

Photosynthesis and community respiration at three depths during a period of stable phytoplankton stock in a eutrophic brackish water culture pond

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ABSTRACT: A 14 d period of dense but stable phytoplankton stock in a brackish water earthen pond (0.2 ha area, 0.7 m depth) was characterized to provide a baseline for study of instability. Results illustrate the potential of ponds to serve as microcosms of natural systems. Primary production and community respiration were assessed by diel curve analysis of oxygen and inorganic carbon sampled every 30 min at 3 depths. Neither stocks nor diel oxygen regimes were destabilized by 2 isolated days of low light, the first accompanied by heavy rainfall. Among nutrient elements, only inorganic nitrogen exhibited marginally limiting values. Daytime net production (dNPP) of oxygen ranged from 0 to $0.26 \text{ mol m}^{-2} \text{ d}^{-1}$, carbon uptake from 0.01 to $0.22 \text{ mol m}^{-2} \text{ d}^{-1}$. Nighttime respiration (nR) approximately matched dNPP, resulting in low mean diel net production (NPP). Minimal estimates of daytime respiration (dR) were substantially greater than nR and dNPP; minimal gross production ($\text{GPP} = \text{dR} + \text{dNPP}$) averaged 2.5 times dNPP. Estimated dR varied with dNPP in a stabilizing negative feedback, possibly mediated by photosynthetic products. Both dNPP and NPP varied with diel irradiance, but nR did not. Both dNPP and nR decreased with depth; positive NPP was concentrated in the upper layer. Stocks and oxygen cycles were more resistant to disturbance by low light than predicted by models assuming 1.0 m pond depth. We suggest for further examination that stability was related to the shallow depth of this pond, which permitted sufficient light penetration to the bottom layer for positive dNPP on most dates.

INTRODUCTION

Phytoplankton communities in earthen culture ponds are important to the success of culture endeavors (Colman & Edwards 1987, Smith & Piedrahita 1988, Boyd 1990). Stability in stock and metabolic activity levels of these communities is critical to maintenance of suitable environmental conditions for cultured animals because phytoplankton are the producers and significant consumers of dissolved oxygen. Pond ecosystems are also of more general interest because they can serve as microcosms of natural water bodies. In eutrophic ponds during warm seasons, water columns may encompass complete photic zones (i.e.

light extinction to less than 1 % of surface irradiance) and exhibit temperature structure similar to that of deep natural waters (Szyper & Lin 1990, Szyper et al. 1992).

Stability of pond stocks and diel oxygen regimes is desirable, but difficult to maintain in the face of environmental variation. As total organic inputs accumulate during a production cycle, phytoplankton concentrations generally increase, as does total organic load unless it is exported by respiration or otherwise controlled. This condition threatens stability beyond the point when standing stocks of phytoplankton and grazers face rate-saturating concentrations of their supporting substrates (nutrients and phytoplankton, respectively), and are unable to make stabilizing functional responses to management- or weather-mediated changes in these concentrations (Caperon et al. 1971, Houde & Schekter 1980). Because artificial control of

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stock levels (by water exchange, for example) is not always feasible during practical culture, preparations are typically made to respond to the consequences of collapsed stocks, for example by mechanical aeration to maintain oxygen concentrations during microbial decomposition of the biomass.

Such destabilization events, colloquially termed 'crashes', continue to disrupt practical culture as well as lake management, despite the existence of comprehensive general models of phytoplankton growth (e.g. Laws et al. 1985). The crash phenomenon has been described repeatedly, but without consistent interpretation (Abeliovich 1967, Barica 1975, Seymour 1980, Motzkin et al. 1982, Boyd 1990, Erez et al. 1990). Modeling and experimentation specific to pond communities have elucidated factors in production (Murphy 1962, Romaine & Boyd 1979, Laws & Malecha 1981, Grobbelaar 1989), but have less frequently addressed the question of stability directly (Krom et al. 1989, Piedrahita 1990, 1991, Szyper et al. 1991).

The interaction among water depth, light penetration, and turbulent mixing is important to the productivity of natural systems (Falkowski 1984, Ferris & Christian 1991, Prezelin et al. 1991), and appears increasingly to be a key to understanding stability of phytoplankton stocks and oxygen regimes in ponds. Theoretical treatments (Murphy 1962, Grobbelaar 1989) indicate that, given nonlimiting nutrients, ponds should be as shallow as possible for their purpose if net primary production is to be optimized. A simulation model incorporating the depth-light interaction found rapid depth reduction to be the most effective practical management action when days of low light threaten to destabilize diel oxygen cycles (Piedrahita 1991). Controlled comparisons of production in ponds of different depths support the theoretical advantage of shallow depth under conditions of high turbidity (Szyper et al. 1991, Szyper & Hopkins 1993).

In this paper, we approach the problem of instability by characterizing pond conditions and community metabolism during a period of stable phytoplankton stock, with attention to light penetration, mixing conditions, and the applicability of ponds as microcosms. From 2 years' records from an automated monitoring system, we have selected a 14 d period of dense (constant Secchi disc depth of 20 cm) but stable stock in a brackish water earthen shrimp production pond. This Secchi depth represents the typically-recommended lower (maximum stock) limit for pond water turbidity consisting primarily of phytoplankton (Boyd 1990). The period included 2 isolated days of low solar irradiance; observations included diel cycles of dissolved oxygen and inorganic carbon at 3 depths; the pond was maintained at the relatively shallow depth of 0.7 m to conserve the facility's limited water supply.

MATERIALS AND METHODS

The 14 d period (September 30 to October 13, 1989) ended the third month of a growout cycle for the commercial shrimp *Penaeus stylirostris*, in an earthen pond of 0.2 ha area, maintained weekly to 0.7 m depth by addition of variable-salinity well water, at the University of Hawaii's Mariculture Research and Training Center on the island Oahu. Shrimp were stocked at 15 ind. m⁻², and fed daily with a custom formula, fishmeal-based feed at 4 % estimated body weight d⁻¹.

Properties of pond water were monitored by both manual and automated methods. Manual water samples were taken daily from a single pond location with a depth-integrating sampler, filtered through glass-fiber filters within 30 min, stored frozen, and analyzed with an automatic analyzer for total ammonia, nitrate (on 4 of 14 dates), nitrite, orthophosphate, and silicate according to adaptations of the methods of Parsons et al. (1984). Similar weekly samples were analyzed for total alkalinity (American Public Health Association 1976) and for salinity by conductivity. Dissolved oxygen concentration (DO), pH, and temperature were measured every 30 min at 3 depths (10, 35, and 60 cm) at a single location (about 5 m from a pond corner) with an automated monitoring system similar to that described by Ebeling & Losordo (1989) and applied by Szyper & Lin (1990) and Green & Teichert-Coddington (1991). Pumps in the pond sequentially filled a plastic pipe receiver on the bank; sensors in the receiver recorded water properties in a data logger. Temperature was measured by thermocouple, pH by gel-filled combination electrode, and DO by polarographic probe. *In vivo* fluorescence was monitored by a flow-through fluorometer (Turner Designs model 10). Fluorescence was related to ambient concentration of chlorophyll *a* (chl *a*) through a series of filtered samples of different concentrations extracted and analyzed by fluorometry (Parsons et al. 1984). The total concentration of all forms of dissolved inorganic carbon (DIC), sometimes termed 'total CO₂', was calculated from pH data and bench analyses of total alkalinity, according to relationships given by Harvey (1966).

A weather station on the bank bordering the pond recorded air temperature, wind speed at 0.5 m above water level, rainfall, and solar irradiance (quantum flux at wavelengths 400 to 700 nm), as means for 30 min intervals.

Components of diel primary production and respiration cycles were calculated for each depth from diel patterns of DO and DIC concentrations according to an adaptation of the method of Hall & Moll (1975) described by Szyper et al. (1992). Observed net rates of change in DO or DIC during sampling intervals were

multiplied by durations of the intervals; these products were summed over appropriate periods. Corrections were made to interval net rates in the top layer for exchange of gases with the atmosphere according to Banks & Herrera (1977) for oxygen and to Weisburd & Laws (1990) for carbon dioxide, using wind speed data and the salinity-dependent saturation values given by Weiss (1970, 1974). The sum of net changes during daylight hours is termed daytime net primary production (dNPP); the sum for nighttime hours is termed night respiration (nR); the sum over 24 h is the total diel net production (NPP = dNPP - nR, taking all diel sums as positive, consistent with their interpretation as areas under curves). Minimal estimates of daytime respiration (dR) were made as described by Hall & Moll (1975) and illustrated under 'Results' below; the morning and evening time end points for this estimate defined the limits of day and night for summations. Minimal estimates of gross production (GPP) were made as $GPP = dNPP + dR$.

Depth-integrated areal rates of production and respiration were calculated by vertically partitioning the 0.7 m water column at midpoints between sampling depths. Statistical analyses were performed as described by Sokal & Rohlf (1981).

RESULTS

Weather conditions during the study period were relatively uniform, with the exceptions of one day of heavy rain, and a variable light regime related to cloud cover (Table 1). Diel mean temperatures ranged from 23.6 to 27.6 °C; wind speeds were light-moderate, with diel means between 0.4 and 1.6 m s⁻¹. Three of 14 days were without recorded rainfall; no other date received more than 2.1 cm except one date with 8.2 cm. Daily quantum flux ranged from 3.4 to 38.7 mol m⁻² d⁻¹; only the day of heavy rain and one other showed less than 19.2 mol m⁻² d⁻¹.

Properties of the pond water similarly exhibited moderate variation (Table 1). Salinity ranged from 13 to 25 ppt, but was nearly constant at 13 to 15 ppt for the last two-thirds of the period. The salinity decrease early in the period is not accounted for by measured rainfall, but moderately heavy rain runs off as sheet wash on this facility, further diluting ponds. Total alkalinity ranged from 83 to 99 mg l⁻¹ as CaCO₃; total ammonia, nitrate, nitrite, and orthophosphate from 0 to 1.3 μmol l⁻¹; and silicate from 60 to 118 μmol l⁻¹.

Phytoplankton standing stock was indexed by *in vivo* fluorescence and by Secchi disc depth (Table 1). The stock was dominated by coccoid cyanobacteria for which confirmed identification could not be made. Both indices documented dense stocks. Secchi disc

Table 1. Weather conditions, concentrations of dissolved materials in pond water, and indices of phytoplankton standing stock during the study period

Measurement	Date 1989:	30 Sep	273	274	275	276	277	278	279	280	281	282	283	284	285	286	13 Oct
	Julian day:	273	274	275	276	277	278	279	280	281	282	283	284	285	286	287	288
Air temperature (°C)	25.6	24.7	25.8	23.6	26.4	25.2	24.5	24.6	25.1	27.6	27.0	25.6	25.3	26.0			
Wind speed at 0.5 m (m s ⁻¹)	1.6	1.3	1.2	1.3	1.6	1.2	1.0	1.2	1.1	1.4	1.5	0.4	0.4	1.1			
Rainfall (cm)	0.6	2.1	1.0	8.2	0.0	1.1	1.4	0.7	1.1	1.6	0.1	0.0	0.0	0.2			
Quantum flux (mol m ⁻² d ⁻¹)	35.9	22.5	38.7	6.2	35.2	23.5	19.2	25.3	35.3	24.3	3.4	30.8	30.0	25.2			
Salinity (ppt)	25	-	-	-	15	-	15	-	-	-	-	-	-	13			
Total alkalinity (mg l ⁻¹)	83	-	-	-	-	-	81	-	-	-	-	-	-	99			
Total ammonia (μmol l ⁻¹)	0.6	0.7	1.1	0.9	0.7	1.1	0.8	0.7	1.3	0.7	0.4	0.4	0.3	0.3			
Nitrite (μmol l ⁻¹)	0.1	0.3	0.1	0.1	0.1	0.1	0.0	0.0	0.1	0.7	0.1	0.1	0.2	0.1			
Nitrate (μmol l ⁻¹)	-	-	0.0	-	-	0.0	-	-	-	-	0.2	0.3	0.3	-			
Orthophosphate (μmol l ⁻¹)	-	0.3	0.1	0.3	0.2	0.1	0.1	0.1	0.1	0.1	0.4	0.1	0.3	0.3			
Silicate (μmol l ⁻¹)	106	118	71	66	67	66	60	68	72	63	103	102	108	107			
Secchi disc depth (cm)	-	-	-	20	20	-	20	-	-	-	-	-	20	20			
Fluorescence (mV)	2459	2464	2508	2364	2376	2422	2343	2378	2375	- ^a							

^a No data for Days 282 to 286. Fluorescence = 2414 mV on Day 287

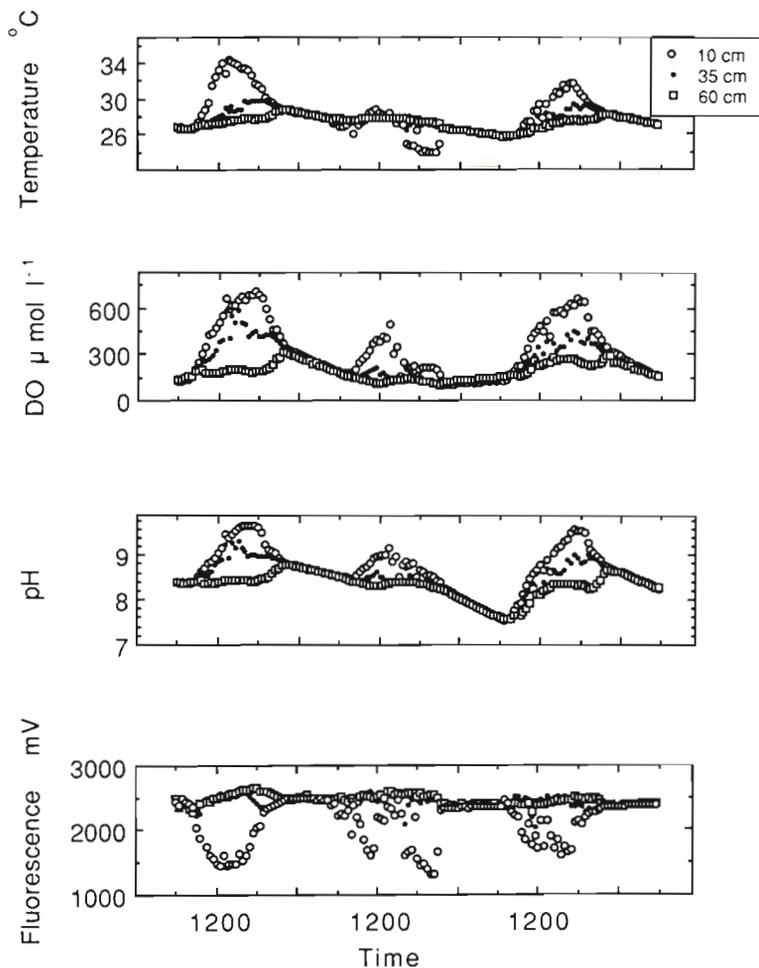


Fig. 1. Diel cycles of temperature, dissolved oxygen concentration (DO), pH, and *in vivo* fluorescence on the third, fourth, and fifth days (Julian Days 275, 276, 277) of the 14 d study period, at 3 depths

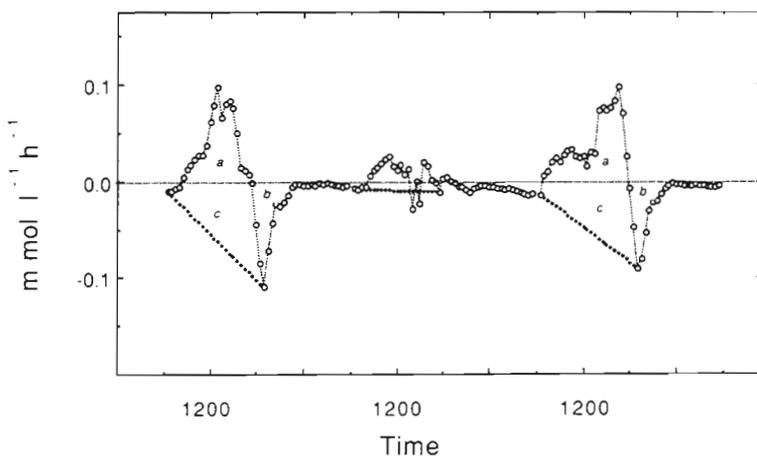


Fig. 2. Diel cycles of rates of change in dissolved organic carbon in the upper water layer on the third, fourth, and fifth days (Julian Days 275, 276, 277) of the 14 d study period. Daytime net primary production is represented by the areas marked 'a', nighttime community respiration by areas 'b', and daytime community respiration by areas 'c'

depth was measured at 20 cm on 6 dates within the period, and was identical the day before the period began; the relationship presented by Almazan & Boyd (1978) predicts a concentration of $460 \mu\text{g l}^{-1}$ chl *a* from 20 cm depth, though high variation is associated with estimates at such small depth values. Fluorescence at 24:00 h (the time chosen to avoid the light-related cycles shown below) varied by less than 10 % during the period. The mean instrument signal of 2410 mV corresponded to an ambient concentration of $402 \mu\text{g chl a l}^{-1}$.

Temperature, DO, pH, and *in vivo* fluorescence exhibited diel cycles that varied with depth as shown in Fig. 1, which includes a cloudy day of rain as the second day of three shown.

Density stratification developed under solar heating during most days, as indicated by the pronounced diel variation in temperature, DO, and pH in the surface layer on the first and third days, in contrast to the relative uniformity and lack of diel pattern in the deepest layer. The temperature plot shows that during the rainy day, fresher surface water was cooler than deeper saline water for several hours; unusual mixing patterns are indicated for this date by the irregular fluorescence trace, which suggests that cells were mixed through different light levels. On all dates, nighttime values of all parameters became uniform with depth following convective mixing during hours following sunset. Pronounced diel fluctuations in fluorescence were seen only in near-surface water; little diel variation is evident even at the middle sampling depth of 35 cm.

Estimation of primary production and community respiration from diel curves of net rates of change is illustrated for surface-layer dissolved inorganic carbon in Fig. 2. Curves pertinent to other depths, and to oxygen, were analyzed similarly. The areas between the horizontal axis and the daytime positive carbon uptake rates (marked 'a' in the figure) represent daytime net primary production (dNPP). The second date shows positive dNPP but is not marked. Negative rates indicate net respiratory release of carbon dioxide to the water; areas between nighttime rates

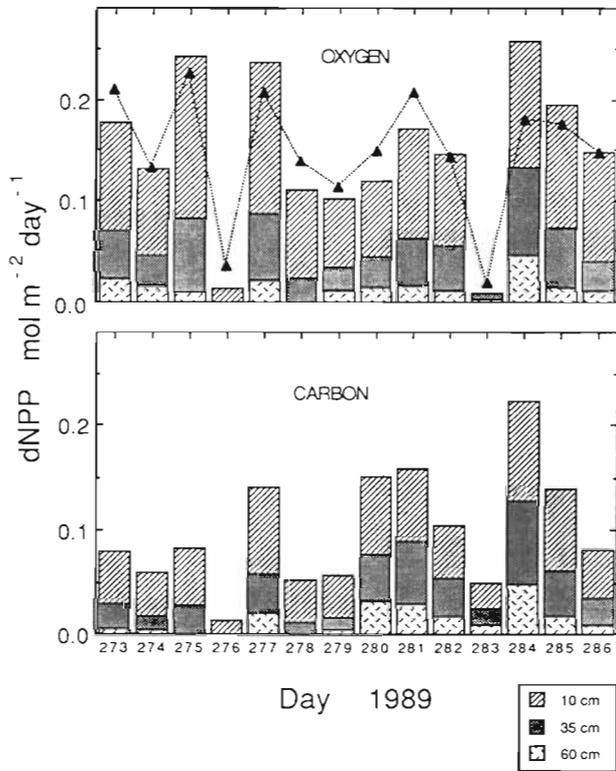


Fig. 3. Daytime net primary production (dNPP) in terms of dissolved oxygen and dissolved inorganic carbon in 3 depth layers during the 14 d study period. The oxygen (upper) plot also shows relative values of daily irradiance on each date (▲)

and the axis ('b') represent nighttime community respiration (nR). Large interval rates of community respiration were evident at dusk, as photosynthesis diminished rapidly with failing light, revealing net rates of change representing respiration (and mixing effects discussed below). These rates diminished (in absolute value) to near zero by midnight, and remained small until dawn. The lines drawn below the daytime rate points, connecting the pre-dawn with post-dusk respiration rates, represent the interpolation recommended by Hall & Moll (1975) for estimating daytime community respiration (dR) as the areas marked 'c'. Gross primary production (GPP) is estimated by addition of the areas of dNPP and dR, i.e. of areas 'a' and 'c'; total diel net production (NPP) is the sum of interval rates through 24 h, which is equivalent to the difference (in absolute value) of areas 'a' - 'b'.

Daytime net primary production of oxygen (Fig. 3) ranged from near 0 to 0.26 mol m⁻² d⁻¹, and followed the temporal pattern of total diel irradiance throughout the study period. The temporal pattern for carbon was similar to that of oxygen, but the correspondence with light was less precise. Water column total dNPP was correlated with irradiance at $r = 0.926$ ($p < 0.01$, $n = 14$) for oxygen and 0.604 ($0.01 < p < 0.05$) for carbon. These relationships showed no evidence of light-saturation.

The distribution of dNPP with depth (Table 2) decreased with light penetration as approximated from

Table 2. Depth distributions of daytime net primary production (dNPP) and nighttime respiration (nR) in the 70 cm water column of the pond with 20 cm Secchi depth. 'Integration limits' are the limits of the depth ranges to which measurements from each sampling depth are applied. The estimated light penetration is derived from the constant Secchi depth of 20 cm according to Poole & Atkins (1929)

Depth (cm)	Function	% of water depth represented	Approx. % surface light penetration	% light absorbed in layer above	% of dNPP		% of nR	
					Oxygen	Carbon	Oxygen	Carbon
0	Integration limit, TOP	-	100	-	-	-	-	-
10.0	Sampling, TOP	32.1	43	57.3	63.8	55.1	54.8	45.4
22.5	Integration limit, TOP/MIDDLE	-	15	-	-	-	-	-
35.0	Sampling, MIDDLE	35.7	5	37.6	26.9	30.9	34.2	38.0
47.5	Integration limit, MIDDLE/BOTTOM	-	2	-	-	-	-	-
60.0	Sampling, BOTTOM	32.1	0.6	4.5	9.3	14.1	11.0	16.7
70.0	Integration limit, BOTTOM	-	0.3	-	-	-	-	-

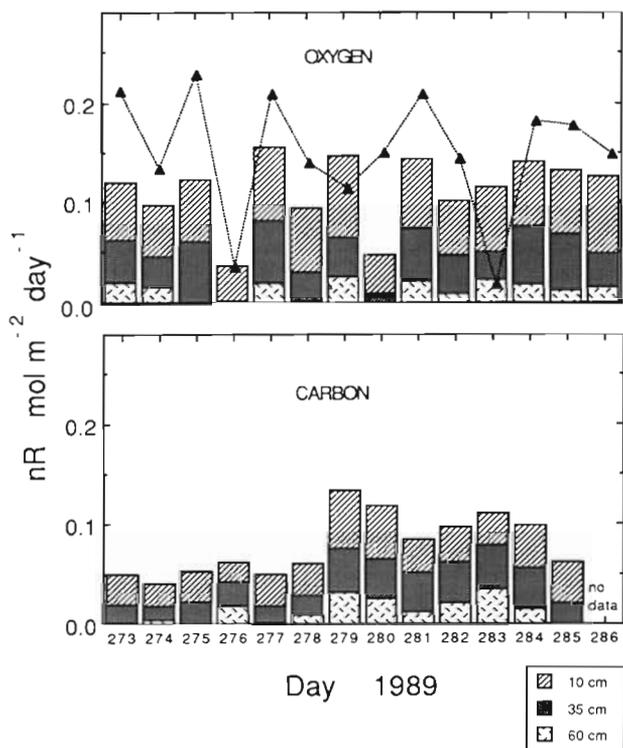


Fig. 4. Nighttime community respiration (nR) in terms of dissolved oxygen and dissolved inorganic carbon in 3 depth layers during the 14 d study period. The oxygen (upper) plot also shows relative values of daily irradiance on each date (\blacktriangle)

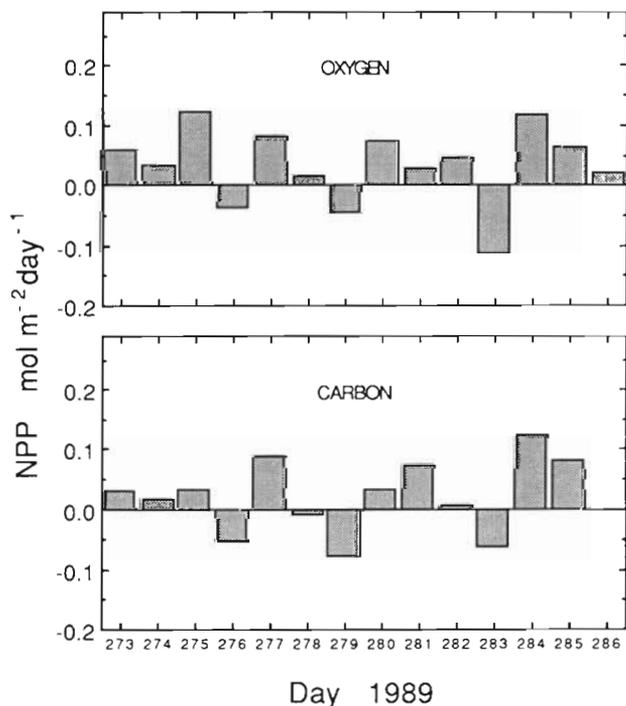


Fig. 5. Total diel net primary production (NPP) in terms of dissolved oxygen and dissolved inorganic carbon in the entire water column during the 14 d study period

the Secchi depth according to Poole & Atkins (1929). The bottom layer showed a substantial average contribution to water-column dNPP despite severe attenuation of light, with positive values of dNPP for oxygen on 12 of 14 dates, and for carbon on 11 of 14 dates.

The temporal pattern of nighttime respiration (nR) did not closely follow the daily irradiance levels (Fig. 4), in contrast to the pattern of dNPP. Mean nR values of 0.112 and 0.078 mol m⁻² d⁻¹ amounted to 78 and 79 % of dNPP for oxygen and carbon, respectively. The average depth distribution was similar to that of dNPP (Table 2).

Total diel net production, NPP (= dNPP - nR), for the water column averaged slightly more than 20 % of dNPP, and exhibited negative daily values more frequently (Fig. 5). NPP was, like dNPP, positively correlated with irradiance, showing coefficients $r = 0.858$ and 0.770 ($p < 0.01$ for both) for oxygen and carbon, respectively. In contrast to the depth patterns of dNPP and nR, however, positive NPP was more stringently confined to the top layer, where the mean values for oxygen and carbon constituted 94.6 % and 87.5 % of the water-column totals, i.e. mean NPP was near zero in the middle and bottom layers.

Daytime respiration (dR) was generally much greater than nR (Fig. 2), with mean values about twice those of nR for both oxygen and carbon. Thus GPP (= dNPP + nR) averaged about 2.5 times the mean values of dNPP, ranging from 0.15 to 0.59 mol m⁻² d⁻¹ for oxygen and from 0.06 to 0.34 mol m⁻² d⁻¹ for carbon. Because these dR estimates are almost certainly significant underestimates (Szyper et al. 1992), temporal and vertical patterns of dR and GPP will not be detailed.

DISCUSSION

Production estimates and diel curves

The areal production estimates presented here are within reported ranges for fertile lakes and freshwater and marine ponds (Table 3). Our diel GPP estimates exhibit a range and maximum similar to those seen by Hephner (1962) in freshwater ponds of similar depth, and by others under different conditions. However, much greater areal rates are possible, as the table also shows. Differences among methods are unlikely to account for the large differences among maximum rates. Neither do the estimated maximum P:B ratios tabulated here vary with maximum areal production. Only the maximum rates observed by Robarts & Zohary (1992) are near theoretical maxima derived by consideration of Bannister's (1974, 1979) model (Laws & Malecha 1981, Baumert & Uhlmann 1983). Both the data of Robarts & Zohary (1992) and the theoretical

Table 3. Areal production rates and maximum P:B ratios in selected fertile environments, designated salt water (SW), brackish water (BW), or fresh water (FW). Original element and rate units reflect methods used by authors; some rates were converted to standardized units and P:B by original authors, others by the authors of this paper, with PQ values from Laws (1991). Maximum P:B ratios are usually not 'assimilation numbers' because light saturation was not assessed. 'N/A' indicates no data available

Source	Environment	Depth (m)	Method	Original element	Original rate unit	Standardized daily C rate (g C m ⁻² d ⁻¹)	Maximum P:B (mg C mg ⁻¹ chl h ⁻¹)
This study	BW shrimp pond	0.7	Diel curve	C	mol m ⁻² d ⁻¹	0.7–4.1	2.7
				O	mol m ⁻² d ⁻¹	1.3–6.5	2.3
Roberts & Zohary (1992)	FW reservoir	~30	¹⁴ C	C	mol m ⁻² h ⁻¹	0.3–30.9	15.9
Erez et al. (1990)	SW fish ponds	0.5	Diel curve	O	g m ⁻² d ⁻¹	5.0	20.4
Schanz & Dubinsky (1988)	FW sewage pond	0.3	Incubation	O	μmol mg Chl ⁻¹ min ⁻¹	~12	5.2
Olah et al. (1986)	FW fish ponds	1.6	Diel curve	O	g m ⁻² d ⁻¹	12.3	N/A
13 cited papers, 1956–1981		Various	Various	O, C	Various	0.1–19.6	N/A
Liang et al. (1981)	7 ponds & lakes	Various	L/D bottle	O	mg l ⁻¹ d ⁻¹	0.5–4.8	N/A
Almazan & Boyd (1978)	FW fish ponds	1	L/D bottle	O	g m ⁻² d ⁻¹	~1–4.5	~5–7
Hepher (1962)	FW fish ponds	0.7–0.9	L/D bottle	O	g m ⁻² h ⁻¹	3.3–6.4	11.5

curve presented by Laws & Malecha (1981) indicate that greater areal production is possible at the chlorophyll concentrations observed in this work.

Our maximum P:B ratios (Table 3) are the lowest we have seen among cases of high areal production, suggesting that the community was nutrient limited at some depths and times. Total inorganic nitrogen exhibited borderline limiting values. The sum of inorganic N concentrations (ammonia, nitrate, nitrite) in daily water-column samples was often less than the half-saturation constants for uptake rates of these materials given by Eppley et al. (1969). The sum was below 1.0 μM on several dates, and may well have been materially lower during daylight in the thermally isolated surface layer. Nearly all available light was absorbed in the water column. Mindful of Preisendorfer's (1986) cautions on use of Secchi depth, we estimated light penetration in Table 2 only to illustrate the extreme conditions of a fertile pond.

Analysis of production in 3 depth layers by means of diel curves is as yet uncommon and presents new problems, though multiple depth analysis was common practice with bottle methods. Of the several advantages of diel curve methods (Hepher 1962, Olah et al. 1978), the most important here is the ability to account for exchange of gases with the atmosphere. The diffusion corrections typically amounted to about 40 % of dNPP with oxygen, and about 30 % with carbon; their importance was much greater (71 to 640 % of dNPP) on the days of low light. We applied atmospheric diffusion corrections only to the surface layer because surface layer concentrations of DO and DIC best characterized the water exposed to the air. This choice affects the distribution of rate estimates among the layers, but does not affect total areal estimates.

Although the likely accuracy of the areal estimates made here is good, the apparent relative contributions of the depth layers to rate processes (Figs. 3 & 4, Table 2) were potentially affected by diffusion of materials among the layers. The irregularity of the diel curves in the middle layer (Fig. 1) suggests weak mixing at some depths during daytime. However, the near-total confinement of NPP to the surface layer weighs against substantial daytime transport of DO to deeper layers by turbulent diffusion. During convective overturn each evening, small but detectable amounts of oxygen were transferred downward (e.g. at about 18:00 h on the first and third days shown in Fig. 1). Consequently, the decrease in surface layer DO is partly due to mixing with deeper water of lesser DO content, and not entirely attributable to surface community respiration. Again, this factor has no effect on total areal

estimates. The similarity in depth distributions of dNPP and nR (Table 2) suggests that mixing effects were relatively small during this period. Three sampling depths represent the minimum number permitting reasonable vertical integration for areal estimates.

Frequent sampling is required to resolve the typical features of diel curves (Fig. 2). Olah et al. (1978) pointed out that 3-point free-water methods (McConnell 1962) miss these features but that 7 sampling times per day made great improvement. More frequent sampling (at least 48 times d^{-1} as done here) is necessary for examination of processes in detail because phytoplankton respond and adapt to environmental changes on relatively short time scales (Ferris & Christian 1991), as illustrated by the diel cycles of fluorescence (Fig. 1). The cycles in the surface layer are expected (Kiefer 1973), but it is noteworthy that such cycles were not observed at middle and bottom depths. This shows the potential to assess diel light adaptation of parts of pond communities isolated at different depths by stratification. The presentation by Szyper et al. (1992) of a photosynthesis-irradiance curve for a pond community responding to the diel light cycle further illustrates ponds' potential as microcosms of natural systems.

Stability

The most remarkable conditions recorded during this study were the stability of the large phytoplankton stock and of the diel oxygen cycles themselves. This stability implies that photosynthetic production was balanced by the aggregate effect of loss factors (respiration, grazing, sedimentation). Although community respiration was the only loss factor assessed directly, it reflects the metabolic activity of grazers and of microbes decomposing sedimented material. The small mean values of total diel NPP (= GPP - dR - nR) for both carbon and oxygen, and their fluctuation between positive and negative daily values (Fig. 5), suggest that community respiration reasonably represents aggregate loss factors and accounts for the observed nearly-steady state. Water-column budgets of both oxygen and inorganic carbon have been used to characterize the net productivity of oceanic regions (Codispoti et al. 1982, Platt et al. 1989, Karl & Hebel 1990).

Environmental conditions were generally favorable for phytoplankton growth and production, but there were compromises to ideal conditions which failed to destabilize this stock. Alkalinity was sufficient at all times (Table 1) to ensure nonlimiting concentrations of DIC (Boyd 1976, Caperon & Smith 1978); wind speeds

were low to moderate, with no significant mixing of sediments into the water column; rainfall, though recorded on 11 of 14 dates, was light on all but 1 date.

Incipient nitrogen limitation, discussed above, was an unrealized potential source of destabilization. It should be noted, however, that concentrations alone are insufficient evidence of limitation in fed or fertilized ponds, because the typical accumulations of organic matter support active remineralization cycles.

The prime example of compromised conditions is provided by the 2 dates on which solar irradiance, and with it dNPP and NPP, fell to low values. In both cases, the following days showed reasonably high irradiance, and exhibited some of the highest values of dNPP and NPP; standing stocks (Secchi depth and *in vivo* fluorescence) were uncompromised. These separate single days of low light were insufficient to destabilize the phytoplankton stocks and diel oxygen regimes, despite that nR for both oxygen and carbon were of 'normal' magnitude during the preceding and following nights, resulting in lower early morning diel minimum oxygen concentrations after dark days.

In general dNPP and dR varied together, as illustrated in Fig. 2 by the low values of dR, dNPP, and irradiance on the second date (Table 1, Day 276). This compensating effect of lower dR on days of low light and production constitutes a negative feedback which favors stability of stocks and oxygen cycles. Szyper et al. (1992) observed that community dR in a dark incubation vessel varied with photosynthetic production, and showed low rates during most of the night as in Fig. 2. Laboratory studies of pure cultures have shown greater mitochondrial respiration in light-exposed cells than in darkened cells, and have suggested its association with anabolic processes or products (Bender et al. 1987, Grande et al. 1989, Weger et al. 1989).

The stock levels themselves were at the upper limit for prudent pond management (Boyd 1990). According to the empirical model presented by Romaine & Boyd (1979), had this Secchi depth been attained in a pond of 1 m depth, diel minimum DO should readily have fallen below $62.5 \mu\text{mol l}^{-1}$ (2.0 mg l^{-1}), and should have reached zero during the 2 periods of low irradiance, yet neither of these conditions was realized. Diel minima (1) never reached zero; (2) were below $31.2 \mu\text{mol l}^{-1}$ (1.0 mg l^{-1}) on only 2 of 14 dates (including the second day of low light but not the first); (3) were otherwise always greater than $62.5 \mu\text{mol l}^{-1}$ (2.0 mg l^{-1}); and (4) exceeded $100 \mu\text{mol l}^{-1}$ on the dates following the lowest excursions. Furthermore, diel minima varied far less with light than would be predicted by Meyer & Brune's (1982) sensitivity analysis of light effects in their model, which also presumed a greater depth. The observed resiliency of this shallow pond system compared with model predictions is consistent with

Piedrahita's (1991) simulations showing that reduced depth was effective in preserving diel oxygen cycles under reduced light.

We suggest that the shallow depth of the pond, and the light-penetration characteristics of its water column, permitted the system to withstand conditions that would have destabilized a deeper pond. More specifically, it may well have been critical that there was positive dNPP in the bottom layer on most dates, which implies by definition that GPP at the 60 cm sampling depth exceeded dR. It is clear that the bottom layer was usually aerobic and photosynthetically active, despite the possibility of 'contamination' of bottom DO levels from above.

The complete data set for the facility contains numerous records of destabilization (rapid increases in Secchi depth), whose severity ranges from catastrophic (very rarely) to scarcely detectable. Records of these events, however, are not useful for analysis of photosynthesis and respiration because most were anticipated or quickly attended by the pond managers with mechanical aeration to preserve the crops. Aeration homogenized the water columns, added unspecified amounts of oxygen to the water, and stabilized diel oxygen cycles though not always stock levels. New experiments will be required to observe community metabolism during destabilization.

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