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The relationship between phytoplankton diversity and community function in a coastal lagoon

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Abstract

The decrease of biodiversity related to the phenomena of global climate change is stimulating the scientific community towards a better understanding of the relationships between biodiversity and ecosystem functioning. In ecosystems where marked biodiversity changes occur at seasonal time scales, it is easier to relate them with ecosystem functioning. The objective of this work is to analyse the relationship between phytoplankton diversity and primary production in St. André coastal lagoon – SW Portugal. This lagoon is artificially opened to the sea every year in early spring, exhibiting a shift from a marine dominated to a low salinity ecosystem in winter. Data on salinity, temperature, nutrients, phytoplankton species composition, chlorophyll *a* (Chl *a*) concentration and primary production were analysed over a year. Modelling studies based on production-irradiance curves were also conducted. A total of 19 taxa were identified among diatoms, dinoflagellates and euglenophyceans, the less abundant group. Lowest diversities (Shannon–Wiener index) were observed just before the opening to the sea. Results show a negative correlation ($p < 0.05$) between diversity and chlorophyll *a* (Chl *a*) concentration (0.2–40.3 mg Chl *a* m^{-3}). Higher Chl *a* values corresponded to periods when the community was dominated by the dinoflagellate *Prorocentrum minimum* (> 90% of cell abundance) and production was maximal (up to 234.8 mg C m^{-3} h^{-1}). Maximal photosynthetic rates (P_{max}) (2.0–22.5 mg C mg Chl a^{-1} h^{-1}) were higher under lower Chl *a* concentrations. The results of this work suggest that decreases in diversity are associated with increases in biomass and production, whereas increases correspond to opposite trends. It is suggested that these trends, contrary to those observed in terrestrial and in some benthic ecosystems, may be a result of low habitat diversity in the water column and resulting competitive pressure. The occurrence of the highest photosynthetic rates when Chl *a* is low, under some of the highest diversities, suggests a more efficient use of irradiance under low biomass–high diversity conditions. Results suggest that this increased efficiency is not explained by potential reductions in nutrient limitation and intraspecific competition under lower biomasses and may be a result of niche complementarity.

Introduction

Biodiversity changes at various temporal and spatial scales (Krebs, 1994). The former may be as large as evolutionary time scales and as small as seasonal or even shorter time scales. The latter may range from latitudinal to local diversity gradients. Given the important shifts observed in biodiversity and the long-term effects of global change, it is important to understand the impact of

these changes on ecosystem functioning and ecosystem services.

Biodiversity (hereafter referred as diversity) is a measure of community structure, whether it is expressed merely as species richness or with a specific index. Production is a measure of community function. Therefore, relating diversity with production is one of the several ways to relate community structure with community function. The relationship between these two parameters has been a topic of much debate over the years, mostly in terrestrial ecology. In spite of all this debate, it is not yet a matter of consensus among the scientific community (e.g. Huston et al., 2000). One question that may be asked about these two parameters, assuming that they are related, is "Which is the cause and which is the effect?". According to some classical ecology textbooks (Krebs, 1994), production may hardly be the cause, since some of the most productive ecosystems have a low diversity. Recent studies on grassland ecosystems suggest that more diverse communities are more productive, because of niche complementarity (Hector et al., 1999; Tilman et al., 2001). This leads to the concept of 'overyielding', when polycultures exhibit higher production than monocultures, due to positive synergies between different species, as in the presence of nitrogen-fixing plants. In such a case, diversity would be the cause of higher production.

When production of different terrestrial ecosystems is compared, from grasslands to rain forests, it is apparent that as diversity increases towards tropical forests, ecosystems have larger gross and net areal productions. But when these values are related to biomass standing stock (the P/B ratio), the opposite seems to be the rule (Fig. 1) (Whittaker & Likens, 1975). Following the same authors, when areal production of continental shelf ecosystems and upwelling zones are compared with production of open ocean ecosystems, the formers exhibit much higher values than the latter, whilst the opposite is true for the P/B ratio. As in terrestrial ecosystems, those with higher biomass standing stocks exhibit higher production but lower P/B ratios than the ones with lower biomass densities (Fig. 1). However, whereas large biomass standing stocks are generally associated with higher diversity in terrestrial ecosystems, the opposite seems to be the rule in pelagic marine ecosystems, where it is generally reported that increased production is associated with decreased diversity (Pearl, 1988; Krebs, 1994). There seems to be a relatively scarcity of field and experimental data relating diversity, production and the P/B ratios in different marine ecosystems, whereas this is a very active field of research in terrestrial ecosystems, with manipulative experiments in current usage (e.g. Hector et al., 1999; Tilman et al., 2001). One of the few works where phytoplankton diversity and production were analysed together is that of Agard et al. (1996). These authors found some empirical evidence to confirm the dynamic equilibrium model of Huston (1979, 1994). According to this model, diversity is reduced by competitive exclusion under conditions of high production and low levels of disturbance, or where production is too slow to allow recovery from mortality. Diversity is therefore maximised at 'intermediate' disturbance and production levels.

Changes in species composition and diversity may produce changes in community level parameters, like phytoplankton growth rate and those parameters regulating the photosynthetic response to irradiance or other limiting factors. It is important to understand how these changes are reflected in ecosystem functioning and ecosystem services. The relationship between photosynthetic rate and irradiance (P–I) is of utmost importance in phytoplankton production studies. The knowledge of the dynamics of the P–I parameters over the annual cycle can be used to estimate primary production over seasonal scales. It may also help to understand some of the mechanisms controlling photosynthesis and operating from the species to the ecosystem level (Macedo et al., 2001).

However, at the present state of knowledge, it is very difficult to relate these parameters with community structure. According to Banse (1982), phytoplankton growth rate changes allometrically with cellular carbon. However, the parameters regulating this allometric relationship are higher for diatoms than for dinoflagellates, predicting higher growth rates for the former than for the latter, when cells exhibit similar carbon contents. Gallegos (1992) observed in the estuary of the Rhode River (Maryland, USA) that the parameters of the P–I curves were higher when phytoplankton blooms were dominated by the diatom

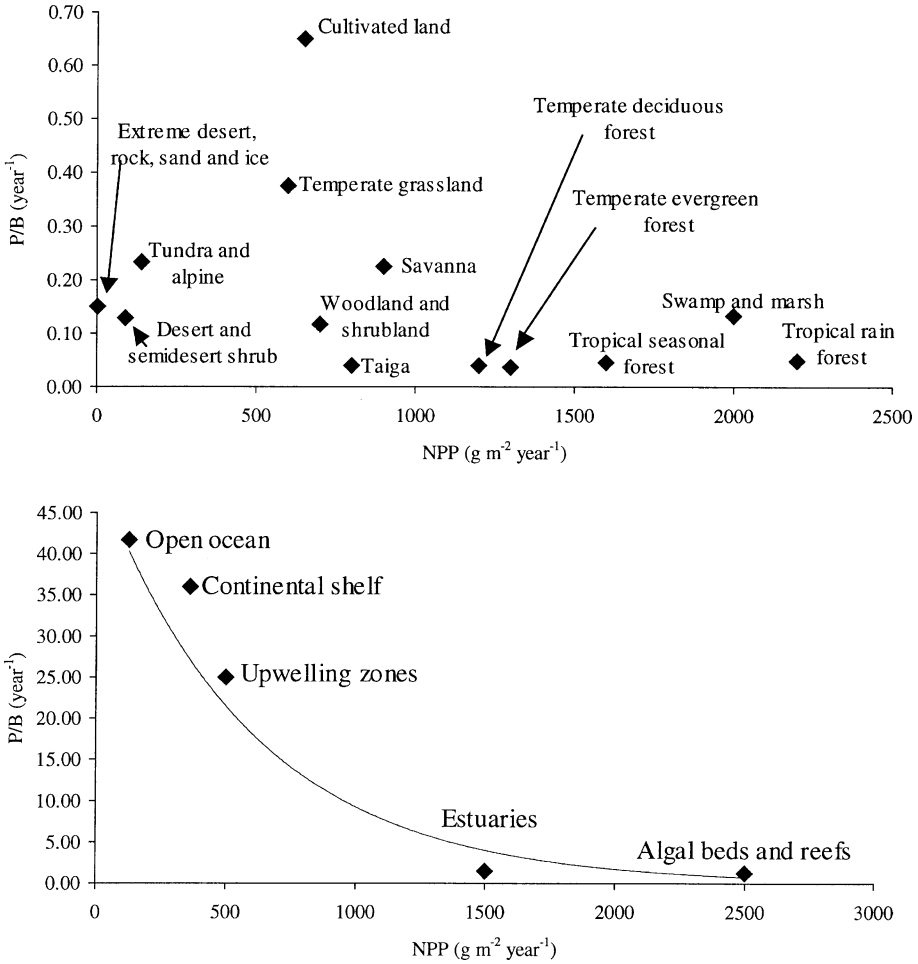

Figure 1. Relationship between areal net primary production and the P/B ratio obtained from data presented in Whittaker & Likens (1975).

Thalassiosira pseudonana Hasle & Heimdal and lower when the blooms were dominated by dinoflagellates. Shaw & Purdie (2001) observed in the UK coastal waters of the North Sea that the October peak in the parameters of the P–I curves coincided with a period in which dinoflagellates accounted for a high proportion of phytoplankton biomass. In a study conducted in Santo André coastal lagoon Macedo et al. (2001) obtained P–I curves every month for a period of 13 months together with phytoplankton species composition and cell counts. A significant Arrhenius type relationship was obtained between light saturated photosynthesis (P_{max}) and temperature when blooms were dominated by the dinoflagellate *Prorocentrum minimum* (Pavillard) Schiller. None of the previous authors related phytoplankton diversity with the P–I curve parameters. Moreover, none separated the effects of species composition from the effects of other environmental variables that may contribute to photoacclimation and photoadaptation of phytoplankton cells, leading to differences in the P–I curve parameters. According to Pahl-Wostl & Imboden (1990) photoresponse has typical time scales between a few minutes and a few hours and corresponds to the time it takes for photosynthesis to reach a steady state response to light. Photoacclimation occurs at time scales of several hours to days and corresponds to changes in cell composition, as chloro-

phyll *a* (Chl *a*) contents per cell. These two processes may mask differences that result from changes in community composition.

Ecosystems that undergo significant changes in species composition over time are suitable to analyse the relationship between diversity and production. This work is about phytoplankton communities in a Portuguese eutrophic coastal lagoon (St. André lagoon, SW Portugal). It is not based on an experimental design specifically defined to analyse the relationship between diversity and production. It is an exploratory study that may help to establish hypothesis about the mentioned relationship to be tested in future works. Therefore, the objective of this work is to get some insight into the following question:

"How is phytoplankton diversity related to phytoplankton community production and photosynthetic rates in a coastal lagoon?"

Methods

The sampling and analytical methods used in this study have been described elsewhere (Macedo et al., 1998, 2001). Therefore, only a brief description will be provided here.

Study area

Santo André Lagoon (38° 05′ N, 8° 47′ W) is a shallow (average annual depth of about 1 m, with a maximum of 5 m in autumn) land-locked coastal system located on the southwest coast of Portugal (Fig. 2). The lagoon is connected with the sea only in two periods: during about one month in March–April, by a man-made channel, and occasionally when seawater overpasses the dunes. In the first situation, low salinity water and sediments are exported and colonisation by marine species occurs. After the lagoon is closed, salinity progressively decreases and organic matter accumulates leading to summer dystrophy (Cancela da Fonseca et al., 1989). The lagoon receives freshwater from six small rivers forming a drainage basin of about 96 km^2. The lagoon can be stratified or vertically mixed, depending on the prevailing environmental conditions (Bernardo, 1990). Fishing is the main economic activity in Santo André Lagoon, although it is also used for recreation. The shifting between a predominantly fresh water ecosystem and a predominantly salt water ecosystem explains the large variability of physical, chemical and biological variables (Table 1).

Sampling and treatment

Physical and chemical variables (temperature, pH, salinity, dissolved nitrogen and phosphorus) Chl *a* concentrations, cell counts and species composition were monitored from January 1998 to January 1999, on a monthly basis (13 sampling campaigns) at one sampling station (Fig. 2). Water samples for phytoplankton biomass, species composition, inorganic nutrients and P–I experiments were collected simultaneously at 0.5 m depth. Samples for P–I determination were collected in the morning and kept in the dark for about 4 h before the incubations (see below).

Chemical analyses

Inorganic nutrient analyses (nitrate, nitrite, ammonia and phosphate) were performed according to the methods described in A.P.H.A. (1992) and Parsons et al. (1984). Total available inorganic carbon was determined in the water samples prior to incubation from pH (pH Meter ESD model 69) and alkalinity measurements according to Parsons et al. (1984). Samples for Chl *a* and phaeopigments (Phae) were filtered onto 0.45 μm membrane filters. Pigments were extracted in 90% acetone and analysed fluorometrically by the method of Yentsch & Menzel (1963) as modified by Holm-Hansen et al. (1965).

Species determination

Samples for species determination and enumeration were preserved with Lugol's solution (Throndsen, 1978) for about 6 months. Phytoplankton cells were counted by the Utermöhl technique in an Olympus IX70 light inverted microscope (Hasle, 1978), using the classification scheme of Drebes (1974), Dodge (1975) and Hasle et al. (1996). Phytoplankton diversity was calculated using the Shannon–Wiener function for each sampling occasion.

Table 1. Main characteristics of St. André lagoon (average ranges from Bernardo, 1990)

Average area	150 ha
Average depth	90–280 cm
Max. depth	225–540 cm
Salinity	1.9–23.5 psu
Temperature	9.5–28.6 °C
Phosphate P-$P0_4$	0.05–3.8 μmol l^{-1}
Nitrate N-$N0_3$	0.2–75.3 μmol l^{-1}
Ammonia N-NH_4	1.4–22.3 μmol l^{-1}
Chl *a*	1.8–61.9 mg m^{-3}
Macrophytes	94–438 g AFDW m^{-2}
Sediment org. matter	6.5–16.6%

P–I experiments

Samples were incubated in the laboratory at the same temperature measured in the field, at the time of sampling and under variable irradiance. Light was provided by 1500 W tungsten halogen lamps. Heat produced by the lights was dissipated using a cold water flow system. Irradiance (0–1445 μmol quanta m^{-2} s^{-1}) was measured by a LI-COR underwater cosine quantum sensor (model LI−192SA) and attenuation was achieved by means of grey PVC nets. Preservation of the spectral characteristics was verified by spectral analysis (see Macedo et al., 1998).

Photosynthetic rates were measured at different irradiances by the standard ^{14}C incubation technique (Steemann Neilsen, 1952) and following the ICES CM 1996/L:3 recommendations. Water samples were placed in 60 ml Winkler bottles and inoculated with 1 ml $NaH^{14}CO_3$ with 10 μCi (371.88 kBq cm^{-3}) (^{14}C Centralen). A dark bottle was used as blank.

P–I parameters were calculated from the photosynthesis and irradiance using the Eiler & Peeters (1988) model (1).

$$P(I) = \frac{I}{aI^2 + bI + c}\left[\text{mg C}(\text{mg Chl } a)^{-1}\text{h}^{-1}\right] \quad (1)$$

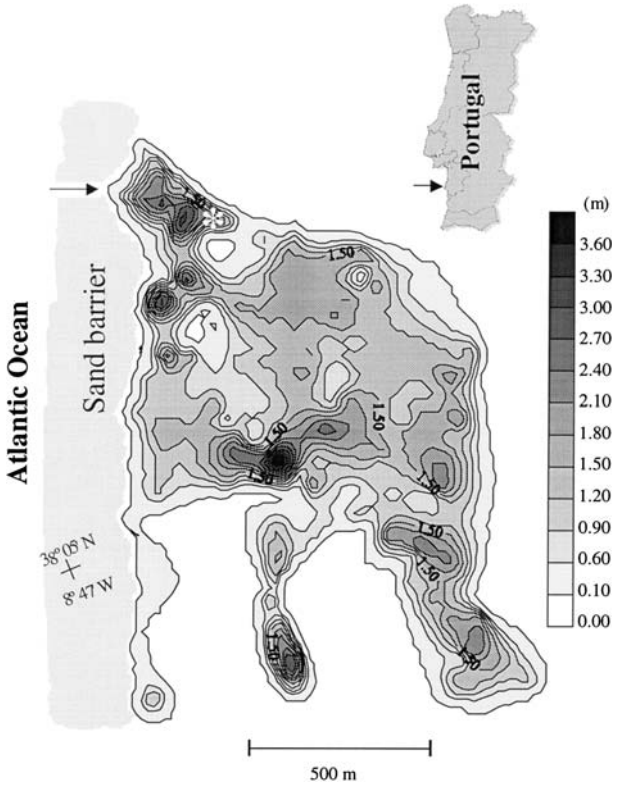

Figure 2. Santo André Lagoon bathymetry. The white asterisk marks the position of the sampling station. The arrow on the upper left corner shows the place where the artificial channel is opened between the Lagoon and the sea (see text).

where:
$P(I)$ – Light limited photosynthetic rate;
I – Irradiance (μmol quanta $m^{-2}\,s^{-1}$);
a, b and c – Adjustment parameters.

By differentiating this function, the parameters α (initial slope), P_{max} (light saturated photosynthesis) and I_{opt} (optimal irradiance) can be expressed as a function of a, b, and c:

$$\alpha = \frac{1}{c}\left[\mathrm{mgC(mgChl}a)^{-1}\,\mathrm{h}^{-1}\,\mu\mathrm{mol\,quanta}^{-1}\,\mathrm{m}^2\,\mathrm{s}\right] \quad (2)$$

$$I_{opt} = \sqrt{\frac{c}{a}}\left[\mu\mathrm{mol\ quanta\ m}^{-2}\,\mathrm{s}^{-1}\right] \quad (3)$$

$$P_{max} = \frac{1}{b + 2\sqrt{ac}}\left[\mathrm{mg\,C(mg\,Chl}\,a)^{-1}\,\mathrm{h}^{-1}\right] \quad (4)$$

A variant of this model combined with an Arrhenius temperature limitation function was also used following Duarte (1995):

$$P(I,t) = \frac{I.\exp(d-(e/t))}{aI^2 + bI + c}\left[\mathrm{mg\,C(mg\,Chl}\,a)^{-1}\,\mathrm{h}^{-1}\right] \quad (5)$$

Where, $P(I,\ t)$ is Light and temperature limited photosynthetic rate; d and e are parameters of the Arrhenius function; and t is Temperature (°C).

A simplification of this model was made in order to reduce the number of parameters to be estimated, by dividing both the numerator and the denominator by exp(d) (Macedo et al., 2001):

$$P(I,t) = \frac{I.\exp(-e/t)}{a'I^2 + b'I + c'} \quad (6)$$

Again, by differentiating this function, the parameters α, P_{max} and I_{opt} can be expressed as a function of a, b, and c. The solution for I_{opt} is as shown before (Eq. (3)) and the solutions for the former two parameters are shown below (Duarte, 1995):

$$\alpha = \frac{\exp(-e/t)}{c} \quad (7)$$

$$P_{max} = \frac{\exp(-e/t)}{b + 2\sqrt{ac}} \quad (8)$$

Thirteen P–I curves were fitted with Eq. (1) (one for each sampling campaign), using the Quasi-Newton non-linear least-squares regression technique (Statistica software). For some campaigns it was possible to obtain a good fit with Eq. (6) as well (see below) (Macedo et al., 2001). Linear regressions (type II) between observed and predicted values were used to verify the fitting equation. For each curve, the slope of the regression line was checked for significant differences from one and the y-intercept was checked for significant differences from zero. The significance of these differences is an indication of a poor fit to observed data (Keller, 1989). Also, analysis of variance was used to test for the significance of the variance explained by the regression line. All statistical analyses were done for a 95% confidence level. P–I curves considered in this study were only those for which all tests confirmed the quality of the obtained fit.

Mathematical simulations

Daily average primary production was calculated for each of the sampling occasions using the above mathematical relationships (1 and 6) integrated over depth and over time with parameters described in Macedo et al. (2001), simulated light intensity data over a 24-h period, with the equations described in Brock (1981) and Portela & Neves (1994), and measured *in situ* temperature.

Macedo et al. (2001) were able to fit Eq. (1) to all obtained datasets (a different parameter set for each sampling occasion) and Eq. (6) only to those datasets (a common parameter set for a total of seven sampling occasions) where the dinoflagellate *Prorocentrum minimum* was the dominant species (> 54% cell abundance). Using Eq. (1) or Eq. (6) for those periods of *P. minimum* dominance should yield similar results, whereas the opposite is true for the remaining periods (cf. – Results). Considering that phytoplankton species dominance shifted between diatoms and dinoflagellates, calculating photosynthetic rates with both equations for all sampling occasions allows us to obtain estimates of expected photosynthetic rates in the case of diatom and dinoflagellate dominance with prevailing light and temperature conditions. Since diatom dominance coincided with higher diversities, comparing obtained results may give some insight into the relationship between diversity and production.

Results

Chl *a* data for St. André lagoon is shown in Figure 3, for years 1984, 1985 (January–December), 1986 (January–May), 1998 and 1999 (January). Phytoplankton cell counts (Figure 3) were directly correlated with Chl *a* ($p < 0.05$).

The results presented in Figure 4 show that during the January 98–January 99 period, lowest phytoplankton diversity was observed in winter, whereas higher values were observed in spring or late summer. Although the correlation between Chl *a* and diversity was not significant ($p > 0.05$), it is apparent that minimum diversity corresponds to some of the highest Chl *a* values, whereas the opposite is true for maximum diversity results (Figs. 3, 4).

In Figure 5, the percentage of different phytoplankton groups over the sampling period is shown. Dinoflagellates and diatoms were the dominant groups. Lower diversities coincided with periods of dinoflagellate dominance, whereas higher diversities coincided with periods of diatom dominance. Dinoflagellate proportion, after the arc sin transformation (Underwood, 1981), is negatively correlated with diversity ($p < 0.05$). A total of 19 taxa were identified among diatoms, dinoflagellates and euglenophyceans, the less abundant group (Macedo et al., 2001).

Temporal variability of P_{max} (Eq. (4), cf. – values reported in Table II of Macedo et al. (2001)) and maximal volume integrated production (MaxProd) – the product of P_{max} and chlorophyll concentration – showed different patterns (Fig. 6). Both parameters exhibited a high variability. P_{max} showed higher values between May and August, with another maximum in October. Minimum values occurred in winter months. MaxProd reached maximum values in some winter months (February and March 1998 and January 1999). However, the lowest value occurred also in winter (January 1999). There is a negative correlation between P_{max} and Chl *a* concentration and the opposite between MaxProd and Chl *a* ($p < 0.05$). P_{max} is directly correlated solely with temperature. MaxProd is directly correlated with nitrogen and the proportion of dinoflagellates ($p < 0.05$). Highest P_{max} values coincided with some of the highest diversities (Figs. 4, 6). Cellular Chl *a*, obtained from the ratio Chl *a* /cell counts, and cellular P_{max}, obtained from the Production/Chl *a* cell counts ratio, are shown in Figure 7. There is a significant correlation between both variables ($p < 0.05$).

Temporal variability of α is shown in Figure 8. No significant correlation was found between the initial slope and any other parameter or variable, except a negative correlation with inorganic phosphorus ($p < 0.05$). However, peaks in α coincide with peaks in diversity (cf. Fig. 4).

Figure 9 depicts the parabolic relationship between diversity and MaxProd. A linear relationship results in a much lower R^2 – 0.436.

In Figure 10 a tree clustering, obtained from the Pearson correlation coefficient, displays two main groups of variables:

(i) An upper group with diversity, equitability, salinity, species richness, P_{max}, temperature, cellular P_{max}, cellular Chl *a*, diatom abundance and α, the initial slope of P–I curves, at a much larger linkage distance;
(ii) A lower group with Chl *a*, cell numbers, pH, MaxProd, the proportion of diatoms, dinoflagellate abundance, the proportion of dinoflagellates, inorganic nutrients and the ratio between nutrient and Chl *a* concentrations.

In Figure 11 the results of the mathematical simulations described above (cf. – Methodology – Mathematical simulations) are presented. The comparisons between both data sets by a one-way ANOVA did not reveal any significant differences ($p > 0.05$).

Discussion

Considering the high variability of Chl *a* data at temporal scales considerably smaller than the sampling intervals depicted in Figure 3, it is clear that the results available are insufficient to adequately describe Chl *a* dynamics. However, it is apparent that the 1998–1999 data are well within the ranges observed in previous works with maximum average Chl *a* concentration reaching ca. 60 mg m^{-3} (Cancela da Fonseca, 1989; Cancela da Fonseca et al., 1989; Bernardo, 1990). All data series show peaks in winter months. Data from 1984, 1985 and 1998 also present peaks in August or September. According to Bernardo (1990), higher Chl *a* concentrations are associated with

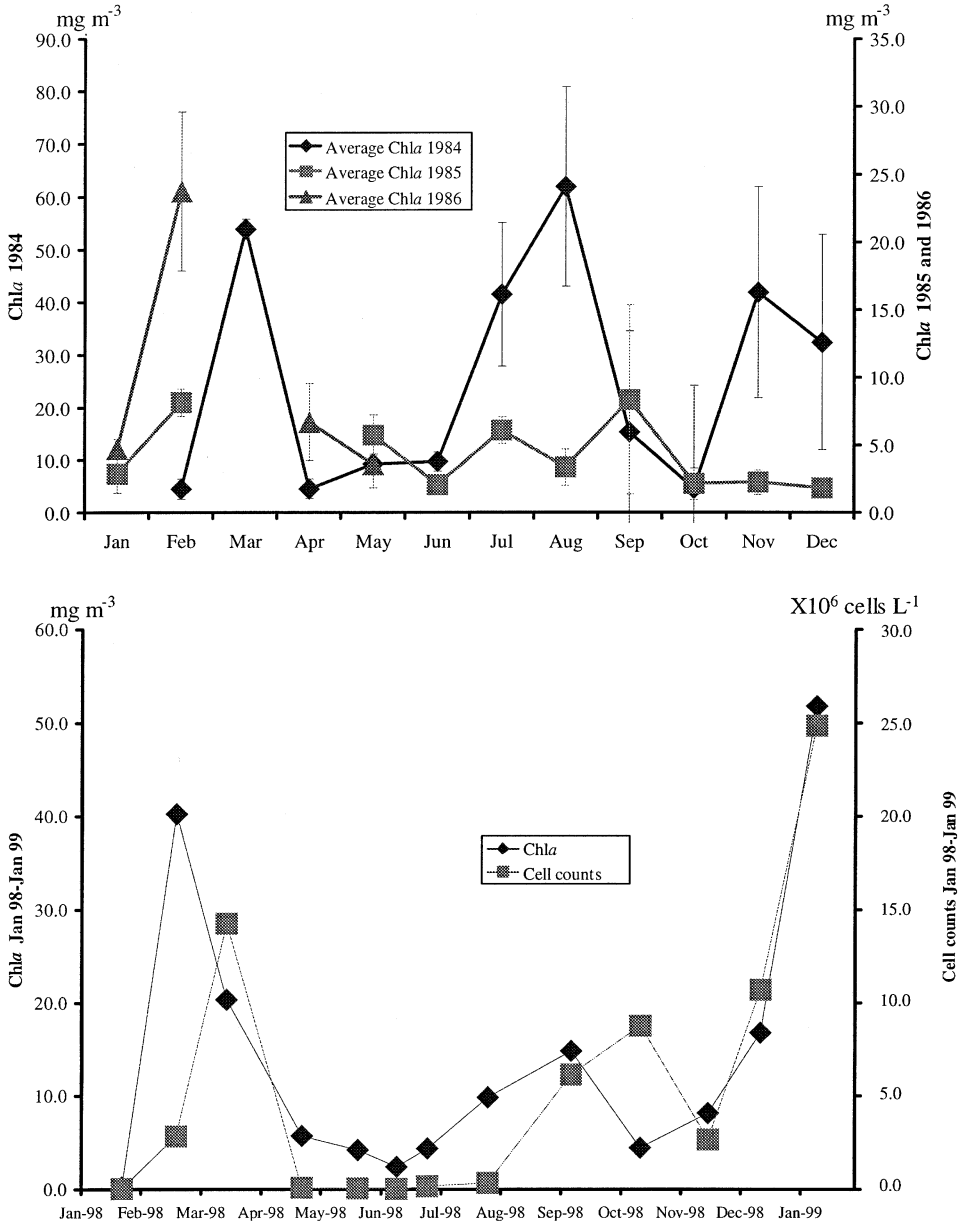

Figure 3. Chl *a* concentrations from several sampling campaigns in St. André lagoon. Data from 1984, 1985 and 1986 was taken from Cancela da Fonseca (1989), Cancela da Fonseca et al. (1989) and Bernardo (1990). Data from 1998–1999 was taken from Macedo et al. (2001). For the period 1998–1999 phytoplankton cell counts are also shown. The values for the period 1984–1986 were based on ca. 17 sampling points over the whole lagoon (also shown the 95% confidence limits). 1998–1999 data was from one sampling location (cf. – Fig. 2).

high nutrient inputs by runoff in winter months and internal nutrient recycling in summer months.

There is a relatively scarcity of data on phytoplankton species richness. In most studies only major taxonomic groups are listed, or proportions of dominant species given. Considering the number of phytoplankton species listed for some coastal ecosystems; e.g. the Rhode river estuary (Maryland, USA) (Gallegos, 1992), the Elbe (Germany), the Shelde (Belgium/The Netherlands) and the Girond (France) estuaries (Muylaert & Sabbe, 1999), the Pearl River estuary (China)

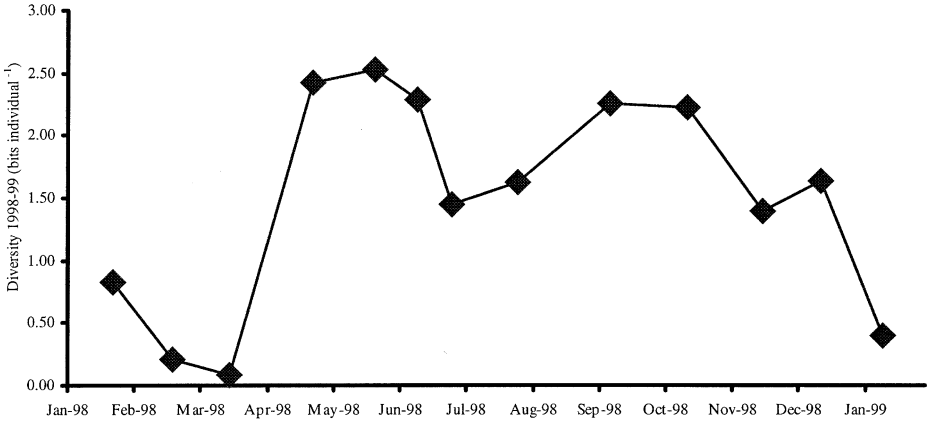

Figure 4. Diversity calculated by the Shannon–Wiener function.

(Huang et al., 2004) and the Bras de Port solar salterns in Santa Pola (Spain) (Estrada et al., 2004), species richness in Santo André lagoon (19 taxa identified) is comparable to the lower values reported – 29 species for the Girond estuary, 18 species for the Rhode river estuary and between 10 and 32 for the Bras de Port solar salterns. However, it is noteworthy that in all these studies the number of samples was much larger than in the present work. The low species richness in Santo André lagoon may partly be explained by the frequent overwhelming dominance of *Prorocentrum minimum* (up to $>90\%$ cell counts) (Macedo et al., 2001) and the alternating periods of low/high salinity (cf. – Methods, Study Area). If the Shannon diversity index is used for comparison, instead of species richness, the range reported in this study (0.08–2.53 bitts individual^{-1}) (Fig. 4)

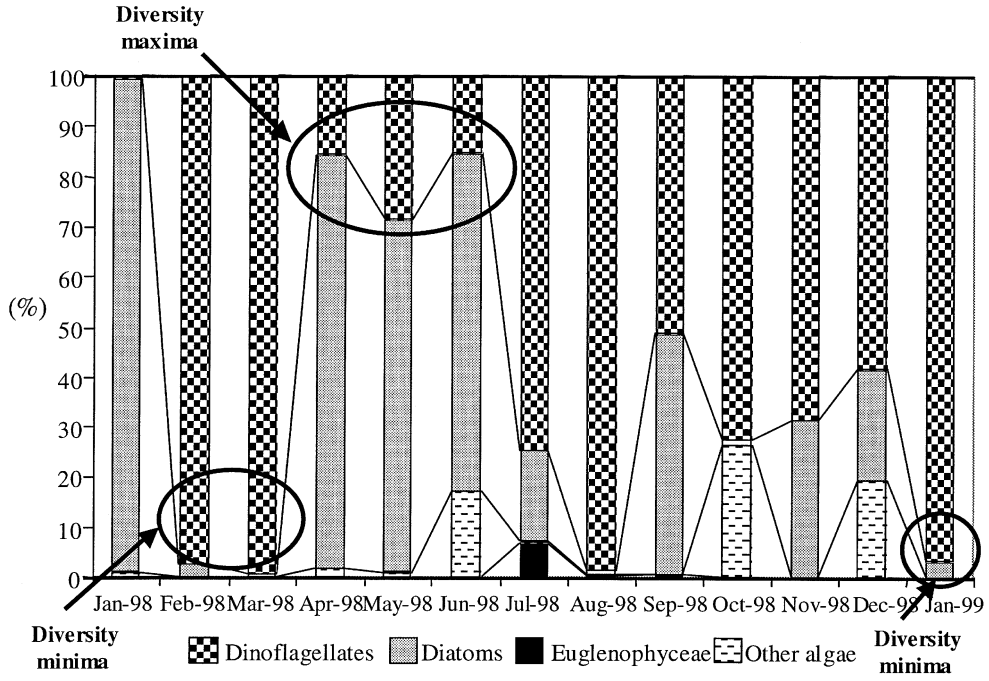

Figure 5. Percentage of phytoplankton groups over the period 1998–1999. Also shown minimum and maximum phytoplankton diversity periods (Adapted from Macedo et al., 2001).

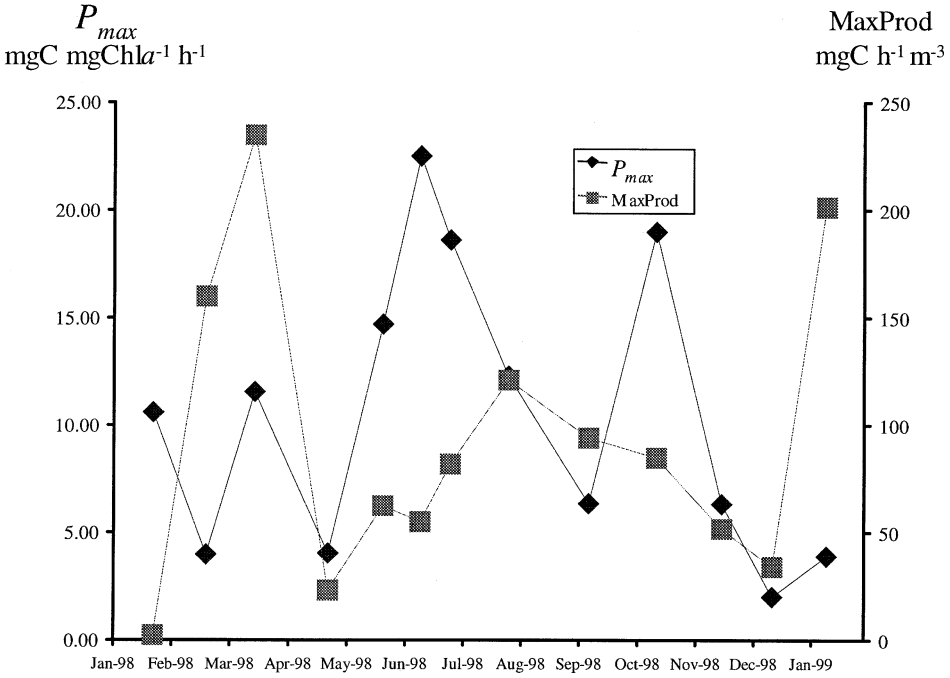

Figure 6. Light saturated photosynthesis (P_{max}) and maximal volume integrated production (MaxProd) (see text).

includes the range reported in Estrada et al. (2004) (0.5 – ca. 2.6 bitts individual^{-1}), the average value reported for the Pearl river estuary (2.47 bitts individual^{-1}) (Huang et al., 2004) and the value reported for the Sado estuary (Portugal) by Peneda et al. (1980) – 1.1 bitts individual^{-1}.

The two groups depicted in Figure 10 (cf. – Results) suggest that higher photosynthetic rates

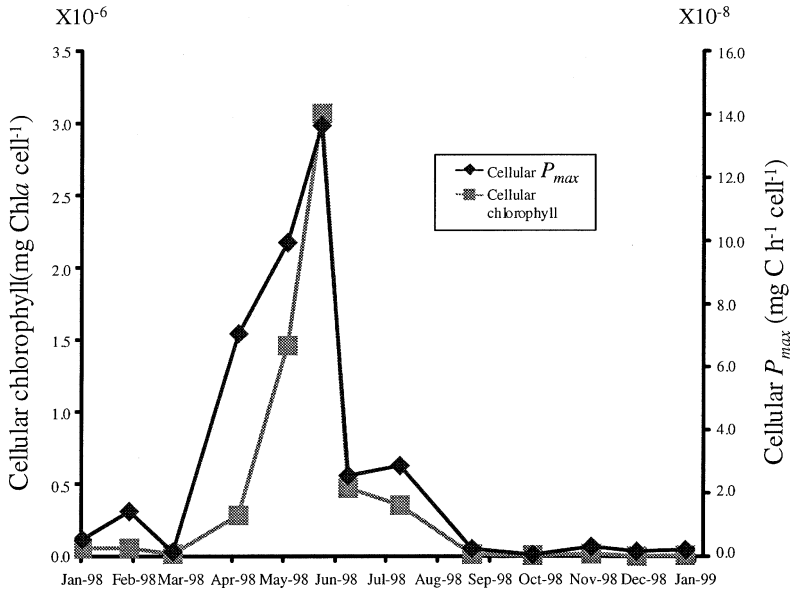

Figure 7. Cellular light saturated photosynthesis (P_{max}) and cellular Chl *a* contents (see text).

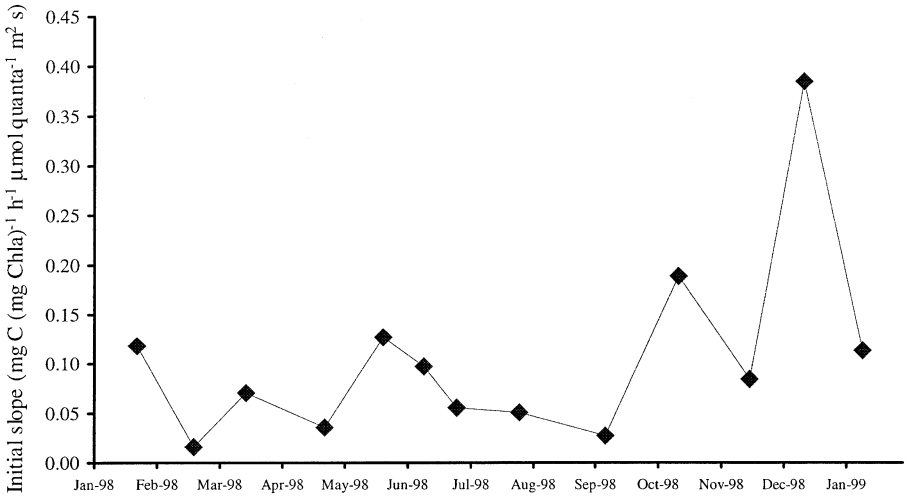

Figure 8. Initial slope (α) of the P–I curves for the study period (see text).

are associated with lower nutrient concentrations and higher temperatures, whereas higher MaxProd values are associated with higher nutrient loads and higher nutrient/Chl *a* ratios. From these results, it is apparent that higher $P_{\max}$ values are not related to release from nutrient limitation. In this work only nitrogen and phosphorus were considered. However, it is expectable that in winter periods, when MaxProd is higher, runoff transports all potentially limiting nutrients to the lagoon. If this is the case, then higher $P_{\max}$ values may be explained mostly by temperature as suggested by the positive and significant correlation referred above (cf. – Results). This is an expected result since P_{max} is known to be a function of the enzymatic processes in photosynthesis and therefore it is temperature dependent (Eppley, 1972; Harrison & Platt, 1980; Davison, 1991). The negative correlation between $P_{\max}$ and Chl *a* concentration and the opposite between MaxProd and Chl *a* concentration ($p < 0.05$) are expected, since the former is calculated from a ratio where Chl *a* is the denominator and the latter is calculated from a product by Chl *a* (cf. – Results). Generally, when Chl *a* is higher, intra and interspecific competition for light and/or nutrients is more likely to occur

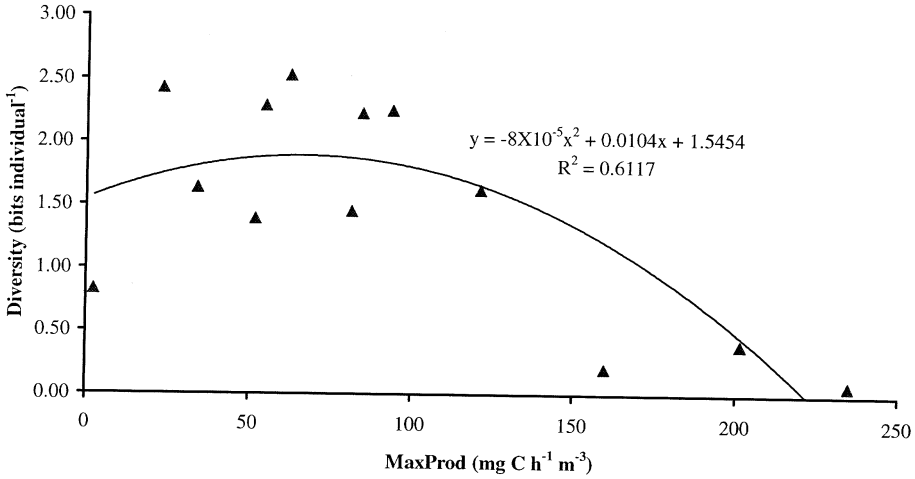

Figure 9. Diversity calculated by the Shannon-Wiener function as a function of maximal volume integrated production – MaxProd (see text).

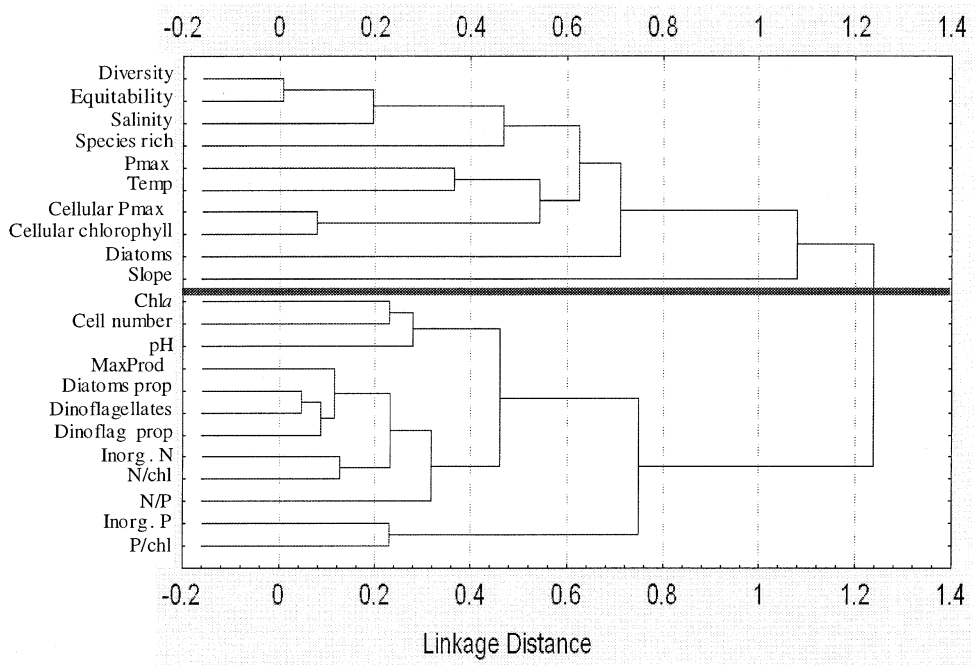

Figure 10. Cluster analysis using the Pearson correlation coefficient and the weighted pair-group average amalgamation scheme. The horizontal line separates two main groups of variables (see text).

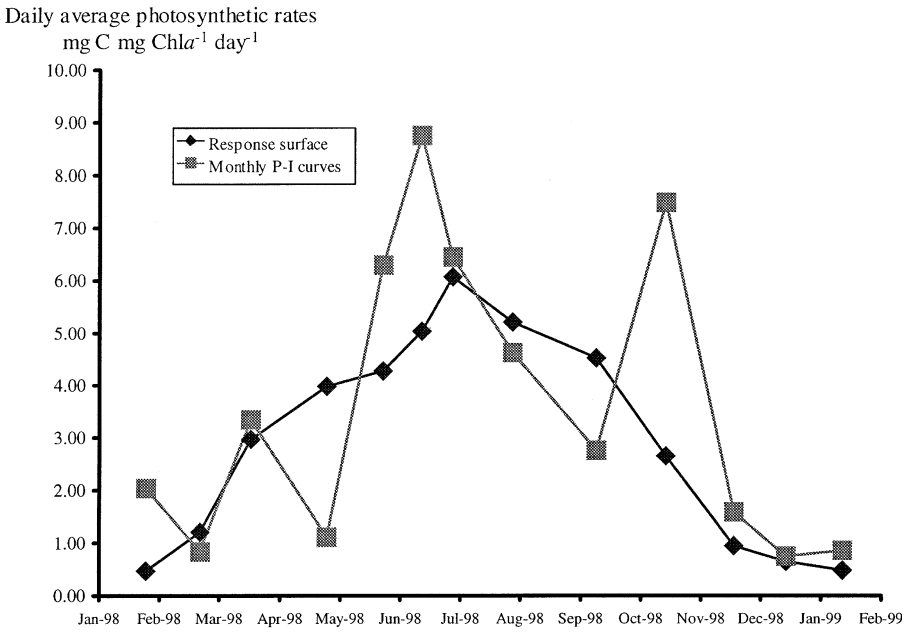

Figure 11. Daily average photosynthetic rates predicted with the P–I curves for each monthly phytoplankton sample, and with the surface response relating photosynthetic rates with irradiance and temperature, for those samples when *Prorocentrum minimum* abundance was larger than 54% of cell counts. The parameters of the P–I curves and of the response surface are described in Macedo et al. (2001) (see text).

reducing P_{max}. Further, low Chl *a* values and corresponding phytoplankton biomasses are not likely to result in high MaxProd, since this is a volume integrated value (cf. – Results).

The coincidence between diversity and α maxima (cf. – Results and Figs. 4, 8) and the fact that α is associated with higher P_{max} and diversity (cf. Results and Fig. 10), suggests that phytoplankton assemblages with higher diversity may also be more efficient at low light levels than lower diversity assemblages.

The absence of significant differences between the two simulated datasets in Figure 11 (cf. – Results) is not surprising because it is apparent that the curve based on the response surface smoothes out the larger variability of the curve calculated with monthly estimates of the photosynthetic parameters. Therefore, it is apparent that long-term (seasonal) average estimates of daily productivity are similar. However, short-term estimates may differ by more than 100%. This demonstrates the importance of having data on the temporal variability of the P–I curve parameters. P_{max} values estimated by the monthly P–I curves are much larger than maximum values obtained with the response surface obtained for the dinoflagellates, and occur in some of the higher diversity periods (Fig. 4). Therefore, it may be speculated that the observed differences were not due solely to temperature effects, already accounted for, but also to community diversity. If this is the case, then niche complementarity may be the explanation.

The results presented here on diversity and production are in contradiction to those of Hector et al. (1999) and Tilman et al. (2001), on grassland communities. Whilst these authors suggest that more diverse communities exhibit larger areal production, the results of this work reveal higher maximal volume integrated production under lower diversity. If niche complementarity is at work in St. André lagoon phytoplankton communities, its effect is reflected not on production but on photosynthetic rates. One might then ask the following question: ''Why more productive phytoplankton assemblages are low in diversity?''

The coexistence of several phytoplankton species under a few limiting resources has been known as the 'paradox of plankton'. It has been explained by the non-equilibrium nature of phytoplankton communities (Krebs, 1994). The model of Huisman et al. (1999) suggested that the coexistence of several phytoplankton species may be explained by the internal dynamics of competitive interactions, capable of generating chaos and opportunities for several species to coexist under a number of limiting resources lower than the number of competing species. According to these authors, if the number of limiting factors increases (different factors for different species), there is more room for more species to coexist. The recent modelling study of Yamamoto & Hatta (2004) provides theoretical evidence for the importance of pulsed nutrient supply in increasing phytoplankton diversity. These authors found that nutrient pulses with 'intermediate frequency' (corresponding to a period of 9 days) maximised the survival of modelled species, in line with the 'Intermediate Disturbance Hypothesis' (IDH) (Connell, 1978). These studies may help to justify the diversity of plankton communities, from internal dynamics and/or external forcing, but they do not explain why more diverse communities produce less biomass in spite of being more efficient.

In one of the rare works where phytoplankton diversity and production were analysed together, Agard et al. (1996) found empirical evidence to support Huston's dynamic equilibrium hypothesis (Huston, 1979, 1994) (cf. – Introduction) – species richness of Caribbean phytoplankton appeared to be maximized under intermediate conditions of disturbance and primary production. On one hand, low production reduces recovery from mortality and may therefore reduce species diversity. On the other hand, higher production may lead to lower diversity through competitive exclusion. The parabolic relationship between diversity and MaxProd obtained in the present work agree with those findings (Fig. 9).

Before trying to explain the observed patterns in Santo André lagoon it is important to recognize that comparing the low diverse and more productive winter phytoplankton assemblages with those observed in spring and summer in St. André lagoon is a bit like comparing two different ecosystems. In winter, the lagoon is predominantly fresh water, whereas in spring and summer the opposite is true. In winter, large nutrient inputs due to rainfall, may give opportunity for some species tolerant to low salinity to reach and

maintain high biomasses. Therefore, competitive exclusion is more likely to occur. Later in the year, the lower nutrient concentrations may limit biomass growth and production. Furthermore, the number of limiting nutrients is likely to increase, generating adequate conditions for the coexistence of more species, according to Huisman's hypothesis. In summer, when rainfall only rarely occurs, nutrient pulses are limited to phosphorus release from the sediments under episodes of bottom anoxia (Bernardo, 1990).

In terrestrial vegetation, although limiting nutrients may be less than coexisting species (Krebs, 1994), niche diversity may be larger, since soil heterogeneity and the plant canopy itself may provide more environmental diversity than the relatively homogeneous water column environments and therefore more opportunities for more species. This may help to explain the differences observed between terrestrial and pelagic ecosystems, concerning the relationship between diversity and production. In fact, similar differences for similar reasons are likely to occur between pelagic and some benthic ecosystems. Algal beds and reefs are generally associated with high diversity and their areal production is among the highest in marine environments (Fig. 1).

From the results discussed so far, the following conclusions may be drawn regarding the St. André lagoon phytoplankton communities:

(1) Phytoplankton communities with lower diversity are dominated by dinoflagellates, exhibit higher cell numbers, Chl *a* concentrations and production, in conjunction with higher nitrogen and phosphorus concentrations, than communities with higher diversity.
(2) The latter are dominated by diatoms, exhibit the highest photosynthetic rates and efficiencies, related with higher Chl *a* cell contents, water temperature, salinity, diversity, species richness and equitability.
(3) These highest photosynthetic rates are not correlated with either inorganic P or inorganic N. Temperature may explain part of the observed results as well as niche complementarity.
(4) Seasonal changes in photosynthetic parameters do not seem to have a major impact on community production averaged over large time scales, but have a major impact at daily time scales.

Furthermore, the following hypothesis may be defined:

(1) Higher nutrient loads in a relatively homogeneous water column may reduce the number of limiting nutrients increasing competitive pressure and leading to high dominance. Low nutrient loads are more likely to result in limitation by more nutrients.
(2) If different species are limited by two or three different nutrients (one per species) there should be more opportunity for more diversity to develop due to non-equilibrium oscillations within the community, following Huisman et al. (1999). More diverse communities are probably more efficient in utilizing irradiance energy due to niche complementarity.

These hypotheses may be tested by experimental designs similar to those employed in terrestrial ecology (Hector et al., 1999; Tilman et al., 2001). These designs imply measuring community production after the random addition of different species and have been criticised by Huston et al. (2000) among other things, due to the fact that random species addition does not mimic either natural or human-caused processes. Ideally, experiments should compare production and photosynthetic rates of different realistic species assemblages, with similar salinity and temperature tolerances, testing simultaneously for the effects of Chl *a* concentration, that is clearly related to photosynthetic rates (see above), and nutrient additions.

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