ICES mar. Sci. Symp., 197: 121–131. 1993

Comparison of in-bottle measurements using ^{15}N and ^{14}C

Aubert Le Bouteiller

Le Bouteiller, A. 1993. Comparison of in-bottle measurements using ^{15}N and ^{14}C. – ICES mar. Sci. Symp., 197: 121–131.

Field data reported in the literature are used for making a direct comparison between primary production estimated by the ^{14}C method and nitrogen uptake measured by the ^{15}N method (nitrate, ammonium, and, at times, urea). C/N uptake ratio values vary widely, from less than 1 to more than 20 (at/at), without any evident relationship with environmental properties or experimental procedure. The mean uptake ratio calculated on the whole data set is found to be equal to 6.7 (n = 99). The question arises whether such a C/N ratio may be considered as the assimilation ratio. For comparison purposes, the constituent ratio of phytoplankton assessed by the slopes of the regression lines relating carbon and nitrogen in particles has also been studied from the literature. This C/N ratio ranges between 5 and 7.5 (at/at) in the ocean, whatever the region, the season, or the phytoplankton present, suggesting that in the field the phytoplankton constituent ratio is probably never very different from the mean ratio found in phytoplankton by Redfield. Different possible sources of uncertainty are discussed to explain discrepancies between C/N uptake values and composition ratios. A lack of standardization in analytical procedures and calculations is evident. A better knowledge of the accurate value of the C/N assimilation ratio in the different oceanic systems is needed, especially for reaching the new production ratio "f" by using the ^{15}N and ^{14}C methods.

Aubert Le Bouteiller: Institut Français de Recherche Scientifique pour le Développement en Coopération (ORSTOM), B.P. A 5. Nouméa, New Caledonia.

Introduction

Since recognition of the potential effect of human activities on the natural evolution of climate, one of the main objectives of most large-scale aquatic ecological research programmes has been to understand the main properties of the ocean and to quantify the global flux of carbon due to biological processes. Undoubtedly, satellites are the most appropriate tools for providing maps of surface chlorophyll distribution derived from ocean colour (Smith and Baker, 1982; Platt and Herman, 1983; Feldman *et al.*, 1984). Algorithms have been proposed for estimating primary production from these satellite images (Smith *et al.*, 1982; Eppley *et al.*, 1985; Platt, 1986; Platt and Sathyendranath, 1988). Furthermore, new production, which represents the exportable component of total production (Dugdale and Goering, 1967), can also be estimated from remote sensing, at least in certain propitious conditions (Dugdale *et al.*, 1989; Sathyendranath *et al.*, 1991). Basically, all the algorithms used to calculate both total and new production clearly require for their construction a fair knowledge of the main primary production processes, and as accurate a "sea truth" as possible. However, despite decades of field studies, factors controlling phytoplankton growth and production are not yet well defined in all aquatic systems, and the absolute magnitude of total and new production is still often wrapped in uncertainty, especially in the case of oligotrophic waters. This is because of the difficulty, both conceptual and technical, of evaluating the daily production of phytoplankton in the natural environment (Peterson, 1980).

Among the numerous methods developed for measuring the primary production of phytoplankton in terms of carbon and nitrogen, use of the tracers ^{14}C and ^{15}N has largely predominated since their introduction by Steemann Nielsen (1952) and Dugdale and Goering (1967) respectively. The ^{14}C method is the standard technique used for estimating primary production in nearly all aquatic ecology laboratories. Relatively easy, rapid, sensitive and precise, this method has received a

number of modifications, reducing many of its original imperfections and increasing the accuracy of the results. One of the recent prevailing recommendations has been the "clean technique" (Fitzwater *et al.*, 1982).

The ^{15}N method is much more delicate, tedious, and time-consuming and requires accurate assessments of dissolved inorganic and particulate organic nitrogen. However, it has been extensively used in many laboratories. Dugdale and Wilkerson (1986) have reviewed most of the difficulties relevant to the method, and have proposed some recommendations for obtaining reliable estimates of phytoplankton nitrogen flux in eutrophic areas. In spite of its difficulties, the ^{15}N method is the only one allowing the distinction between new production based on nitrate uptake from regenerated production based for the most part on ammonium utilization (Dugdale and Goering, 1967).

When primary production (^{14}C) and new production (^{15}N) have been measured, the percent new production (Dugdale and Goering, 1967), of "f" factor such as defined by Eppley and Peterson (1979), can be calculated with the relationship:

$$f = \rho\, ^{15}N\text{-}NO_3 \times 6.6/\rho\, ^{14}C$$

ρ is the rate of C or N uptake, and 6.6 is the assimilation ratio C/N (at/at) assumed equal to the constituent ratio determined in phytoplankton by Redfield (1958).

If "f" and primary production are known, "f" provides direct access to the rate of new production, which is the true fertility index of an area. Primary production is expressed in terms of carbon while new production is measured in terms of nitrogen. Hence, the relationship between carbon fixation and nitrogen uptake has to be clearly defined in the field in order to calculate "f".

When all the forms of N uptake are assessed simultaneously, the rate of total nitrogenous production is obtained. Since the ^{14}C method gives the rate of total carbon fixation, the absolute magnitude of primary production can be approached by two different ways, the ^{15}N and ^{14}C methods. A direct comparison between the two is then possible.

The C/N composition ratio

Comparison between ^{14}C and ^{15}N utilization requires knowledge of the range of values in which the C/N assimilation ratio is expected to vary. If the physiological processes leading to the synthesis of new cellular material were in balance during the course of experiments, then assimilation ratios would resemble those of cellular composition (McCarthy and Nevins, 1986a). In cultures of phytoplankton under nutrient or light limitation, the C/N constituent ratio may vary within brief periods from the Redfield ratio of 6.6 to about 20, or more, according to the growth rate limitation (Goldman, 1984). In the field, the C/N constituent ratio of phytoplankton is not always directly measurable, because of the difficulty of separating algal cells from the non-algal particulate material. However, the relative concentrations of particulate carbon (PC) and particulate nitrogen (PN) in the field are considered to reflect the chemical composition of phytoplankton (Goldman *et al.*, 1979).

The regression lines linking (PC) and (PN) calculated for a great number of different oceanographic situations are reported in Table 1. The residual carbon for $N = 0$ would correspond to carbonaceous compounds that do not covary with nitrogen (Copin-Montegut and Copin-Montegut, 1983). The slopes of the regression lines represent the C/N ratio due to phytoplankton, but also in part to zooplankton and some microheterotrophs and detritus. However, it is assumed that these slopes give a good indication of the C/N constituent ratio of phytoplankton, especially when phytoplankton are known to predominate, as for example during coastal upwelling blooms. From the data in Table 1 it appears that differences between regions and systems are very small, even when coastal upwelling areas are compared with the extreme oligotrophic areas, such as the tropical Atlantic or the southwestern Pacific between 7°S and 15°S. The slopes of the regression lines C/N vary in a narrow range, from 5.1 to 7.6 (model II), and are generally close to the Redfield ratio. Interestingly, Herbland and Le Bouteiller (1983) and Eppley *et al.* (1992) have tested the effect of the nutrient abundance in stratified situations and found that both slopes and intercepts of the relationships between PC and PN were independent of the presence or absence of nitrate. Within the euphotic layer, PC/PN does not seem to exhibit any significant vertical gradient with respect to light or nutrients.

In the Guinea Dome, the size distribution of PC/PN in seston indicates that the $<1\ \mu m$ fraction shows the same properties as the total fraction (Table 1). Assuming that the non-algal matter has no particular effect on C/N, the chemical composition of picophytoplankton, which represents nearly 50% of total phytoplankton in that area (Le Bouteiller *et al.*, 1992), would not be different from large algal cells.

All these results provide clear evidence of a striking consistency in the chemical structure of the organic matter. This suggests that in the oceanic photic layer the constituent ratio of phytoplankton would be close to the C/N ratio of algal cells growing at a maximum growth rate (Goldman, 1980). From an empirical approach, there are many indications that, at least on average, the assimilation ratio should not be very different from the C/N Redfield ratio.

Table 1. Linear regression analysis between carbon and nitrogen in particles (PC = Y; PN = X, both in micromoles). Slope and Y-intercept were calculated with the model I method. When X and Y are simply measured and are not under the control of the investigator, model II is more appropriate (Sokal and Rohlf, 1969). The slope of the regression line using model II is also given. PIRAL and PROPPAC cruises were conducted by ORSTOM, France (unpublished data). Size fractionations during PIRAL cruises were presented by Fukaï (1991) and Le Bouteiller *et al.* (1992).

	Model I				Model II	
Area	Slope	Y-int	n	r	Slope	Reference
Indian Ocean 23°S to 46°S	5.45	0.59	82	0.996	5.47	Copin-Montegut and
Antarctic Ocean	5.49	0.10	62	0.996	5.51	Copin-Montegut (1983)
Tropical Atlantic	5.21	0.63	29	0.977	5.33	Copin-Montegut (1983)
Morocco upwelling	5.32	2.55	60	0.971	5.48	Copin-Montegut (1983)
Mauritania upwelling	4.93	1.66	55	0.973	5.07	Copin-Montegut (1983)
Mediterranean Sea	5.89	0.30	296	0.975	6.04	Copin-Montegut (1983)
All data	5.44	0.73	658	0.980	5.55	Copin-Montegut (1983)
Equat. Atlantic 0°,4°W	6.00	0.75	100	0.92	6.52	Herbland and
NO_3-rich water 0°,4°W	6.08	0.64	71	0.89	6.83	Le Bouteiller (1983)
W. Pacific 15°S 173°E	5.26	1.29	48	0.81	6.49	Lemasson, Cremoux, 1985
Guinea Dome 12°N 22°W	6.18	1.34	107	0.92	6.72	PIRAL cruises, 1986
<1 μm, 12°N 22°W	5.23	1.44	97	0.77	6.79	PIRAL cruises, 1986
Pacific 5°N–14°S 165°E	6.12	0.85	137	0.81	7.56	PROPPAC cruise, 1987
Upwelling, Pacific 0° 165°E	5.65	1.48	91	0.79	7.15	PROPPAC cruise, 1988
Pacific 7°S 165°E	5.15	1.10	81	0.75	6.87	PROPPAC cruise, 1989
Pacific 15°N–12°S 135°W	5.70	1.60	67	0.82	6.95	Peña *et al.* (1991)
Pacific 15°N–15°S 150°W	4.98	1.21	64	0.81	6.15	Eppley *et al.* (1992)

The C/N assimilation ratio

Still today it is not easy to carry out and obtain reliable measurements of production with either the ^{14}C method (Gieskes and Kraay, 1984; Grande *et al.*, 1989) or the ^{15}N method (Glibert *et al.*, 1982; Harrison, 1983; Laws *et al.*, 1985; Garside, 1991). The variance within a data set is often fairly small (Le Bouteiller and Herbland, 1984; Lohrenz *et al.*, 1988b; Williams and Purdie, 1991), but comparisons between different data sets are still disappointing (Richardson, 1991). Moreover, in most oceanic systems large changes in primary production rate are apt to occur within the course of a few days (Herbland and Le Bouteiller, 1982; Lohrenz *et al.*, 1988a; Platt *et al.*, 1989; Fukaï, 1991), such that comparison between C and N uptake measured at different times may have no real significance. Finally, the sine qua non condition to achieve for a reasonable comparison between C and N production consists in considering only the data sets of $\rho^{14}C$ and $\rho^{15}N$ which have been obtained simultaneously in well-controlled experimental conditions.

Most research reported in the literature deals with total nitrogen production of phytoplankton in oceanic waters, generally ^{15}N-NO_3 and ^{15}N-NH_4 uptake, and, at times, ^{15}N-urea uptake. Some research also includes simultaneous ^{14}C fixation measurements. A strict comparison between C and N production is then possible.

The data summarized in Table 2 concern a great number of regions, different seasons, and various situations. The range of variations in $\rho^{14}C/\rho^{15}N$ (Table 2) appears clearly much larger than that of PC/PN (Table 1).

There are two explanations for this discrepancy: (1) The uptake ratio C/N may change according to the environmental factors, thus reflecting the physiological response of the natural assemblages of phytoplankton to the experimental conditions during incubation. (2) When used in the field, the ^{14}C or ^{15}N methods over- or underestimate the actual rate of C or N production, for many different technical reasons; the main ones will be detailed later.

Some of the first values in Table 2 (for example MacIsaac and Dugdale, 1972; McCarthy, 1972; MacIsaac *et al.*, 1974) reflect a large predominance of C fixation over N uptake, whatever the studied system. When $\rho^{14}C/\rho^{15}N$ exceeds 15 or 20 (atomic), experimental procedures are probably to be suspected rather than a lack of balance between uptake and composition. Paradoxically, several studies in nutrient-rich waters of coastal upwellings present also relatively high $\rho C/\rho N$: Morocco (Slawyk *et al.*, 1978), Mauritania (Slawyk *et al.*, 1978), Peru in 1976 (Wilkerson *et al.*, 1987), and Namibia (Probyn, 1988, and Estrada and Marrase, 1987). It is difficult to suggest that nitrogen deficiency might explain these observations.

Conversely, the data summarized in Table 2 suggest that nutrient-depleted waters do not involve significantly higher C/N uptake ratios in the open ocean. This is to be compared to the lack of clear effect of oligotrophic conditions upon the PC/PN ratio (Table 1).

Table 2. Assimilation ratios C/N (at/at) calculated from primary production (^{14}C method) measured in sea water in parallel with total nitrogen production (^{15}N method): nitrate, ammonium and, at times, urea uptake. IS and SIS: *in situ* and "simulated" *in situ* incubations.

Position	Reference	^{15}N-compounds	Incubation	C/N Mean	C/N Range	n
Atlantic 26°–42°N 65°W	Dugdale and Goering (1967)	NO_3,NH_4	24 h SIS	9.5	1.6–34	7
Upwelling Peru	MacIsaac and Dugdale (1972)	NO_3,NH_4	24 h SIS	11.7	6.4–22	6
Eastern Pacific	MacIsaac and Dugdale (1972)	NO_3,NH_4	24 h SIS	75.7	14–178	4
Eastern Pacific	MacIsaac and Dugdale (1972)	NO_3,NH_4	24 h SIS	27.7	–	1
Eastern Mediterranean	MacIsaac and Dugdale (1972)	NO_3,NH_4	24 h SIS	20.8	–	1
Western Mediterranean	MacIsaac and Dugdale (1972)	NO_3,NH_4	24 h SIS	15.7	7.8–46	8
Coast of California	McCarthy (1972)	NO_3,NH_4, urea	24 h SIS	11.2	8.8–14.6	4
N. Pacific Central Gyre	Eppley *et al.* (1973)	NO_3,NH_4, urea	24 h SIS	5.07	3.0–7.65	3
Upwelling NW Africa	MacIsaac *et al.* (1974)	NO_3,NH_4	24 h SIS	15.5	11.7–24	4
Upwelling Morocco	Slawyk *et al.* (1978)	NO_3,NH_4	24 h SIS	13.7	4.1–31.2	5
Upwelling Mauritania	Slawyk *et al.* (1978)	NO_3,NH_4	24 h SIS	32.6	26.3–36.9	4
Saanich Inlet	Harrison (1978)	NO_3,NH_4	24 h SIS	4.92	–	1
Southern California Bight	Harrison (1978)	NO_3,NH_4	24 h SIS	6.88	–	1
Eastern Canadian Arctic	Harrison *et al.* (1982)	NO_3,NH_4	24 h SIS	4.74	1.8–7.4	14
Middle Atlantic Bight	Harrison *et al.* (1983) Falkowski *et al.* (1983)	NO_3,NH_4	6 h SIS	4.06	2.6–7.5	8
Eastern Canadian Arctic	Harrison *et al.* (1985)	NO_3,NH_4, urea	24 h SIS	8.27	3.4–26.7	7
NW Atlantic 40°N 65°W	McCarthy and Nevins (1986a)	NO_3,NH_4, urea	3–4 h SIS	9.36	4.5–23	5
NW Atlantic 40°N 65°W	McCarthy and Nevins (1986b)	NO_3,NH_4, urea	4 h SIS	7.60	5.1–9.5	5
Upwelling Peru, 1976	Wilkerson *et al.* (1987)	NO_3,NH_4	6 h SIS	14.9	–	29
Upwelling Peru, 1977		NO_3,NH_4	6 h SIS	7.07	–	14
NW Atlantic, coast mixed	Harrison and Wood (1988)	NO_3,NH_4	24 h SIS	5.56	–	1
NW Atlantic, frontal		NO_3,NH_4	24 h SIS	7.65	5.83–9.48	2
NW Atlantic, stratified	Harrison and Wood (1988)	NO_3,NH_4	24 h SIS	11.5	1.93–21	2
NW Atlantic, oceanic	Harrison and Wood (1988)	NO_3,NH_4	24 h SIS	10.1	6.60–12.8	4
Upwelling Namibia	Probyn (1988), Estrada and Marrase (1987)	NO_3,NH_4, urea	4–6 h SIS	12.1	–	10
Eastern equatorial Pacific	Murray *et al.* (1989)	NO_3,NH_4	24 h IS	7.12	3.7–11.2	4
Antarctic, spring 1983	Smith and Nelson (1990)	NO_3,NH_4	24 h SIS	4.17	2.2–6.4	15
Antarctic, autumn 1986		NO_3,NH_4	24 h SIS	2.43	0.75–5.0	6
Eastern Pacific, VERTEX	Knauer *et al.* (1990)	NO_3,NH_4	24 h IS	5.25	1.96–10.2	6
Pacific 8°N–15°N 150°W	Dugdale *et al.* (1992)	NO_3,NH_4	6 h SIS	6.80	—	4
Pacific 1°N–6°N 150°W	Dugdale *et al.* (1992)	NO_3,NH_4	6 h SIS	7.50	–	4
Pacific 0° 150°W	Dugdale *et al.* (1992)	NO_3,NH_4	6 h SIS	7.40	–	4
Pacific 2°S–8°S 150°W	Dugdale *et al.* (1992)	NO_3,NH_4	6 h SIS	4.10	–	4
Pacific 10°S–15°S 150°W	Dugdale *et al.* (1992)	NO_3,NH_4	6 h SIS	0.94	–	3

$\rho C/\rho N$ were often observed below 5 (atomic) in the eastern Canadian Arctic (Harrison *et al.*, 1982, 1985) and also in the marginal ice zone of the Weddell Sea (Smith and Nelson, 1990). This leads to the hypothesis that the C/N uptake ratio would be specifically lower than the Redfield ratio in subpolar waters. This result is not corroborated by PC/PN analyses in the Antarctic Ocean (Table 1), but low $\rho^{13}C/\rho^{15}N$ uptake ratios were also observed at 60°S and 66°S by Collos and Slawyk (1986).

When all the data from Table 2 are considered (except those from Dugdale and Goering, 1967; MacIsaac and Dugdale, 1972; Slawyk *et al.*, 1978), a good correlation between $\rho^{14}C$ and $\rho^{15}N$ (total) is obtained ($r = 0.87$; $n = 104$). The mean assimilation ratio is 6.7 ($C/N = 6.70 \pm 0.97$; $n = 104$). One may conclude that, on the average, the C/N assimilation ratio is not significantly different from the expected Redfield ratio. This is undoubtedly an important result.

Sources of uncertainty in C/N uptake ratio

The results in Table 2 have not all been obtained by exactly the same methodology. Some experiments were carried out *in situ* while most of them were "simulated" *in situ* incubations, which could have some consequences (Lohrenz *et al.*, 1992), although not necessarily appreciable, upon the uptake ratio C/N (Slawyk *et al.*, 1976). The length of incubation time is probably the

most important factor to consider for the present comparison. Short-term and long-term experiments lead to an approximation of gross and net production respectively. Many studies in the field have shown that C and N have not the same evolution within bottles during incubations, from the uptake by photosynthetic and possibly heterotrophic processes, till incorporation into autotrophic and, depending upon the ecosystem, into heterotrophic organisms. Brief uptake experiments seem to lead to a predominance of carbon uptake (Slawyk *et al.*, 1978). Conversely, in nitrogen limited waters, the ammonium incorporation by phytoplankton is potentially very rapid (Glibert and Goldman, 1981; Dortch *et al.*, 1982). Hence, low short-term C/N uptake ratios may occur. During daytime, photosynthesis directly depends on available light, whereas nitrogen uptake may occur at night. In the open ocean, NO_3 is almost never taken up in darkness (Nelson and Conway, 1979), except in very nitrogen-poor waters (Cochlan *et al.*, 1991), while dark NH_4 uptake seems much more important, varying from 10 to 100% of light uptake (Cochlan *et al.*, 1991). However, a significant amount of inorganic N uptake is probably due to heterotrophic bacteria (Laws *et al.*, 1985; Harrison *et al.*, 1992). Because of nocturnal respiration and excretion of carbon (Eppley and Sharp, 1975; Laws *et al.*, 1987; Harris *et al.*, 1989), it appears evident that processes occurring at night are very important to take into account here. As a consequence, a 24 h incubation seems to give a better representation of average daily rates of carbon and nitrogen assimilation (Eppley *et al.*, 1973).

Nevertheless, in addition to the light effect, several problems arise when the incubation time exceeds about 12 h, mainly related to respiration, excretion, and regenerative processes, such that the C and N uptake rates may become non-parallel. When long incubations are performed, the risk of a "bottle effect" increases (Gieskes *et al.*, 1979; Chavez and Barber, 1987; Wilkerson and Dugdale, 1992), especially when very delicate picophytoplankton are present (Murphy and Haugen, 1985). Besides, the ^{15}N uptake rate may increase during incubation due to ^{15}N addition in the sample, which needs to be corrected by the use of the Michaelis-Menten equation (Paasche and Kristiansen, 1982). Ammonium regenerated during incubation may also influence N flux measurements by causing underestimation of the uptake rate because of isotope-dilution of the $^{15}NH_4$ concentration (Glibert *et al.*, 1982). Laws (1984) has shown that this isotope dilution was overestimated by Glibert *et al.* (1982) owing to an inappropriate method of calculation, and because of using Reeve Angel filters through which many picoplankton pass easily (Le Bouteiller *et al.*, 1992). Harrison and Harris (1986) also found that isotope dilution was significant and, if ignored, could account for 1.5 to 3-fold underestimates in computed uptake rates. Kanda *et al.* (1987) described a new practical calculation procedure to correct the underestimate caused by isotope dilution.

Moreover, a discrepancy has been observed between disappearance of nitrate or ammonium such as measured chemically, and uptake of the same compounds by the ^{15}N method (Price *et al.*, 1985; Dugdale and Wilkerson, 1986; Slawyk *et al.*, 1990). Although not fully explained, the difference between these two approaches leads to a limit on incubation periods of 6 h or less. Many investigators, however, still use 12 or 24 h.

The consequence of relatively short experiments, where incubation artifacts are limited, is that an extrapolation is needed to obtain daily production. Experiments summarized in Table 2 comprise incubation periods ranging from 3 to 24 h. Many results of short incubations have been simply expressed as $mM\ m^{-3}\ h^{-1}$ (Harrison *et al.*, 1983; Wilkerson *et al.*, 1987; Harrison and Wood, 1988; Probyn, 1988), which is not fully satisfactory for the present purpose. McCarthy and Nevins (1986a) converted the hourly rates measured during a 3 or 4 h incubation period to a daily rate by multiplying both nitrate and ammonium uptake rates by 24. Dugdale *et al.* (1992) chose another procedure: after 6 h incubation, the hourly uptake rates of NO_3 and NH_4 were multiplied by 12 and 18 respectively to obtain a daily rate. Knauer *et al.* (1990) observed that after 6, 12, and 24 h time-course experiments NO_3 uptake did not deviate from linearity. However, NH_4 uptake rates over 1–6 h were approximately 2.5 times greater than those after 24 h. Based on these findings, Knauer *et al.* (1990) have not corrected NO_3 uptake rates after 24 h incubations, but NH_4 uptake rates have been revised upwards and multiplied by a factor of 2.5 to correct for the observed non-linearity.

All these various analytical procedures and calculations may explain part of the discrepancy between carbon fixation and total nitrogen uptake (Table 2). Great differences appear clearly in the corrections applied to the calculation of daily rates, taking into account both isotope dilution and length of incubation. A lack of standardization in methods is evident.

Several authors have measured urea taken up by phytoplankton in addition to nitrate and ammonium (Table 2). In the nitrate-rich coastal waters, urea represents 10 to 30% of total N uptake (McCarthy *et al.*, 1977; Probyn, 1985; L'Helguen, 1991), but may become negligible when nitrate concentration is high (Kokkinakis and Wheeler, 1987, 1988). In Arctic and Antarctic waters, the urea uptake rate ranges from 10 to 50% (Probyn and Painting, 1985; Wheeler and Kokkinakis, 1990). Phytoplankton have probably the highest affinity for urea in oligotrophic regions (Eppley *et al.*, 1977; Kanda *et al.*, 1985; Price and Harrison, 1988). For example, the urea contribution in the Central North Pacific Gyre ranges from 27 to 57% of total N uptake,

generally more than nitrate uptake (Eppley *et al.*, 1973; Sahlsten, 1987). These results provide clear evidence that in a number of regions, and especially in oceanic areas, urea utilization by phytoplankton represents at least 10% and usually 20 or 30% of total N uptake, which is far from negligible when all the forms of dissolved nitrogen used by phytoplankton are taken into account. As mentioned above for other factors, the results in Table 2 do not show significantly lower $\rho^{14}C/\rho^{15}N$ when urea uptake has been measured in addition to nitrate and ammonium. Too many causes of variations probably interact in a relatively too small data set.

Dissolved organic nitrogen also contributes to the nutrition of phytoplankton (Antia *et al.*, 1991). However, recent studies have shown that in the oligotrophic northeast Pacific, dissolved organic nitrogen flux represented a relatively insignificant component of the nitrogen balance in the surface ocean (Harrison *et al.*, 1992).

The data quality

Actually, most sets of $\rho C/\rho N$ ratios in Table 2 present wide variations around the Redfield ratio, and so any systematic over- or underestimation of C or N production rate is impossible to detect. The number of chemical and biological parameters to be measured for only one comparison is undoubtedly the source of much uncertainty, especially in oligotrophic systems where most of the methods reach their analytical limits. The diversity of experimental procedures used by authors (see above) is another evident cause of discrepancy.

In oceanic primary productivity studies there is no suitable diagnostic index by which the production of different areas could be compared and tested. There is no means for deciding if, in one given time and space, the true rate of primary production such as measured by the ^{14}C or ^{15}N technique has actually been achieved. Even the amount of production data collected in a region is not the required criterion of quality because of possible systematic bias.

However, there are two approaches often used to test the level of *in situ* production. The first consists in standardizing production by light (Platt, 1969), chlorophyll (Platt and Subba Rao, 1973), or by both light and chlorophyll (Morel, 1978; Platt *et al.*, 1988). The other approach requires the results of different methods run simultaneously to be compared (^{14}C, ^{13}C, ^{15}N, O_2, . . .).

Production has generally been divided by chlorophyll in the first approach. In the tropical open ocean, and probably also in many other ecosystems, the vertical profiles of productivity index (g C g^{-1} Chl *a* h^{-1}) seem always to present the same typical pattern, whatever the nitrate depth distribution may be (Le Bouteiller and Herbland, 1984): a low value at the surface due to inhibition of photosynthesis by light excess, a subsurface maximum at 10 or 20 m depth (20–30% of surface light), and a very regular decrease downwards, down to the bottom of the photic zone. Tests of data quality and regional comparisons are possible with the productivity index, and especially with the maximum value in the profile.

For example, Thomas (1970) observed that in nutrient-poor waters of the tropical Pacific Ocean, the productivity index was near 3 on average, and up to 5 g C g^{-1} Chl *a* h^{-1} in rich waters, but "the difference between the two was not great". More recently, much higher subsurface productivity indices have been measured in deep blue tropical seas: 7.3 to 18.9 g C g^{-1} Chl *a* h^{-1} (Williams *et al.*, 1983), 11.6 to 15.3 (Herbland and Le Bouteiller, 1983), up to 15 (Gieskes and Kraay, 1986), and around 10 g C g^{-1} Chl *a* h^{-1} (Laws *et al.*, 1984, 1987, 1990). A mean maximum productivity index of only 59 g C g^{-1} Chl *a* d^{-1} was observed by Cullen *et al.* (1992) in the equatorial Pacific at 155°W.

Comparison of primary production measurements using ^{14}C and ^{15}N methods (Table 2) has led to the conclusion that, on average, the assimilation ratio C/N is not significantly different from the composition ratio (Table 1). This approach, however, cannot be used to test the absolute magnitude of C or N production rate without the certainty that in the system studied the C/N assimilation ratio is close to the Redfield ratio. This statement clearly must be reinforced in the future.

The f ratio

Total primary production (^{14}C) may be compared indirectly with nitrogen production (^{15}N) through the "f" factor (Eppley and Peterson, 1979), which can be obtained in three different ways:

$$f = \rho\,^{15}N\text{-}NO_3/\rho\,^{15}N\text{-}(NO_3, NH_4, \text{urea}) \quad (1)$$

$$f = \rho\,^{15}N\text{-}NO_3 \times 6.6/\rho^{14}C \quad (2)$$

$$f = \rho\,^{15}N\text{-}NO_3 \times 6.6/\rho^{13}C \quad (3)$$

Provided primary production is consistently estimated by the methods using ^{14}C, ^{13}C, or ^{15}N, then "f" must be found equivalent in a given system whatever the tracer used.

Table 3 gives some recent values of "f" measured in the tropical and subtropical Atlantic and Pacific open oceans, where the seasonal signal is always expected to be relatively low. All results are remarkably consistent and independent of the methods used. Knauer *et al.* (1990) have compared "f" obtained with relationships 1 and 2, and found 0.11 and 0.16 respectively for a large

Table 3. Some recent results of f-ratio measurements in the tropical and subtropical Atlantic and Pacific Oceans. New production estimated by the ^{15}N method, and total production estimated by the ^{15}N, ^{14}C, or ^{13}C methods.

Position	Date	Reference	Incubation	Methods	f-ratio
13°N 22°W	Oct 1976	Slawyk and Collos (1982)	SIS	$^{13}C^{15}NO_3$ $^{15}NH_4$ $^{15}NO_2$ ^{15}N-urea	0.02–0.20
5°S to 30°N	Nov 1982	Kanda *et al.* (1985)	SIS	^{13}C $^{15}NO_3$	0.11
170°E to 110°W	Feb 1983	Kanda *et al.* (1985)			
0° 4°W	Feb 1979	Le Bouteiller (1986)	IS	^{14}C $^{15}NO_3$	0.05–0.25
	Jan 1980	Le Bouteiller (1986)			
28°N 155°W	Aug 1985	Sahlsten (1987)	SIS	$^{15}NO_3$ $^{15}NH_4$ ^{15}N-urea	0.14
2°30S 84°W	Jun 1987	Murray *et al.* (1989)	IS	$^{15}NO_3$ $^{15}NH_4$	0.29
0°55S 87°W		Murray *et al.* (1989)			0.22
2°47N 86°W		Murray *et al.* (1989)			0.24
4°26N 85°W		Murray *et al.* (1989)			0.17
32°N to 39°N	Jun Jul	Harrison (1990)	IS	$^{15}NO_3$ $^{15}NH_4$	0.07–0.28
55°W to 65°W					
9°N to 10°N	Mar Apr	Harrison (1990)	SIS	$^{15}NO_3$ $^{15}NH_4$	0.43–0.84
89°W to 94°W					
33°N 139°W	1987–1988	Knauer *et al.* (1990)	IS	$^{15}NO_3$ $^{15}NH_4$ ^{14}C	0.11–0.16
150°W	Feb Mar	Dugdale *et al.* (1992)	SIS	^{14}C $^{15}NO_3$	
8°N to 15°N	1988				0.06
1°N to 6°N		Dugdale *et al.* (1992)			0.13
0°		Dugdale *et al.* (1992)			0.24
2°S to 8°S		Dugdale *et al.* (1992)			0.13
10°S to 15°S		Dugdale *et al.* (1992)			0.07
135°W	Apr 1988	Peña *et al.* (1992)	SIS	$^{14}C^{15}NO_3$	
4°N to 16°N		Peña *et al.* (1992)			0.22
2°N to 6°S		Peña *et al.* (1992)			0.39
12°S to 15°S		Peña *et al.* (1992)			0.09

number of data from the Vertex time-series site. At 150°W, Dugdale *et al.* (1992) also found general consistent agreement between total production values computed from ^{15}N and ^{14}C measurements, except south of 10°S where "f" values calculated with Equation (2) were about four times higher than values calculated with Equation (1). This observation probably results from very low primary production values estimated with the ^{14}C method from 10°S to 15°S, as confirmed by other recent ^{14}C results (Barber and Chavez, 1991) in similar conditions. Such an underestimation of the rate of primary production (^{14}C method) evidenced by comparison with the nitrogen production (^{15}N method) measured simultaneously gives an example of common problems arising in primary productivity experiments. The interest in direct comparison between the results of two independent methods used in parallel is thus clearly demonstrated. Some experimental artifacts are difficult to put into evidence in the field studies. They are probably more frequent than generally thought.

Most "f" values in Table 3 lie between 0.10 and 0.25, even when nitrate was present at the surface in the equatorial upwelling of both the Pacific and Atlantic Oceans. Dugdale *et al.* (1992) found an overall mean "f" factor of 0.17 at 150°W (15°N to 15°S), which is in strong agreement with the median value calculated from all data reported in Table 3. This mean "f" = 0.17 seems to represent the typical magnitude of the tropical open ocean. Dugdale *et al.* (1992) observed the lowest "f" values in the nitrate-depleted waters (see their Fig. 3), but they did not find any clear relationship between "f" and the nitrate concentration in nutrient-rich waters. Similarly, neither "f" nor nitrate uptake were directly correlated to the nitrate concentration in the equatorial Atlantic, as long as ambient NO_3 exceeded about 0.1 μM (Le Bouteiller, 1986). By contrast, total primary production and new production were strongly correlated, and "f" varied as a function of the chlorophyll concentration (Fig. 1). These relationships suggest that in the tropical open ocean, factors controlling the chlorophyll concentration are more important to consider for interpreting results of C and N production measurements than the NO_3 concentration. Chlorophyll, size, and composition of phytoplankton are related. In the equatorial Atlantic, Le Bouteiller and Herbland (1984) have shown that in waters containing 1 mg m^{-3} of total chlorophyll *a*, about 50% of chlorophyll belonged to organisms passing through a 3 μm filter, and the percentage approximated 75% in oligotrophic waters. In addition, in stratified tropical situations, the euphotic zone

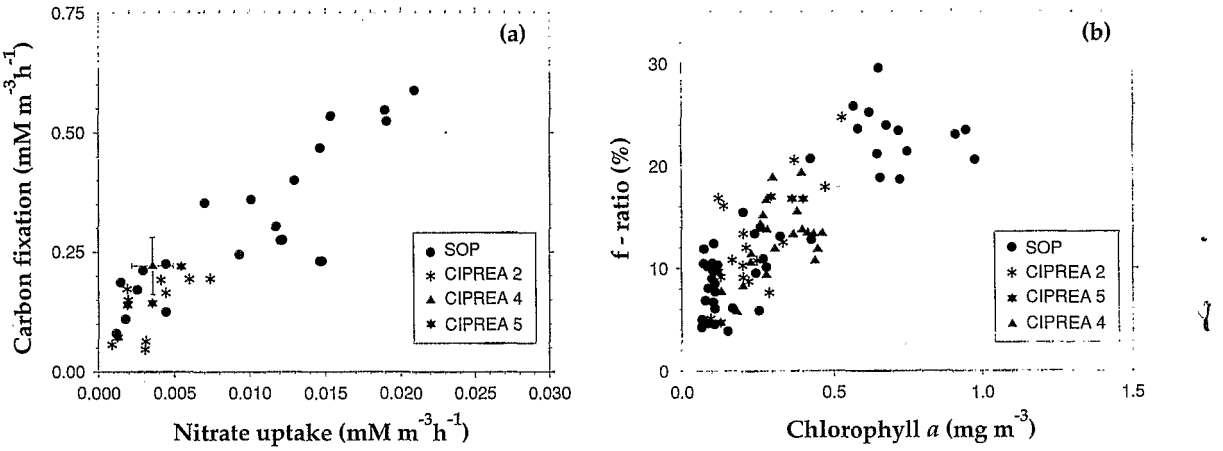

Figure 1. (a) Primary production (^{14}C) vs ^{15}N-NO_3 uptake. Results from four studies at the fixed position 0° 4°W in the Atlantic Ocean; 24 days of *in situ* incubations (11 h) from dawn to dusk. CIPREA 4 cruise: all data (n = 41) are represented by only one point (mean ± SD). Data from nitrate-poor waters (NO_3 <1 μM) were excluded. Redrawn from Le Bouteiller (1986). (b) f-ratio (%) vs chlorophyll *a*. Same data set as in Figure 1 (a), including data from nitrate-depleted waters.

was found to be divided into two parts: an upper nitrate-depleted layer in which cyanobacteria were always numerically predominant, closely linked with chorophyll *a* in the <1 μm fraction which accounted for 60% of total chorophyll *a* on average; a lower nutrient-rich layer in which chlorophyll >1 μm dominated, belonging mainly to eukaryotic microalgae (Le Bouteiller *et al.*, 1992). Size fractionation experiments have suggested that picophytoplankton have a preference for ammonium and the larger cells a preference for nitrate (Le Bouteiller, 1986). As a consequence, the new production ratio "f" would be directly related to the relative abundance of large cells able to take up nitrate (Fig. 1b), and the chlorophyll concentration would reflect the size structure of phytoplankton.

Field data (Table 2) show than on average, $\rho C/\rho N$ actually equals C/N assessed in phytoplankton (Table 1). If we suppose that the assimilation ratio is indeed 6.6 in most regions, then many data in Table 2 show that C production is up to twice N production or, inversely, four to five times lower than N production. Over- or underestimation of C or N production would be the cause of such great discrepancies. Further measurements of total C and N uptake rates are needed in the future in order to reduce such uncertainty and to enable calculation of N uptake from C production measurements. The number of nitrogenous sources taken up by phytoplankton, the necessity to obtain reliable data of NH_4 and urea concentrations in sea water (McCarthy, 1980, 1981), the correction of isotope dilution in ^{15}N-NH_4 and ^{15}N-urea utilization, and the conversion of short-term incubation measurements to daytime N assimilation, are some of the main difficulties to resolve in total N production estimation. Although never really simple, total production seems nevertheless much easier to obtain in terms of carbon than nitrogen. When the C/N assimilation ratio of phytoplankton is known in a system, then the simplest way to obtain "f" lies in measuring new production by the ^{15}N method and total production by the ^{14}C or the ^{13}C method.

Acknowledgements

I am grateful to R. Le Borgne, G. Slawyk, and two anonymous referees for their most valuable comments.

References

Antia, N. J., Harrison, P. J., and Oliveira, L. 1991. The role of dissolved organic nitrogen in phytoplankton nutrition, cell biology and ecology. Phycologia, 30: 1–89.

Barber, R. T., and Chavez, F. P. 1991. Regulation of primary productivity rate in the equatorial Pacific Ocean. Limnol. Oceanogr., 36: 1803–1815.

Chavez, F. P., and Barber, R. T. 1987. An estimate of new production in the equatorial Pacific. Deep-Sea Res., 34: 1229–1243.

Cochlan, W. P., Price, N. M., and Harrison, P. J. 1991. Effects of irradiance on nitrogen uptake by phytoplankton: comparison of frontal and stratified communities. Mar. Ecol. Prog. Ser., 69: 103–116.

Collos, Y., and Slawyk, G. 1986. ^{13}C and ^{15}N uptake by marine phytoplankton. IV. Uptake ratios and the contribution of nitrate to the productivity of Antarctic waters (Indian Ocean sector). Deep-Sea Res., 33: 1039–1051.

Copin-Montegut, C., and Copin-Montegut, G. 1983. Stoichiometry of carbon, nitrogen, and phosphorus in marine particulate matter. Deep-Sea Res., 30: 31–46.

Cullen, J. J., Lewis, M. R., Davis, C. O., and Barber, R. T.

1992. Photosynthetic characteristics and estimated growth rates indicate grazing is the proximate control of primary production in the equatorial Pacific. J. Geophys. Res., 97: 639–654.

Dortch, Q., Clayton, J. R., Thoreson, S. S., Bressler, S. L., and Ahmed, S. I. 1982. Response of marine phytoplankton to nitrogen deficiency: decreased nitrate uptake vs enhanced ammonium uptake. Mar. Biol., 70: 13–19.

Dugdale, R. C., and Goering, J. J. 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. Limnol. Oceanogr., 12: 196–206.

Dugdale, R. C., Morel, A., Bricaud, A., and Wilkerson, F. P. 1989. Modelling new production in upwelling centers: a case study of estimating new production from remotely sensed temperature and color. J. Geophys. Res., 94: 18119–18132.

Dugdale, R. C., and Wilkerson, F. P. 1986. The use of ^{15}N to measure nitrogen uptake in eutrophic oceans: experimental conditions. Limnol. Oceanogr., 31: 673–689.

Dugdale, R. C., Wilkerson, F. P., Barber, R. T., and Chavez, F. P., 1992. Estimating new production in the equatorial Pacific Ocean at 150°W. J. Geophys. Res., 97: 681–686.

Eppley, R. W., Chavez, F. P., and Barber, R. T. 1992. Standing stocks of particulate carbon and nitrogen in the Equatorial Pacific at 150°W. J. Geophys, Res., 97: 655–661.

Eppley, R. W., and Peterson, B. J. 1979. Particulate organic matter flux and planktonic new production in the deep ocean. Nature, 282: 677–680.

Eppley, R. W., Renger, E. H., Venrick, E. L., and Mullin, M. N. 1973. A study of plankton dynamics and nutrient cycling in the central gyre of the North Pacific Ocean. Limnol. Oceanogr., 18: 534–551.

Eppley, R. W., and Sharp, J. H. 1975. Photosynthetic measurements in the central North Pacific: the dark loss of carbon in 24 h incubations. Limnol. Oceanogr., 20: 981–987.

Eppley, R. W., Sharp, J. H., Renger, E. H., Perry, M. J., and Harrison, W. G. 1977. Nitrogen assimilation by phytoplankton and other microorganisms in the surface waters of the Central North Pacific Ocean. Mar. Biol., 39: 111–120.

Eppley, R. W., Stewart, E., Abott, M. R., and Heyman, U. 1985. Estimating ocean primary production from satellite chlorophyll. Introduction to regional differences and statistics for the Southern California Bight. J. Plankton Res., 7: 57–70.

Estrada, M., and Marrase, C. 1987. Phytoplankton biomass and productivity off the Namibian coast, pp. 347–356. *In* Benguela 86. Ed. by A. I. L. Payne, J. A. Gulland and K. H. Brink. S. Afr. J Mar. Sci. 5.

Falkowski, P. G., Vidal, J., Hopkins, T. S., Rowe, G. T., Whitledge, T. E., and Harrison, W. G. 1983. Summer nutrient dynamics in the Middle Atlantic Bight: primary production and utilization of phytoplankton carbon. J. Plankton Res., 5: 515–537.

Feldman, G., Clark, D., and Halpern, D. 1984. Satellite color observations of the phytoplankton distribution in the eastern equatorial Pacific during the 1982–1983 El Nino. Science, 226: 1069–1071.

Fitzwater, S. E., Knauer, G. A., and Martin, J. H. 1982. Metal contamination and its effect on primary production measurements. Limnol. Oceanogr., 27: 544–551.

Fukai, E. 1991. Importance du picoplancton autotrophe dans la biomasse et la production primaire des eaux marines oligotrophes. Atlantique tropical oriental et Mer des Sargasses. PhD thesis. University P. and M. Curie, Paris, 182 pp.

Garside, C. 1991. Shift-up and nitrate kinetics of phytoplankton in upwelling systems. Limnol. Oceanogr., 36: 1239–1244.

Gieskes, W. W. C., and Kraay, G. W. 1984. State-of-the-art in the measurement of primary production. *In* Flows of energy and materials in marine ecosystems, pp. 171–189. Ed. by M. J. R. Fasham. Plenum Press, New York.

Gieskes, W. W. C., and Kraay, G. W. 1986. Floristic and physiological differences between the shallow and the deep nanoplankton community in the euphotic zone of the open tropical Atlantic revealed by HPLC analysis of pigments. Mar. Biol., 91: 567–576.

Geiskes, W. W. C., Kraay, G. W., and Baars, M. A. 1979. Current ^{14}C methods for measuring primary production: gross underestimates on oceanic waters. Neth. J. Sea Res., 13: 58–78.

Glibert, P. M., and Goldman, J. C. 1981. Rapid ammonium uptake by marine phytoplankton. Mar. Biol. Lett., 2: 25–31.

Glibert, P. M., Lipschultz, F., McCarthy, J. J., and Altabet, M. A. 1982. Isotope dilution models of uptake and remineralization of ammonium by marine phytoplankton. Limnol. Oceanogr., 27: 639–650.

Goldman, J. C. 1980. Physiological processes, nutrient availability, and the concept of relative growth rate in marine phytoplankton ecology. *In* Primary productivity in the sea, pp. 179–193. Ed. by P. G. Falkowski. Plenum Press, New York.

Goldman, J. C. 1984. Oceanic nutrient cycles. *In* Flows of energy and materials in marine ecosystems, pp. 137–170. Ed. by M. J. R. Fasham. Plenum Press, New York.

Goldman, J. C., McCarthy, J. J., and Peavy, D. G. 1979. Growth rate influence on the chemical composition of phytoplankton in oceanic waters. Nature, 279: 210–215.

Grande, K. D., Williams, P. J. leB., Marra, J., Purdie, D. A., Heinemann, K., Eppley, R. W., and Bender, M. L. 1989. Primary production in the North Pacific gyre: a comparison of rates determined by the ^{14}C, O_2 concentration and ^{18}O methods. Deep-Sea Res., 36: 1621–1634.

Harris, G. P., Griffiths, F. B., and Thomas, D. P. 1989. Light and dark uptake and loss of ^{14}C: methodological problems with productivity measurements in oceanic waters. Hydrobiol., 173: 95–105.

Harrison, W. G. 1978. Experimental measurements of nitrogen remineralization in coastal waters. Limnol. Oceanogr., 23: 684–694.

Harrison, W. G. 1983. Use of isotopes. *In* Nitrogen in the marine environment, pp. 763–807. Ed. by E. Carpenter and D. Capone. Academic Press, New York.

Harrison, W. G. 1990. Nitrogen utilization in chlorophyll and primary productivity maximum layers: an analysis based on the f-ratio. Mar. Ecol. Prog. Ser., 60: 85–90.

Harrison, W. G., Douglas, D., Falkowski, P. G., Rowe, G., and Vidal, J. 1983. Summer nutrient dynamics of the Middle Atlantic Bight: nitrogen uptake and regeneration. J. Plankton Res., 5: 539–556.

Harrison, W. G., and Harris, L. R. 1986. Isotope-dilution and its effects on measurements of nitrogen and phosphorus uptake by oceanic microplankton. Mar. Ecol. Prog. Ser., 27: 253–261.

Harrison, W. G., Harris, L. R., Karl, D. M., Knauer, G. A., and Redalje, D. G. 1992. Nitrogen dynamics at the VERTEX time-series site. Deep-Sea Res., 39: 1535–1552.

Harrison, W. G., Head, E. J. H., Conover, R. J., Longhurst, A. R., and Sameoto, D. D. 1985. The distribution and metabolism of urea in the eastern Canadian Arctic. Deep-Sea Res., 32: 23–42.

Harrison, W. G., Platt, T., and Irwin, B. 1982. Primary production and nutrient assimilation by natural phytoplankton populations of the Eastern Canadian Arctic. Can. J. Fish. aquat. Sci., 39: 335–345.

Harrison, W. G., and Wood, L. J. E. 1988. Inorganic nitrogen uptake by marine picoplankton: evidence for size partitioning. Limnol. Oceanogr., 33: 468–475.

Herbland, A., and Le Bouteiller, A. 1982. The meanders of equatorial currents in the Atlantic Ocean: influence on the biological processes. Océanogr. Trop., 17: 15–25.

Herbland, A., and Le Bouteiller, A. 1983. Dynamique du phytoplancton et matière organique particulaire dans la zone euphotique de l'Atlantique Equatorial. Mar. Biol., 72: 265–278.

Kanda, J., Laws, E. A., Saino, T., and Hattori, A. 1987. An evaluation of isotope dilution effect from conventional data sets of ^{15}N uptake experiments. J. Plankton Res., 9: 79–90.

Kanda, J., Saino, T., and Hattori, A. 1985. Nitrogen uptake by natural populations of phytoplankton and primary production in the Pacific Ocean: regional variability of uptake capacity. Limnol. Oceanogr., 30: 987–999.

Knauer, G. A., Redalje, D. G., Harrison, W. G., and Karl, D. M. 1990. New production at the VERTEX time-series site. Deep-Sea Res., 37: 1121–1134.

Kokkinakis, S. A., and Wheeler, P. A. 1987. Nitrogen uptake and phytoplankton growth in coastal upwelling regions. Limnol. Oceanogr., 32: 1112–1123.

Kokkinakis, S. A., and Wheeler, P. A. 1988. Uptake of ammonium and urea in the northeast Pacific: comparison between netplankton and nanoplankton. Mar. Ecol. Prog. Ser., 43: 113–124.

Laws, E. A. 1984. Isotope dilution models and the mystery of the vanishing ^{15}N. Limnol. Oceanogr., 29: 379–386.

Laws, E. A., Ditullio, G. R., Carder, K. L., Betzer, P. R., and Hawes, S. 1990. Primary production in the deep blue sea. Deep-Sea Res., 37: 715–730.

Laws, E. A., Ditullio, G. R., and Redalje, D. G. 1987. High phytoplankton growth and production rates in the North Pacific subtropical gyre. Limnol. Oceanogra., 32: 905–918.

Laws, E. A., Harrison, W. G., and Ditullio, G. R. 1985. A comparison of nitrogen assimilation rates based on ^{15}N uptake and autotrophic protein synthesis. Deep-Sea Res., 32: 85–95.

Laws, E. A., Redalje, D. G., Haas, L. W., Bienfang, P. K., Eppley, R. W., Harrison, W. G., Karl, D. M., and Marra, J. 1984. High phytoplankton growth and production rates in oligotrophic Hawaiian coastal waters. Limnol. Oceanogr., 29: 1161–1169.

Le Bouteiller, A. 1986. Environmental control of nitrate and ammonium uptake by phytoplankton in the Equatorial Atlantic Ocean. Mar. Ecol. Prog. Ser., 30: 167–179.

Le Bouteiller, A., Blanchot, J., and Rodier, M. 1992. Size distribution patterns of phytoplankton in the Western Pacific: towards a generalization for the tropical open ocean. Deep-Sea Res., 39: 805–823.

Le Bouteiller, A., and Herbland, A. 1984. Carbon fixation and productivity index in relation to chlorophyll and light in the equatorial Atlantic ocean. Océanogr. trop., 19: 161–179.

Lemasson, L., and Cremoux, J.-L. 1985. Programme "PROCAL". Croisière PROLIGO. N. O. J. Charcot, Noumea: ORSTOM. Rapp. Missions, Sci. Mer, Océanogr. biol. 40 pp.

L'Helguen, S. 1991. Absorption et régénération de l'azote dans les écosystèmes pélagiques du plateau continental de la Manche occidentale. PhD thesis, Université de Bretagne Occidentale, Brest. 212 pp.

Lohrenz, S. E., Arnone, R. A., Wiesenburg, D. A., and De Palma, I. P. 1988a. Satellite detection of transient enhanced primary production in the western Mediterranean Sea. Nature, 335: 245–247.

Lohrenz, S. E., Wiesenburg, D. A., DePalma, I. P., Johnson, K. S., and Gustafson, D. E. 1988b. Interrelationships among primary production, chlorophyll, and environmental conditions in frontal regions of the western Mediterranean Sea. Deep-Sea Res., 35: 793–810.

Lohrenz, S. E., Wiesenburg, D. A., Rein, C. R., Arnone, R. A., Taylor, C. D., Knauer, G. A., and Knap, A. H. 1992. A comparison of *in situ* and simulated *in situ* methods for estimating oceanic primary production. J. Plankton Res., 14: 201–221.

MacIsaac, J. J., and Dugdale, R. C. 1972. Interactions of light and inorganic nitrogen in controlling nitrogen uptake in the sea. Deep-Sea Res., 19: 209–232.

MacIsaac, J. J., Dugdale, R. C., and Slawyk, G. 1974. Nitrogen uptake in the northwest Africa upwelling area: results from the CINECA-Charcot II cruise. Téthys, 6: 69–76.

McCarthy, J. J. 1972. The uptake of urea by natural populations of marine phytoplankton. Limnol. Oceanogr., 17: 738–748.

McCarthy, J. J. 1980. Nitrogen. *In* The physiological ecology of phytoplankton, pp. 191–233. Ed. by I. Morris. University of California Press, Berkeley, CA.

McCarthy, J. J. 1981. The kinetics of nutrient utilization. *In* Physiological bases of phytoplankton ecology, pp. 211–233. Ed. by T. Platt. Can. Bull. Fish. aquat. Sci., 210.

McCarthy, J. J., and Nevins, J. L., 1986a. Sources of nitrogen for primary production in warm-core rings 79-E and 81-D. Limnol. Oceanogr., 31: 690–700.

McCarthy, J. J., and Nevins, J. L., 1986b. Utilization of nitrogen and phosphorus by primary producers in warm-core ring 82-B following deep convective mixing. Deep-Sea Res., 33: 1733–1788.

McCarthy, J. J., Taylor, W. R., and Taft, J. L. 1977. Nitrogenous nutrition of the plankton in the Chesapeake Bay. I. Nutrient availability and phytoplankton preferences. Limnol. Oceanogr., 22: 996–1011.

Morel, A. 1978. Available, usable, and stored radiant energy in relation to marine photosynthesis. Deep-Sea Res., 25: 673–688.

Murphy, L. S., and Haugen, E. M. 1985. The distribution and abundance of phototrophic ultraplankton in the North Atlantic. Limnol. Oceanogr., 30: 47–58.

Murray, J. W., Downs, J. N., Strom, S., Wei, C.-L., and Jannash, H. W. 1989. Nutrient assimilation, export production and ^{234}Th scavenging in the eastern equatorial Pacific. Deep-Sea Res., 36: 1471–1489.

Nelson, D. M., and Conway, H. L. 1979. Effects of the light regime on nutrient assimilation by phytoplankton in the Baja California and northwest Africa upwelling systems. J. Mar. Res., 37: 301–318.

Paasche, E., and Kristiansen, S. 1982. Nitrogen nutrition of the phytoplankton in the Oslofjord. Est. Coast. Shelf Sci., 14: 237–250.

Peña, M. A., Harrison, W. G., and Lewis, M. R. 1982. New production in the central equatorial Pacific. Mar. Ecol. Prog. Ser., 80: 265–274.

Peña, M. A., Lewis, M. R., and Harrison, W. G. 1991. Particulate organic matter and chlorophyll in the surface layer of the equatorial Pacific Ocean along 135°W. Mar. Ecol. Prog. Ser., 72: 170–188.

Peterson, B. J. 1980. Aquatic primary productivity and the ^{14}C-CO_2 method: a history of the productivity problem. Ann. Rev. Ecol. System, 11: 359–385.

Platt, T. 1969. The concept of energy efficiency in primary production. Limnol. Oceanogr., 14: 653–659.

Platt, T. 1986. Primary production of the ocean water column as a function of surface light intensity: algorithms for remote sensing. Deep-Sea Res., 33: 149–163.

Platt, T., Harrison, W. G., Lewis, M. R., Li, W. K. W., Sathyendranath, S., Smith, R. E., and Azam, A. F. 1989.

Biological production of the oceans: the case for a consensus. Mar. Ecol. Prog. Ser., 52: 77–88.

Platt, T., and Herman, A. W. 1983. Remote sensing of phytoplankton in the sea: surface-layer chlorophyll as an estimate of water-column chlorophyll and primary production. Int. J. Remote Sensing, 4: 343–351.

Platt, T., and Sathyendranath, S. 1988. Oceanic primary production: estimation by remote sensing at local and temporal scales. Science, 241: 1613–1619.

Platt, T., Sathyendranath, S., Cavernhill, C. M., and Lewis, M. R. 1988. Ocean primary production and available light: further algorithms for remote sensing. Deep-Sea Res., 35: 855–879.

Platt, T., and Subba Rao, D. V. 1973. Some current problems in marine phytoplankton productivity. Fish. Res. Bd Can. Tech. Rep. N°370. 90 pp.

Price, N. M., Cochlan, W. P., and Harrison, P. J. 1985. Time course of uptake of inorganic and organic nitrogen by phytoplankton in the Strait of Georgia: comparison of frontal and stratified communities. Mar. Ecol. Prog. Ser., 27: 39–53.

Price, N. M., and Harrison, P. J. 1988. Urea uptake by Sargasso Sea phytoplankton: saturated and *in situ* uptake rates. Deep-Sea Res., 35: 1579–1593.

Probyn, T. A. 1985. Nitrogen uptake by size-fractionated phytoplankton populations in the southern Benguela upwelling system. Mar. Ecol. Prog. Ser., 22: 249–258.

Probyn, T. A. 1988. Nitrogen utilization by phytoplankton in the Namibian upwelling region during an austral spring. Deep-Sea Res., 35: 1387–1404.

Probyn, T. A., and Painting, S. J. 1985. Nitrogen uptake by size-fractionated phytoplankton populations in Antarctic surface waters. Limnol. Oceanogr., 30: 1327–1332.

Redfield, A. C. 1958. The biological control of chemical factors in the environment. Am. Sci., 46: 205–221.

Richardson, K. 1991. Comparison of ^{14}C primary production determinations made by different laboratories. Mar. Ecol. Prog., Ser., 72: 189–201.

Sahlsten, E. 1987. Nitrogenous nutrition in the euphotic zone of the Central North Pacific Gyre. Mar. Biol., 96: 433–439.

Sathyendranath, S., Platt, T., Horne, E. P. H., Harrison, W. G., Ulloa, O., Outerbridge, R., and Hoepffner, N. 1991. Estimation of new production in the ocean by compound remote sensing. Nature, 353: 129–133.

Slawyk, G., and Collos, Y. 1982. ^{13}C and ^{15}N uptake by marine phytoplankton: II. Results from a tropical area (Guinea Dome). Rapp. P.-v. Réun. Cons. int. Explor. Mer, 180: 209–213.

Slawyk, G., Collos, Y., Minas, M., and Grall, J.-R. 1978. On the relationship between carbon-to-nitrogen composition ratios of the particulate matter and growth rate of marine phytoplankton from the northwest African upwelling. J. exp. mar. Biol. Ecol., 33: 119–131.

Slawyck, G., MacIsaac, J. J., and Dugdale, R. C. 1976. Inorganic nitrogen uptake by marine phytoplankton under *in situ* and simulated *in situ* incubation conditions: results from the northwest African upwelling region. Limnol. Oceanogr., 21: 149–152.

Slawyck, G., Raimbault, P., and Gentilhomme, V. 1990. On the discrepancies between a colorimetric and isotopic method for measuring nitrate utilization in nutrient-depleted waters: implications for the design of experimental protocols in new production studies. Hydrobiol., 7: 333–339.

Smith, R. C., and Baker, K. S. 1982. Oceanic chlorophyll concentrations as determined by satellite (Nimbus-7 Coastal Zone Color Scanner). Mar. Biol., 66: 269–279.

Smith, R. C., Eppley, R. W., and Baker, K. S. 1982. Correlation of primary production as measured aboard ship in Southern California coastal waters and as estimated from satellite chlorophyll images. Mar. Biol., 66: 281–288.

Smith, W. O., and Nelson, D. M. 1990. Phytoplankton growth and new production in the Weddell Sea marginal ice zone in the austral spring and autumn. Limnol. Oceanogr., 35: 809–821.

Sokal, R. R., and Rohlf, F. J. 1969. Biometry. The principles and practice of statistics in biological research. W. H. Freeman and Co., San Francisco.

Steemann Nielsen, E. 1952. The use of radio-active carbon (C^{14}) for measuring organic production in the sea. J. Cons. perm. int. Explor. Mer, 18: 117–140.

Thomas, W. H. 1970. On nitrogen deficiency in tropical Pacific oceanic phytoplankton: photosynthetic parameters in poor and rich water. Limnol. Oceanogr., 15: 380–385.

Wheeler, P. A., and Kokkinakis, S. A. 1990. Ammonium recycling limits nitrate use in the oceanic subarctic Pacific. Limnol. Oceanogr., 35: 1267–1278.

Wilkerson, F. P., and Dugdale, R. C., 1992. Measurements of nitrogen productivity in the equatorial Pacific. J. Geophys. Res., 97: 669–679.

Wilkerson, F. P., Dugdale, R. C., and Barber, R. T. 1987. Effects of El Niño on new, regenerated, and total production in eastern boundary upwelling systems. J. Geophys. Res., 92: 14347–14353.

Williams, P. J. leB., Heinemann, K. R., Marra, J., and Purdie, D. A. 1983. Phytoplankton production in oligotrophic waters: measurements by the ^{14}C and oxygen techniques. Nature, 305: 49–50.

Williams, P. J. leB., and Purdie, D. A. 1991. *In vitro* and *in situ* derived rates of gross production, net community production and respiration of oxygen in the oligotrophic subtropical gyre of the North Pacific Ocean. Deep-Sea Res., 38: 891–910.