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**VARIABILITY OF SURFACE PLANKTONIC COMMUNITY METABOLISM
IN RESPONSE TO COASTAL UPWELLING EVENTS
IN THE RIA DE VIGO (NW SPAIN).**

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Abstract

Measurements of microbial photosynthetic and respiration rates based on oxygen light:dark incubations were carried out twice weekly, from April to November 1991, at a fixed station in the Ria de Vigo (N.W. Spain). Wind driven upwelling events in the Ria sustained high but very variable chlorophyll a biomasses (mean: 6.0 ± 4.2 , range: $0.2-17.5 \mu\text{g l}^{-1}$), gross photosynthetic (GP) rates (mean: 37.4 ± 30.2 , range: $0.9-123.3 \mu\text{mol O}_2 \text{ l}^{-1} \text{ d}^{-1}$), GP:Chl a ratios (mean: 5.2 ± 2.3 , range: $0.9-11.6 \mu\text{g C } (\mu\text{g Chl a})^{-1} \text{ h}^{-1}$) and respiration rates (mean: 12.3 ± 9.7 , range: $0.6-46.5 \mu\text{mol O}_2 \text{ l}^{-1} \text{ d}^{-1}$) in the surface planktonic community. Chlorophyll increases were associated with both upwelling and relaxation conditions. During the spring-summer period dominated by regular upwelling and relaxation events, the GP:Chl a ratio (Productivity Index), showed consistent correlations with the density of the surface layer but was independent of temperature, nutrient and planktonic dominance. From April to the end of June, upwelling typically depressed photosynthetic activity while in July-August upwelling was associated with increases in autotrophic activity. Respiration rates showed a more complex pattern and varied on a shorter time-scale than did chlorophyll a biomass or photosynthetic productivity suggesting a rapid growth or physiological response of heterotrophic organisms to very transient physical and biological situations.

Introduction

Upwelling ecosystems are usually considered as immature ecosystems with a food web typically based on "new production" of organic matter by fast growing diatoms. The planktonic community is then characterized by a high photosynthesis to respiration ratio, the new production being exported and remineralized out of the system (Packard 1979) thus generating a strong spatial heterogeneity. Under an intermittent coastal upwelling regime such as the one characterizing the Rias of the North West coast of Spain (Fraga 1981, Blanton et al. 1984), the occurrence of stratified and unstratified periods allows the maturation of the planktonic community (autotrophs/heterotrophs, prey/predators, diatoms/dinoflagellates) and its vertical segregation during the periods of stabilization (Figueiras & Pazos 1991, Figueiras & Rios 1993). How the different components of those complex communities respond to upwelling and relaxation is one of the major objectives of upwelling area studies.

Since the 1950's, phytoplankton ecology has been regularly studied in the Rias Baixas, especially in regards to the annual phytoplanktonic succession (e.g. Margalef et al. 1955) and its relation with the hydrographic regime (e.g. Figueiras & Niell 1987). Short-term variability of phytoplankton biomass and composition on a time scale of less than a week has been monitored consistently. The present study, based on a twice-weekly sampling frequency is an attempt to outline the major consequences of strong hydrographic variability created by an intermittent upwelling regime on the planktonic community in

terms of both autotrophic and heterotrophic activity at the surface.

Materials and methods

From the 15 April to the 11 November 1991, sampling was carried out twice a week (typically between 9.00 and 10.30) at a fixed station ($42^{\circ}14'1''\text{N}$, $8^{\circ}46'9''\text{W}$) in the Ria de Vigo (Fig. 1). Samples were collected with 5 l PVC Niskin bottles provided with rotating thermometer frames. Three depths were sampled: surface, 1% of light determined by a LICOR underwater quantum sensor and 40 m (8 m above the bottom). Salinity was calculated from the equation (6) of UNESCO (1981) from conductivity measurements with an AUTOSAL 8400A salinometer. Aliquots for nutrient determination were frozen at -20°C after sampling and analysed by Technicon AA11 systems following Hansen and Grasshoff (1983) with some modifications (Alvarez-Salgado et al. 1992, Mouriño & Fraga 1985). Chlorophyll a was determined after filtration through Whatman GF/F filters by the fluorometric method (Yentsch & Menzel 1963) using a Turner Designs 10000R fluorometer. The abundances of bacteria, pico- and nanoflagellates were determined by epifluorescence microscopy using the DAPI-induced fluorescence method (Porter & Feig 1980). Photosynthetic cells were identified by autofluorescence under blue light excitation (Davis & Sieburth 1982).

For the community oxygen metabolism study, 25 l of water from each depth were pooled in three darkened carboys and gently shaken before subsampling. Size-fractionation of the

community was performed by gravity filtration through 10 μm mesh. From 15 April to 3 September, prefiltration through 150 μm mesh was carried out. After 3 September the samples were incubated without prefiltration. Incubations usually began within 2 to 3 h after sampling. Daily net photosynthetic and respiration rates of the phytoplankton community were estimated with the oxygen light-dark bottle method (Strickland & Parsons 1972). Triplicated 120 ml light and dark bottles were incubated for 24 h *in situ*.

Oxygen titration was performed by a SIS microprocessor controlled titrator system using the colorimetric Winkler method. Rates of net photosynthesis (NP), gross photosynthesis (GP) and respiration (R) are expressed in $\mu\text{mol O}_2 \text{ l}^{-1} \text{ d}^{-1}$.

The chlorophyll a content of the samples used for primary production experiments was also analysed as described above. These chlorophyll data were used for the normalization of GP to Chl a referred to as the Productivity Index (PI) expressed in $\mu\text{g C } (\mu\text{g Chl a})^{-1} \text{ h}^{-1}$. Oxygen production values were converted to carbon using a PQ of 1.36 (Rios & Fraga 1987).

Results

During the upwelling season 1991, regular intrusions of Eastern North Atlantic Water (ENAW) in the Ria de Vigo imposed a strong hydrographic variability at the fixed station as represented by the temporal evolution of bottom and surface temperatures (Fig. 2A) and nitrate+nitrite concentrations at 40 m, at the 1% light depth and at the surface (Fig. 2B). Maxima in the surfacewards transport of the dense bottom water

were reflected in the surface density values on 22 April, 6 May, 20 May, 6 June, 20 June, 4 July, 29 July and 12 August (annotated with arrows on the date axis). These events were associated with marked decreases in sea surface temperature during the thermally stratified season from mid-April to mid-October together with strong influxes of nitrate in the bottom layer at the fixed station. Nitrate concentrations $>6 \mu\text{M}$ were regularly measured at the 1% LD ($12 \pm 4 \text{ m}$) with concentrations $>2 \mu\text{M}$ being observed on five occasions at the surface.

Chl a concentrations, gross photosynthesis and respiration rates remained high at the surface during the period of sampling (Table 1) averaging respectively $6.0 \mu\text{g Chl a l}^{-1}$ ($\pm 70\%$), $37 \mu\text{mol O}_2 \text{ l}^{-1} \text{ d}^{-1}$ ($\pm 81\%$) and $12.3 \mu\text{mol O}_2 \text{ l}^{-1} \text{ d}^{-1}$ ($\pm 79\%$). The autotrophic community was largely dominated by organisms $>10 \mu\text{m}$ which accounted for 66% of the biomass and 77% of the gross photosynthesis while in contrast 60% of the community oxygen consumption was by organisms $<10 \mu\text{m}$ (Table 1).

Chl a concentrations at the surface (Fig. 3A) showed marked seasonal differences with major increases associated with the upwelling events of early spring ($>15 \mu\text{g l}^{-1}$) and mid-August ($\approx 14 \mu\text{g l}^{-1}$) while a third bloom in the autumn, consisting of a series of short lived peaks $>10 \mu\text{g l}^{-1}$ decreasing in intensity towards the winter, was initiated during the longest relaxation period when stratification was strongest. In contrast, in June-July, concentrations appeared relatively low with peaks $<10 \mu\text{g l}^{-1}$.

The evolution of the productivity index (Fig. 3B) in the surface layer did not show such a pronounced seasonal trend as for Chl a since high values were regularly observed during the

upwelling season (average of $5.25 \pm 2.30 \mu\text{g C } (\mu\text{g Chl a})^{-1} \text{ h}^{-1}$). From the 15 April to 6 August, highly significant linear relationships were observed between PI at the surface and the superficial water density over periods of 3 to 6 weeks (Fig. 4). As a single factor, density variation explained 63% ($0.005 < p < 0.001$) of the variations of the productivity index observed from 15 April to 30 May, 93% ($p < 0.001$) from 3 to 27 June and 76% ($0.005 < p < 0.001$) from 1 July to 6 August. High surface temperature and increased water column stratification as estimated by the 0-40 m density, corresponded to discontinuities in the parameters characterizing the relationships with the slope evolving from -3.44 ($r=0.793$, $n=11$) in April-May, to -8.70 ($r=0.985$, $n=7$) in June and +4.77 ($r=0.871$, $n=8$) in July-August. Contrasts were also apparent over time, with greater significance between PI and the density estimated 2 days before the sampling in the first period, 1.5 days before in the second and the day of the sampling in the third period. During those three periods, although PI was not statistically correlated with Chl a, each maximum of PI (range: $6.09-9.09 \mu\text{g C } (\mu\text{g Chl a})^{-1} \text{ h}^{-1}$) preceded a maximum of biomass in surface (range: $4.16-16.71 \mu\text{g Chl a l}^{-1}$). The delay observed between both varied from none (29 July) to 11 days (2-13 May) but corresponded typically to the 3 to 4 days separating each sampling.

The temporal evolution of the respiration rates showed marked short-term variability, especially at the beginning of the summer (Fig. 3C). Higher rates were measured during the thermally stratified period (mid-April to mid-October). From mid-May to mid-July heterotrophic activity was depressed when

the maxima in upwelling were observed while it increased during the two last upwelling events. From 22 August to 19 September, a steady increase, significantly correlated with the increase in surface temperature ($r=+0.877$, $p<0.05$) contrasted with the short-lived peaks observed in June-July. However, physical variability of the water column alone is insufficient to explain the strong short-term variability of respiration rates. Figure 5 illustrates how the structure of the heterotrophic community and its interactions with the phytoplanktonic community might explain this variability. In the $<10\mu\text{m}$ fraction, which was responsible for 60% of the heterotrophic activity, two groups of data were isolated. In Figure 5A, one group (G1) showed a marked increase of the respiration rate with chlorophyll concentration in the $<10\mu\text{m}$ fraction (Chl a values $>4 \mu\text{g l}^{-1}$ were observed during the marked increase in surface temperature in September) while a second group (G2), corresponding to the highest rates measured during the sampling season (including most of the peaks of respiration observed in May-June), was associated with low Chl a concentrations in the small fraction but showed a clear tendency to increase as the photosynthetic activity in the larger fraction increased (Fig. 5B). Correlation between epifluorescence counts and respiration rates (Table 2) indicated that small heterotrophic flagellates (pico- and nanoflagellates) were associated with the respiration data of the first group while bacteria gave the major contribution to the variation of the respiration rates measured in the second group.

Discussion

The study carried out in the Ria de Vigo during the upwelling season 1991 showed that the intermittent intrusions of deep oceanic water in the Ria occurred with an approximate frequency of 2 weeks and allowed the development of high autotrophic biomass and production and high heterotrophic activity as well as strong interactions within the planktonic community.

The response of the planktonic community to upwelling events appears very complex and the interpretation of this response based on data from a single fixed station is not necessarily easy.

The three significant and contrasting relationships found between the productivity index of the surface community and the surface density within the three consecutive periods 15 April-30 May, 3 June-27 June and 1 July to 6 August underline two currently observed aspects of phytoplankton response to upwelling: the lag-time following upwelling stress (MacIsaac et al. 1985, Wilkerson & Dugdale 1987, Dortch & Postel 1989, Duarte 1990) and the control of phytoplanktonic production by physical processes (Huntsman & Barber 1977, Small & Menzies 1981). Since those relationships were apparently independent of temperature, phytoplanktonic succession and nutrient influx with the deep water (Moncoiffé et al., in prep.), it is suggested that phytoplanktonic productivity was controlled overall by the physical variability of the surface layer associated with the succession of upwelling, relaxation and stratification during the period dominated by regular upwelling and relaxation events.

In the Ria de Vigo, because of the scarcity of freshwater input, surface density depends mainly on the strength of the upwelling and the rate at which thermal stratification is re-established. The strength of the upwelling will determine the stress applied to the system while the vertical stability will condition the degree of maturity of the ecosystem in terms of the nitrogen source supporting phytoplankton growth, trophic relationships and light adaptation. In conditions of weak stratification (April-May) high phytoplankton biomasses were rapidly reached following the maximum of density at the surface while nitrate concentrations fell to values $<1 \mu\text{M}$ in the photic layer suggesting a rapid growth response of the phytoplankton. However, the productivity index varied little and its slight decrease following the maximum of density could either be due to higher concentration of non-functional Chl a or to photoinhibition known to occur when a water sample taken from a mixed water column is exposed to high irradiances (Huntsman & Barber 1977, Harris 1980). Once the seasonal thermocline was established (June, July, August), upwelling occurrences had major consequences on the productivity index of the phytoplanktonic community resulting either in low values in June (61 and 89% lower than under stratified conditions), or in high values in July-August decreasing by 85 and 81% under relaxation conditions. Negative relationships between phytoplanktonic community and stability have usually been interpreted with reference to the low average light regime experienced by the microalgae during strong mixing and its increase as the water column stabilizes as a progressive adaptation to high surface irradiances (Malone et al. 1983,

Demers & Legendre 1982). In an upwelling area, it could also be related to the time-lag necessary for adaptation of the upwelled cells (Wilkerson & Dugdale 1987) or phytoplanktonic population (Duarte 1990) to near surface conditions. A positive relationship or the absence of lag would correspond to either a preconditioning of the upwelled cells to high irradiances (MacIsaac et al. 1985) or to a fertilization of nutrient-limited surface population (Dortch & Postel 1989).

The respiration rates measured (mean and range) were highest than the values for surface coastal waters reviewed by Williams (1984). Organisms $<10\ \mu\text{m}$ (mainly small flagellates and bacteria), by accounting for 60% of the oxygen respired by the whole microplankton fraction and representing on average 44% (± 66) of the gross photosynthetic production against 20% (± 18) for the organisms $>10\ \mu\text{m}$, appear as a major component of the biological transfer of organic matter in the surface layer during the upwelling season. More surprising is the relatively weak dependence of the respiration rate on the physical evolution of the surface layer, especially during the summer time, since previous seasonal studies of small flagellates and bacteria activity have revealed a strong temperature influence (Marrasé et al. 1992, Velimirov & Walenta-Simon 1992). Although the respiration rates in this fraction remained $<10\ \mu\text{mol O}_2\ \text{l}^{-1}\ \text{d}^{-1}$ when the temperature fell below 15°C , the lack of correlation at higher temperature was probably related to the partitioning of the heterotrophic community into two fractions. In the first fraction respiration rates increased with chlorophyll concentration in $<10\ \mu\text{m}$ fraction and were significantly correlated with the small flagellates

population. In the second fraction, respiration rates increased with the photosynthetic activity in the $>10\ \mu\text{m}$ fraction and was more closely related to variations of the bacterial biomass. Without however explaining totally the short-term respiration variability observed in June-July, those correlations suggest the rapid establishment of complex relationships between the different components of the community (through remineralization and grazing activity in the small fraction) following upwelling events. The dependence of bacterial production on photosynthetic production through the release of extracellular organic compounds (EOC) by photosynthetically active cells is well established. In the present instance where the bacterial population was separated from the main source of EOC (organisms $>10\ \mu\text{m}$) by prefiltration, the correlation observed between respiration in the small fraction and photosynthetic activity of the larger organisms would require an accumulation of EOC in the surface layer. Such an accumulation does not seem to be of general occurrence (Riemann & Sondergaard 1984) although it has been observed in the Peruvian upwelling system (Sellner 1981). Furthermore, bacteria assimilation rates depend strongly on the quality of the dissolved organic matter (Sell & Overbeck 1992).

In conclusion, the Ria de Vigo appears as a very productive ecosystem both in terms of photosynthetic and heterotrophic production. The diversity of the trophic relationships in the microplanktonic community observed at the surface is likely to be reflected by a similar diversity of larger predators giving rise to the high productivity of the Galician Rias. The

importance of upwelling strength relative to the seasonal thermal stratification in regulating phytoplankton productivity is likely to have, together with upwelling frequency, a major influence on the interannual variability of exploitable resources.

Acknowledgements

The authors would like to thank the staff of the Marine Biology Station in Portaferry and of the Instituto de Investigaciones Mariñas in Vigo for their help during the project. Special thanks go to Ricardo Casal for his assistance during the work at sea and to Ana Mosquera for the epifluorescence counts. G.M. is also grateful to the IIM for providing accommodation and scientific facilities during the seven months study in the Ria. This work was supported by CEC MAST Contract N° 0017 on the Control of Phytoplankton Dominance.

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Table 1. Means, coefficient of variation (C.V.), range and numbers of observations (n) at the surface of chlorophyll a (Chl a, $\mu\text{g l}^{-1}$), gross photosynthesis (GP, $\mu\text{mol O}_2 \text{ l}^{-1} \text{ d}^{-1}$) and respiration (R, $\mu\text{mol O}_2 \text{ l}^{-1} \text{ d}^{-1}$) for the whole sample (TOT) and for $>10 \mu\text{m}$ fraction as proportion of total.

		Chl a	GP	R
TOT	mean	6.0	37.5	12.3
	C.V.	70	81	79
	range	0.2-17.5	0.9-123.3	0.6-46.5
	n	61	49	49
$>10 \mu\text{m}$		(66 \pm 20)%	(77 \pm 27)%	(40 \pm 28)%

Table 2. Correlation coefficients recorded for the two groups of surface data G1 (n=27) and G2 (n=11) between respiration rates in $<10 \mu\text{m}$ fraction (R $<10 \mu\text{m}$) and epifluorescence counts of bacteria, autotrophic (A) and heterotrophic (H) picoflagellates and nanoflagellates (bold type: $p < 0.05$).

	G1	R $<10 \mu\text{m}$ G2
H. nanoflagellates	+0.634	-0.065
H. picoflagellates	+0.663	+0.045
A. nanoflagellates	+0.427	+0.127
A. picoflagellates	+0.210	+0.318
Bacteria	+0.224	+0.577

Figure Legends

Figure 1. The Rias Baixas on the North-West coast of Spain and the Ria de Vigo with the position of the fixed station.

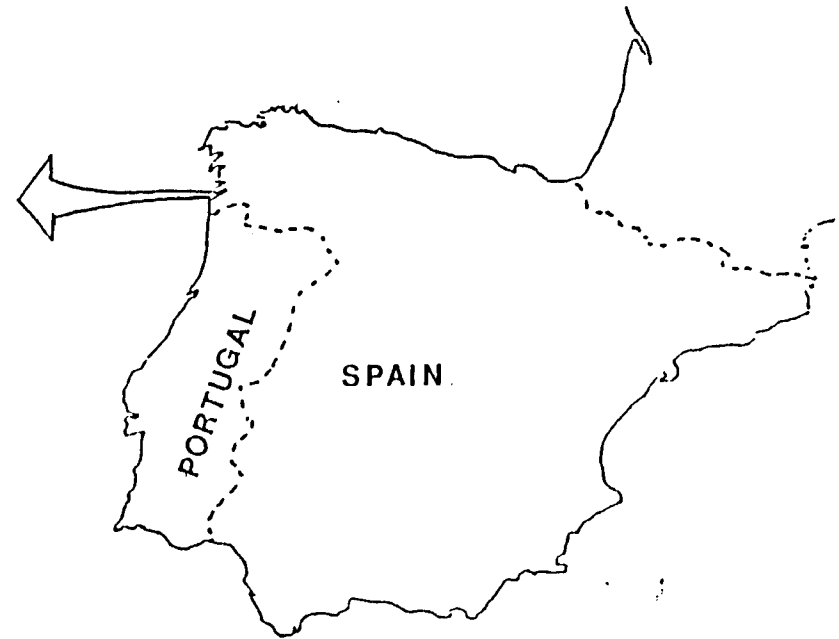
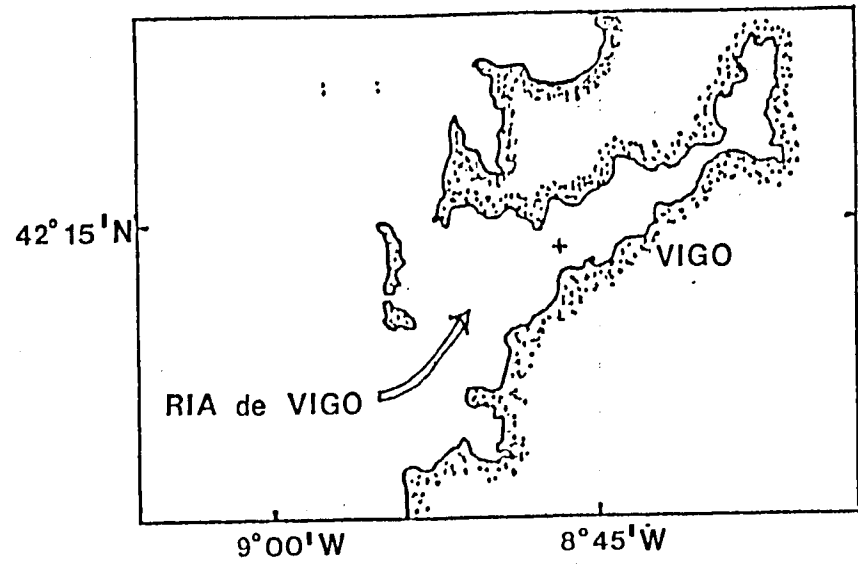
Figure 2. Temporal evolution of: A) temperature at 40 m (thin line) and surface (bold line); B) nitrate + nitrite at 40 m (thin line), 1% light depth (crosses) and surface (bold line). Arrows on the date axis denote the maxima of density observed at the surface.

Figure 3. Temporal evolution at the surface of: A) chlorophyll a, B) productivity index and C) respiration rate, in the whole sample.

Figure 4. Surface community productivity index (PI) versus surface density during the following periods of the survey: A) 15 April-30 May, B) 3 June-27 June, C) 1 July-6 August. (0), (-1.5) and (-2) denote respectively the values measured on the day of sampling and the values derived by interpolation 1.5 or 2 days prior to sampling.

Figure 5. A) Respiration $<10 \mu\text{m}$ ($\mu\text{mol O}_2 \text{ l}^{-1} \text{ d}^{-1}$) versus chlorophyll a $<10 \mu\text{m}$ ($\mu\text{g l}^{-1}$). Open circles denote the data used in Figure 5B and referred to as "G2" in the text. B) Respiration $<10 \mu\text{m}$ versus productivity index $>10 \mu\text{m}$ ($\mu\text{g C} (\mu\text{g Chl a})^{-1} \text{ h}^{-1}$) relationship in G2.

Figure 1



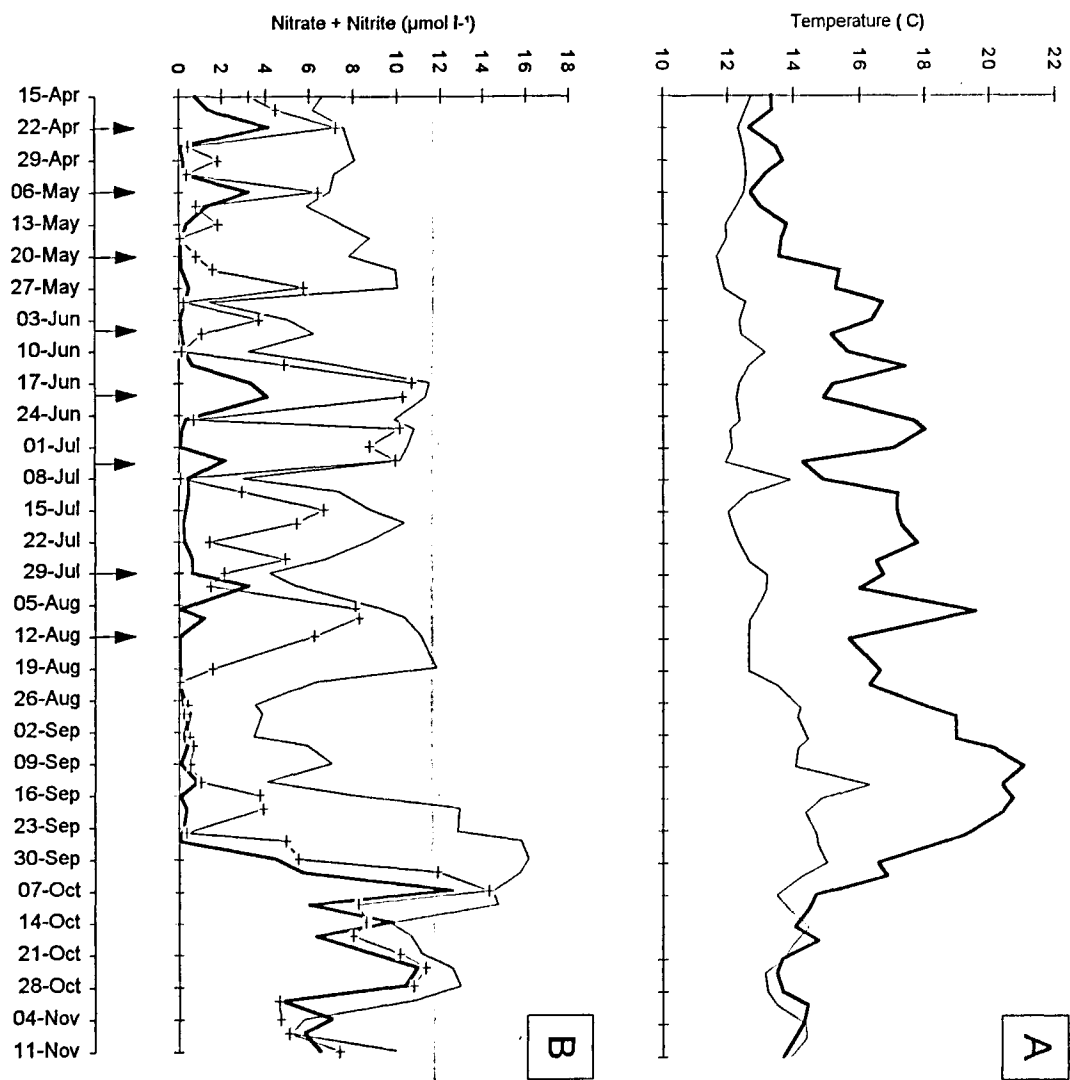


Figure 2

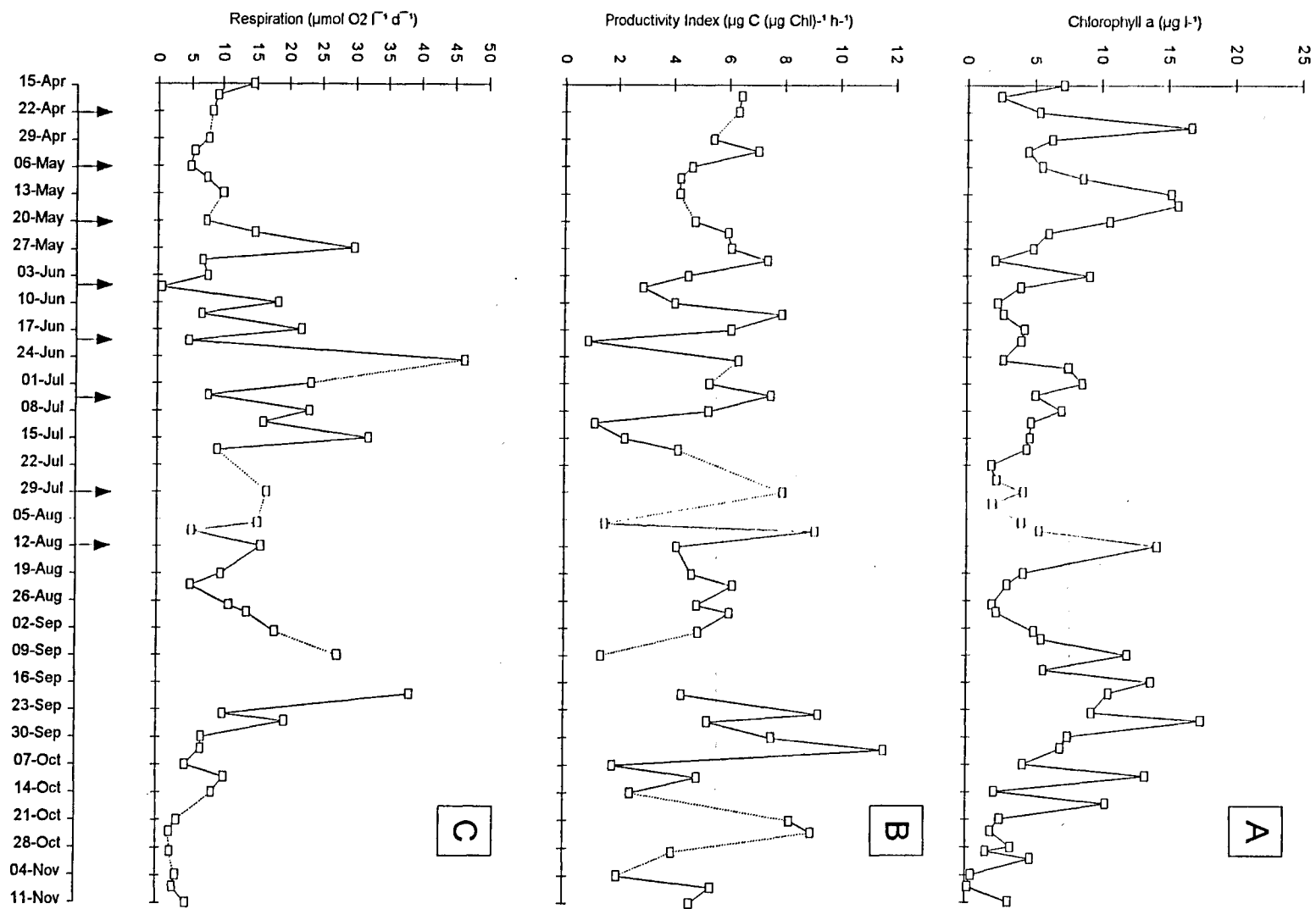


Figure 3

Figure 4

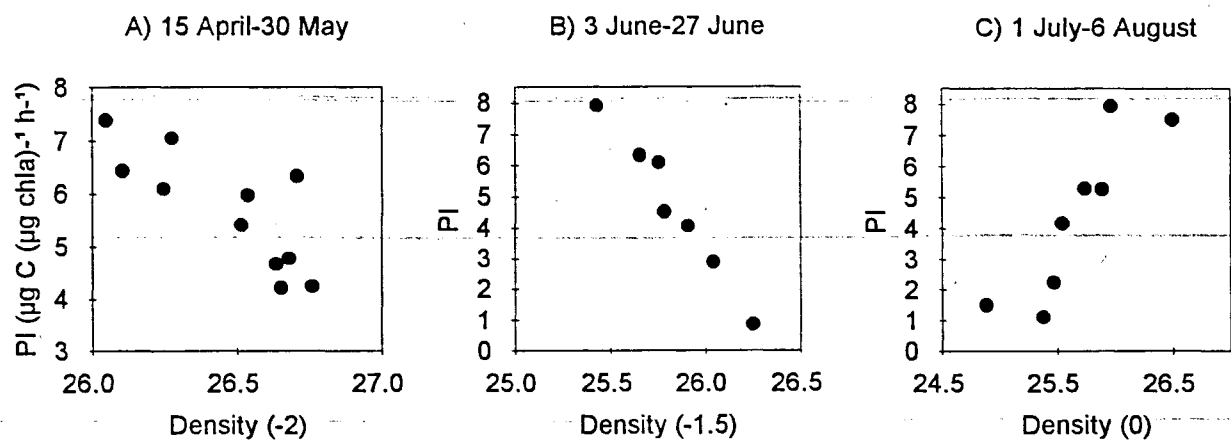


Figure 5

