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On the Controls of Phytoplankton Abundance and Production in Coastal Lagoons[1]

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ABSTRACT

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The diversion of the Ebro River water to irrigate rice paddies and subsequent drainage into coastal lagoons results in a shift from the seawater-dominated phase of the water column of the lagoons from December to May, to a freshwater-dominated phase for the remainder of the year. The species composition of phytoplankton within the lagoons changes accordingly. This ecosystem level shift provides a unique opportunity to discuss the relationships between phytoplankton productivity and abundance and nutrient concentrations and the effect of water turnover on productivity of phytoplankton.

During the freshwater phase, the nutrient concentrations and ratios are such that nutrients seem unlikely to limit phytoplankton production. During the seawater phase, relatively more dissolved inorganic nitrogen (DIN) than phosphorus (SRP) is consumed, the DIN:SRP ratio in the water is lowered below the Redfield ratio, the loss of nitrogen from the water is similar in magnitude and concurrent to the increase in particulate N, and changes of the DIN:SRP ratio and production rates are inversely related. All these relationships point to the phytoplankton uptake as a mechanism lowering DIN. The assemblage of marine phytoplankton species prefers to use nitrate rather than ammonium. The turnover rate of the water in the lagoons is not slow enough for nitrogen recycling mechanisms to supply sufficient N for P to become the limiting element of the phytoplankton growth.

ADDITIONAL INDEX WORDS: *Phytoplankton, nitrogen, phosphorus, water turnover, freshwater, seawater, coastal lagoons.*

INTRODUCTION

Geochemical arguments based on observed concentrations of dissolved solids and particulate nutrients in seawater suggest that the supply of phosphorus ought to limit net primary production (NPP) in the sea over the long term (10^3 yr or more) (REDFIELD, 1958; BROECKER and PENG, 1982). The results of enrichment experiments (SCHINDLER, 1974; CARPENTER and CAPONE, 1983; VALIELA, 1984; HOWARTH, 1988), however, show that over shorter time scales (days to months) available phosphorus is the principal control of net phytoplankton production in freshwater, while available nitrogen controls NPP in marine coastal waters.

Concentrations of inorganic nitrogen are generally higher in freshwater than in marine waters (VALIELA, 1984). There are probably many mechanisms that cause this difference, including different supplies of N and P in fresh and seawater. The external inputs of N into freshwater ecosystems are relatively large (as much as 13 mM N m^{-2} d^{-1}) compared to those entering marine ecosystems (which may receive up to 2.5 mM N m^{-2} d^{-1}) (SEITZINGER, 1988).

Another mechanism that might produce lower concentrations of dissolved inorganic nitrogen in the coastal water column is denitrification within anoxic coastal sediments, which may reduce the amounts of regenerated N relative to amounts of regenerated P (NIXON, 1981).

Differences may also be a consequence of differences in rate of water turnover. If water exchange rate in a particular water body is high enough, internal biogeochemical mechanisms—fixation, regeneration, uptake—may be insufficient to alter nitrogen and phosphorus concentrations (SMITH, 1984). Rapid turnover may be in part a reason why in many marine water bodies primary production seems to be nitrogen-limited in the short term because nitrogen cycling is slower than phosphorus. If water turnover is slow, the mechanisms that supply nitrogen internally (fix-

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ation and regeneration) could provide sufficient nitrogen, and NPP could become phosphorus-limited. SMITH (1984) made the argument for total organic production, but it is of interest to see if it might apply to net primary production in freshwater or coastal marine systems that have relatively low rates of water turnover, and which might thus be limited by phosphorus rather than nitrogen supply.

The matter of nutrient limitation in fresh vs. coastal waters and the role of turnover rates can be studied in the coastal lagoons of the Ebro Delta. These lagoons have seasonal hydrological cycles in which about half the year the water column is dominated by seawater and the remainder of the year freshwater dominates the water column. This ecosystem-scale experiment creates a situation in which there ought to be a switch from nitrogen limitation of net primary production during the seawater phase to phosphorus limitation during the freshwater phase, if inferences from the enrichment experiments are correct.

The objectives of this paper are, first, an examination of relationships between nutrient concentrations and phytoplankton productivity and abundance in systems dominated alternatively by seawater and by freshwater, and second, an evaluation of the effect of rate of water turnover on productivity of phytoplankton.

METHODS

Forty percent of the surface of the Ebro Delta (total area 320 km^2) is used for the cultivation of rice in paddies. While the rice crop is growing, freshwater from the Ebro River is continuously pumped through irrigation canals into the paddies, and out into coastal lagoons of the Delta (Figure 1). After the rice crop has been harvested in early fall, the pumping of freshwater into the paddies stops, and so does the flow of freshwater into the coastal lagoons. Seawater gradually replaces the freshwater in the lagoons and enters the lagoons mainly through the canals connecting the lagoons directly with the sea. Thus, the lagoons change from a freshwater-dominated water column during the rice-growing season (April–October) to a seawater-dominated water column in winter.

The very shallow water column in Encanyissada and Tancada lagoons studied (mean depth 44 and 37 cm, respectively) appears to be well mixed throughout the year by the near-continuous winds that blow commonly at 50 km hr^{-1} and faster (COMÍN, 1984). The oxygen content of the water ranges between 4 and 10 ml l^{-1}, 100–150% saturation, with very few exceptions (COMÍN, 1984).

Distinctive assemblages of algae occur during the freshwater (Bacillariophyceae-Chlorococcales-Cyanophyceae) and the seawater (*Dunaliella-Tetraselmis-Hemiselmis*) phases in the lagoons (COMÍN, 1984). There are also related changes in zooplankton: *Calanipeda aquaedulcis, Notholca* sp. and *Synchaeta* sp. populations dominate the zooplankton during winter and early spring and *Acanthocyclops vernalis, Hexartha* and *Brachionus* spp. populations dominate during late spring, summer and autumn (MENÉNDEZ and COMÍN, 1986).

Two sampling stations were established in different basins of the two lagoons studied (Figure 1). Water samples were collected at 10 cm depths using a Niskin bottle on 18 occasions between May, 1978 and May, 1979. Unfiltered water samples were stored frozen, and concentrations of chlorophyll *a*, chloride, nitrate, nitrite, ammonium, and soluble reactive phosphate were analyzed in the laboratory (STRICKLAND and PARSONS, 1965) not later than one month after collection. Production rates were measured "*in situ*" on the same dates as water sampling, using the ^{14}C technique (VOLLENWEIDER, 1969). One microcurie of radioactivity ($H^{14}CO_3^-$) was introduced into three 125 ml transparent bottles, one of which was opaque, and the bottles were incubated at 10 cm depth for 2 hr between 1100 and 1500 hr. Water was filtered using 0.8 μm pore size membrane filters, and then 2.5 ml of 0.001 N HCl were also filtered to prevent precipitation of ^{14}C, and activity was determined by liquid scintillation.

Phytoplankton counts were done on a subsample of 10 ml for each station in each lagoon. The subsamples were fixed with Lugol's solution, concentrated by settling, and were counted using an inverted microscope (UTERMOHL, 1958; VOLLENWEIDER, 1969). At least 400 individuals of each of the species accounting all together for 80% of the total cell density were counted at 890 ×. The rest of the species were counted in a volume of 0.1 ml of sample at 890 ×. Further descriptions of the study area and methods are provided in COMÍN (1984).

The minimum volumes of seawater, V_s, of chloride concentration, Cl_s, needed to produce the observed increases in chloride concentration (Figure 2a) in the lagoons from January to April–May, were calculated separately month by month using

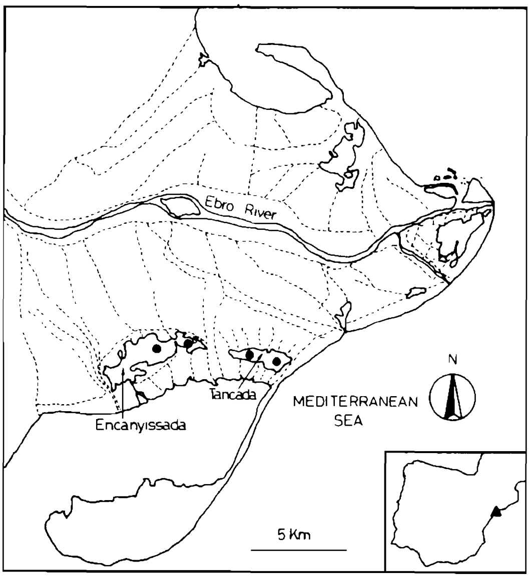

Figure 1. Sketch map of the Ebro River Delta in NE Spain. The coastal lagoons used in this study are Encanyissada (E) and Tancada (T). The dashed lines show the principal (mostly man-made) canals that convey and drain water into and out of rice fields and the lagoons. The inset shows site of Ebro Delta in the Iberian Peninsula.

the equation $V_{L,t}Cl_{L,t} + V_sCl_s = V_{L,t+1}Cl_{L,t+1}$, where $V_{L,t}$, $V_{L,t+1}$ and $Cl_{L,t}$, $Cl_{L,t+1}$ are, respectively, the water volumes and chloride concentrations of the lagoon in two consecutive sampling times. The volumes of water present each month in the lagoons, V_L, were calculated using monthly data on depth and area of the lagoons (Comín, 1984). The volumes, V_s, were then taken to be the volume of seawater that entered the lagoons per month. These estimates of flux are underestimates, since they only include net changes over intervals of about one month. Changes over shorter periods were neglected by our calculations. Tides are not important in this zone of the Mediterranean Sea and, certainly, not considerable in the lagoons. Seawater exchanges occur at irregular intervals due to storms. The sums of the monthly fluxes of seawater (V_s) entering Encanyissada and Tancada derived from chloride measurements (Table 1) can furnish a rough estimate of rate of seawater flow (R_s) and turnover of water during the seawater phase (T_s) in the lagoons, since from Figure 2 we know that the rate of salinity increase per time is not constant.

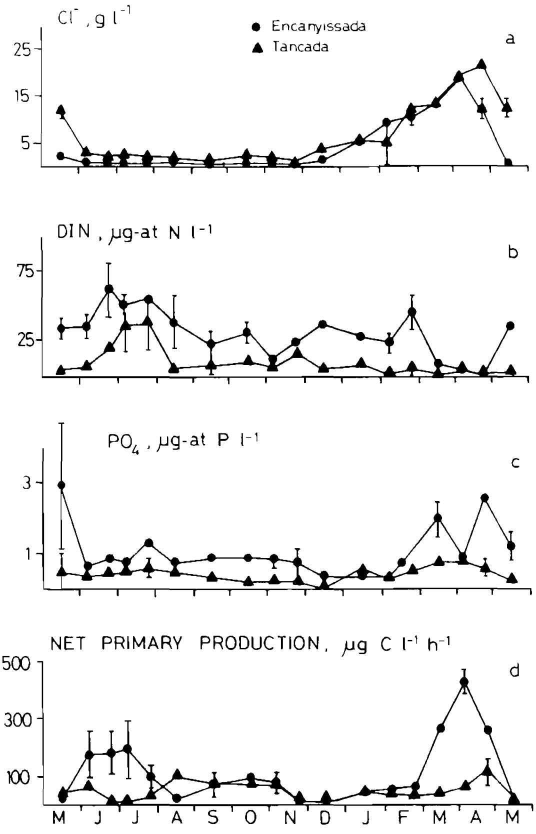

Figure 2. Chloride concentration (a), dissolved inorganic nitrogen (b), soluble reactive phosphorous as phosphate (c) and phytoplankton primary production (d) in the Ebro lagoons. Data shown as mean standard error (= range) for the two stations sampled from each lagoon.

Calculations regarding phytoplankton were done using data on chlorophyll from Comín (1984), conversion ratios of chlorophyll to biomass (1:62), carbon to biomass (45% C), and Redfield ratios for phosphorus and nitrogen contents of phytoplankton (Valiela, 1984). Then we regressed changes in particulate N and P (due to changes in number of cells per water volume unit) vs. changes in dissolved inorganic N and P in the water (due to presumed uptake by phytoplankton).

RESULTS AND DISCUSSION

Water Regime

As a result of the entrance of seawater into the lagoons through the winter, salinity (measured as

Table 1. *Estimates of duration of the sea- and freshwater phases in Encanyissada and Tancada lagoons, and estimates of water flow and turnover times for each of the two phases. Data on volumes are from* Comín *(1984).*

	Encanyissada	Tancada
Volume of lagoon (m^3) (V)	2,443,100	672,400
Seawater phase:		
Duration (days) (D_s)	130	150
Volume of seawater flowing into lagoon (m^3) (V_s)	2,215,660	672,080
Rate of seawater flow (m^3 day^{-1}) (R_s)	17,040	4,480
Turnover of water of lagoon (mo^{-1}) (T_s)	0.23	0.20
Freshwater phase:		
Duration (days) (D_f)	235	215
Volume of freshwater flowing into lagoon (m^3) (V_f)[1]	10,377,840	2,651,810
Rate of freshwater flow (m^3 day^{-1}) (F_f)	44,160	12,330
Turnover of water in lagoon (mo^{-1}) (T_f)	0.60	0.60

[1] The entry in the table refers to the volume entering the lagoons during the entire freshwater phase. This total volume was extrapolated to the entire freshwater phase based on calculations on the 50-day period during which chlorinity decreased from seawater to freshwater concentrations (and hence made our calculation of freshwater flow possible). The water flows during the 50-day period were 2,208,100 m^3 for Encanyissada and 616,690 m^3 for Tancada

chloride concentration) increased and reached 18–21 g Cl l^{-1} (Figure 2a). The salinity of the two lagoons decreased suddenly in early spring, when freshwater from rice paddies began to flow through the drainage canals into the lagoons (Figure 2a). The drop in salinity in Encanyissada occurred about one month before that in Tancada, and salinity was higher in Tancada (2.01 ± 0.8 g Cl l^{-1}) than in Encanyissada (0.75 ± 0.39 g Cl l^{-1}) throughout the freshwater phase.

At least 4,480 m^3 of seawater must have entered Tancada per day, while for Encanyissada the flux was about 17,040 m^3 day^{-1} (Table 1). The volumes of the two lagoons differ, however, so that the turnover of water (T_s) did not differ significantly between the two lagoons. During the seawater phase the water in Tancada turned over ($T_s = R_x/V \times$ days mo^{-1}) about 0.2 times per month (4,480 m^3 day^{-1}/672,080 m^3 × 30 days mo^{-1}), while in Encanyissada it turned over 0.23 times mo^{-1} (17,400 m^3 day^{-1}/2,215,600 m^3 × 30 days mo^{-1}).

Similar calculations were performed to estimate the flux of freshwater into the lagoons during the spring and early summer. In Tancada, it took about 50 days (D_f, April to June) for salinity to drop to freshwater levels (Figure 2a). Thus at least 616,690 m^3 (this volume, V_f, refers to water level during April to June, and hence differs from the average volume shown in Table 1) must have flowed in from the rice paddies during those 50 days. We can divide V_f/D_f and conservatively estimate a flow rate (F_f) of about 12,330 m^3 day^{-1} (Table 1). In Encanyissada, the equivalent calculation is 44,160 m^3 day^{-1} (2,208,100 m^3 in 80 days during April and May) (Table 1 and Figure 2a).

The salinity in the lagoons did not change during mid summer to fall (Figure 2a). This makes it impossible to calculate inflows of freshwater from charges on chloride concentration. Rice growth requirements for water increase late in the summer, so the drainage out of the paddies must also increase, but evapotranspiration also increases. We conservatively assumed that the rates of flow of freshwater entering the lagoons during the summer remained the same as in spring. At this conservative rate, the turnover of lagoon water during the freshwater phase would be about 0.6 times per month (12,330 m^3 day^{-1}/616,090 m^3 × 30 days mo^{-1}) for both Tancada and Encanyissada (44,160 m^3 day^{-1}/2,208,100 m^3 × 30 days mo^{-1}). The minimum turnover of water during the entire freshwater phase is thus about three times as fast as that during the seawater phase.

We can therefore estimate that during the seawater phase the water in the lagoons is replaced at least once every five to six months; that is, once during the entire seawater phase. In contrast, during the 6–7 month long freshwater phase, the water in the lagoons turns over at least four times.

As the previous calculations are coarse estimates, it is desirable to corroborate them with an independent check. We can perform an independent comparison of the relative rates of water renewal in the lagoons during the fresh and seawater phases using data on primary production

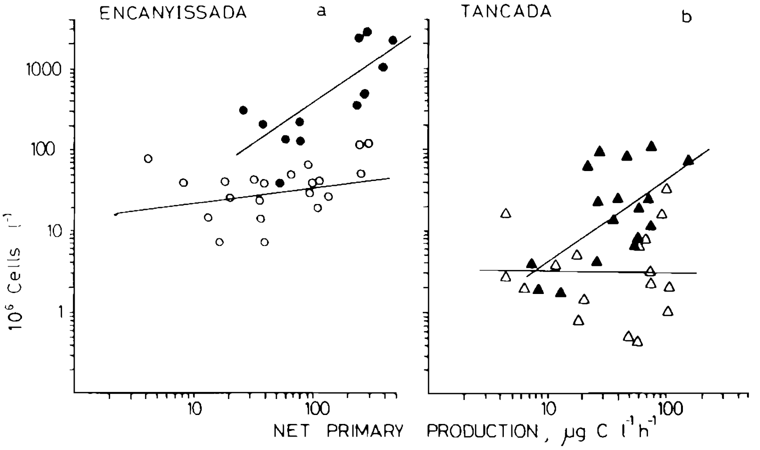

Figure 3. Abundance of phytoplankton cells vs. productivity in the two lagoons. Black symbols refer to the seawater phase and white symbols to the freshwater phase. Samples whose chlorinity exceeded 4 g Cl l^{-1} were assigned to the seawater phase.

and abundance of phytoplankton (Figure 3). During the seawater phase, cell abundance increased at higher levels of productivity. During the freshwater phase, in contrast, cell abundance did not increase at higher productivities; there were clearly some major cell losses during the freshwater phase, in excess of losses during the seawater phase. Note that all this occurred within approximately the same total range of productivity during the two phases. In general, a similar production rate was obtained by lower number of cells during the freshwater phase than during the seawater phase. Of course, different grazing rates could be involved, but zooplankton abundance is not high enough to control phytoplankton growth (MENÉNDEZ and COMÍN, 1986). The NPP data suggest that water turnover during the freshwater phase may be high enough for the lagoons to resemble a chemostat whose flow rate washes out cells fast enough to prevent increases in cell density, in spite of high production rates. In contrast, during the seawater phase, rates of water flow may have been slow enough for cell abundance to increase inside the lagoons as productivity increased.

Nutrients

The concentrations of dissolved inorganic nitrogen in the water of the Ebro lagoons ranged between less than 1 to about 75 µg at N l^{-1} (Figure 2b). There were two peaks, one in winter and one in summer, both followed by decreases.

The two major components of DIN, ammonium and nitrate, have different seasonal patterns (Figure 4), suggesting that simple passive mixing of salty and freshwater end-members is not sufficient explanation for the seasonal changes in con-

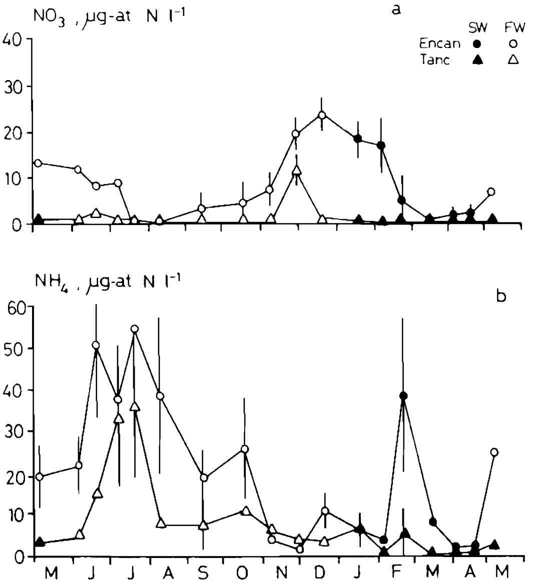

Figure 4. Nitrate (a) and ammonium (b) concentrations in the two lagoons over time. The seawater and freshwater phases are indicated as SW and FW. Data shown as mean standard errors.

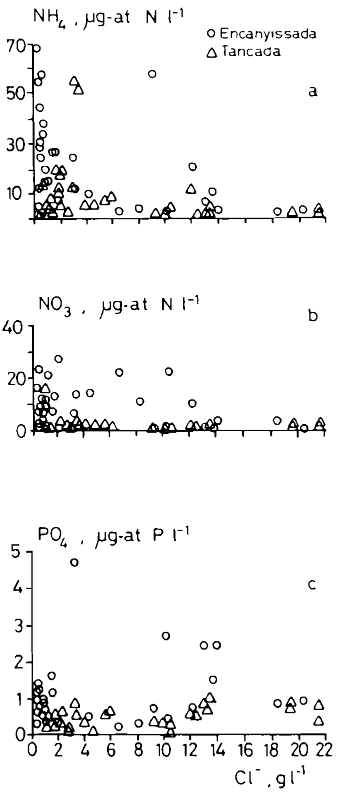

Figure 5. Nutrient concentrations in relation to chloride concentration.

centrations. Neither NO_3 nor NH_4 show a clear relation to salinity, as would be the case if simple mixing determined nutrient concentrations (Figure 5). Concentrations of nitrate and ammonium show a wide scatter in the freshwater phase; NO_3 and NH_4 concentrations at chloride concentrations below 1 g l^{-1} ranged from near 0 to 70 and 27 µg at N l^{-1} of NH_4 and NO_3, respectively (Figure 5). The concentrations of NH_4 and NO_3 diminished in saltier water. Most points in Figure 5 lie below a linear mixing line, however, so it seems that input and transformation mechanisms other than passive mixing have to be involved. The net effect of such mechanisms is very variable, particularly at lower salinities. We, therefore, need to see what additional mechanisms may be involved in the seasonal patterns of nitrate and ammonium.

Inputs are more important than transformation mechanisms within the lagoons early in the growing season since rice paddies are fertilized with urea, which hydrolyzes to produce ammonium. The flows of nitrogen as ammonium and nitrate from the rice paddies are probably the cause of the peaks in the lagoons during early and mid summer (Figure 4). FORÉS and COMÍN (1987) reported 45.2 ± 8.7 µg at N-NH_4 l^{-1} and 29.7 ± 5.7 µg at N-NO_3 l^{-1} in water leaving the newly irrigated paddies during May, June and July. By mid summer, there were much less NH_4(9.5 ± 9) and NO_3 (2.5 ± 2.1) leaving the paddies and entering the lagoons. Thus, transformation mechanisms within the lagoons must be more important than inputs during mid summer and early autumn. Denitrification may be the cause of the mid-summer drop in nitrate, since rates of denitrification are markedly temperature dependent (KAPLAN *et al.*, 1979; FOCHT and VERSTRAETE, 1977).

As the rice-growing season and freshwater flow ended (November–December), there were high nitrate concentrations in the lagoons and low concentrations of ammonium (Figure 4). The rates of accumulation of NO_3 in the water from August to December are 2 and 5.7×10^{-7} mol l^{-1} day^{-1} in the two lagoons. These rates are comparable to the average of 4.8 10^{-7} mol l^{-1} day^{-1} reported for nitrification in the water column of various coastal areas (KAPLAN, 1983).

Uptake by phytoplankton may account for some decrease in nitrate and ammonium during the seawater phase (Figure 4). We checked to see if this could be qualitatively significant by comparing losses in DIN from the water to see if these losses may have been of the same magnitude as the amount of N that appeared as cells in the water during periods of phytoplankton growth (Table 2).

The relation of growth to uptake had a substantial scatter (Table 2), as could be expected from the very rough method of calculation. The only significant relationship was that of changes in dissolved nitrogen and cell N during the seawater phase. As particulate N increased, there were concomitant decreases in the concentration of DIN. The relationship is not 1:1 but the variability of the data is too large to speculate on the significance of a departure from 1:1. In any case, the relationship suggests that algal uptake is a quantitatively significant mechanism that may reduce concentration of DIN in the water column of the lagoons during the seawater phase. The relatively fast rate of water turnover during the freshwater phase (Table 1) precludes the estab-

Table 2. *Regressions of the changes in DIN and DIP in water in relation to changes in particulate N and P in the lagoons during the seawater and freshwater phases. The changes were calculated between sampling dates, which were approximately monthly. NS: not significant; *: significant at 95% level.*

Regression Equation	F Value	r
Seawater phase		
Change in DIN = $-3.0293 + (-0.3175)$Part N	7.707*	−0.63
Change in DIP = $0.1529 + 0.023$ Part P	0.034 NS	0.05
Freshwater phase		
Change in DIN = $2.9238 + 0.2281$ Part N	0.768 NS	0.20
Change in DIP = $-0.1585 + 0.0945$ Part P	0.457 NS	0.16

lishment of a clear algal N to water DIN relationship.

Concentrations of NH_4 were lowered during peaks in production, but not depleted from the water column of the Ebro lagoons (Figure 4b). Nitrate, however, was more clearly depleted (Figure 4a) during periods of high productivity (Jun.–July and Feb.–Apr., Figure 2d). This phenomenon suggests that denitrification may also be responsible for the winter loss of NO_3. Unfortunately, we cannot say with confidence that denitrifiers were responsible for the lowered nitrate concentrations, because there are several reports of uptake of NO_3 by phytoplankton in the presence of substantial amounts of NH_4 (GLIBERT *et al.*, 1982; ANDERSON *et al.*, 1984; CARPENTER and DUNHAM, 1985; PRICE *et al.*, 1985; FLYNN and BUTLER, 1986; QUEGUINER *et al.*, 1986). FLYNN AND BUTLER (1986) showed that natural phytoplankton from a coastal bay could show relatively fast nitrate uptake rates at concentrations of ammonium of 10–30 μg at l^{-1}. Such concentrations of ammonium are very close to the range found in the Ebro lagoons during Dec.–Mar. (Figure 4). Nitrate uptake rates by phytoplankton of a frontal, nutrient-richer station in the Strait of Georgia were higher than in a stratified, nutrient-poorer station, even though there was more ammonium in the frontal station (PRICE *et al.*, 1985).

It is thus not unprecedented that Ebro lagoon phytoplankton could take up nitrate at ambient ammonium concentrations. The recent literature and our results therefore suggest that for some reason brackish lagoon or estuarine algae may do better in nitrate-rich water than in ammonium-rich water. Perhaps the uptake of NO_3 and NH_4 varies in relation to the relative saturation of the internal N pool (FLYNN and BUTLER, 1986), since the uptake of nitrate seems to occur mainly in DIN-rich water. It is important to evaluate rates of microbial N loss in the lagoons in order to know the relative importance of different transformation mechanisms.

Phosphate concentrations in the Ebro lagoons ranged from 0 to 3 μg at l^{-1} (Figure 2c). There is no clear trend of phosphate concentration and chlorinity (Figure 5c), so it is evident that phosphate is not a passive tracer of the mixing of fresh and salty water. Water leaving rice paddies contained 2–5 μg at l^{-1} from May through October (FORÉS and COMÍN, 1987). These values are higher than those recorded during the freshwater phase in the lagoons (Figure 2c), so some process—chemical precipitation, adsorption, uptake by producers—removes phosphate during the freshwater phase. Uptake by phytoplankton cells may be relatively unimportant in phosphate removal, since we found no relation between losses of DIP from the water and increases in particulate P in cells during the freshwater phase (Table 2), but fast turnover of water makes a relationship unlikely during the freshwater phase.

During the winter seawater phase, in contrast to the summer freshwater phase, there was an accumulation (more prominent in Encanyissada than in Tancada) of phosphate in the water column. The accumulation suggests that phosphate was not limiting the growth of producers during the seawater phase. This additional phosphate was not brought in by seawater, since the saltiest water ranged between 0.4 and 1 μg at l^{-1} (COMÍN, 1984; and Figure 4) and, further, the phosphate peak in the two lagoons differed considerably (Figure 2c). It seems most likely that the winter phosphate peak reflects benthic or water column remineralization during a time of slower water turnover.

Abundance, Productivity and Composition of Phytoplankton

Productivity of phytoplankton of the Ebro Delta lagoons was low from fall to winter (Figure 2d),

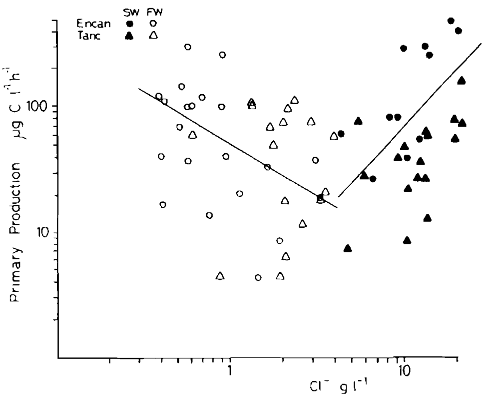

Figure 6. Productivity vs. chlorinity in the Ebro lagoons. Encanyissada values are circles, while Tancada values are shown as triangles. Values for the seawater phase are black symbols, and those for the freshwater phase are white symbols.

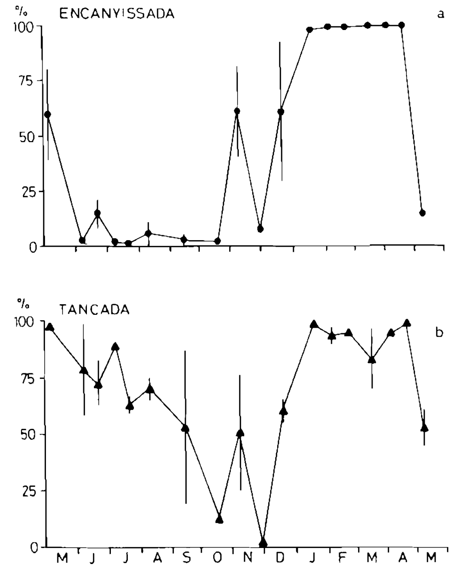

Figure 7. Percent of marine species (see text for definition) of phytoplankton in the Ebro lagoons over time. Mean standard errors shown by bars.

presumably limited by low light because this is the period of the year of the lowest Secchi disk depths which were due to suspended sediment by intense and frequent winds (Comín, 1984). There was a spring bloom (Feb.–May) which was ended by the changes in salinity brought about by freshwater inputs from ricepaddies. The change from sea to freshwater led to very low production rates in May. At the same time, there were fewer phytoplankton species and cells than earlier or later in the year (Comín, 1982). Productivity increased again in June–July in Encanyissada, while being variable in Tancada.

The somewhat different schedules of changes in salinity in Encanyissada and Tancada (Figure 2a) were not clearly reflected in the seasonal productivity data (Figure 2d), but there was a relationship between productivity and salinity (Figure 6). The productivity in the lagoons varied by at least one order of magnitude at any time throughout the year and at every salinity (Figure 6). The variability of productivity (the vertical scatter around the two lines of Figure 6) was not altered in the two regimes, but the level of productivity changed as salinity changed. Higher production was at the lowest and highest salinities. This was the result of the establishment of either fresh or more marine phytoplankton assemblages (Comín, 1982) when water at either end of the spectrum was available. The transition between fresh and seawater reduced phytoplankton production, likely due to increases in turbidity and osmotic stress.

To express the relative abundances of marine and fresh phytoplankton species, we totaled the abundances of all marine species and expressed this as a percent of all phytoplankton cells in the sample. The average of such calculations for the two stations for each date of sampling is shown as it changed over time in Figure 7. We used the term "marine" species to refer to the assemblage of "marine" species consisting of cosmopolitan nanoplanktonic species that are commonly found in waters variously affected by the sea, from brackish to full seawater (Comín, 1984).

The change from freshwater to marine species and back to freshwater species was very pronounced in Encanyissada (Figure 7a). In Tancada, there are similar shifts, except that there was a much more gradual change from the marine to freshwater species assemblage during the warm part of the year. This may be related to the persistence of saltier water in Tancada during this period (Figure 2a).

Relation of Nutrient Limitation and Hydrologic Regime

If conclusions based on the results of enrichment experiments (Schindler, 1974; Carpenter and Capone, 1983; Valiela, 1984) are correct, there ought to be a switch in the nutrients limiting phytoplankton production in the Ebro Delta lagoons, from N in the salty winter water to P in the fresh summer water. Some clues to this switch are: (1) phosphate concentrations in the water of the lagoons during the freshwater phase were lower than in water draining rice paddies; (2) the concentration of phosphate in the lagoons increased during the seawater phase; and (3) the calculated increases in particulate N were significantly related to the measured decreases in DIN from water in the lagoons during the seawater phase.

Although there were important depletions of P (Figure 2) and of NO_3 and NH_4 (Figure 4) at certain times of the year, phytoplankton productivity was not related to the concentrations of individual nutrients, even though nutrient concentrations ranged over two orders of magnitude, and production over three orders of magnitude. Nixon (1982) reached the same conclusion after reviewing similar data for various coastal lagoons. Many processes are involved at the same time for a clear relationship to emerge.

As another way to examine the questions, changes in N to P ratios can be used as a rough indication of nitrogen or phosphorus limitation (Jaworski, 1981). During the freshwater phase, chlorinity did not vary very much, and there were no trends in the N/P values (Figure 8), most of which were considerably above 16:1, even though most of the direct measurements of denitrification, N-fixation and regeneration of nutrients in coastal environments indicate that the effect of these important processes is to decrease the N/P ratio below 16:1 (Valiela and Teal, 1979; Nixon, 1981; Seitzinger *et al.*, 1984; Seitzinger, 1988). The regression of N/P and chlorinity was not significant. The net effect of the mechanisms affecting nitrogen and phosphorus concentrations did not change the N/P ratio during the freshwater phase.

As water became saltier during the seawater phase (Figure 2), there was a notable and significant decrease in N/P from about 100:1 to 1:1 (Figure 8). Nutrient uptake by phytoplankton may have been an important process that lowered the ratio N:P during the seawater phase suggesting that marine species of phytoplankton (Figure 7) removed N preferentially, since N/P in water reached levels considerably below the Redfield ratio (Figure 8) and below the N/P ratio in the bay from where seawater enters the lagoons (Delgado, 1986). As the seasonal cycle was completed and water from the rice paddies was pumped into the lagoons during spring, the water in the lagoons quickly returned to very low salinities of less than 1 g l^{-1}, and to N/P values that exceeded 16:1. The N/P of water entering the lagoons was around 30 during the rice-growing season (Comín, 1984); this is roughly the average ratio evident throughout the freshwater phase in the lagoons (Figure 8). Water flow overwhelmed the impact of internal nutrient cycling within the lagoons during the freshwater phase.

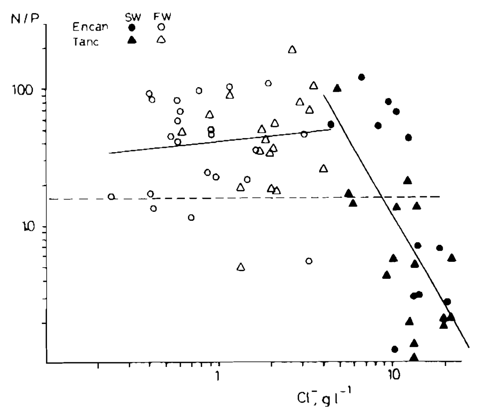

Figure 8. Ratio of dissolved inorganic nitrogen to soluble reactive phosphorous vs. chlorinity of water in the Ebro lagoons. Symbols as in Figure 5. Horizontal dashed line shows N/P ratio = 16.

If ratios of N to P reflect nutrient limitation of phytoplankton growth, there should be some relation of productivity to N/P (Figure 9). In spite of significant scatter, the data show a significant negative regression for the seawater phase (log productivity = 2.088 − 0.307 log(N/P), F = 5.429*, r = −0.42), while the relationship is not significant for the freshwater phase (log productivity = 2.071 − 0.291 log(N/P), F = 1.584, n.s., r = −0.21, line not shown).

There are two possible interpretations of the data of Figure 9. Higher production rates during the seawater phase could be associated with low N/P, that is, the phytoplankton production is phosphorus stimulated during the seawater phase. Alternatively, phytoplankton removed more N than P during intervals of time between samplings and grew in some proportion to nutrients—par-

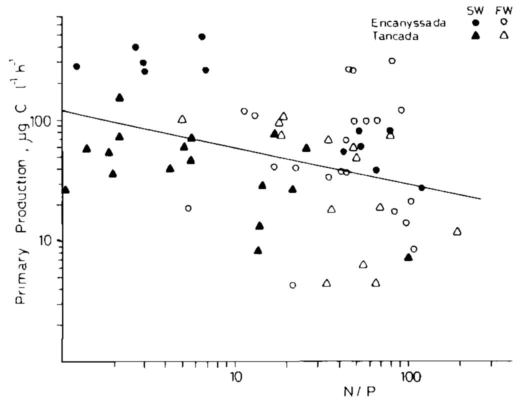

Figure 9. Productivity of phytoplankton in Ebro lagoons vs. N/P in water. Symbols as in Figure 5. The regression for the freshwater phase data (open symbols) was not significant (see text) and the line is not shown. The regression line shown is for the seawater phase values.

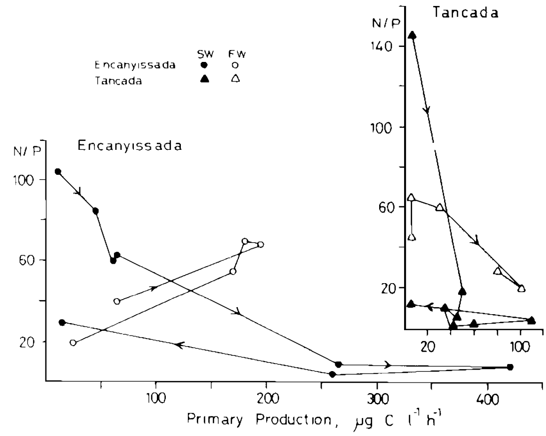

Figure 10. Changes in ratio of N to P during the time course of the two major seasonal phytoplankton blooms. (SW: bloom during the seawater phase of the hydrological year; FW: bloom during the freshwater phase of the hydrological year). Arrows on lines indicate sequence over time.

ticularly N—removed. The latter is a more reasonable option, since algal blooms do not appear instantaneously; lags in response of phytoplankton blooms to nutrient availability may take up to one month (Figure 2). If algal uptake is indeed large enough to result in measurable changes in concentration of dissolved nutrients, there should be a resulting coupling of primary production and nutrient loss (and to N/P) expressed during the course of the bloom. We have two such blooms in the lagoons, one during the seawater phase, one during the freshwater phase (Figure 2d).

Detailed time courses during blooms in fact show well defined relationships between increases and decreases in primary production, and N/P (Figure 10). First, the data from Encanyissada (Figure 10) show that as production increased during the freshwater phase, the N/P increased. This suggests that more P than N was removed from the water by the growing phytoplankton. As production increased during the seawater phase bloom, the N/P was lowered. This suggests that relatively more N than P had been removed, and the N/P was lowered to the vicinity of the Redfield ratio.

In Tancada (Figure 10), there was a decrease in N/P as production increased during both the freshwater and seawater blooms. The data for the freshwater phase thus are contrary to the Encanyissada results. An explanation for the different results may be that Tancada is much slower to achieve a truly freshwater phytoplankton assemblage. In fact, the species composition of the phytoplankton found during the "freshwater" phase in Tancada contains a significant proportion of marine species (Figure 7). Tancada, thus, does not show as complete a shift to a freshwater response as Encanyissada. Such remarkable changes of the N/P ratio over time in the different phases of the hydrological cycles in the lagoons suggest a close coupled relation of growth of the assemblage of phytoplankton species to short-term changes of ambient N/P. We cannot demonstrate the cause–effect relation between nutrients and uptake by phytoplankton. We need additional data to separate the role of, for example, denitrification from that of nutrient uptake by phytoplankton. There is circumstantial evidence that points to uptake by phytoplankton as a mechanism that, at least in part, may lower DIN in the water column of the Ebro lagoons during the seawater phase: (1) inverse relationship between changes in N/P and production rates, described in previous paragraph, (2) loss of nitrogen from water is similar in magnitude and concurrent to the increase in particulate N, and (3) the reduction of dissolved inorganic nitrogen and marked lowering of N/P below Redfield ratio during the seawater phase. These observations are consistent with the notion that phytoplankton growth during winter may have been limited by the supply of nitrogen.

The turnover of seawater in the Ebro lagoons in winter is in a range of several months, similar to the turnover of others slow enough—2 months to over 1 year (SMITH, 1984)—for biogeochemical mechanisms to furnish enough nitrogen to supply demands by producers. In spite of the slow turnover of water during the seawater phase, the N to P ratios suggest that nitrogen is depleted relative to phosphorus during the seawater phase. If this is so, the water turnover is not slow enough for nitrogen recycling mechanisms to supply sufficient N for P to become the limiting element. In fact, the concentrations of phosphate in the Ebro Delta lagoons were highest during the seawater phase (Figure 2c), the time of year when water turnover was slowest. At least for the Ebro lagoons, water turnover is not readily related to N or P limitation.

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□ RESUMEN □

Las lagunas costeras del delta del Río Ebro tienen agua dulce de mayo a Diciembre porque reciben grandes cantidades de agua excedente del riego de arrozales. Durante el resto del año, la salinidad aumenta progresivamente hasta igualar a la del mar debido a que el intercambio de agua tiene lugar exclusivamente con el mar. La composición específica del fitoplancton cambia de acuerdo con estos cambios. Este experimento a nivel de ecosistema permite discutir las relaciones de la abundancia y productividad del fitoplancton con las concentraciones de nitrógeno inorgánico disuelto (DIN) y fósforo reactivo soluble (SRP) del agua y el efecto potencial de la tasa de renovación del agua sobre la productividad del fitoplancton en dos situaciones separadas en el tiempo, agua dulce y agua marina, en la misma cubeta.

Durante la fase de agua dulce, las concentraciones de nutrientes y la relación DIN:SRP son tales que parece improbable que los nutrientes limiten la producción del fitoplancton. Durante la fase de alta salinidad, disminuye más el nitrógeno que el fósforo, la relación DIN:SRP disminuye por debajo de 16:1, la pérdida de nitrógeno del agua es similar en magnitud y concurrente con el aumento de nitrógeno particulado, y los cambios de la relación DIN:SRP y de la tasa de producción están inversamente relacionados. Todas estas relaciones indican que la captación por el fitoplancton es un mecanismo determinante de la disminución del DIN. Los resultados indican que el fitoplancton de las lagunas prefiere el uso de nitrato antes que el de amonio. La tasa de renovación del agua de las lagunas no es lo suficientemente baja como para que se recupere el deficit de nitrógeno respecto al fósforo relacionado con el crecimiento algal.