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New production and production of large phytoplankton (>5 µm) on the Scotian Shelf (NW Atlantic)

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ABSTRACT: New phytoplankton production (P_{new}; nitrate uptake) and production of large phytoplankton (>5 µm, P_L; carbon fixation) were monitored on the Scotian Shelf (Northwest Atlantic) every month for 1 yr. On a daily basis, P_{new} and P_L were seldom the same. When nitrate uptake accounted for less than 20% of total primary production (f-ratio < 0.2), P_L was generally higher than P_{new}. Above this threshold, P_{new} was higher than P_L. This was true independently of actual production, i.e. the difference between P_{new} and P_L depended on the f-ratio and not on the level of primary production (high or low). When averaged over periods of 6 mo or more, P_L and P_{new} were roughly balanced. Over the year, P_{new} and P_L were equivalent, i.e. 121.8 and 115.2 mg C m^{-2} d^{-1}, respectively. Assuming that the system was in steady state, which implies a balance between new and exported production, these results lead to the conclusion that at time scales of 6 mo or more, exportable production (P_L) was equivalent to new production.

KEY WORDS: New production · Nitrate uptake · Carbon uptake · Phytoplankton · Size fractionation

INTRODUCTION

The fate of phytoplankton production in oceans can be schematically reduced to 2 broad pathways, which mainly depend on the size of phytoplankton and on hydrodynamic conditions (e.g. Legendre & Le Fèvre 1989): (1) part of pelagic primary production is recycled within the euphotic layer, and is thus called recycled production; (2) the remainder (called export production) is exported out of the euphotic layer, either directly (sinking of intact phytoplankton) or indirectly (fecal pellets of grazers, respiratory CO_2 of vertically migrating organisms, etc.). Assuming that pelagic marine ecosystems are in steady state, the amount of biogenic matter lost to export from the euphotic layer must be replaced by the production of the same quantity of organic matter. Furthermore, assuming that nitrogen is the nutrient that limits primary production in oceans, the rate of this replacement is controlled by the import of allochthonous (or new) nitrogen in the euphotic layer (mainly NO_3^- and N_2), and is thus called new production (P_{new}) (Dugdale & Goering 1967). Within the context of the above assumption, the amount of biogenic carbon exported must be in stoichiometric balance with the amount of nitrogen imported.

A rough simplification consists in dividing the system into 2 main pathways: (1) input of new nitrogen (NO_3^-) to the euphotic layer (mainly by hydrodynamic events such as upwelling), followed by production of large phytoplankton (e.g. >5 µm) and export of biogenic matter; (2) regeneration of nitrogen within the euphotic layer (mainly as NH_4 and urea), leading to the production of small phytoplankton (e.g. <5 µm) and recycling of biogenic matter within the euphotic layer. These 2 pathways are generally identified as the herbivorous (or traditional) food chain and the microbial food web, respectively (e.g. Azam et al. 1983, Cushing 1989). However, it is obvious that these 2 pathways are a simplification, and that phenomena occurring in most pelagic ecosystems correspond to an intermediate situ-

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ation. For example, it is likely that there is no one-to-one relationship between the production of large phytoplankton (P_L) and new production (P_{new}), because large phytoplankton use both nitrate and regenerated nitrogen (e.g Kokkinakis & Wheeler 1988). In addition, there is no strict equivalence between P_L and export production because, even if large phytoplankton are the part of primary production which is most readily exportable, they are not actually all exported. Overall, not much is known about the relationship between P_{new} and P_L.

The present study was undertaken to assess, on time scales from 1 d to 1 yr, the relationship between new production by the whole phytoplankton assemblage (P_{new}) and the production of large phytoplankton (P_L), on a temperate continental shelf.

MATERIALS AND METHODS

Sampling and laboratory analyses. Sampling was conducted monthly at 3 stations on the Scotian Shelf (Northwest Atlantic; Fig. 1), from March 1991 through March 1992. Stations were chosen to be representative of different hydrodynamic and biological conditions. Stn A was located at the shelf break where it was assumed that waters were generally upwelled. Stn B was located on the northeastern part of the shelf and was assumed to be representative of average conditions on the shelf. The position of Stn C was moved from month to month in order to track conditions existing in the center of an anticyclonic circulation.

At each station, samples were collected at 10 optical depths within the euphotic layer, at noontime ±2 h, using 8 l Niskin bottles. The optical depths corresponded to 10 irradiance levels in incubators on board the ship, ranging from 100% to 1% of irradiance at the sea surface. The light source for incubation was a 400 W super metal halide Optimarc lamp, and the incubators were cooled by surface water circulation. The samples were prescreened on 333 µm mesh and kept in dark isothermal containers until the beginning of measurements (within 1 h of sampling).

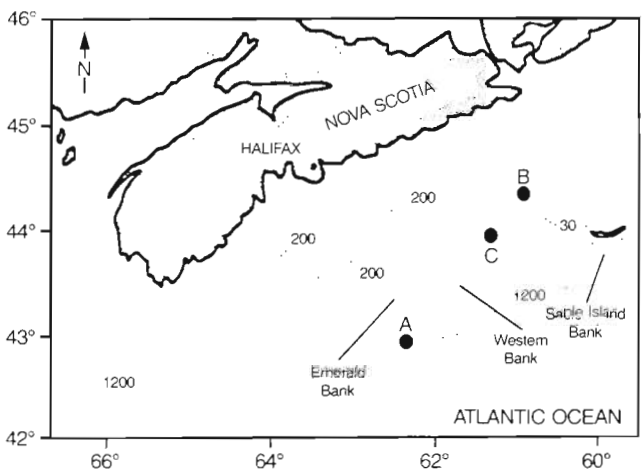

Fig. 1 The Scotian Shelf, showing the location of the sampling stations. Stn C was moved each month, but it was always located in the same general area and is thus represented as a fixed station. Isobaths given in meters

Nitrate concentrations were not analysed on board. Water was filtered on Whatman GF/F filters and frozen until analysis, which was performed later in a shore laboratory with an autoanalyser (Alpkem), following Parsons et al. (1984).

For production estimates, 1 l flasks containing 900 ml of sample from each depth were inoculated with $NaH^{13}CO_3$ (ca 120 µmol) and $K^{15}NO_3$ (between 0.1 and 1 µmol, depending on the concentration of nitrate expected to be present in the environment). Immediately after isotope additions, samples were placed in incubators for periods of 4 to 6 h. These periods represented a compromise to minimize the effects of decrease in isotope during incubation and initial surge uptake, which may reduce the accuracies of N uptake estimates (Dugdale & Wilkerson 1986). At the end of incubation, each sample was divided into 2 parts. The first half was directly filtered on 21 mm precombusted Whatman GF/F filters (0.7 µm) to assess nitrogen and/or carbon uptake for the whole phytoplankton assemblage. The second half was sequentially filtered on 25 mm Poretics 5.0 µm filters and on precombusted GF/F filters, thus providing the uptake by the small (ca 0.7 to 5.0 µm) size fraction. The GF/F filters were kept frozen until analysis.

Analyses were performed on dessicated GF/F filters (dried for 6 h at 65°C), with a CHN analyser coupled to a tracermass spectrometer (Europa Scientific). This instrument measures the amount of particulate organic carbon (POC) and particulate organic nitrogen (PON), and the percent concentration of ^{15}N and ^{13}C in the particulate organic matter, at the end of incubation.

Calculations of nitrate and carbon uptake rates. Specific nitrate uptake rates (h^{-1}) were calculated as:

$$V_n = \frac{\left({}^{15}N_p - {}^{15}N_0\right)}{\left({}^{15}N_d - {}^{15}N_0\right)T} \quad (1)$$

where $^{15}N_p$ is the concentration of ^{15}N (atom %) in the particulate phase after incubation, $^{15}N_0$ is the concentration of ^{15}N (atom %) in the particulate phase at time zero (i.e. natural concentration in the particulate phase), $^{15}N_d$ is the concentration of ^{15}N in the dissolved phase at time zero (i.e. following the ^{15}N enrichment), and T is the incubation time (h). The letter n stands for nitrate.

Transport rates (ρ_n in mg-at. $N\text{-}NO_3^-$ m^{-3} h^{-1}) were calculated as:

$$\rho_n = PON_f V_n \quad (2)$$

where PON_f is the concentration of particulate organic nitrogen (mg-at. N m^{-3}) after incubation. Eq. (1) is the same as Eq. (2) in Dugdale & Wilkerson (1986). Eq. (2) is the same as Eq. (4) in Collos (1987).

Nitrate uptake rates were converted to daily rates as follows: (1) estimated hourly N uptake rates were divided by the fraction of daily irradiance represented by the hourly irradiance at sampling time; (2) assuming a dark:light uptake ratio of 0.1 for NO_3^- (Probyn 1988), dark N uptake rates were calculated by multiplying the N hourly uptake rates by 0.1 and by the duration of the dark period (in hours). Daily NO_3^- uptake rates are the sum of (1) and (2).

Specific carbon uptake rates (h^{-1}) were calculated using the following equation:

$$V_c = \frac{({}^{13}C_p - {}^{13}C_0)}{({}^{13}C_d - {}^{13}C_0)T} \quad (3)$$

where ${}^{13}C_p$ is $\%\,{}^{13}C$ in the particulate phase after incubation, ${}^{13}C_0$ is $\%\,{}^{13}C$ in the particulate phase at time zero, ${}^{13}C_d$ is $\%\,{}^{13}C$ in the dissolved phase at time zero, and T is the incubation time (h). This equation was adapted from Eq. (1) above, which is normally used for calculating specific nitrogen uptake rates. As for nitrogen, carbon transport rates (mg-at. C m^{-3} h^{-1}) were calculated as:

$$\rho_c = POC_f V_c \quad (4)$$

where POC_f is the concentration of particulate organic carbon (mg-at. C m^{-3}) at the end of the incubation. This gives uptake rates for the total assemblage (ρ_T) and for the small size fraction (ρ_S). Uptake rates for large phytoplankton (ρ_L) were obtained by subtraction, i.e. $\rho_L = \rho_T - \rho_S$.

Carbon uptake rates were converted to daily rates by dividing the hourly C uptake rate by the fraction of daily irradiance represented by the hourly irradiance at sampling time.

Values of both ρ_n and ρ_c were integrated over the euphotic layer. In order to compare new production (nitrate uptake by the whole population) and primary production (carbon fixation) of large phytoplankton, new production was converted to equivalent carbon according to Eqs. (1) and (4) in Dugdale et al. (1992):

$$\rho_{new}(\text{mg-at. C m}^{-2}\text{d}^{-1}) = \rho_n(\text{mg-at. N m}^{-2}\text{d}^{-1}) \times 6.6\,(\text{C N}^{-1}) \quad (5)$$

where ρ_n is the transport rate of nitrate, integrated over the euphotic layer, for the whole assemblage, and 6.6 is the Redfield ratio (at./at.). Finally, ρ_{new}, ρ_T and ρ_L (mg-at. C m^{-2} d^{-1}) were converted into P_{new}, P_T and P_L (mg C m^{-2} d^{-1}), for comparison with values reported in the literature.

The *f*-ratio is the proportion of new to total production (new N uptake/total N uptake; Eppley & Peterson 1979). One way to obtain this ratio is by using the following equation (Dugdale et al. 1992):

$$f = P_{new} / P_T \quad (6)$$

RESULTS

There was no obvious relationship between nitrate transport rates normalized (or not; not shown) to chlorophyll *a* (ρ_n/chl *a*) and the concentrations of nitrate measured at different depths (Fig. 2). Similarly, there was no systematic correspondence between the integrated daily new production (P_{new}) and the production by phytoplankton >5 µm (P_L) (Fig. 3).

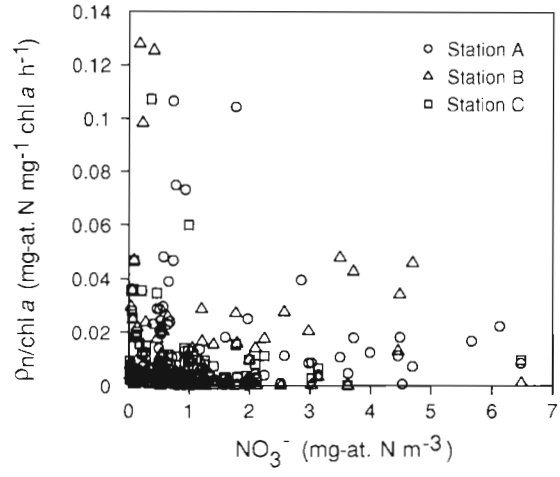

Fig. 2. Transport rate of nitrate normalized to chlorophyll *a* (ρ_n/chl *a*) as a function of nitrate concentration

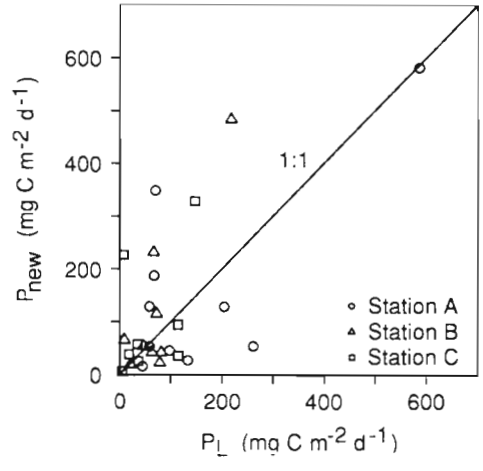

Fig. 3. New production (P_{new}) as a function of the production by large phytoplankton (P_L). Values were integrated over the euphotic layer. The 1:1 line is given for visual reference

Another way to compare P_{new} and P_L is to calculate the relative difference between the 2 types of production, using the index ΔP:

$$\Delta P = (P_L - P_{new})/(P_L + P_{new})$$

$\Delta P = -1$ when $P_L = 0$, $\Delta P = 0$ when $P_L = P_{new}$, and $\Delta P = 1$ when $P_{new} = 0$. Fig. 4 shows seasonal changes of ΔP, P_{new}, P_L, nitrate concentration and the f-ratio. The 3 stations generally exhibited the same trends. In general P_L tended to be higher than P_{new} ($\Delta P > 0$), except during September and October 1991 and February 1992 ($\Delta P < 0$). In March 1992, the only available data are for Stn A, where $\Delta P = 0$ ($P_L = P_{new}$). P_{new} was low until autumn (September–October 1991), when it suddenly increased before a drastic decrease, to increase again in February and March 1992. Except for the high values of March 1992, variations of P_L tended to be smaller but more frequent than those of P_{new}. P_L often increased and decreased during the year, but not in any major way. Nitrate concentrations were high in April 1991 and March 1992, and low during the remainder of the year. Annual variations of the f-ratio tended to show the same trend as those of P_{new}, with high values in September–October 1991 (up to 0.9) and in February–March 1992 (up to 0.8). Even if ΔP, P_{new}, P_L, NO_3^- and the f-ratio appeared to be positively or negatively correlated, statistical analyses (pairwise correlations; Table 1) did not evidence, except in 2 cases, significant relations between variables.

Table 1. Pairwise correlations between ΔP and P_{new}, P_L, NO_3^- and the f-ratio, respectively (vertically integrated values), for data from the 3 stations (A+B+C) and each station separately. Data are illustrated in Fig. 4. $^{ns}p > 0.05$, $^{*}p < 0.05$

	Stns A+B+C	Stn A	Stn B	Stn C
ΔP vs P_{new}	−0.47*	−0.53^{ns}	−0.49^{ns}	−0.60^{ns}
ΔP vs P_L	0.24^{ns}	0.17^{ns}	0.00^{ns}	0.41^{ns}
ΔP vs NO_3^-	−0.02^{ns}	−0.05^{ns}	−0.36^{ns}	0.06^{ns}
ΔP vs f-ratio	−0.21^{ns}	−0.88	0.64^{ns}	0.57^{ns}

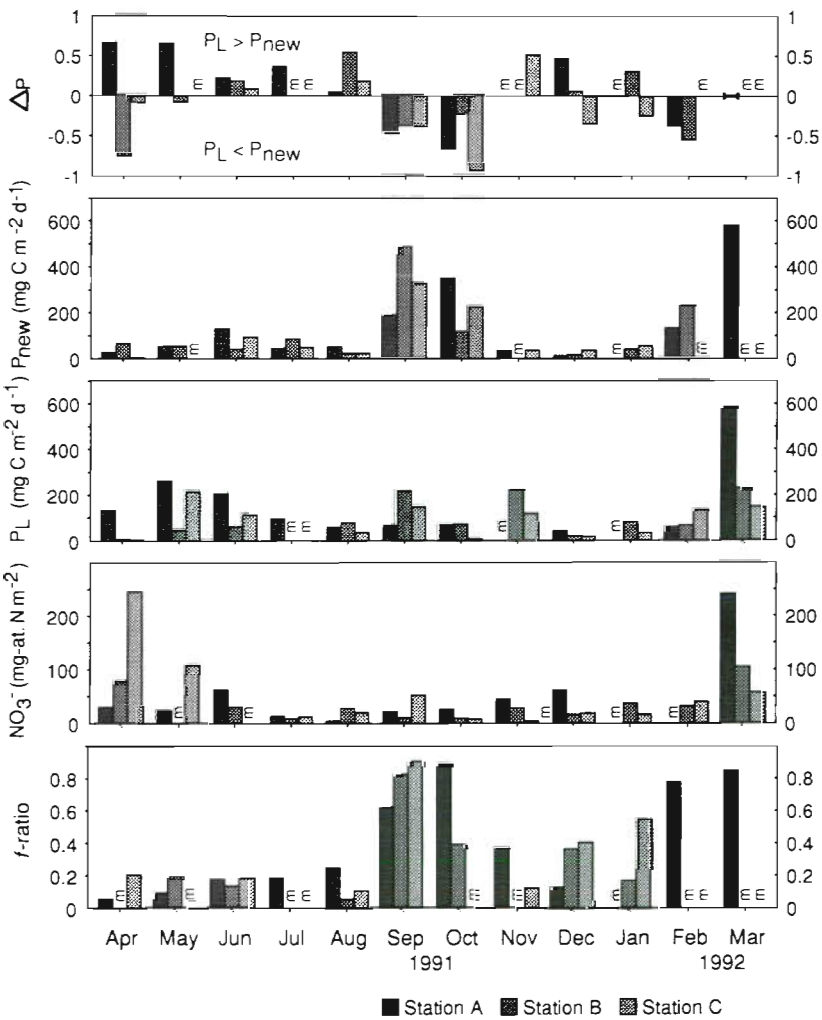

Fig. 4. Temporal variations of the difference index (ΔP), new production (P_{new}), production of large phytoplankton (P_L), nitrate concentration, and the f-ratio. All values were integrated over the euphotic layer. m: missing data

There was an inverse relationship between ΔP and the f-ratio (Fig. 5). Visually, the data tended to cluster in 2 subsets. A first group, characterized by f-values < 0.2, was located in the steepest part of the scatter plot, whereas the second group, where $f \geq 0.2$, was located in the part of the scatter plot with a weaker slope. Data were divided into almost the same 2 subsets when split relative to $\Delta P = 0$. In each subset, the relationship between ΔP and the f-ratio is linear.

Given that subsets based on ΔP or f are about the same, only results for the latter are given. Fig. 6 compares P_{new} and P_L within each subset. When $f < 0.2$, all the data points were below the 1:1 line, indicating that $P_L > P_{new}$, i.e. large phytoplankton likely took up both new and regenerated nitrogen. In contrast, when $f \geq 0.2$, values were in most cases above the 1:1 line; thus $P_{new} > P_L$, which indicates that both large and small phytoplankton took up new nitrogen.

Table 2 gives the daily (month by month) and mean values of P_L, P_{new}, the f-ratio and ΔP. The striking result of this table is that, when averaged

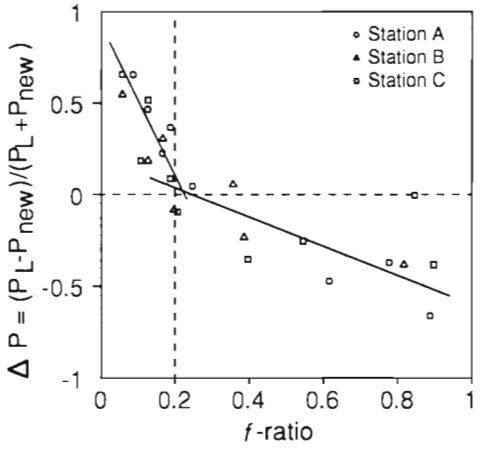

Fig. 5. Difference index (ΔP) as a function of the f-ratio. Calculations were made with values integrated over the euphotic layer For $f < 0.2$, f-ratio = 0.92 – 4.16ΔP (r^2 = 0.50) and, for $f \geq 0.2$, f-ratio = 0 21 – 0.81ΔP (r^2 = 0.38) (model II linear regressions)

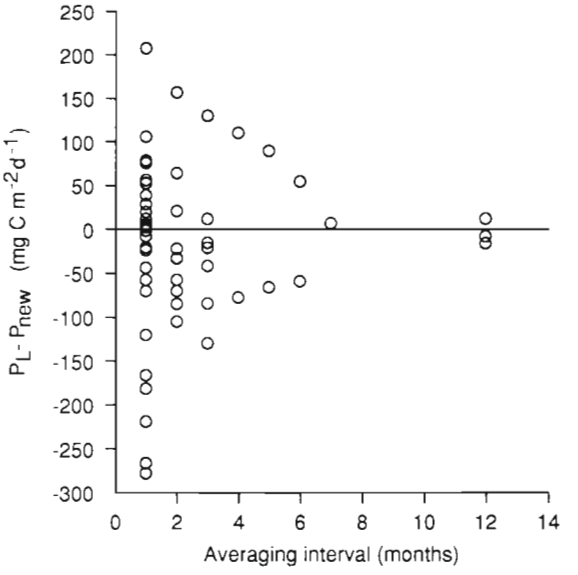

Fig. 7 Differences between P_L and P_{new} as a function of the time interval (months) over which the average values of P_L and P_{new} were calculated. For the time interval of 1 mo, values are not averages but those actually determined

over the year, P_L and P_{new} were very similar Unpaired t-tests on means (Table 3) confirm that, on the annual time scale, there was no significant difference between P_L and P_{new}, for each station separately and for the 3 stations pooled together. Given these results, it was important to assess the smallest time scale for which P_L and P_{new} were balanced on the Scotian Shelf. Because of the lack of replicates, analysis of variance could not be used, so that data were examined visually. For each station, monthly P_L and P_{new} values were averaged over different time intervals. For example, averages over 2 mo intervals were calculated for April and May, June and July, and so on up to February and March; averages over 3 mo intervals were calculated for April, May and June, and so on up to January, February and March; etc. Because of missing data, the longest interval over which averages could be computed was 7 mo. Annual averages were calculated using all values of P_L and P_{new} available for the 12 mo period. Fig. 7 shows variations of $P_L - P_{new}$ as a function of various time intervals, the 1 mo values corresponding to individual months (Table 2). Obviously, there were much more data for the short than for the long time intervals. In spite of this contraint, a general trend emerges. Over short time intervals, variability of $P_L - P_{new}$ was very high, e.g. $|P_L - P_{new}|$ ranged from 0 to ca 300 mg C m^{-2} d^{-1} on a monthly basis. As the time interval increased, the extreme values of $|P_L - P_{new}|$ tended to decrease. Finally, for time intervals of 6 mo and more, $|P_L - P_{new}|$ values were small.

DISCUSSION

It is often assumed that, because an ecosystem is in steady state, new production (mainly nitrate uptake) must be balanced by export (e.g. Eppley & Peterson 1979). This assumption is based on the hypothesis that nitrogen is the nutrient that limits primary production. In the present study, we found no relationship (i.e. no Michaelis-Menten-type kinetics) between nitrate up-

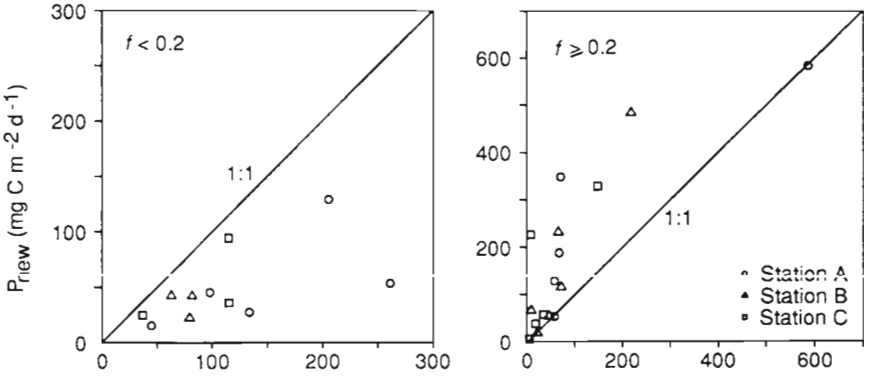

Fig. 6. New production (P_{new}) as a function of the production by large phytoplankton (P_L), for $f < 0.2$ and $f \geq 0.2$. The 1:1 line is given for visual reference

Table 2. Values, integrated over the euphotic layer, of P_L and P_{new} (mg C m^{-2} d^{-1}), the *f*-ratio and the index $\Delta P = (P_L - P_{new})/(P_L + P_{new})$. Average P_L, P_{new} and *f*-ratio are the sums of values in the column divided by the number of observations; average ΔP values are computed from average P_L and P_{new}

Stn	Date	P_L	P_{new}	*f*-ratio	ΔP
A	17 Apr 91	133.8	27.8	0.1	0.7
	19 May 91	261.6	54.0	0.1	0.7
	18 Jun 91	205.7	129.6	0.2	0.2
	23 Jul 91	98.4	45.8	0.2	0.4
	21 Aug 91	59.4	53.8	0.3	0.1
	12 Sep 91	68.3	188.4	0.6	−0.5
	09 Oct 91	71.3	349.5	0.9	−0.7
	13 Nov 91		35.8	0.4	
	14 Dec 91	44.9	16.0	0.1	0.5
	17 Feb 92	59.1	129.3	0.8	−0.4
	10 Mar 92	587.2	583.6	0.9	0.0
	Average	159.0	146.7	0.4	0.0
B	20 Apr 91	9.4	66.6		−0.8
	22 May 91	47.1	54.9	0.2	−0.1
	20 Jun 91	63.2	43.0	0.1	0.2
	20 Jul 91		88.0		
	25 Aug 91	79.6	23.1	0.1	0.6
	15 Sep 91	218.5	484.7	0.8	−0.4
	11 Oct 91	72.9	116.3	0.4	−0.2
	14 Nov 91	225.6			
	10 Dec 91	22.1	19.6	0.4	0.1
	08 Jan 92	81.9	42.9	0.2	0.3
	19 Feb 92	67.0	233.3		−0.6
	13 Mar 92	229.9			
	Average	101.6	117.2	0.3	−0.1
C	21 Apr 91	5.6	6.8	0.2	−0.1
	24 May 91	214.5			
	22 Jun 91	114.8	95.1	0.2	0.1
	25 Jul 91		50.5		
	26 Aug 91	37.2	25.4	0.1	0.2
	17 Sep 91	148.0	329.7	0.9	−0.4
	13 Oct 91	8.4	227.4		−0.9
	20 Nov 91	115.4	36.6	0.1	0.5
	13 Dec 91	18.5	38.7	0.4	−0.4
	13 Jan 92	35.1	58.3	0.6	−0.3
	22 Feb 92	135.2			
	15 Mar 92	146.7			
	Average	89.0	96.5	0.4	0.0
	Total average (Stns A+B+C)	115.2	121.8	0.4	0.0

Table 3. Unpaired *t*-tests on mean P_L and P_{new} (in mg C m^{-2} d^{-1}). For all tests, there is no significant difference between means ($p > 0.05$)

Stn	Mean P_L	Mean P_{new}	*t*
A	159.0	146.7	0.17
B	101.6	117.2	−0.31
C	89.0	96.5	−0.19
A + B + C	115.2	121.8	−0.20

take, even when corrected for biomass differences, and nitrate concentrations (Fig. 2). This is not unusual. Dortch & Postel (1989) reported the same for several of their measurements, and even inverse relationships between nitrogen concentration and uptake. According to Le Bouteiller (1986), such a lack of relationship could indicate that nitrate was not limiting on the Scotian Shelf. However, because many environmental variables other than nitrogen concentration (e.g. vertical mixing, water temperature, irradiance, species composition) influence production, the half-saturation constant for nitrate (K_s, NO_3^-) should be a better indicator than Fig. 2 of possible limitation by NO_3^-. Since that constant is not available for the Scotian Shelf, we used the value 0.50 ± 0.11 µg-at. N l^{-1} given by Dortch & Postel (1989). During the sampling year and at the 3 stations, 66% of the values of nitrate were >0.50 µg-at. N l^{-1} which indicates that, most of the time, nitrate was probably not limiting.

When data from all stations and seasons were pooled (Fig. 3), there was no obvious relationship between P_{new} and P_L. Similarly, relative differences (ΔP) between P_L and P_{new} did not allow a better assessment of the relationship between the 2 types of production throughout the year (Table 1). There were few significant correlations of ΔP with other variables, i.e. changes in ΔP were inversely related to changes in P_{new} when data from the 3 stations were pooled and to changes in *f*-ratio at Stn A. Thus, it can be concluded that P_L and P_{new} were likely driven by a combination of several factors.

The lack of relationship between P_{new} or the *f*-ratio and the absolute concentration of nitrate indicated that new production was not driven by nitrate or that nitrate was rapidly used. This is consistent with the results of Probyn (1988) for the Namibian upwelling region and those of Glibert et al. (1991) for the plume of the Chesapeake Bay (USA) estuary, but in disagreement with those reported by Harrison et al. (1987) for numerous areas, including the Scotian Shelf.

There was a threshold in the proportion of new to total production (nitrate uptake/total production, i.e. the *f*-ratio) below which $P_{new} > P_L$ and above which $P_L > P_{new}$. This threshold was ca 20% on the Scotian Shelf. This means that when $f \geq 0.2$ ($P_{new} > P_L$), nitrate was taken up by both large and small phytoplankton. In contrast, below this threshold ($P_L > P_{new}$), large phytoplankton took up both new and regenerated nitrogen.

It follows from our results that P_{new} and P_L were seldom equivalent, on a daily basis. This is not surprising, for a number of reasons. The correspondence which is sometimes assumed to exist between new production and that of large phytoplankton is a simplification, because large phytoplankton can use regenerated nitrogen and small phytoplankton can assimilate

nitrate (e.g. Furnas 1983). In addition, Kirchman et al. (1992) reported nitrate uptake by bacteria, even if generally low. Similarly, P_L is not a direct estimate of the exported production, but rather of that part of primary production which is most readily exportable. As pointed out by Legendre & Le Fèvre (1989), small phytoplankton incorporated into aggregates can be exported, and part of the large phytoplankton is recycled in the euphotic layer. Also, grazing by tunicates can contribute to the export of small phytoplankton (Fortier et al. 1994)

In the present study, P_{new} (in terms of carbon) was calculated using the Redfield ratio. On short time scales, the uptake of carbon and nitrate may be uncoupled (Banse 1994) and the C:N uptake ratio can vary between <1 and >10 (review of Le Bouteiller 1993). It follows that using the Redfield ratio may not be appropriate for converting new production (i.e. nitrate uptake) in terms of carbon at short time scales. The Redfield ratio is a mean value for the elemental composition of phytoplankton, i.e. it reflects carbon and nitrogen uptake over long time scales. It may thus be assumed that, for values of P_{new} averaged over periods of several months to 1 yr, the Redfield ratio provides a realistic estimate of the mean carbon and nitrogen uptake rates. At these time scales, the Redfield ratio can be used to convert new production from nitrogen to carbon. This could explain why P_{new} and P_L were balanced at relatively long time scales only. Additional factors can contribute to explaining the lack of daily equivalence between P_{new} and P_L, e.g. the uptake of NH_3 transported by the atmosphere and N_2 fixation, which are generally not measured even if, strictly speaking, they are part of new production (e.g. Legendre & Gosselin 1989). Finally, measurements, as is the case in most studies, did not take into account the production and export of dissolved organic matter.

Despite all the above uncertainties and approximations and also the temporal (months) and spatial (stations) variations in ΔP, estimates of P_L and P_{new} were equivalent at the annual scale, for each station and for the 3 stations pooled (Tables 2 & 3). Examination of different time scales indicated that P_L and P_{new} were approximately balanced on time scales of 6 mo and more (Fig. 7), which is rather short. Legendre & Gosselin (1989) and Platt et al. (1989) pointed out that, in order for masses to be balanced, steady state must be assumed on appropriate spatial and temporal scales. From the present study, it appears that there was a balance between new and exportable production at relatively short time scales.

Again, the balance between P_L and P_{new} does not mean that the 2 terms are equivalent (i.e. that large phytoplankton take up only nitrate). Actually, even if nitrate uptake was almost completely due to the large size fraction during the spring bloom (up to 95%), small phytoplankton accounted for at least 50% (and up to 85%) of total nitrate uptake during the remainder of the year (Dauchez et al. in press).

The conclusions that P_L and P_{new} were balanced over time scales of 6 mo or more and that the 2 terms are not equivalent may appear paradoxical. The first conclusion comes from a comparison of P_L and P_{new}, both expressed in mg C m^{-2} d^{-1}. P_L is the carbon uptake by large phytoplankton, whereas P_{new} is the new production of total phytoplankton, i.e. total nitrate uptake (large + small phytoplankton) multiplied by the Redfield ratio in order to transform new (nitrate) production from nitrogen into carbon. The second conclusion is based on estimates of new production (in terms of nitrogen) only, for the small and large phytoplankton. Results did show that nitrate was taken up by the 2 size fractions. Moreover, large phytoplankton are known to use both nitrate and regenerated nitrogen (Kokkinakis & Wheeler 1988). In summary, both large and small phytoplankton use nitrate, and large phytoplankton use both nitrate and regenerated nitrogen. Thus, on long time scales, the uptake of regenerated nitrogen by large phytoplankton could compensate for the uptake of nitrate by small phytoplankton. This would agree with the results of the present study, i.e. P_L (production of large phytoplankton, which used new and regenerated nitrogen) balanced P_{new} (new production by small and large phytoplankton), on time scales of 6 mo or more.

An interesting point in the present study is the similarity between the 3 sampling stations. In spite of the different locations and depths, P_L and P_{new} were balanced on the same time scales at all stations. This can be explained by the fact that factors that control P_L and P_{new} (periods of stratification/destratification, nitrate concentration, water temperature and irradiance) were similar at the 3 stations.

From an ecological point of view, the results of the present study are of great interest. Because the euphotic layer is in steady state, it is often assumed that new and exported production are balanced on a long, but indeterminate time scale. For this reason, it is difficult to assess the annual export of biogenic carbon. Even if P_{new} and P_L are not perfect estimates of new and exported production, one can assume that they are rather good approximations of them. The fact that the 2 sets of values were balanced at time scales from 6 mo to 1 yr offers the possibility of assessing the annual export of carbon by estimating either the total uptake of nitrate or the production of large phytoplankton. When both values are estimated, it is possible to obtain some idea of the time scale over which the euphotic layer is in steady state.

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