnologists addressed this question by constructing signal-response functions relating changes in the availability of P (the most limiting factor in freshwater) with some measure of change in the productivity or biomass of phytoplankton, and the high strength of such correlations is the basis of conceptual models and the basis for nutrient management. However, such kinds of relationships are difficult to find in coastal marine waters, and nutrient input alone is a poor predictor for algal blooms (Cloern, 2001).

In a previous study we showed some evidence of the planktonic food web response to changes in nutrient input dynamics in the Mar Menor coastal lagoon (Pérez-Ruzafa et al., 2002). Due to run-off from agricultural lands over the last decade, there is a generalized eutrophication process. During the 90s, agriculture started to change from dry crop farming with low amounts of nitrogen fertilizers to intensive irrigated crops with nitrogen fertilization, using waters diverted from the Tajo to the Segura river. From 1988 to 1997, nitrate concentrations increased from lower than  $1 \mu\text{mol N l}^{-1}$ , throughout the year, to concentrations of up to  $8 \mu\text{mol l}^{-1}$ . By contrast, phosphate values, usually higher than  $2 \mu\text{M}$  in 1988, seem now to be the limiting factor during most of the year. Comparative analyses between 1988 and 1997 revealed that, in spite of changes in nutrient input which stimulated the growth of larger phytoplankton cells, there were no significant differences in the pelagic size-spectra slope which followed a similar seasonal trend for both years. We concluded that size structure in these assemblages can be subject to top-down control by large gelatinous zooplankton, mainly two alloctonous jellyfish species (*Rhizostoma pulmo* and *Cotylorhiza tuberculata*) which have colonized the lagoon over the last decade and since 1995 have occurred in large numbers (Pérez-Ruzafa et al., 2002).

In this paper, spatial and temporal changes in nutrients, chlorophyll *a* and suspended matter in the Mar Menor lagoon are analysed in relation to rainfall, salinity, water temperature and ichthyoplanktonic assemblages. The main aim is to detect the relationships between hydrological, climatic and biological factors.

## Materials and methods

### Study area

The Mar Menor is a sheltered lagoon located in SE Spain, a semi-arid region of the SW Mediterranean (Fig. 1). The bottom is covered mainly by a meadow of *Cymodocea nodosa*-*Caulerpa prolifera*,

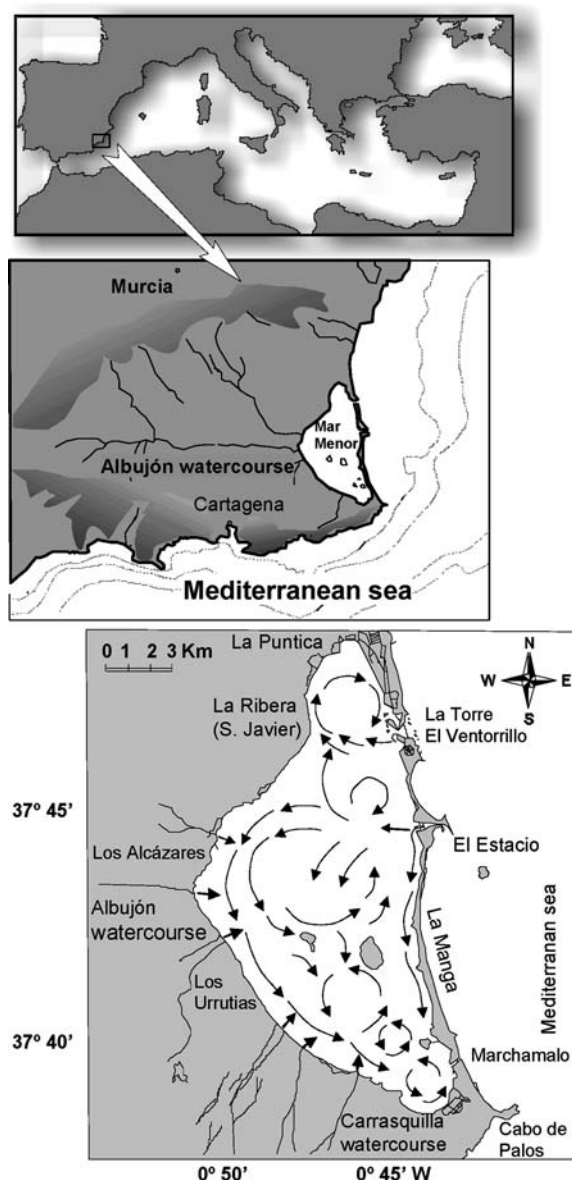


Figure 1. Geographical location of the Mar Menor lagoon, main watercourses and connection channels with the Mediterranean sea and circulatory patterns inside the lagoon.

whose biomass was estimated at  $280 \text{ g dw m}^{-2}$  (Pérez-Ruzafa et al., 1989, Terrados & Ros, 1991). The mean annual rainfall is less than 300 mm and potential evapotranspiration is close to 900 mm (López Bermúdez et al., 1981). The net hydric balance attained an annual deficit above  $600 \text{ mm m}^{-2} \text{ year}^{-1}$ . Climatic and hydrological features coupled to the geomorphology of the lagoon make it behave like a concentration basin.

Until recent years, there were no permanent watercourses flowing into the lagoon. There are, nevertheless, more than twenty cataclinal watercourses in the watershed, most of them discharging into the southern basin of the lagoon, but its functioning became conditioned by a sporadic and torrential rainfall regime (Fig. 1). Among these, the Albuñón watercourse, the main collector in the drainage basin, is an exception at present, as it maintains a regular flux of water due to changes in agricultural practices and related phreatic rising (Pérez-Ruzafa & Aragón, 2002).

The run-off from the drainage basin plus direct rainfall yields a mean discharge of  $27.9\text{--}122 \text{ Hm}^3$  while  $155\text{--}205 \text{ Hm}^3$  evaporates, thus resulting in a hydric deficit ranging from 38 to  $115 \text{ Hm}^3$  per year which is compensated by salt water input from the Mediterranean sea and regulated by differences in the sea level between the lagoon and the open sea (Arévalo, 1988; Pérez-Ruzafa, 1989; Pérez-Ruzafa et al., 1991). Circulation within the lagoon is mainly conducted by the wind (Fig. 1).

### Sampling design

Spatial and temporal variations of hydrological conditions, nutrients and chlorophyll *a* concentrations were analysed using two sets of data that spatially covered the lagoon. According to the terrestrial and marine influence, 20 sampling stations were grouped in 5 zones, so that each zone was represented by 4 replicate sampling units (Fig. 2). In 1997, weekly surveys were conducted from February to December, while by-monthly surveys were made from May 2002 to May 2003.

Water samples were taken at an approximate depth of 1 m with a Niskin bottle, or by pumping. Samples for nutrient analysis were kept in the dark at  $4^\circ \text{C}$  in the field and stored at  $-28^\circ \text{C}$ . Nitrate ( $\text{NO}_3\text{-N}$ ), nitrite ( $\text{NO}_2\text{-N}$ ), ammonia ( $\text{NH}_4\text{-N}$ ) and

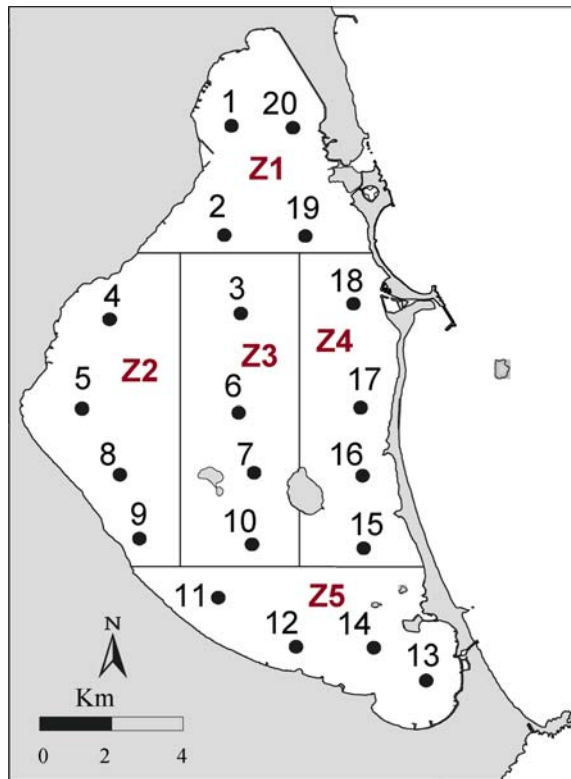


Figure 2. Location of sampling stations (1–20) in the Mar Menor lagoon and organization of the sampling area in zones (Z1–Z5) for spatial analyses.

phosphate ( $\text{PO}_4\text{-P}$ ) were determined following the methods described by Parsons et al. (1984). In 1997, salinity was determined with a Beckman RS 7B salinometer. In 2002–2003, *in situ* determinations were performed using a WTW Multiline F/Set3 multiple probe. Chlorophyll *a* was analysed with the spectrophotometric methods reported by Parsons et al. (1984). The field sampling for ichthyoplankton composition studies was carried out using a 500  $\mu\text{m}$ -gauze net in 1997. The methodology is described in detail in Pérez-Ruzafa et al. (2004).

#### Data analysis

Mean water temperature, salinity, nutrient concentration and chlorophyll *a* were analysed with a 3-factor ANOVA (Underwood, 1997), considering the orthogonal factors; Year (1997, 2002/2003); Season (winter, spring, summer, and autumn); and Zone (1–5). All sources of variation were considered as fixed factors.

Relationships among the considered variables were tested with the Pearson's correlation. A multiple linear regression models (GLM) with stepwise forward selection of variables (using  $p < 0.05$  as the inclusion and/or rejection criterion) were used to determine the best linear models accounting for the observed variation of chlorophyll *a* estimates. To explore the response of variables at different time scales two different matrices were used in the analyses, one matrix with the raw data and the other with monthly means. In addition, different time lags between chlorophyll estimates and the remaining variables were considered adding two new columns to the respective matrix with a lag of one ( $t+1$ ) and two ( $t+2$ ) weeks, respectively, for raw data, and with a lag of one and two months, respectively, for mean monthly data.

To explore the spatio-temporal patterns of the measured variables, a Principal Component Analysis (PCA) using normalised data was performed on the monthly means at each zone matrix, using the Primer 5.1 package.

## Results

The rainfall in 1997 and 2002/2003 showed differing conditions. Although there are no significant differences among mean rainfall in both years the interaction year  $\times$  season results marginally significant ( $p = 0.1$ ) with the 2002–2003 period showing a drier summer and autumn and a more rainy winter. Monthly mean rainfall in the four meteorological stations in the Mar Menor area during the study period was 21.99 mm in 1997 and 26.39 mm in 2002–2003 (Fig. 3). Rainfall periods were April to May, September and December in 1997. In 2002 rainfalls were concentrated in April and to a much lesser extent in September, and only in the southern basin. The rainiest month was January, 2003, with a mean rainfall in the area of 123.2 mm.

Water temperature showed a regular seasonal cycle (Fig. 4). Maxima were reached in August (30 °C) and minima in February (11.2 °C). Temperature did not show significant differences between zones but did show significant differences for the interaction year  $\times$  season ( $p < 0.001$ ) (Fig. 5), since the 2002–2003 period showed a

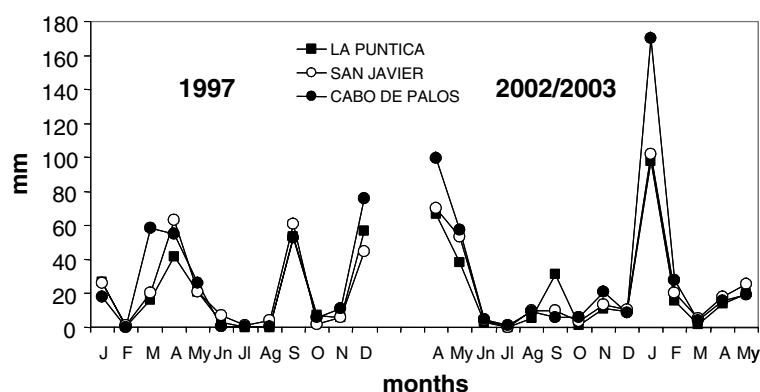


Figure 3. Rainfall regime in the Mar Menor watershed in 1997 and from April 2002 to May 2003.

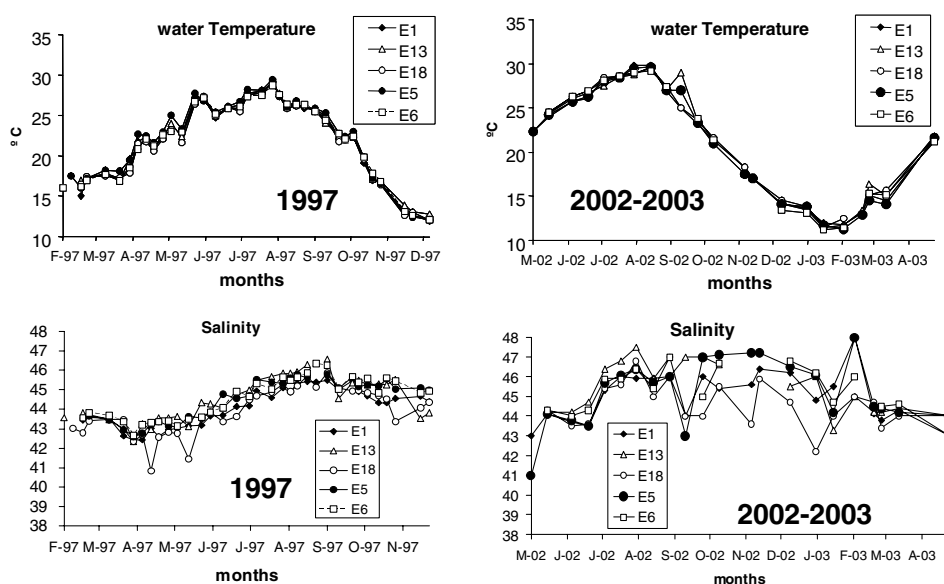


Figure 4. Temporal dynamics of water temperature and salinity at the Menor lagoon in 1997 and from April 2002 to May 2003.

hotter spring-to-autumn period and a colder winter than 1997.

Salinity showed heterogeneous spatial and temporal behaviour with a minimum of 38.1 and a maximum of 51 psu (Fig. 4). The maximum was reached in September 2002 after a period of very low rainfall. The minimum was attained in April and May of 1997 close to the mouth of El Estacio channel, the main inlet communicating the lagoon with the Mediterranean. Spatial differences are low but highly significant among zones ( $p < 0.01$ ) with minimum values at zone 1, in the northern basin, and maximum ones at zone 5, in the

southern basin. The interaction of year  $\times$  season is also highly significant ( $p < 0.001$ ) with highest values in 2002–2003 and reaching a maximum difference between years in winter, the driest period (Fig. 5).

Nitrate showed heterogeneous spatial and temporal behaviour on a daily scale (Fig. 6a), but with some trends at seasonal and yearly scales. Values higher than 4–6  $\mu\text{M}$  were common during the entire study period. Highest values reached 45  $\mu\text{M}$  in a one-off event in April 1997. Nitrate concentration values turned out to be significantly different between zones, with higher concentrations

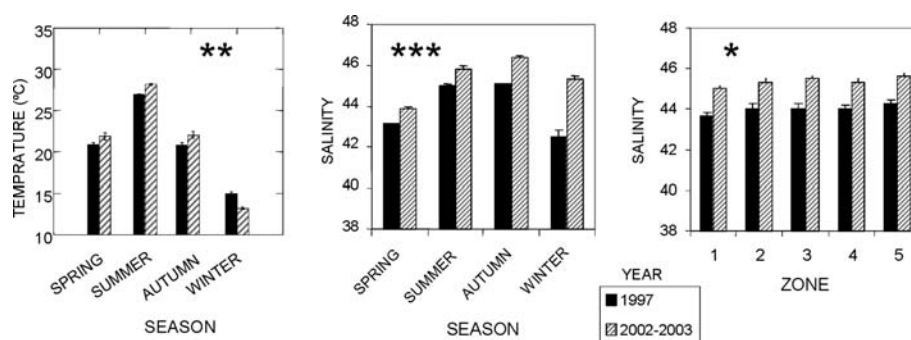


Figure 5. Seasonal, zonal and interannual patterns (mean values  $\pm$  MSE) of water temperatures and salinity according to the results of the analyses of variance (\*\*\* $p$  = 0; \*\* $p$  < 0.0001; \* $p$  < 0.01).

in zone 2, the area of the Albuñón watercourse mouth. Differences are also significant for the interaction of year  $\times$  season ( $p$  < 0.05) with higher values in 2002–2003. Maximum values appeared in spring in 1997 and in winter in 2002–2003 (Fig. 7a).

Nitrite and ammonia showed lower values than nitrate, rarely reaching concentrations higher than  $0.5 \mu\text{M}$  (Fig. 6b and c). They also showed heterogeneous spatial and temporal behaviour on a daily scale. Nitrite showed significant differences among zones with a slightly higher concentration in the zone 2 (Fig. 7b). Differences are also significant for the interaction of year  $\times$  season with higher values in spring, and in 1997 with respect to 2002–2003.

Phosphate usually showed values lower than  $1 \mu\text{M}$  (Fig. 6d). There was a peak reaching  $8.74 \mu\text{M}$  in April 1997. Two isolated peaks ( $27.17$  and  $23.86 \mu\text{M}$ ) were observed in July and August 2002 at sampling stations 9 and 11, just off the locality of “Los Urrutias”. Such peaks in phosphorous concentrations seem to be related to a malfunction in local urban waste water collectors. Significant differences for Phosphate only show up for the interaction year  $\times$  season ( $p$  < 0.001), with a strong reduction in P input in spring and winter 2002–2003 with respect to 1997 (Fig. 7c).

Chlorophyll  $a$  usually showed values lower than  $4 \text{ mg m}^{-3}$  (Fig. 8a), reaching a maximum of  $7.49 \text{ mg m}^{-3}$  at sampling station 9 in June, 2002. This showed a significant effect in the interactions year  $\times$  season ( $p$  < 0.001), year  $\times$  zone ( $p$  < 0.001) and season  $\times$  zone ( $p$  < 0.001) (Fig. 8b). Maximum concentrations took place in spring at zones

2 (close to the mouth of the Albuñón watercourse) and 5 (in the southern basin), and minimum concentrations took place in winter. Zones 1, 2 and 5 showed a similar seasonal behaviour between years, with maxima in spring and autumn and minima in winter; meanwhile zones 3 and 4 both had their maxima in summer.

Ichthyoplankton dynamics in the lagoon for 1997 have been described in Pérez-Ruzafa et al. (2004). The abundance of larvae in the lagoon increased slightly from March, rising abruptly at the end of summer, and reaching the maximum mean density ( $2341.6 \pm 356.3 \text{ SE larvae } 1000 \text{ m}^{-3}$ ) in October. *Gobius niger*, *Pomatoschistus marmoratus*, *Engraulis encrasicolus* and *Callionymus risso* were the main species that contributed to this peak. *Gobius paganellus*, *Parablennius gattorugine* and the pelagic species *Aterina boyeri* had their respective peaks in September and *Parablennius pilicornis* and *Parablennius tentacularis* in August. Other species such as *Aphia minuta* and *Parablennius sanguinolentus*, *Symphodus mediterraneus*, *Diplecogaster bimaculata*, *Belone belone* and *Tripterygion tripteronotus* experienced maximum abundance in spring. *Solea vulgaris*, *Solea lascaris* and *Gobius cobitis* larvae occurred in February and March. *Sardina pilchardus* larvae were abundant in April with a second peak in November. Mean annual densities showed a generally increasing gradient from north to south with the central part of the main circulation gyres as areas of concentration. The minimum ( $227.9 \text{ larvae } 1000 \text{ m}^{-3}$ ) was recorded at station E1 and the maximum ( $1058.6 \text{ larvae } 1000 \text{ m}^{-3}$ ) at station E10 (see more details in Pérez-Ruzafa et al., 2004).

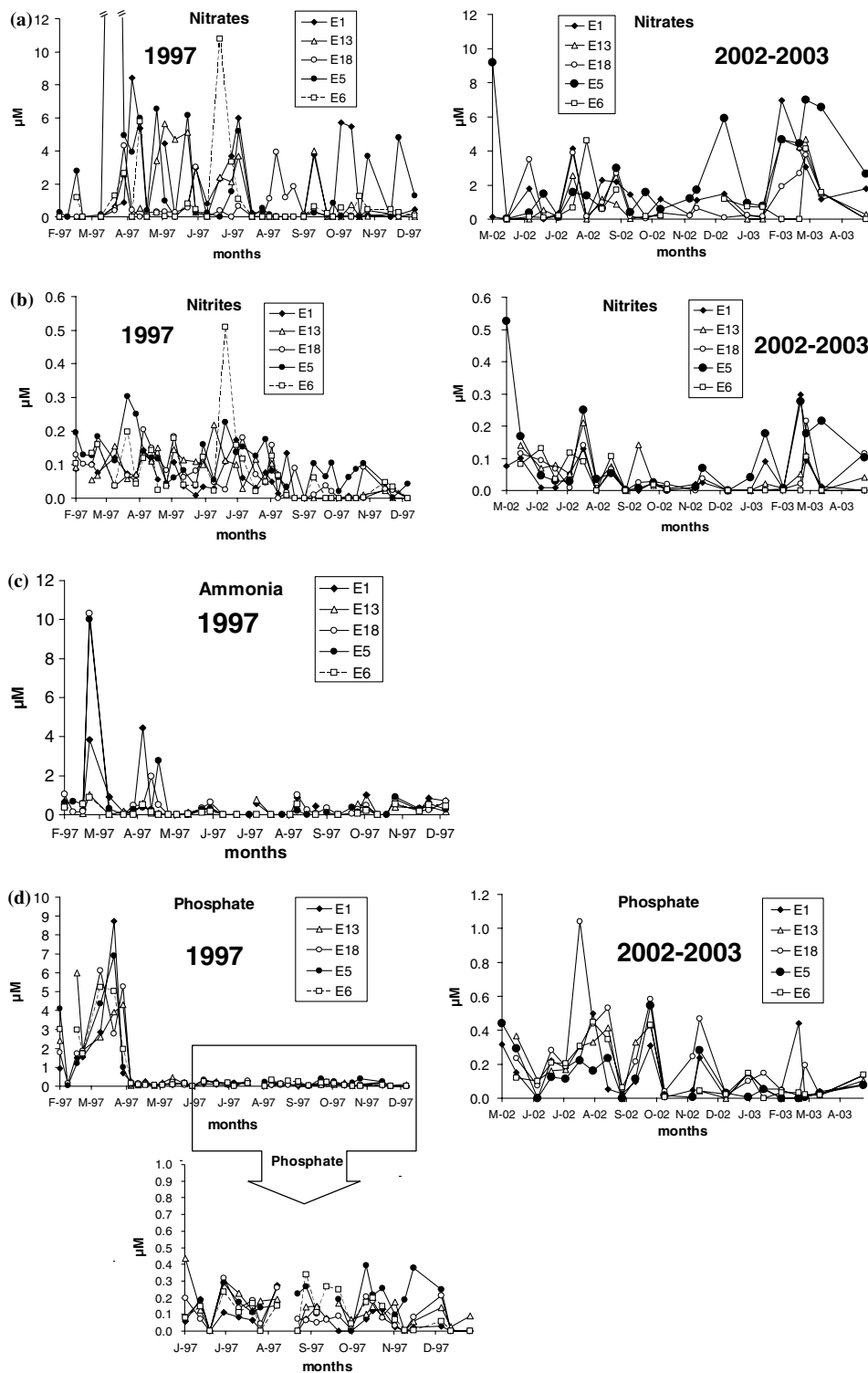


Figure 6. Temporal dynamics of nutrient concentration in surface waters at the Mar Menor lagoon during the sampling period. (a) nitrates; (b) nitrites; (c) ammonia (not sampled in 2002–2003 period); (d) phosphate (note the change in scale in 2002–2003 period).

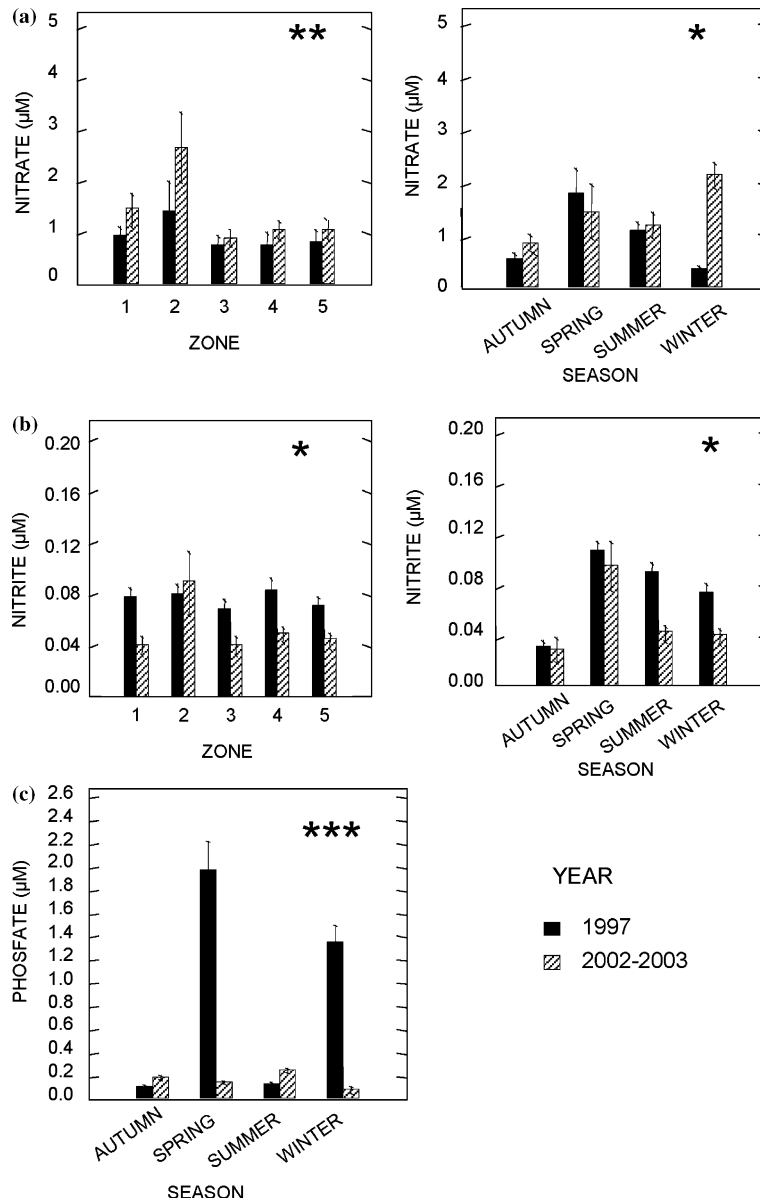


Figure 7. Seasonal, zonal and interannual patterns in nutrient concentration in the Mar Menor lagoon (mean values  $\pm$  MSE) according to the results of the analyses of variance (\*\* $p < 0.01$ ; \*\* $p < 0.005$ ; \* $p < 0.05$ ).

The magnitude of temporal variability precludes detecting spatial patterns with ordination techniques, and the PCA detects only temporal (seasonal and monthly) patterns (Fig. 9). The first two ordination axes explain 57.4% of the total variance in data. The first axis, which explains 40.3% of the total variance on its own, represents most of the seasonal variation. In the negative part we find the samples taken in winter

(February and March) associated to Phosphate, suspended solids and ammonia concentrations. In the positive part we find mid autumn samples (October). The variables which seem to explain this distribution are salinity, chlorophyll *a* and temperature. The second component, which explained an additional 17.1% of the variance, is represented by variations in the nitrate concentration, separating spring samples, in the negative



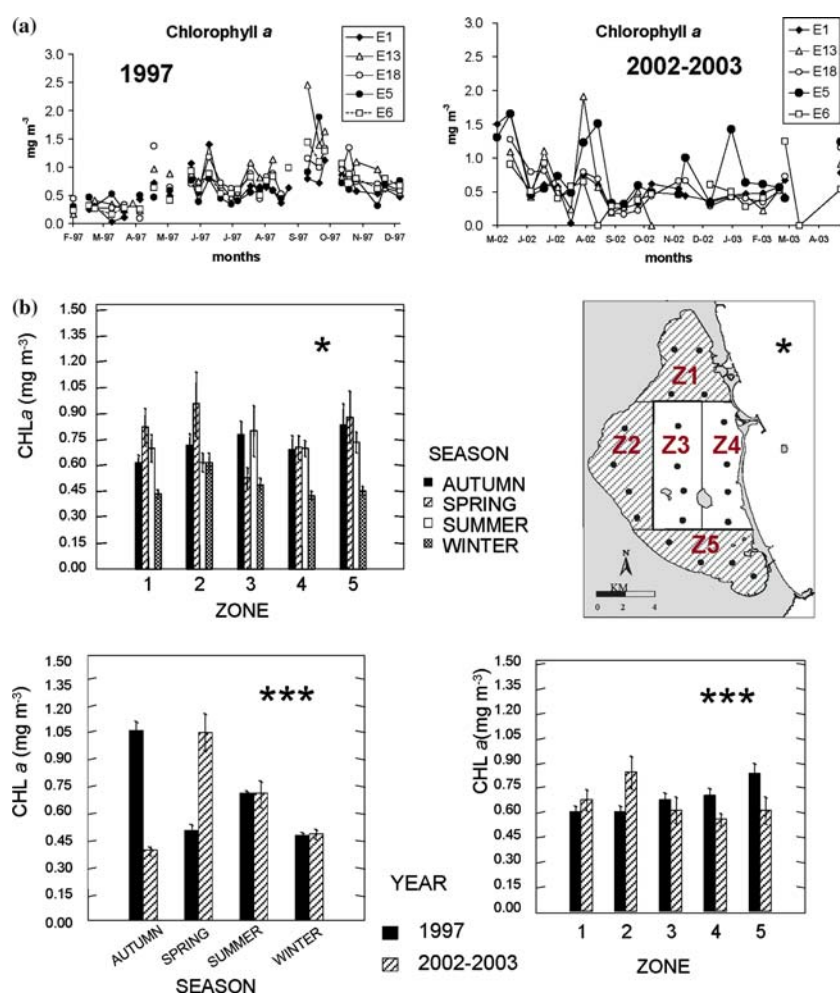


Figure 8. Temporal dynamics (a) and seasonal, zonal and interannual patterns (b) of chlorophyll *a* concentration at the Mar Menor lagoon during the sampling period. The map shows the significant groups for the interaction season  $\times$  zone. (\*\* $p = 0$ ; \*\* $p < 0.005$ ; \* $p < 0.05$ ).

part, from winter and autumn samples, in the positive one.

Correlations between chlorophyll *a* concentrations in raw data and environmental variables are not in agreement with traditional models (model I *sensu* Cloern, 2001). Chlorophyll *a* is negatively correlated with phosphate, nitrate and nitrite. However, it is positively correlated with ichthyoplankton abundance, and especially with larvae density in the previous week (Table 1). Nitrate is positively correlated with nitrite and temperature, while phosphate is negatively correlated with salinity. Correlations between mean monthly-averaged chlorophyll *a* and environmental data

show different results (Table 2). Chlorophyll is now positively correlated with phosphate, nitrate and nitrite, as well as with salinity and suspended solids. In most cases, the highest correlations are found with a time lag of two months ( $t+2$ ). However this variable still maintains a high correlation with ichthyoplankton abundance within a given month. Run-off seems to control the nutrient input regime, as phosphate, nitrite and nitrate are significantly correlated with rainfall (Pearson's  $r = 0.73, 0.53$  and  $0.44$ , respectively).

Multiple regressions with forward selection of variables show similar results: a negative relationship with nutrients and a positive one with

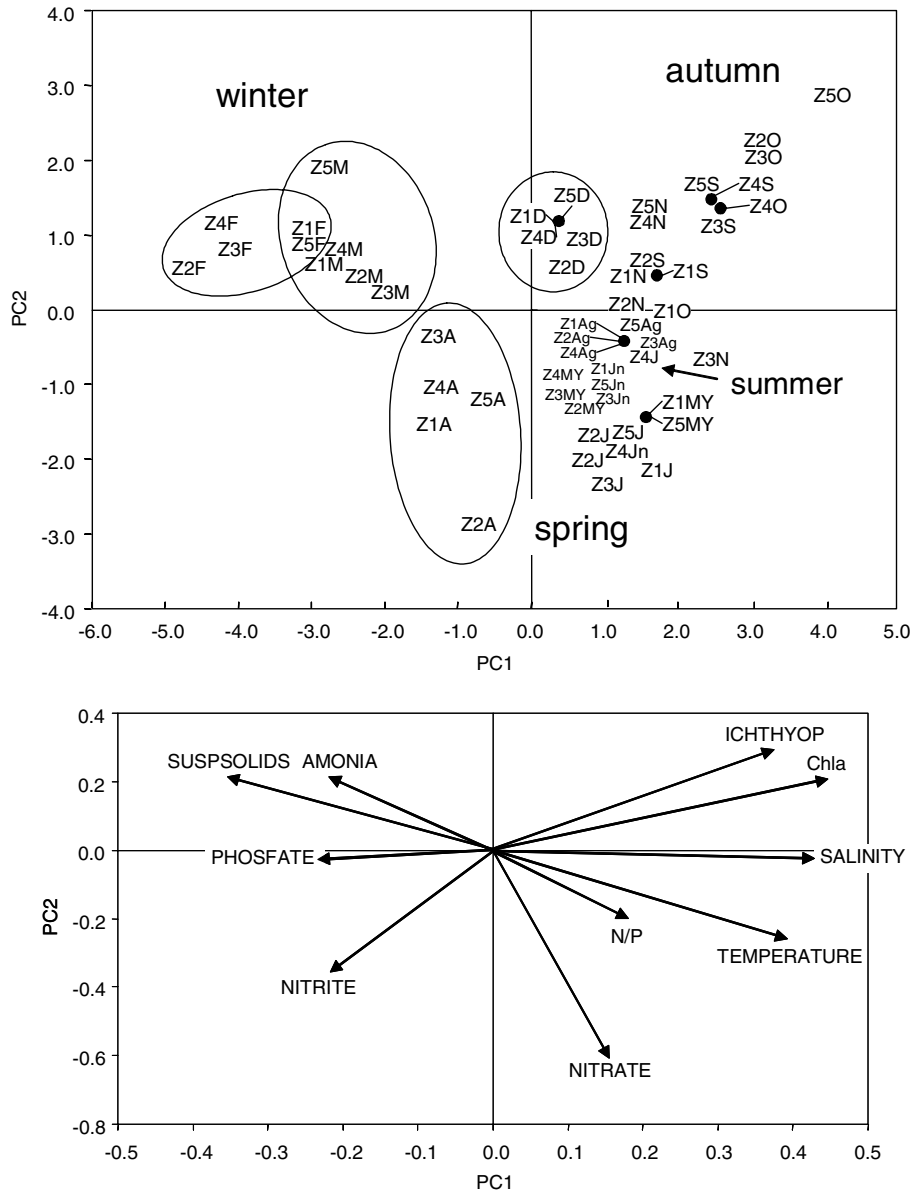


Figure 9. Results of the Principal Component Analysis. The biplot ordination diagram for monthly means for zones (a) and variables which explain the ordination (b) are reported. Numbers corresponds to the zone number, letters corresponds to the initial of the month, and black dots refer to aggregation of samples. PC1 explains 40.3% of the total variance of data and PC2 a 17.1%.

ichthyoplankton (adjusted  $R^2 = 0.35$ ; cases included = 513) according to the model:

$$\begin{aligned}
 Chla = & 0.52 - 5 \cdot N - 0.07 \cdot P + 3.97 \cdot 10^{-6} \cdot S^3 \\
 & + 28.69 \cdot N^2 - 48.31 \cdot N^3 \\
 & + 6.98 \cdot 10^{-5} \cdot I
 \end{aligned}
 \tag{1}$$

where: Chla = chlorophyll a, N = nitrite, P = phosphate, S = salinity and I = ichthyoplankton.

A higher percentage of variance is explained by the model describing a chlorophyll a concentration when a time lag of one week is introduced. This model includes three variables as follows (adjusted  $R^2 = 0.51$ ; cases included = 494):



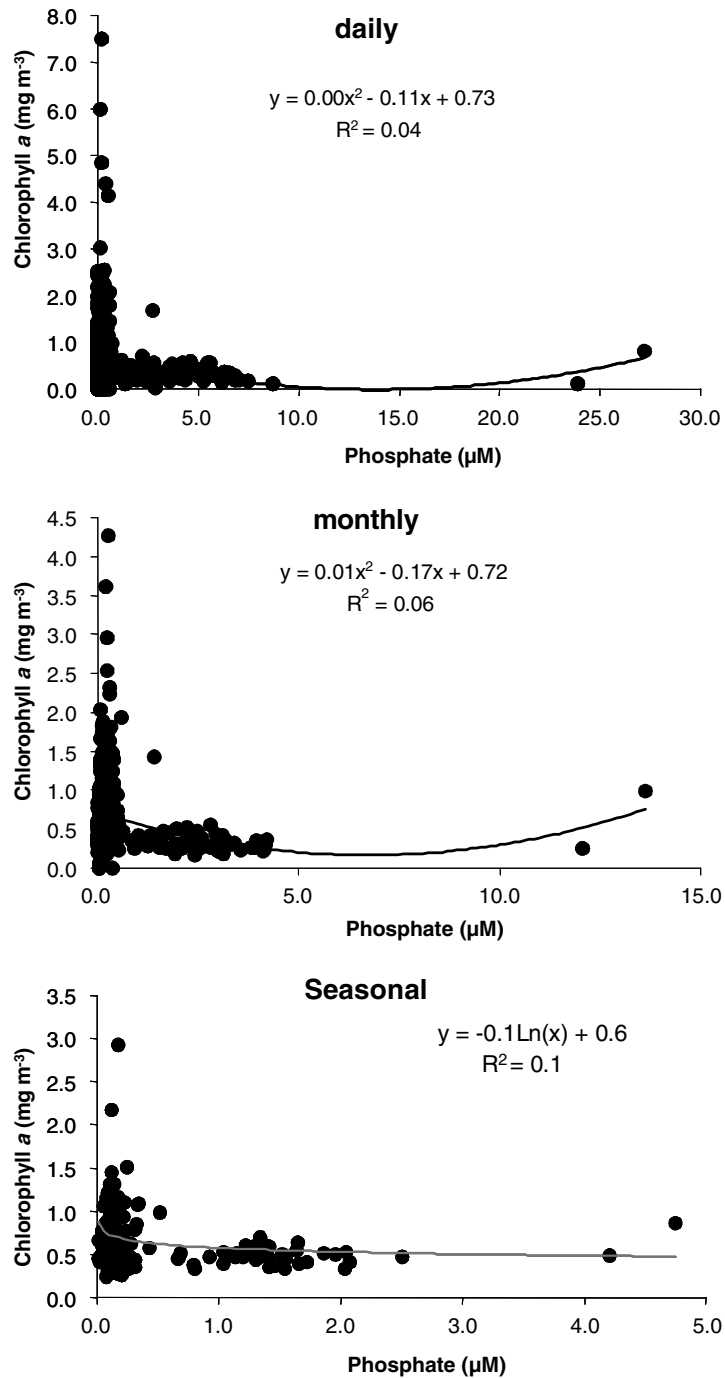


Figure 10. Relationship between chlorophyll *a* concentration and phosphate in the water column at different temporal scales.

Single regressions confirm the day in response of chlorophyll *a* and top levels in the trophic web, and the complex relationship that this variable maintain with nutrients. The relationships with phosphate are negative except for high concen-

trations of phosphate. The adjusted  $R^2$  increases from 0.04 for daily data, to 0.06 with monthly means and 0.1 for seasonal means (Fig. 10). The relationships with nitrate are also exponentially negative for raw data and monthly means

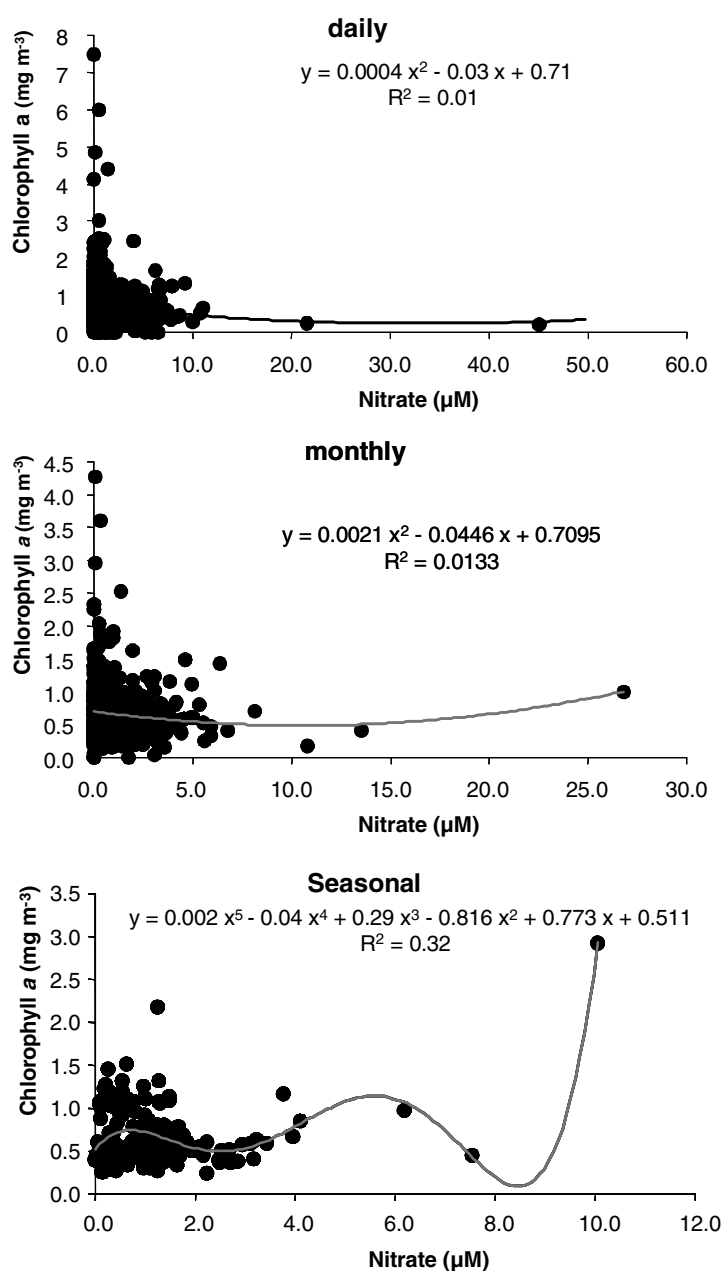


Figure 11. Relationship between chlorophyll *a* concentration and nitrate in the water column at different temporal scales.

(adj.  $R^2 = 0.01$ ) but become more robust, including up to five degree terms, (adj.  $R^2 = 0.3$ ) for seasonal means (Fig. 11). The only linear positive relationship is maintained with ichthyoplankton, which also increases from daily data (with a time lag of one week) (adj.  $R^2 = 0.3$ ) to seasonal data (adj.  $R^2 = 0.7$ ) (Fig. 12). The strength of the correlation between chlorophyll *a*

and fish larvae density, when seasonal means are compared, is remarkable.

### Discussion

In the Mar Menor, since late 80s, there is a continuing tendency towards an increase in the

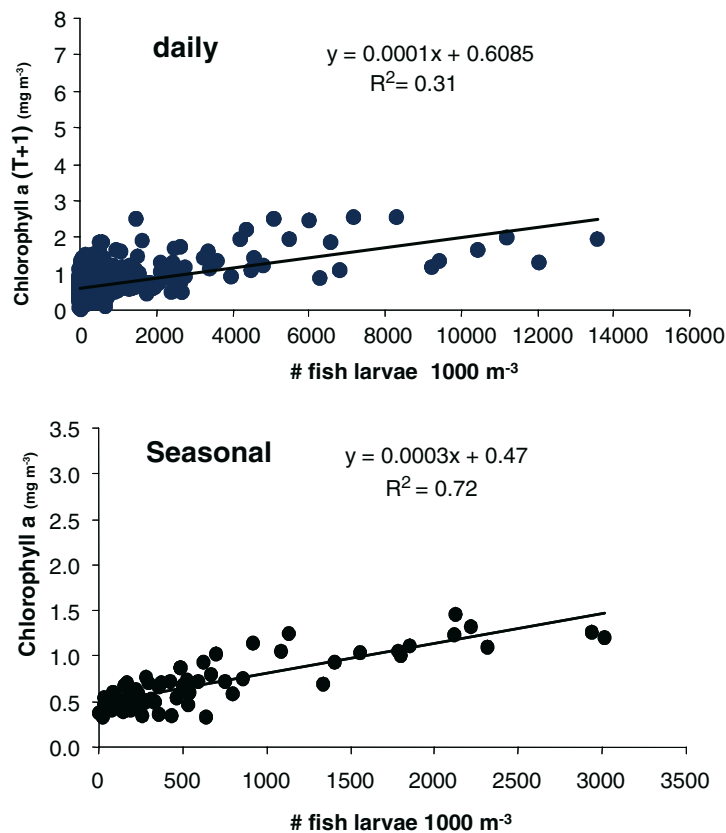


Figure 12. Relationship between chlorophyll *a* concentration and ichthyoplankton abundance in the water column at different temporal scales.

input of DIN due to an increase in agricultural run-off and a decrease in phosphate delivery due to the amelioration of wastewater works. Our results show that correlations between chlorophyll *a* concentrations and environmental variables in daily data disagree with traditional models which suppose a direct response of phytoplankton-related variables to nutrient loadings (Phase I conceptual I of Cloern, 2001). In our case, relationships with nutrients are negative, suggesting that phytoplankton controls nutrient concentrations. Chlorophyll *a* concentrations show complex relationships (involving quadratic and cubic terms) with multiple variables and nitrate and phosphorous seem to alternate as limiting factors depending, probably, on their relative concentrations and the concentration of chlorophyll. In fact, while the relationship between monthly mean of chlorophyll *a* concentrations and nitrate or phosphate concentrations

did not show any temporal pattern, a yearly cycle emerges when the monthly mean chlorophyll concentration is related to the N to P ratio (Fig. 13). The comparison between 1997 and 2002/2003 showed different temporal dynamics, but with important regularities. Phosphorous acts as the main limiting factor in both years. The Redfield N to P ratio seems to act as an attractor for the chlorophyll *a* oscillations, which also showed the same maximum and minimum limits for both years. At the same time, the negative correlations between daily chlorophyll and phosphorous and nitrate concentrations and the fact that such relationships became positive when considering time lags in the relationship between chlorophyll and nutrients or when data are factored in at higher time scales (monthly or seasonal) suggests a very rapid response by the primary producers to nutrient enrichment.

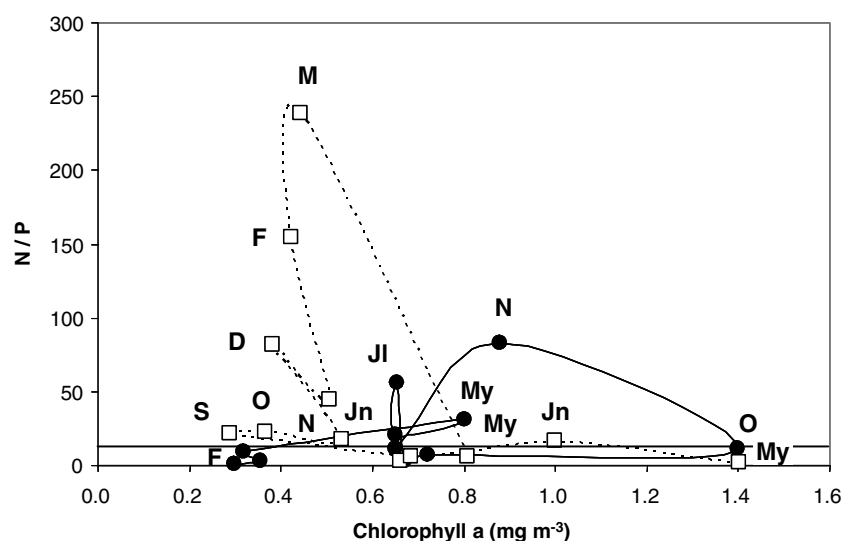


Figure 13. Temporal dynamics of the relation between monthly mean chlorophyll *a* concentration and the inorganic N to P ratios in the water column in the Mar Menor lagoon during 1997 (continuous line) and 2002–2003 period (dashed line). Horizontal line corresponds to N:P = 16.

On the other hand, the strength of the correlation between chlorophyll *a* concentrations and fish larvae density, both for weekly data with a time lag of one week and when seasonal means are compared, is significant, suggesting a top-down control of the trophic web. This agrees with previous data on the effect of jellyfish on the biomass spectra (Pérez-Ruzafa et al., 2002).

The variation of the relationship between fish larvae density and chlorophyll *a* concentrations shows seasonal dynamics with a limit cycle (Fig. 14) which is similar to that simulated by Scheffer (1998) for zooplankton and algae interactions. As stated by the latter author, the oscillations (or different amplitude in the case of the distinct sampling stations) on the limit cycle can be biologically explained as the result of overshoots due to a delayed response in the population density of herbivores to the amount of available food, or differences in the assemblage structure and life cycles which would introduce homeostatic controls and time lags in the responses of the successive trophic levels.

The results suggest, in agreement with Cloern (2001), that the problem of coastal eutrophication must involve consideration of several process and factors and, probably, different time scales for response throughout the trophic web. The resulting complex system would be an important

component of the filter, *sensu* Cloern (2001), which modulates the response to the signal of change in nutrient loading in estuarine and coastal marine ecosystems.

The response of planktonic food webs to nutrient enrichment in coastal marine ecosystems varies greatly worldwide due to the broad range of both direct and indirect effects of the eutrophication process (Kerfoot & Sih, 1987; De Angelis, 1992; Scheffer, 1998). When bottom-up control exists, the general patterns described include the substitution of macrophytes by macroalgae at the benthic level as a first step and then a change to a phytoplankton based system with anoxic events originating when light penetration is severely affected by phytoplankton density (Nienhuis, 1992). However, the response of ecosystems to nutrient load increase differs widely because biological control mechanisms of the eutrophication process are not always the same. Predation can be a very efficient control mechanism providing alternative energy flow pathways in the food web by removing excess biomass generated by excess nutrients (Pérez-Ruzafa et al., 2002).

Because of the observed shifts in the response and the top-down control exerted by the different trophic levels on their resources, a detailed analyses of the responses in the different fractions of the biomass spectra would probably give valuable

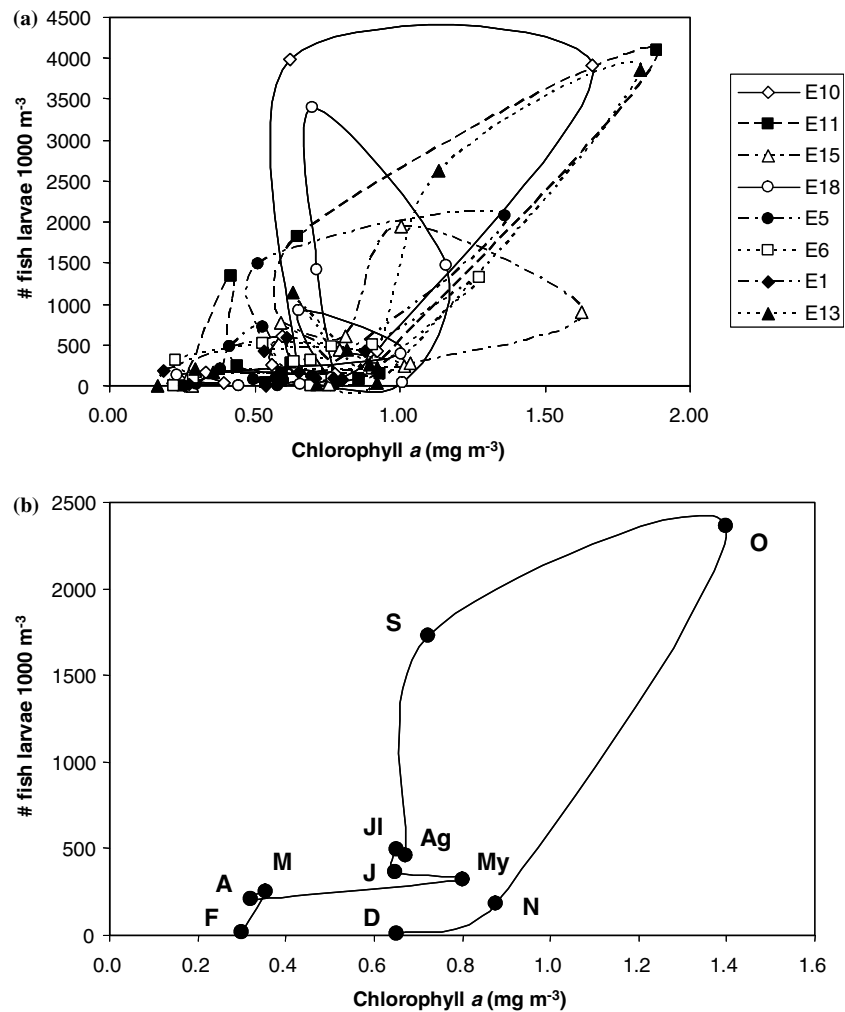


Figure 14. Relationship between fish larvae density and chlorophyll *a* concentration in several sampling stations in the Mar Menor lagoon during 1997 (a) and averaged for all the lagoon (b) showing a regular seasonal cycle.

information about the homeostatic and regulatory controls in these environments and would probably explain the differences in response between simple and complex or freshwater and marine ecosystems.

Therefore, the response of the system can adjust either to model I or model II *sensu* Cloern (2001), depending on the temporal scale considered, and one of the more effective filters seems to be the trophic network. In model II, the system response is so rapid that positive correlations are probably only detected two or three steps down the food-chain, after a time lag of several days, or at high temporal scales.

### Acknowledgements

This study has been partially supported by different agreements with the Consejería de Agricultura, Agua y Medio Ambiente (Dirección General de Agricultura y Pesca for 1997 data, and Dirección General del Medio Natural for 2002 data) of the Región de Murcia. We also thank to the Club Náutico de Lo Pagán for harbour facilities.

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