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Photosynthesis, respiration and nitrogen supply of plankton populations in stratified, frontal and tidally mixed shelf waters

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ABSTRACT: Results of parallel photosynthesis and respiration measurements in stratified, frontal and mixed shelf waters using $^{14}CO_2$ and oxygen methods are described. Particulate ^{14}C fixation appeared to give an underestimate of gross photosynthesis. Estimates of net photosynthetic rates are compared with observed microheterotroph and calculated (from appropriate carbon biomass data) mesozooplankton respiration rates. In each of the 3 systems microheterotrophs were the major energy consumers. In surface stratified waters, turnover of plankton carbon was rapid compared to that in the light-limited, mixed water system and, under certain conditions, the phytoplankton may obtain > 50 % of their nitrogen requirement from ammonium excretion by zooplankton. Development of dinoflagellate blooms in the frontal region could be explained in terms of high rates of nitrate assimilation at the base of the thermocline, upward movement of the cells and low grazing mortality.

INTRODUCTION

Estimates of primary production in the sea based on measurements of $^{14}CO_2$ assimilation in the light over periods < 6h are now considered to represent rates of gross, rather than net, photosynthetic carbon fixation especially for incubation light intensities close to the compensation point (Dring and Jewson, 1982). For proper ecological interpretation of primary production data, compatible information about phytoplankton respiration (Steemann Nielsen, 1955; Laws, 1975), or the compensation irradiation for the uptake and loss of CO_2 (Hobson and Guest, 1983) is required. From data on plant photosynthesis and respiration, together with values for the total biomass contributing the net photosynthesis, the growth rates of natural phytoplankton communities can be calculated (Riley, 1941). Furthermore, the quantities of organic carbon available for secondary production can be determined if temporal changes in the plant standing stock are known (Cushing, 1957). However, due to the difficulties of distinguishing autotrophic and heterotrophic organisms in natural plankton populations, reliable estimates of phytoplankton respiration (Steemann Nielsen and Hansen, 1959) and standing stock (Eppley et al., 1977) are not easy to obtain. This is particularly important problem to resolve for transitional hydrographic regions (e.g. close to frontal systems), where spatial and temporal variations in the light environment of the phytoplankton populations are likely to lead to considerable variations in the proportion of photosynthetic carbon lost directly through plant respiration.

In considering phytoplankton growth in stratified waters, the availability of nitrogen (or any limiting nutrient) must also be taken into account; continual losses from the surface waters, due mainly to incorporation into organisms at higher trophic levels, the sinking of particulate material and the formation of refractory dissolved organic compounds, have to be balanced by renewal processes across the pycnocline (or frontal boundary) in order to maintain the production cycle (Eppley et al., 1979, Eppley and Peterson, 1979). The relative importance of physical (vertical and horizontal mixing) and biological (migration and aggregation of plankton, *in situ* regeneration) factors

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in controlling the supply of nitrogen under varying conditions of thermocline development is not clearly understood.

In this paper, these problems are considered for stations in mixed, frontal and stratified waters of the western English Channel, with particular reference to data on the partitioning of particulate organic carbon in the water column obtained in July–August 1981 (Holligan et al., 1984). Measurements of photosynthesis, respiration, zooplankton ammonium excretion and the distribution of nitrate across the seasonal thermocline are used to calculate rates of photosynthesis, respiration and input of inorganic nitrogen to surface water for representative vertical profiles of plankton carbon.

METHODS

The 3 stations were located in the western English Channel approximately midway between England and France in seasonally stratified (Station E5, 49°05' N 06°37' W), frontal (Station F, 49°20' N 04°35' W) and tidally mixed (Station M, 49°22' N 03°15' W) waters (Pingree et al., 1978).

Water samples were obtained with 30 l Niskin bottles, decanted with minimal agitation into glass carboys, and stirred gently immediately before subsampling. Methods for measuring hydrographic properties (temperature, inorganic nutrients, chlorophyll) and plankton carbon, as well as information on the species composition of the plankton populations, have been given by Holligan et al. (1984).

Measurements of photosynthesis by the ^{14}C technique were made by incubating water samples in 130 ml glass bottles in the presence of about 5 µCi $H^{14}CO_3$ (supplied by the Radiochemical Centre, Amersham) for 3.5 to 7 h. The stock ^{14}C solutions (~ 20 µCi ml^{-1}) were made up in 10^{-3} N NaOH, irradiated overnight under an ultraviolet lamp to break down any labelled organic compounds, and filtered through a 0.2 µm membrane filter. All incubations were carried out *in situ* by suspending 4 bottles (3 light, 1 dark) at depths appropriate to the penetration of light and vertical distribution of chlorophyll. After incubation each bottle was shaken thoroughly, an aliquot withdrawn to determine total radioactivity, and the remainder filtered on a 0.45 µm membrane filter and dried. Radioactive carbon in the media samples and on the filters was assayed by liquid scintillation counting (Pingree et al., 1976). Release of labelled dissolved organic carbon by the cells was not measured, and rates of carbon fixation in the light bottles were not corrected by subtraction of the dark bottle value. Surface and subsurface irradiance was monitored with two Lambda Quantum (400 to 700 nm) sensors, and the attenuation coefficient calculated from the subsurface light profile.

Oxygen determinations were made at sea using an automated precise Winkler procedure with photometric detector, based on the system described by Williams and Jenkinson (1982). Reagents and standardisation of the technique, using iodate, were according to recommendations of Carritt and Carpenter (1966). Water samples were incubated and subsequently analysed in nominally 125 ml borosilicate Pyrex glass bottles. Individual bottle volumes (corrected to 20 °C) were determined by weight to a minimum precision of 0.01 %. Bottles were filled directly from a 30 l Niskin sampler subsequent to decanting off water for the hydrographic and $^{14}CO_2$ measurements. Light incubations were conducted *in situ* at the same depth as those for $^{14}CO_2$ by suspending bottles on a common line from a surface buoy tethered to the ship. Respiration measurements were made in a deck incubator at ± 2 C° of surface sea temperature by enclosing bottles in black polyethylene bags. Incubations were conducted over periods of between 3 and 24 h and all reported values were the mean of 4 replicates.

For the measurement of excretion rates, copepods were collected with a 200 µm net from a depth of 10 m between 2000 and 2200 h. Within 1 h of collection 10 to 50 animals were added to 50 ml glass bottles containing 0.2 µm filtered sea water. Incubations lasted for 3.5 h at 15 °C in the dark, after which a subsample of seawater was removed from each experimental and control bottle, and immediately analysed for ammonium by the method of Liddicoat et al. (1975). Experimental animals were then collected on a 200 µm mesh, counted and dried for subsequent nitrogen analysis using a Carlo Erba elemental analyser.

The vertical distribution of nitrate was determined from continuous hydrographic records obtained by pumping from a fixed depth within the thermocline (Pingree et al., 1977). The internal wave structure allows nitrate to be estimated at various levels within the temperature gradient, and any bias due to differential smoothing (Anderson and Okubo, 1982) of the two parameters is removed by taking data for successive troughs and crests of the internal waves.

Consistent with Holligan et al. (1984), the term mesozooplankton refers to all organisms collected on a 200 µm mesh, and microzooplankton to organisms passing through a 200 µm mesh but retained by 80 µm. The term 'microheterotroph', in the present context, is defined as all heterotrophic organisms adequately sampled within the respiration bottles (125 ml) and includes bacteria, protozoa and most of the microzooplankton taxa (see Table 3a, Holligan et al., 1984).

RESULTS

Primary production

Results of parallel oxygen and ^{14}C photosynthesis measurements are summarised in Table 1. In 1981 the phytoplankton was dominated by diatoms in the mixed water at Station M, by the dinoflagellate *Gyrodinium aureolum* in the frontal region at F, and by various small flagellates at the stratified station E5 (Holligan et al., 1984). Data for Station E5 in June 1982, when the subsurface chlorophyll maximum was composed mainly of diatoms remaining from the spring outburst, are included for comparison.

Table 1. Comparative measurements of photosynthesis by oxygen and $^{14}CO_2$ methods

Station	Date	Depth of incubation (m)	Ambient nitrate concentration (μM)	Period of incubation (h)	Chlorophyll *a* concentration (mg m^{-3})	Oxygen concentration (% sat.)	Photosynthetic rate mg m^{-3} h^{-1} O_2	Photosynthetic rate mg m^{-3} h^{-1} C	Molar flux ratio $\left(\frac{+\Delta O_2}{-\Delta CO_2}\right)$
E 5	26. 7. 81	7	< 0.1	6.3	0.34	104.2	12.5 ± .3	2.2 ± .01	2.2 ± .1
		17	< 0.1		0.35	102.2	9.2 ± .4	1.4 ± .04	2.4 ± .1
	27. 7. 81	7	< 0.1	5.6	0.26	106.4	10.0 ± 1.3	2.4 ± .1	1.6 ± .2
		17	< 0.1		1.45	109.3	37.3 ± .4	7.0 ± .2	2.0 ± .1
		26	~ 1.0		2.81	100.2	40.7 ± .6	5.6 ± .8	2.7 ± .4
E 5	1. 6. 82	2	0.4	6.5	0.44	105.9	11.2 ± 1.3	1.8 ± .1	2.3 ± .3
		5	0.4		0.45	106.1	9.5 ± .8	1.5 ± .01	2.4 ± .2
		10	0.5		0.48	106.2	8.8 ± 1.0	1.5 ± .1	2.3 ± .3
		20	~ 3.0		2.92	110.1	27.7 ± 2.9	2.3 ± .2	4.5 ± .4
F	30. 7. 81	1	0.1	3.5	54.8	145.7	532 ± 11	126 ± 11	1.6 ± .1
	31. 7. 81	1	0.1	4.25	34.9	132.0	251 ± 3	59 ± 7	1.6 ± .2
M	24. 7. 81	4	0.1	6.2	1.25	–	65.2 ± .9	15.2 ± .1	1.6 ± .1
		10	0.1		1.47	105.2	63.8 ± 1.9	14.0 ± .4	1.7 ± .1
	25. 7. 81	4	0.1	4.1	1.48	–	64.7 ± 2.7	15.2 ± .9	1.6 ± .1
		10	0.1		1.65	105.0	35.8 ± 1.3	6.6 ± .3	2.0 ± .1

The overall correlation ($r = 0.99$) between the 2 techniques for measuring photosynthetic rates is comparable to that observed for estuarine and inshore phytoplankton communities (Williams et al., 1979) and those from oligotrophic water (Williams et al., 1983). This gives confidence that either technique can be used to measure gross primary production provided, in the case of the ^{14}C method, that losses due to exudation are taken into account. In order to make an exact comparison between the 2 methods, the photosynthetic quotient (P.Q.), i.e. the molar flux ratio for O_2 production and CO_2 assimilation, is needed. It is possible to calculate a 'theoretical P. Q.', if the pattern of nitrogen assimilation (i. e. the nitrogen source and in the case of nitrate, the C/N assimilation ratio) of the plant cells is known. The P.Q. is also influenced, but to a lesser extent, by the pattern of carbon assimilation of the cells (i.e. the biochemical composition). In the case of the 'carbon P.Q.', an assumed value of 1.25 (Williams et al., 1979) is adequate for the present purposes.

For the experiments described here, the mean carbon to nitrogen ratio for particulate material (which will reflect the C/N assimilation ratio of the phytoplankton) averaged 8.1 (Holligan et al., 1984), although ratios down to 6.5 were found for the chlorophyll maximum at E5 on 1 June 1982. Assuming a C/N assimilation ratio of 8 for the algae, P.Q. values of 1.2 and 1.6 would be expected for ammonium and nitrate assimilation respectively (Williams et al., 1979).

The observed molar flux ratios (Table 1) were generally 35 to 50 % greater than those anticipated from theoretical considerations. The reason for significance of this discrepancy are not clear. Calibration errors are not thought to be a likely explanation; the oxygen technique was standardised using gravimetrically prepared solutions of iodate (Carritt and Carpenter, 1966), and the ^{14}C activity determined with attention to Peterson's (1980) recommendations on scintillation counting. No measurements were made of extracellular ^{14}C photosynthate production, which will lead to an underestimation of total CO_2 fixation (see, for example, Davies and Williams, 1984). For natural phytoplankton populations recent estimates of net release of extracellular labelled products have generally been about 10 % of the total carbon fixed for incubation times ≤ 6 h (e.g. Mague et al., 1980; Iturriaga and Zsolnay, 1983, Joint and Pomroy, 1983). In relation to the present study, a 10 % exudation of total fixed carbon would only account for a minor part of the discrepancies between the oxygen and carbon experiments.

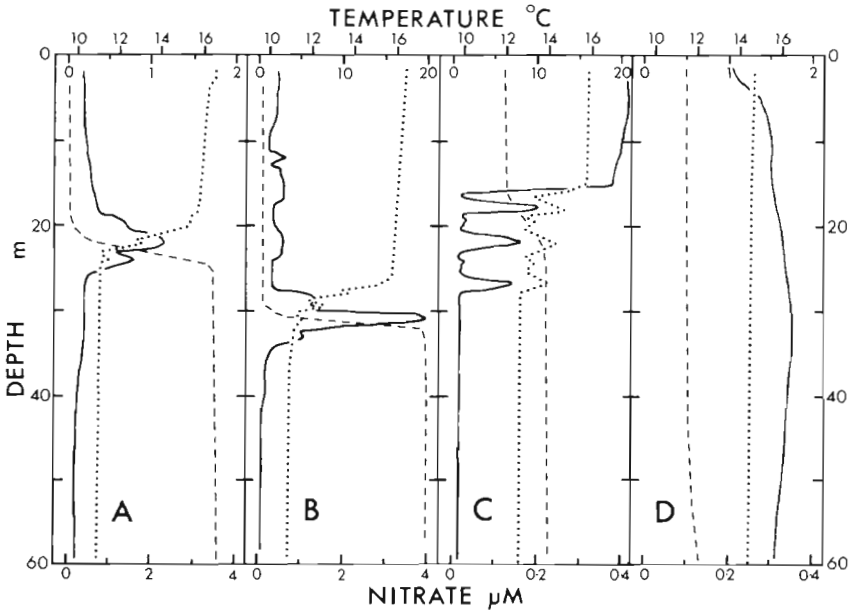

Fig. 1. Vertical distributions of temperature (···), chlorophyll *a* (——), and nitrate (– – –) in the upper 60 m of the water column. (A) Station E5, 28 July, 1981; (B) Station E5, 27 July, 1981; (C) Station F, 1 Aug, 1981; (D) Station M, 25 Jul, 1981. Lower scales on top axis: chlorophyll *a* concentrations (mg m^{-3}). Corresponding downwelling irradiance profiles for (A), (C) and (D) are shown in Fig. 1. of Holligan et al. (1984)

Also, since maximum assimilation rates were relatively high (9 to 12 mg C [mg chl. *a*]$^{-1}$h^{-1}) at Stations E5 and M, there is no reason to suspect abnormally high rates of exudation. In experiments with cultures in which carbon uptake was measured by chemical analysis (Myers and Cramer, 1949) and in other studies with natural populations (McAllister et al., 1961 Davies and Williams, 1984) high O_2/CO_2 molar flux ratios have been found, especially at low light intensities, when nitrate was known or presumed to be the nitrogen source. These observations suggest that there may be some biochemical explanation for high photosynthetic quotients during nitrate assimilation, although the possibility that the ^{14}C method underestimated carbon assimilation cannot be ruled out.

Ambient levels of nitrate, nitrite and ammonium in surface waters were generally < 0.2 µM. Only for the samples from the thermocline at E5 (26 m on 27 July 1981, and 20 m on 1 June 1982), where subsurface chlorophyll maxima are characteristically associated with the nitrate gradient between surface and bottom waters (Fig. 1), was there any direct evidence for nitrate assimilation from variations in P.Q. values. In the mixed water column at Station M, some input of nitrate was probably maintained by remineralisation in the sediments, whereas in the surface layers overlying the thermocline at Stations E5 and F ammonium regenerated by herbivorous organisms is likely to have been the major source of nitrogen for the phytoplankton.

Results of the 1981 *in situ* ^{14}C experiments at each of the three stations were evaluated for reference vertical profiles, for which detailed plankton (Holligan et al., 1984) and hydrographic (Fig. 1) data were obtained.

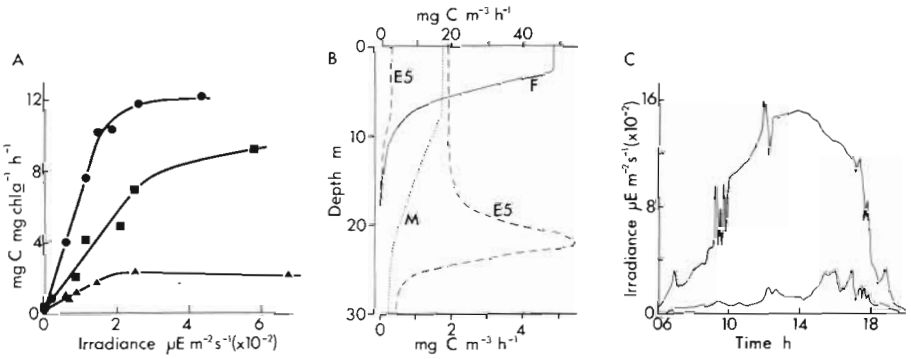

Fig. 2. (A) Photosynthesis (*in situ* ^{14}C method) – light curves for E5 (■), F (▲) and M (●) in Jul–Aug 1981. Each point represents the mean of 3 observations. Curves drawn by eye. (B) Calculated gross photosynthetic production profiles for surface irradiance values of 1600 µE m^{-2} (all 3 stations) and 200 µE m^{-2} s^{-1} (E5 only). Each profile derived from light and chlorophyll profiles (Fig. 1A, C, D) and photosynthesis-irradiance curves (Fig. 2A), assuming that wind mixing at the surface prevents photoinhibition. Upper production scale applies to F and M, lower to E5. (C) Daily irradiance plots obtained on the ship for 24 Jul, 1981 (high light) and 1 Aug, 1981 (low light)

Table 2. Respiration data for Stations E5, F and M

Station	Date	Sample depth (m)	Incubation period (h)	Chlorophyll *a** concentration (mg m^{-3})	Respiration rate (mg O_2 m^{-3} d^{-1})
E 5	26. 7. 81	7	7.0	0.34	69 ± 12
		17	7.0	0.35	78 ± 9
		50	7.0	0.16	2.4 ± 6.5
	27. 7. 81	7	5.6	0.26	103 ± 20
		17	5.6	1.45	167 ± 20
		26	5.6	2.81	120 ± 15
		50	5.6	0.19	30 ± 25
	28. 7. 81	7	5.0	[0.20]	74 ± 7
		17	5.0	–	152 ± 16
		26	5.0	–	125 ± 12
		50	5.0	[0.15]	10 ± 18
	9. 8. 82	5	24.0	0.18	55 ± 4
	10. 8. 82	5	12.0	0.16	74 ± 10
	10. 8. 82	5	24.0	0.16	50 ± 5
F	30. 7. 81	4	3.5	54.8	1718 ± 130
	31. 7. 81	4	4.25	34.9	1323 ± 67
		10	5	28.3	912 ± 16
	1. 8. 81	50	11.5	0.26	43 ± 10
	5. 8. 82**	4	24	50.8	1066 ± 16
	6. 8. 82**	5	11	29.5	621 ± 25
		5	24	29.5	504 ± 5
M	24. 7. 81	10	6.2	1.47	144 ± 15
	25. 7. 81	10	4.1	1.65	61 ± 42
		10	12	[1.6]	94 ± 11
		5	8.5	[1.4]	145 ± 34
		10	8.5	[1.4]	104 ± 13
		20	8.5	[1.5]	78 ± 24
		30	8.5	[1.6]	124 ± 38
		50	8.5	[1.7]	110 ± 15

* Values in parentheses are inferred from *in vivo* fluorometer records
** Position 49° 39′ N 05° 06′ W

Rates of carbon fixation were normalised against chlorophyll, and plotted as standard photosynthesis-light curves (Fig. 2A). From information on the vertical distributions of light and chlorophyll (Fig. 1) at each station, primary production profiles (Fig. 2B) were then constructed for a range of surface light conditions. Surface water was considered to be well mixed by wind so that, even under midday sunshine conditions, the influence of photoinhibition on rates of photosynthesis was negligible. The effects of light absorption by chlorophyll (self-shading) and by water are clearly apparent by comparing the production and chlorophyll profiles for each station, and at E5 it seems that there was significant production within the subsurface chlorophyll maximum only above a threshold surface irradiance of ~ 400 μE m^{-2} s^{-1}.

Finally, values of daily gross primary production were calculated for observed extremes of daily irradiance (Fig. 2C). Due to the discrepancies between O_2 and CO_2 measurements, these are considered as minimal estimates of primary production, particularly for Station E5. They are interpreted in relation to the standing stock of plant carbon and to compatible estimates of community respiration in the next section (Table 3).

Respiration

The 1981 respiration measurements at Stations E5, F and M, together with comparable data obtained in 1982 for E5 surface water and a *Gyrodinium aureolum* bloom close to Station F, are summarised in Table 2. Daily integral values for respiration were calculated for the whole water column (Table 3) by interpolation of the discrete depth measurements, with appropriate scaling against chlorophyll for the dinoflagellate population. All measurements were made with 125 ml water samples and are interpreted in terms of the combined activity of phytoplankton and microhetero-

Table 3. Estimates of plankton standing stocks, photosynthesis and respiration for stratified (E5), frontal (F) and mixed (M) waters in 1981

Station	E 5			F			M
Depth range (m)	0–30	30–120	Total (120 m)	0–16	16–96	Total (96 m)	Total (76 m)
Standing stocks (g Cm^{-2})[1]							
Particulate organic	8.5	19.3	27.8	33.5	17.3	50.8	20.3
Phytoplankton	0.4	0.4	0.8	25.7	4.3	30.0	7.0
Microheterotrophs	0.6	0.6	1.2	1.6	1.0	2.6	1.3
Mesozooplankton	0.8	1.1	1.9	0.1	0.8	0.9	1.1
Photosynthetic rate (g Cm^{-2} d^{-1})[2]	0.10–0.60 (0.15–0.90)	– –	0.10–0.60 (0.15–0.90)	0.68–2.7 (0.92–3.6)	– –	0.68–2.7 (0.92–3.6)	0.52–2.8 (0.70–3.8)
Respiration (g Cm^{-2} d^{-1})							
Observed	0.88	0.12	1.00	3.1	1.0	4.1	2.5
Calculated phytoplankton[3]	*0.10*	–	*0.10*	*3.1*	*0.5*	*3.6*	*2.0*
Calculated microheterotroph[4]	*0.57*	*0.48*	*1.05*	*1.50*	*1.05*	*2.55*	*1.20*
Calculated mesozooplankton[5]	*0.05*	*0.07*	*0.12*	*0.01*	*0.05*	*0.06*	*0.07*
Sum of calculated rates	*0.72*	*0.55*	*1.27*	*4.61*	*1.60*	*6.21*	*3.27*
Specific respiration rate (d^{-1})[6]	0.88	0.12	0.50	0.11	0.19	0.13	0.30
Maximum phytoplankton growth rate (d^{-1})[7]	1.17			−0.023			0.16

[1] For details see Holligan et al. (1984). Surface depth intervals of 30 and 16 m at Stations E 5 and F correspond to vertical distribution of chlorophyll *a* in the wind mixed and thermocline layers (Fig. 2 B); carbon distributions have been interpolated accordingly. Microheterotrophs include bacteria, protozoans and microzooplankton

[2] Minimum and maximum values derived from ^{14}C experiments correspond to cloudy and sunny weather conditions respectively (Fig. 2). No corrections have been made for the exudation of organic carbon. Values in parentheses are gross rates based on oxygen measurements

[3] Calculated as 0.06 P_{max} for stations E 5 and M

[4] Calculated assuming a specific respiration rate of 1.5 gO_2 [g dry weight]$^{-1}$ d^{-1}, a carbon to dry weight ratio of 1:2, and R. Q. = 0.85 (see text and Williams, 1981)

[5] Calculated assuming a specific respiration rate of 0.1 gO_2 [g dry weight]$^{-1}$ d^{-1}, and the carbon to dry weight and R. Q. values given above (see text and Williams, 1981)

[6] Calculated from observed respiration rates and total standing stock of autotroph + microheterotroph carbon

[7] Calculated as doublings d^{-1} (Cullen and Eppley, 1981) from net photosynthetic rate (i.e. measured photosynthesis under optimal illumination minus calculated algal respiration) and standing stock of autotroph carbon

trophs (bacteria, protozoans and microzooplankton). For the reference profiles at E5, F and M in 1981, the microheterotrophs were calculated to be equivalent to 150, 6 and 16 %, respectively, of the plant biomass in the euphotic zone (Holligan et al., 1984).

Values for oxygen consumption within blooms of the dinoflagellate, *Gyrodinium aureolum*, can be considered due to plant respiration alone. Comparison of the specific respiration values (i.e. oxygen consumption per unit chlorophyll *a* or cell carbon) shows that rates in 1981 (incubation times < 5 h) were about 50 % greater than those in 1982 (incubation times 11 to 24 h). Since the specific photosynthetic oxygen production at an equivalent light intensity was 2 to 3 times higher in 1982 (Fig. 3) than in 1981 (a precise comparison cannot be made due to differences in incubation times and *in situ* light conditions), this may indicate a real difference between the two populations. However, it could also reflect a decrease in respiration with incubation time as, in the 1982 experiment, the rate over the first 11 h was ~ 1.5 times that observed between 11 and 24 h (Table 2). The potential for net oxygen production within the *G. aureolum* blooms, which can give saturation values as high as 170 % (unpublished observations), is shown clearly in Fig. 3 (Station F). On the other hand, when maximum photosynthetic rates are relatively low as in 1981, the combination of shelf-shading and respiration appears to lead to a negative growth rate for the population as a whole, even under optimal conditions of surface irradiance. Another important point to note is that the respiration rate of *G. aureolum*, expressed relative to cell chlorophyll *a* or carbon (Table 3), is comparable to values estimated by Steemann Nielsen and Hansen (1959) for other natural phytoplankton populations; the higher respiration values measured in 1981 are equivalent to about 6 % of the maximum observed photosynthetic rate (7 mgC [mg Chl *a*]$^{-1}$; Pingree et al., 1976)

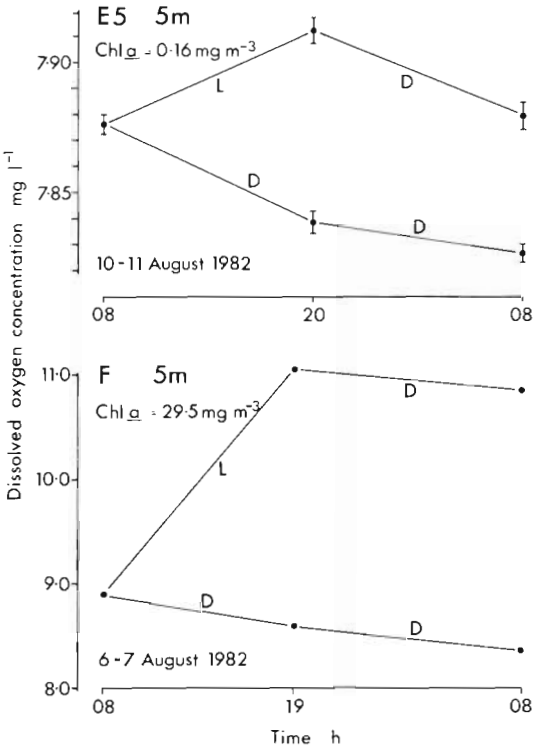

Fig. 3. Changes in dissolved oxygen concentration in light (L) and dark (D) bottles with time. Lines connect dissolved oxygen determinations. Standard errors of means, shown for E5 experiment, were less than diameter of dots for F. Position of Station F (1982): 49°39' N 05°06' W

for *G. aureolum*. This implies, however, that the same respiration rate is maintained at higher growth rates (Laws and Caperon, 1976).

For the stratified water at E5, which was characterised by a chlorophyll-poor wind mixed layer and a subsurface chlorophyll maximum, the respiration rates on the four sampling occasions were remarkably consistent (Table 2). The highest values were associated with elevated chlorophyll levels in the upper part of the thermocline, but were not coincident with the chlorophyll maximum itself (compare the 17 and 26 m samples for 1981). Respiration rates for surface waters were similar on both years, and the 24 h incubation times for 1982 indicate that phytoplankton production and microheterotroph consumption were in close balance with one another (e.g. Fig. 3). In turn, this suggests that the capacity of seasonally stratified waters to support the production of mesozooplankton and larger organisms is effectively regulated by variations of plant production within the thermocline. Calculations of integral photosynthesis and respiration rates from the 1981 data (Table 3) show that the net primary production was positive even during cloudy weather, but was generally insufficient to meet the demands of the heterotrophs. However, allowing for the possibility that the ^{14}C-method underestimated photosynthetic rates (values based on the O_2 measurements are given in parentheses in Table 3), it is possible to envisage a situation of material balance under optimal light conditions (i.e. sunny days).

In the tidally mixed environment at Station M, planktonic organisms were uniformly distributed throughout the water column. The respiration measurements were more variable than at the other two stations, but a mean value for the water column indicates that the balance between respiration and photosynthesis fluctuated with surface irradiation (Table 3). This conforms with the expected pattern of events in a situation where the water depth approximates to the critical depth (Sverdrup, 1953) so that growth of the phytoplankton population tends to be restricted by light rather than by nutrients. Calculations from the plankton carbon data imply that the bulk of water column respiration at Station M is attributable to the phytoplankton (Table 3), and that gross primary production is a poor indicator of secondary production rates. This is probably the reason for lower standing stocks of heterotrophs at this station as compared with E5 even though integral gross photosynthesis rate was much greater.

In Table 3, estimates of respiratory demands based on the biomass data are also presented. The calculations are approximate (e.g. no temperature corrections were attempted), using the coefficients listed by Williams (1981) to provide mean rates for the mesozooplankton (0.1 g O_2 consumed [g dry weight]$^{-1}$ d^{-1}) and the microheterotrophs (1.5 g O_2 [g dry weight]$^{-1}$ d^{-1}). Within these restrictions, there is reasonably good agreement between the respiration rates determined from *in vitro* oxygen changes and those estimated from microscope biomass data for the plankton populations above the thermocline at Stations E5 and F and throughout the water column at Station M. The calculated rates below the thermocline appear to be too high; this implies, not surprisingly, that the heterotrophic organisms at and above the thermocline are metabolically more active than those below, and that the coefficients adopted by Williams (1981) are only appropriate to the former situation. The other feature to emerge is the relatively small contribution made by the mesozooplankton towards community respiration. The calculated mesozooplankton respiration rates are < 10 % of those of the total zooplankton and are comparable to the results for the CEPEX experiments (Williams, 1981).

From the photosynthesis and respiration data the maximum potential growth rates of the phytoplankton (i.e. under optimal light conditions) can be estimated. These values are given in Table 3 and illustrate the very different dynamic states of the populations in

stratified, mixed and frontal waters. At Station F, plant carbon is abundant but, due mainly to the effects of light limitation and respiration, the *Gyrodinium aureolum* is calculated to have a negative growth rate. By contrast, at E5, the plant carbon is low but could have a doubling time of 1 d or less; the range in daily values for primary production is similar to that reported by Joint and Pomroy (1983) for stratified water in the Celtic Sea. The phytoplankton in the mixed water appears intermediate with respect to both biomass and growth rate.

Renewal and regeneration of nitrogen in stratified waters

For stratified waters in which combined inorganic nitrogen is depleted in the surface layers but remains relatively high (mainly as nitrate) below the thermocline or pycnocline, the vertical gradients and fluxes of nitrogen are of fundamental importance in controlling phytoplankton growth. In the context of the profiles for Stations E5 and F (Fig. 1) 2 important questions are: what is the relative importance of nitrate renewal from below the thermocline and ammonium regeneration in the surface layers for phytoplankton growth, and how do surface phytoplankton blooms in frontal regions accumulate nitrogen to the extent that particulate N exceeds maximum winter levels of nitrate N?

In a region of strong tides, the supply of nitrate to the surface layers is likely to be determined by vertical mixing rather than isopycnal transport or other effectively horizontal processes. The consistent observation that nitrate reaches its minimal surface value within or close to the thermocline chlorophyll maximum (Pingree et al., 1977) indicates that the phytoplankton in this layer are actively assimilating nitrate and also that, as the nitrate gradient in the upper part of the thermocline (density gradient) is zero, there can be no significant mixing of nitrate into the surface layer. It is possible, therefore, to make an estimate of nitrate uptake in the thermocline given appropriate data on the nitrate (N) and temperature (T) gradients and values for the vertical heat flux between the surface and bottom layers.

The vertical heat flux (F_H) and nitrate flux (F_N) can be defined in terms of the vertical diffusion coefficient K for any depth (Z) interval –

$$F_H = \frac{H}{C_p P} = -K \frac{\delta T}{\delta Z} \quad (1)$$

where C_p = specific heat at constant pressure; P = the density of sea-water.

and

$$F_N = -K \frac{\delta N}{\delta Z} \quad (2)$$

Substituting for K gives

$$F_N = F_H \cdot \frac{S}{\Delta T} \cdot \Delta N \quad (3)$$

where

$$S = \left(\frac{\Delta T}{\Delta N}\right)\left(\frac{\delta N}{\delta T}\right)$$

in which the units for ΔN are $\mu g\ NO_3$–N cm^{-3} if F_H is expressed as cal $cm^{-2}\ d^{-1}$.

Values of S were estimated from nitrate and temperature profiles associated with weak and strong chlorophyll maxima in the region of E5 (Fig. 4). The

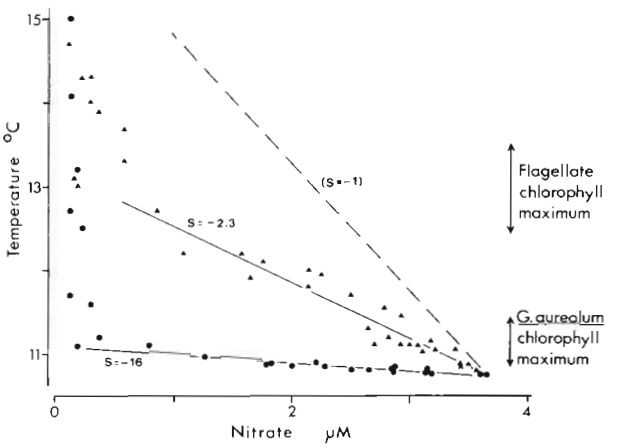

Fig. 4. Temperature-nitrate plots for chlorophyll profiles dominated by *Gyrodinium aureolum* (●) and by small flagellates (▲) at Station E5 on 27 and 28 Jul, 1981. Maximum chlorophyll concentrations were ~2 and 20 mg m^{-3} (Fig. 1A, B). Lines show relative gradients of changes in temperature to changes in nitrate (S). Dashed line (S = −1); expected distribution of nitrate if there was no uptake in the thermocline (i.e. changes in nitrate universely proportional to those in temperature)

weak maximum, composed mainly of small flagellates (< 10 μm in diameter), showed the highest chlorophyll *a* concentrations (< 2 mg m^{-3}) close to the mid-point of the temperature gradient (Fig. 1) and a small value for S. By contrast, the strong maximum, which represented the western extent of the *Gyrodinium aureolum* bloom around Station F (see Holligan et al., 1983, 1984 for further details), was characterised by chlorophyll levels up to 20 mg m^{-3} at the base of the thermocline within 0.5 C° of the bottom water temperature (Fig. 1) and a large S value. Using typical summer values for ΔN and ΔT, the potential vertical nitrate fluxes and equivalent rates of photosynthetic carbon fixation corresponding to the 2 values of S were then calculated for Stations E5 and F (Table 4). They indicate that the downward displacement and steepening of the nitrate gradient by *G. aureolum* can lead to net primary production rates as high as 3 g C $m^{-2}\ d^{-1}$.

The flux of nitrate into the weak chlorophyll maximum (S = −2.3) at Station E5 at the end of July 1981

Table 4. Potential vertical fluxes of nitrate at Stations E5 and F

	Depth of BML (m)	Average temp. increase of BML April–July[1] (°C)	Vertical heat flux into BML (F_H) (cal cm^{-2} d^{-1})	Temp. difference across thermocline (ΔT)[1] (°C)	Nitrate difference across thermocline (ΔN)[1] (μg NO_3–N cm^{-3})	Relative gradient of changes in temperature to changes in nitrate (S)[2]	Vertical nitrate flux out of BML (F_N) (μg NO_3–N cm^{-2} d^{-1})	Equivalent 'new' carbon production[3] (g C m^{-2} d^{-1})
E5	90	1.0	100	5	0.070 (5 μM)	− 2.3	3.22	0.26
						−16	22.4	1.79
F	75	2.5	208	3.5	0.042 (3 μM)	− 2.3	5.74	0.46
						−16	39.94	3.19

BML = bottom mixed layer
[1] Typical values from previous observations; see Pingree et al. (1976) and Holligan (1981)
[2] Maximum and minimum values based on the 2 nitrate profiles shown in Fig. 4
[3] Net values for primary production based on a $^C/_N$ ratio of 8.0 for phytoplankton

was probably somewhat lower than that given in Table 4, due mainly to relatively low nitrate concentrations (~ 0.052 μg NO_3-N cm^{-3} or 3.7 μM) in the bottom water compared to other years (Holligan, 1981). In relation to the production data given in Table 3, a more realistic value is 24 mg N m^{-2} d^{-1} which is equivalent to a net primary production rate of 0.19 g C m^{-2} d^{-1}. Therefore about half the total plant production under average light conditions (Table 3) appears to have been based on nitrate uptake, although the relative rates of nitrogen and carbon assimilation by plant cells in the thermocline at any one time are likely to have been variable due to light dependent fluctuations in photosynthesis (Fig. 2B).

The high nitrate fluxes predicted for the subsurface *Gyrodinium aureolum* populations (S = −16) provide the first realistic explanation of the phenomena of surface particulate N accumulation (as plant cells) and bottom nitrate depletion (see Fig. 1) that are characteristic of bloom conditions. Thus when F_N is high it will tend to exceed the regeneration rate (R_N) for nitrate in the bottom water (depth h) so that ΔN will decrease. A time scale for this effect can be calculated from the relationship.

$$\frac{\delta \Delta N}{\delta t} \cdot h = R_N h - F_N \qquad (4)$$

Substituting for F_N (Eq 3), assuming R_N is constant, and solving for t gives

$$t = -\frac{1}{k} \ln \left(\frac{R_N - k\Delta N}{R_N - k\Delta N_o} \right) \qquad (5)$$

where

$$k = F_H \cdot \frac{S}{\Delta T} \cdot \frac{1}{h}$$

is assumed constant for S = −16 (Table 4), and ΔN_o and ΔN are respectively the differences in nitrate concentration across the thermocline at the start of the bloom (t = o) and after t days.

As a first approximation it can be assumed that, when the summer chlorophyll maximum is weakly developed and *Gyrodinium aureolum* is not dominant, changes in ΔN are slight so that $R_N \simeq F_N/h$ (i.e. nitrate production in the bottom water due to presumed nitrification processes is equivalent to nitrate losses due to upward mixing and uptake in the thermocline). If this value for R_N is applied to conditions when *G. aureolum* is abundant in the thermocline (note that the total standing stock of heterotrophs appears to remain relatively constant; Table 3), the period for ΔN to be reduced to 0.02 ΔN_o (Fig. 1C) is calculated to be 34 d for typical starting conditions at Station F (Table 4). This gives good agreement with the time scale of about one month based on field observations (Holligan et al., 1983) for bloom development. Furthermore, the accumulation of particulate plant nitrogen in the surface waters at F (Table 3) is equivalent to that estimated to have been removed from below the thermocline.

It appears therefore that the ability of *Gyrodinium aureolum* to form dense populations in frontal regions can be explained in terms of nitrate uptake in the thermocline and upward movement of the cells into the surface layer. Although diel vertical migrations have not been observed for this species in the western English Channel comparable to those described for other dinoflagellates (Cullen et al., 1982), it is possible that the cells move up and down over longer time scales in order to obtain nitrate at the base of the thermocline. Restrictions on the assimilation of nitrate by *G. aureolum* are likely to be set by the depth of the thermocline, which affects the light available for photosynthesis in the nitrate gradient as well as vertical distance over which the cells have to move. Conditions in the deeper thermocline at E5 may be limiting in these respects, as this station generally represents the western extent of the frontal dinoflagellate blooms.

The potential rate of nitrogen regeneration by zoo-

Table 5. Ammonium excretion by dominant copepod species at Stations E5 and F

Species	Station	Number of observations	Body N (µg)	Excretion rate µg NH_4-N copepod^{-1} h^{-1}	Excretion rate % body−N d^{-1}
Calanus helgolandicus	E 5	8	18.2	0.025	3.3
	F	5	16.0	0.027	4.1
Paracalanus parvus•	E 5	3	1.1	0.009	19.1
Metridia lucens	E 5	2	9.0	0.044	11.7
Centropages typicus	E 5	1	3.3	0.008	5.8

• Mixed copepodites

plankton can be estimated from the experimental data on ammonium excretion (Table 5). *Calanus helgolandicus* and copepodites of *Paracalanus*, as representatives of the meso- and microzooplankton groups, gave excretion rates of 3.7 % (mean of value for Stations E5 and F) and 19.1 % of body nitrogen per day respectively which are consistent with other observations for copepods of similar size (Corner and Davies, 1971; Ikeda, 1974). These values, taken with the biomass and C : N ratio data given by Holligan et al. (1984) allow the total ammonium regeneration for the surface mixed layer to be estimated (Table 6).

This approach assumes that a single excretion rate can be applied to all organisms within a given size fraction, that the results of short-term incubation experiments immediately after capture are representative of *in situ* excretion rates, and that ammonium is the principal nitrogenous excretory product (Corner and Davies, 1971). The latter assumption is probably correct, although urea might also be important (Eppley et al., 1973). Finally diurnal vertical migration is not taken into account. This probably does not affect the results for the microzooplankton but the pronounced migratory activity of the mesozooplankton at E5 may have had a significant influence on the spatial pattern of nitrogen regeneration.

Within these restrictions, it appears that the contribution of zooplankton excretion to the nitrogen flux in the surface layer at E5 when *Gyrodinium aureolum* is absent (i.e. the chlorophyll sub-surface maximum is weakly developed) considerably exceeds that from nitrate penetrating the thermocline (Table 6). However, as the input of nitrate is increased either through uptake by dinoflagellates at the base of the thermocline or through tidal mixing (compare Stations E5 and F; Table 4), regeneration is likely to supply a much lower proportion of the nitrogen required by the phytoplankton. The excretion experiments also showed that most of the ammonium was released by the microzooplankton at both stations.

As a first approximation, the estimated rates of ammonium-N excretion below the thermocline at Stations E5 and F (Table 6) are equivalent to the estimated upward fluxes of nitrate (Table 4). Since there is no significant increase in the concentrations of ammonium or nitrite in the bottom water during summer, the ammonium is likely to be converted to nitrate by nitrifying bacteria under conditions of low illumination (Olson, 1981). The range in rates of nitrification (0.02 to 0.08 µM l^{-1} d^{-1}) implied by estimates of the upward flux of nitrate under non-bloom conditions (Table 4) and of ammonium excretion in the bottom water (Table 6)

Table 6. Potential NH_4-N regeneration through zooplankton excretion at Stations E5 and F

Station		Nitrogen regeneration via excretion (µg NH_4-N cm^{-2} d^{-1})			Zooplankton regeneration as % of vertical nitrate flux• out of BML
		Microzooplankton	*Mesozooplankton*	Total	
E 5	0–30 m	5.15	2.43	7.58	34–235
	30–120 m	3.60	5.04	8.64	–
	Total	8.75	7.47	16.22	–
F	0–16 m	2.92	0.80	3.72	9.3–65
	16–96 m	5.70	2.33	8.03	–
	Total	8.62	3.13	11.75	–

• Based on maximum and minimum values given in Table 4. BML = bottom mixed layer

are compatible with the maximum rates measured in coastal California waters (Ward et al., 1982). This suggests that the nitrogen cycle in the stratified shelf waters is maintained during the summer months largely by processes occurring within the water column as opposed to the surface sediments.

DISCUSSION

The aim of this investigation of summer plankton populations in stratified, frontal and mixed shelf waters has been to establish firstly how light and inorganic nutrient (nitrate) supply affect rates of net primary production, and secondly whether the microheterotrophs are important consumers of plant carbon. The phytoplankton populations in the three situations are typically quite different – mainly small flagellates showing a well defined subsurface chlorophyll maximum under stratified conditions, dinoflagellate blooms in the frontal region and diatoms in the tidally mixed waters – and specific differences in their physiological and behavioural properties (Cullen and Eppley, 1981) have yet to be examined in detail. However, compatible measurements of photosynthesis and respiration have shown basic differences between these contrasting hydrographic regimes in terms of both the relative biomass and the rates of turnover of primary and secondary producers. These appear to be of fundamental importance in understanding the dynamic properties of the 3 types of plankton community.

At all 3 stations the photosynthetic quotient values were higher than predicted for ammonium or nitrate assimilation. These discrepancies between the oxygen and ^{14}C methods for measuring photosynthesis are probably due in part to the exudation of organic substances, and to other physiological or biochemical properties that influence the balance between oxygen production and carbon uptake. However, it is also possible that the ^{14}C estimates of gross photosynthetic carbon fixation were too low by as much as 30 % at Stations M and F (assuming mainly NH_4 assimilation) and up to 50 % at E5 (assuming NH_4 and NO_3 assimilation for the surface and thermocline layers respectively).

The respiration measurements represent the mean of seven replicate samples and gave consistent results, the main uncertainty being an apparent reduction in oxygen consumption with time by *Gyrodinium aureolum* during long incubation periods. The data for F and M were consistent with previous observations on the respiration of natural phytoplankton populations (Steemann Nielsen and Hansen, 1959) so that net primary production rates at these two stations can be calculated with some confidence. At Station E5 both the carbon biomass data, and the high specific respiration rate indicate that respiration was dominated by the microheterotrophs so that, even though it was not possible to estimate phytoplankton respiration directly, it certainly represented only a small proportion of total respiration. For all three stations the phytoplankton growth rates (Table 3) were calculated on the basis of optimal light conditions (Fig. 2C). However, the effect of lower average light levels will be offset by any underestimation of gross photosynthesis by the ^{14}C method, so that these values may represent reasonable approximations of actual growth rates. The main difference between the stations was that the phytoplankton growth rate appeared to be positive under all light conditions only at E5, whereas at Station M it probably fluctuated between negative and positive values according to daily irradiance levels, and at F was generally negative at the time of the observations due to self-shading effects.

The estimated vertical fluxes of nitrate for Station E5 (Table 4) indicate that the supply of 'new' nitrate-nitrogen resulting from vertical mixing and assimilation in the subsurface chlorophyll maximum supports up to 50 % of total net primary production during the summer in regions with a well developed thermocline ($\Delta T > 5$ °C) and low standing crop of chlorophyll (< 20 mg m^{-2}). This value is similar to that suggested by Harrison (1980) for West Atlantic shelf waters with comparable rates of annual production. It was also shown that the position of the chlorophyll maximum in the thermocline as well as the behavioural responses of the phytoplankton (Cullen and Eppley, 1981) are critical in determining how much nitrate (or other nutrients) can be extracted from the bottom water Attempts to estimate (Pingree and Pennycuick, 1975) or model (Tett, 1981) primary production in stratified shelf waters in terms of vertical mixing across the seasonal thermocline must be related to precise information about the distributions of nitrate and/or phytoplankton. Any displacement of the chlorophyll maximum towards the base of the thermocline is likely to be associated with increases in total primary production and in the proportion of 'new' as opposed to 'regenerated' production.

In the case of subsurface *Gyrodinium aureolum* populations the high daily nitrate fluxes and inferred carbon fixation rates given in Table 4 represent maximum initial values which are reduced as nitrate is depleted in the bottom water and as light levels in the thermocline fall due to population growth and self-shading. The good correspondence between the observed and calculated rates of bloom development ($\sim$ 30 d), and between nitrate depletion of the bottom water and phytoplankton-N accumulation in the sur-

face layers are convincing evidence that the general mechanism for bloom formation, based on nitrate assimilation within the thermocline, is correct. Furthermore, as supposed from data on zooplankton distributions (Holligan et al., 1984) and the rate of increase in cell density (Holligan et al., 1983), it is unlikely that the grazing mortality of *G. aureolum* is significant. Further work is still needed to substantiate earlier observations (Pingree et al., 1976) of high assimilation rates for *G. aureolum* in the thermocline, although they must be a prerequisite of bloom formation. The factors that determine the rate of development and extent of the blooms are not certain, although physical conditions within the thermocline – in particular vertical stability – are probably critical in allowing the chlorophyll maximum to persist at the base of the temperature gradient.

The estimates of nitrogen regeneration by zooplankton, as compared to the potential nitrogen demand for phytoplankton production and to the vertical flux of nitrate through the thermocline, indicate the importance of recycling by zooplankton, especially the 80 to 200 µm fraction in the surface water at E5. This observation is consistent with the work of Harrison (1978) who concluded that the microplankton (< 183 µm) may be the primary nitrogen remineralizers. In the present work, the significance of protozoans and bacteria in regeneration has not been estimated, but a general agreement has been found between phytoplankton nitrogen requirement and regeneration by the > 80 µm zooplankton.

Other studies have emphasised the importance of nitrogen regeneration by zooplankton in comparable environments. For example, Eppley et al. (1973), working in the central north Pacific estimated the ratio between zooplankton excretion and phytoplankton assimilation to range from 0.4 to 0.5 for ammonium and 0.4 to 1.1 for urea. Off northwest Africa Smith and Whitledge (1977) reported that zooplankton supplied 44 % of the ammonium and 25 % of the total nitrogen demand of the phytoplankton, and they concluded that these were unusually high values for eutrophic areas. In the Peruvian upwelling system Dagg et al. (1980) found that the larger copepods contributed only 3 % of the ambient excretory nitrogen daily, suggesting that the abundant small copepods must be important in such systems (see also Dagg and Cowles, 1982; Paffenhöfer, 1982).

To conclude, the phytoplankton population in mixed water is formed mainly of chain forming diatoms which are kept up in the surface layers by tidal mixing. Due to the combined effects of low mean light levels in the whole water column and respiration, the growth rate of the plant population is variable but, on average, low. The respiration data indicated a correspondingly low specific metabolic activity for the microheterotroph community. By contrast, positive net primary production by populations of flagellates is apparently maintained in stratified waters, giving growth rates > 1 d^{-1} during clear weather when there is sufficient light for photosynthesis in the thermocline chlorophyll maximum. Under these conditions a very active microheterotroph population is found, with high specific respiration rates and rapid regeneration of inorganic nitrogen. Close to the frontal boundary where the thermocline is relatively shallow (< 20 m), *Gyrodinium aureolum* is often abundant, giving large standing crops of particulate material. This is apparently achieved by assimilation of nitrate at the base of the thermocline but the physiological and behavioural mechanisms for the maintenance of cell nitrogen in persistent surface blooms have still to be investigated.

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LITERATURE CITED

Anderson, J. J., Okubo, A. (1982). Resolution of chemical properties with a vertical profiling system. Deep Sea Res. 29: 1013–1019

Carritt, D. E., Carpenter, J. H. (1966). Comparison and evaluation of currently employed modifications of the Winkler method for determining dissolved oxygen in seawater; a NASCO report. J. Mar. Res. 24: 286–317

Corner, E. D. S., Davies, A. G. (1971). Plankton as a factor in the nitrogen and phosphorus cycles in the sea. Adv. mar. Biol. 9: 101–204

Corner, E. D. S., Newell, B. S. (1967). On the nutrition and metabolism of zooplankton. IV. The forms of nitrogen excreted by *Calanus*. J. mar. biol. Ass. U.K. 43: 485–493

Cullen, J. J., Eppley, R. W. (1981). Chlorophyll maximum layers of the Southern Californian Bight and possible mechanisms of their formation and maintenance. Oceanologica Acta 4: 23–32

Cullen, J. J., Horrigan, S. G., Huntley, M. E., Reid, F. M. H. (1982). Yellow water in La Jolla Bay, California, July 1980. 1. A bloom of the dinoflagellate, *Gymnodinium flavum* Kofoid and Swęzy. J. exp. mar. Biol. Ecol. 63: 67–80

Cushing, D. H. (1957). The effect of grazing in reducing the primary production: a review. Rapp. P.-v. Rèun. Cons. int. Explor. Mer 144: 149–154

Dagg, M. J., Cowles, T (1982). Grazing by copepods in the Peru upwelling. Deep Sea Res. 29A: 147

Dagg, M. J., Cowles, T., Whitledge, T., Smith, S., Howe, S., Judkins, D. (1980). Grazing and excretion by zooplankton in the Peru upwelling system during April 1977. Deep Sea Res. 27A: 43–59

Davies, J. M., Williams, P. J. leB. (1984). Verification of ^{14}C and O_2 derived primary organic production measurements using an enclosed ecosystem. J Plankton Res. (in press)

Dring, M. J., Jewson, D. H. (1982). What does ^{14}C uptake by phytoplankton really measure? A theoretical modelling approach. Proc. R. Soc. B 214: 351–368

Eppley, R. W., Peterson, B. J. (1979). Particulate organic matter flux and planktonic new production in the deep ocean. Nature, Lond. 182: 677–680

Eppley, R. W., Harrison, W. G., Chisholm, S. W., Stewart, E. (1977). Particulate organic matter in surface waters off southern California and its relationship to phytoplankton. J. mar. Res. 35: 671–696

Eppley, R. W., Renger, E. H., Harrison, W. G. (1979). Nitrate and phytoplankton production in southern California coastal waters. Limnol. Oceanogr. 24: 483–494

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

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

Harrison, W. G. (1980). Nutrient regeneration and primary production in the sea. In Falkowski, P. G. (ed.) Primary productivity in the sea. Plenum Press, New York, p. 433–460

Hobson, L. A., Guest, K. P. (1983). Values of net compensation irradiation and their dependence on photosynthetic efficiency and respiration in marine unicellular algae. Mar. Biol. 74: 1–7

Holligan, P. M. (1981). Biological implications of fronts on the northwest European Shelf. Phil. Trans. R. Soc. A302: 547–562

Holligan, P. M., Harris, R. P., Newell, R. C., Harbour, D. S., Head, R. N., Linley, E. A. S., Lucas, M. I. Tranter, P. R. G., Weekley, C. M. (1984). The vertical distribution and partitioning of organic carbon in mixed, frontal and stratified waters of the English Channel. Mar. Ecol. Prog. Ser. 14: 111–127

Holligan, P. M., Viollier, M., Dupouy, C., Aiken, J. (1983). Satellite studies on the distributions of chlorophyll and dinoflagellates blooms in the western English Channel. Contin. Shelf Res. 2: 81–96

Ikeda, T. (1974). Nutritional ecology of marine zooplankton. Memoirs of the Faculty of Fisheries Hokkaido University 22: 1–97

Iturriaga, R., Zsolnay, A. (1983). Heterotrophic uptake and transformation of phytoplankton extracellular products. Botanica mar. 26: 375–381

Joint, I. R., Pomroy, A. J. (1983). Production of picoplankton and small nanoplankton in the Celtic Sea. Mar. Biol. 77: 19–27

Laws, E. A. (1975). The importance of respiration losses in controlling the size distribution of marine phytoplankton. Ecology 56: 419–426

Laws, E., Caperon, J. (1976). Carbon and nitrogen metabolism by *Monochrysis lutheri*: measurement of growth-rate-dependent respiration rates. Mar. Biol. 36: 85–97

Liddicoat, M. I., Tibbits, S., Butler, E. I. (1975). The determination of ammonia in sea water. Limnol. Oceanogr. 20: 131–132

Mague, T. H., Friberg, E., Hughes, D. J., Morris, I. (1980). Extracellular release of carbon by marine phytoplankton; a physiological approach, Limnol. Oceanogr. 25: 262–279

McAllister, C. D., Parsons, T. R., Stephens, K., Strickland, J. D. H. (1961). Measurements of primary production in coastal sea water using a large volume plastic sphere. Limnol. Oceanogr. 6: 237–258

Myers, J., Cramer, M. (1948). Metabolic conditions in *Chlorella*. J. gen. Physiol. 32: 103–109

Olson, R. J. (1981). Differential photoinhibition of marine nitrifying bacteria: a possible mechanism for the formation of the primary nitrite maximum. J. mar. Res. 39: 227–238

Paffenhöfer, G.-A. (1982). Grazing by copepods in the Peru upwelling. Deep Sea Res. 29A: 145–146

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

Pingree, R. D., Holligan, P. M., Head, R. N. (1977). The survival of dinoflagellate blooms in the Western English Channel. Nature, Lond. 265: 266–269

Pingree, R. D., Holligan, P. M., Mardell, G. T. (1978). The effects of vertical stability on phytoplankton distribution in the summer on the northwest European shelf. Deep Sea Res. 25: 1011–1028

Pingree, R. D., Holligan, P. M., Mardell, G. T., Head, R. N. (1976). The influence of physical stability on spring, summer and autumn phytoplankton blooms in the Celtic Sea. J. mar. biol. Ass. U.K. 56: 845–873

Pingree, R. D., Pennycuick, L. (1975). Transfer of heat, fresh water and nutrients through the seasonal thermocline. J. mar. biol. Ass. U.K. 55: 261–274

Riley, G. A. (1941). Plankton studies. IV. Georges Bank. Bull. Bingham Oceanographic Collection 7: 1–74

Smith, S. L., Whitledge, T. E. (1977). The role of zooplankton in the regeneration of nitrogen in a coastal upwelling system off northwest Africa. Deep Sea Res. 24: 49–56

Steemann Nielsen, E. (1955). The interaction of photosynthesis and respiration and its importance for the determination of ^{14}C discrimination in photosynthesis. Physiologia Plantarum 8: 945–953

Steemann Nielsen, E., Hansen, V. K. (1959). Measurements with the carbon-14 technique of the rates of respiration in natural populations of phytoplankton. Deep Sea Res. 5: 222–233

Sverdrup, H. U. (1953). On conditions for the vernal blooming of phytoplankton. J. Cons. 18: 287–295

Tett, P. (1981). Modelling phytoplankton production at shelf-sea fronts. Phil. Trans. R. Soc. A 302

Ward, B. B., Olson, R. J., Perry, M. J. (1982). Microbial nitrification rates in the primary nitrite maximum off southern California. Deep Sea Res. 29: 247–255

Williams, P. J. leB. (1981). Microbial contribution to overall plankton community respiration – studies in enclosures. In Grice, G. D., Reeve, M. R. (ed.) Marine mesocosms: biological and chemical research in experimental ecosystems. Springer-Verlag, Heidelberg, p. 305–321

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

Williams, P. J. leB., Jenkinson, N. W. (1982). A transportable microprocessor-controlled precise Winkler titration suitable for field station and shipboard use. Limnol. Oceanogr. 27: 576–585

Williams, P. J. leB., Raine, R. C. T., Bryan, J. R. (1979). Agreement between the ^{14}C and oxygen methods of measuring phytoplankton production: reassessment of the photosynthetic quotient. Oceanologica Acta 2: 411–416

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