Plankton community respiration and its relationship to chlorophyll *a* concentration in marine coastal waters

Plankton
Respiration
Chlorophyll *a*
Coastal waters
Microheterotrophs

Plancton
Respiration
Chlorophylle *a*
Eaux littorales
Microhétérotrophes

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ABSTRACT

Rates of plankton community respiration and chlorophyll *a* levels were measured in water samples collected at several times of the year in the North Sea, and during July in the English Channel. Planktonic community respiration rates ranged from 0.025 to 0.830 µmol O_2 l^{-1} h^{-1}. At low and moderate chlorophyll *a* concentrations (0-5 µg l^{-1}) the correlation between algal biomass and community respiration was not significant. However, respiration and chlorophyll *a* did correlate significantly and positively at chlorophyll *a* levels in excess of 5 µg l^{-1}. This is discussed in terms of the relative contribution to the total community respiration of autotrophs and microheterotrophs. It is argued that at low and moderate chlorophyll *a* concentrations, the microheterotrophs make the most substantial contribution to community respiration rates whilst at exceptionally high concentrations of chlorophyll *a* autotrophic dark respiration can be the dominant component of the plankton community respiration in the water column. The ratio of respiration to maximum photosynthesis (R/P_{max}%) is considered to be a useful indicator of the trophic balance of the plankton community. The range of this ratio varied from 2.2 to 75.9, lowest values being recorded in water masses with high rates of net algal growth.

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RÉSUMÉ

Relation entre chlorophylle *a* et taux de respiration du plancton dans les eaux littorales

Nous avons mesuré la chlorophylle *a* et le taux de respiration provenant de communautés planctoniques prélevées dans la Manche en juillet et dans la Mer du Nord à différentes époques de l'année. Les valeurs du taux de respiration sont comprises entre 0.025 et 0.830 µmol O_2 l^{-1} h^{-1}. Lorsque la concentration en chlorophylle *a* est inférieure à 5 µg l^{-1}, aucune corrélation significative n'existe

entre la biomasse phytoplanctonique et le taux de respiration de l'ensemble du plancton. Par contre, les deux paramètres sont étroitement liés dès que la teneur en chlorophylle *a* excède 5 µg l^{-1}. L'explication proposée repose sur la dominance d'espèces autotrophes ou d'espèces hetérotrophes quant à leurs contributions au taux de respiration global. Il est montré qu'aux faibles concentrations en chlorophylle *a*, les espèces microhétérotrophes contrôlent le taux de respiration global, tandis qu'aux concentrations élevées le mode de respiration autotrophe domine.
De ce fait, le rapport entre le taux de respiration et le taux maximum de photosynthèse (R/P_{max}%) peut servir à exprimer l'équilibre trophique de la communauté planctonique. Ce rapport évolue entre 2,2 et 75,9, et les valeurs inférieures sont enregistrées dans des masses d'eau connaissant un taux élevé de croissance nette des espèces phytoplanctoniques.

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INTRODUCTION

Respiration, defined as a biologically controlled oxidation of organic compounds (Burris, 1980), is the major consumption process of photosynthetically fixed carbon in the marine water column. Knowledge of respiration rates is essential for the quantification and modelling of energy and carbon flux within marine food webs. However, the relative contribution of the various metabolic groups to total planktonic respiration has yet to be established.

Data on plankton community respiration rates are remarkably sparse in the literature, particularly when compared to the number of photosynthesis measurements that have been reported (Peterson, 1980). This scarcity can mainly be attributed to the low routine precision of the Winkler assay, the established chemical method for measuring dissolved oxygen in sea water, and the low sensitivity of oxygen electrodes for measuring small changes in dissolved oxygen concentration in discrete samples. Both these approaches have been unsuitable for measuring changes in oxygen concentration in low to moderately productive waters *e.g.* oceanic oligotrophic waters. The alternative approach to measuring total plankton respiration has been to determine the biochemical activity of the electron transport system (ETS) using an enzyme assay procedure (Packard *et al.*, 1971; Packard, 1985). Although the principle behind this technique is reasonably straightforward, acceptance of the method has suffered from problems of interpretation of results (Williams, 1984).

Direct measurements of respiration from changes in dissolved oxygen concentration in the dark are now reliable due to substantial improvements in the precision of the Winkler titration technique (Bryan *et al.*, 1976; Williams and Jenkinson, 1982) and new approaches to using oxygen electrochemical sensors (Langdon, 1984; Smith and Horner, 1982). Thus potential artifacts associated with prolonged incubations (Steemann Nielsen, 1952) or preconcentration of natural plankton samples (Pomeroy and Johannes, 1968; Holm-Hansen *et al.*, 1970; Souza Lima, 1971) have been eliminated for respiration measurements.

Until comparatively recently (Williams, 1981 *a*) the notion that microheterotrophs (< 200 µm), including bacteria and protozoa (*e.g.* microflagellates, loricate and aloricate ciliates), played only a minor role in the structure and function of marine plankton communities had led to the suggestion that most of the oxidation of photoassimilated carbon is carried out by the larger members of the zooplankton or the photoautotrophs themselves (Steele, 1974). In the last decade, due to considerable improvements in techniques available for measuring bacterial biomass (Hobbie *et al.*, 1977; Porter and Feig, 1980) and production (Hagstrom *et al.*, 1979; Fuhrman and Azam, 1982), the role of planktonic microorganisms in the sea has undergone a thorough re-examination and evidence has been put forward to suggest that bacteria can be one of the major direct consumers of photosynthetically fixed carbon (Azam *et al.*, 1983 ; Linley *et al.*, 1983). In agreement with these results there is evidence suggesting that respiratory activity by the small fraction of the plankton (< 3 µm) can be significant (Williams, 1981 *b*; Kuparinen, 1984; Harrison, 1986). However, as yet few studies have attempted to determine the relative contribution of photoautotrophic and microheterotrophic oxygen consumption to overall plankton community respiration. Also, there has been little attention focused on the difference between the relative algal oxygen demand of low phytoplankton biomass communities and phytoplankton bloom populations.

We present here data on rates of plankton community respiration measured at various times of the year in several regions of the southern and central North Sea and during a summer bloom of the dinoflagellate *Gyrodinium aureolum* in the western English Channel. Results are discussed in terms of the relative contribution of the photosynthetic and non-photosynthetic organisms to the planktonic community respiration rates under different concentrations of phytoplankton biomass as indicated from measurements of chlorophyll *a*.

Data on the ratio of respiration to maximum rate of photosynthesis expressed as a percentage (R/P_{max}%) are also included in this paper. There is little information in the literature regarding respiration to photosynthesis ratios for

natural plankton communities. Most of the data available refers to unialgal culture studies (Humphrey, 1975; Falkowski and Owens, 1978; Geider and Osborne, 1989; Grande *et al.*, 1989). The R/P_{max} ratio of phytoplankton in culture has been shown to be an indicator of the physiological state of the algae (Ryther, 1954) and respiration rate has been suggested to be a small proportion of the photosynthetic rate in rapidly growing phytoplankton (Peterson, 1980; Smith, 1982). Also, plankton community respiration rates have been found to be lower at the beginning of a bloom period than when the bloom is scenescent (Keller and Riebesell, 1989). In this paper R/P_{max} ratios estimated from waters containing algal populations in different stages of development are presented. This ratio is proposed as a useful index of the trophic balance of the plankton community.

MATERIALS AND METHODS

Study areas

Water samples were collected from the southern and central North Sea during the months of March, April, May, June, July and October 1989, while on board the RV *Challenger* and in the English Channel during July 1987 on board the RV *Frederick Russell.* Measurements in North Sea waters were made opportunistically on several research cruises undertaken as part of the British Natural Environmental Research Council North Sea Project. The majority of the sampling sites were located in the shallow (less than 50 m) well mixed waters of the southern bight between latitudes 51°18'N and 53°00'N and between longitudes 1°50'E and 4°00'E, with most samples being taken in Dutch coastal waters, between latitudes 52°10'N and 52°50'N and longitudes 3°00'E and 3°40'E. Exceptions were during May, June and July when sampling was extended to areas in the stratified Central North Sea, between latitudes 54°10'N and 55°50'N and between longitudes 1°10'W and 7°00'E. In the English Channel measurements were made at station F87 at about 49°14'N and 4°30'W, in a bloom of the dinoflagellate *Gyrodinium aureolum* (Garcia and Purdie, 1991).

Photosynthesis and respiration measurements

Natural samples were collected from surface waters using 10 or 30 l Niskin bottles and dispensed through silicon rubber tubing into 125 or 60 ml borosilicate glass bottles. Incubation time varied between 3 and 17 hours and samples were held within 2°C of ambient seawater temperature. Dissolved oxygen concentration was measured using a precise, automated microprocessor controlled Winkler titration technique similar to that described by Williams and Jenkinson (1982). Respiration rates were determined from the difference between zero time and dark incubated measurements of oxygen. A series of six screened deck incubators was used to measure photosynthesis from oxygen production under various natural light levels (100, 58, 28, 19, 10, 5.2 % of surface incident irradiance) as described by Garcia (1989).

Since respiration is a process common to both heterotrophic and autotrophic organisms, rates measured in untreated natural samples (*i.e.* without prefiltration) are regarded as plankton community respiration rates (Williams, 1984). In practice, however, there is an upper limit to the size of planktonic organism studied, which is constrained by the volume of incubation containers used (usually less than 200 ml) in relation to the low density of larger organisms, *i.e.* mainly zooplankton.

Size-fractionation procedure

Natural water samples were fractionated by reverse filtration by gravity through large diameter (142 mm) 3 µm pore sized Nuclepore filters cemented to perpex tubing (Williams, 1981 *b*).

Chlorophyll *a* measurements

Duplicate samples were filtered onto Whatman GF/F filters and stored frozen until analysis on return to the laboratory. Chlorophyll *a* was extracted by homogeneization of filters in 90 % acetone and the concentration determined fluorometrically, correcting for phaeopigments, in an Aminco fluoro-colorimeter as described by Parsons *et al.* (1984). The concentration of a commercial standard solution of chlorophyll *a* (extracted from *Anacystis nidulans*, Sigma Ltd.) was determined spectrophotometrically in a Pye Unicam SP6-350 using the equations of Lorenzen (1967).

RESULTS AND DISCUSSION

Plankton community respiration rates measured during this study span one order of magnitude, ranging from 0.025 to 0.83 µmol O_2 l^{-1} h^{-1} (Tab. 1). This range is in agreement with other published data for coastal areas, reviewed by Williams (1984).

Regression analysis indicated rates of community respiration, expressed as µmol O_2 l^{-1} h^{-1}, to be significantly correlated ($p < 0.001$) with both, chlorophyll *a* concentration ($r = 0.88$; Fig. 1), and water temperature($r = 0.59$; Fig.2). In laboratory grown cultures an increase in the rate of respiration with increasing temperature has been observed for both phytoplankton (Morgan and Kalff, 1979; Verity,

Table 1

Plankton community respiration and photosynthesis rates measured in the North Sea during March, April, May, June, July and October 1989, in the English Channel during July 1987 and in Southampton water during June 1980.
**Data from Southampton water from June 1980 taken from Shamsudin (1980).*

Date	Temp. (°C)	Chl *a* ($\mu g\ l^{-1}$)	Respiration $\mu molO_2\ l^{-1}h^{-1}$)-	Spec. respiration ($\mu molO_2\ \mu gChl^{-1}h^{-1}$)	Inc. time (hours)	P_{max} ($\mu molO_2\ l^{-1}h^{-1}$)	R/P_{max} (%)
06.80*	19.0	6.7	0.33	0.049	-	-	-
06.80*	19.0	22.0	0.76	0.034	-	-	-
06.80*	19.0	23.5	0.83	0.035	-	-	-
07.87	16.8	12.8	0.68	0.053	4.0	4.01	16.9
07.87	16.4	11.2	0.60	0.053	4.0	1.80	33.4
07.87	16.8	11.7	0.79	0.068	4.0	2.84	27.7
07.87	16.9	10.1	0.70	0.070	4.0	1.96	35.7
07.87	16.9	12.2	0.59	0.048	4.0	2.24	26.3
07.87	16.4	11.2	0.65	0.058	4.0	-	-
07.87	16.9	10.1	0.52	0.052	4.0	-	-
07.87	16.9	14.1	0.63	0.045	4.0	-	-
07.87	16.9	12.2	0.66	0.054	4.0	-	-
03.89	8.1	-	0.05	-	12.0	0.37	14.3
03.89	7.0	-	0.05	-	12.0	0.53	10.0
03.89	-	-	-	0.05	-	3.0	-
03.89	-	-	0.05	-	6.5	-	-
04.89	7.0	1.5	0.05	0.033	14.0	0.49	10.3
04.89	6.9	1.2	0.08	0.062	13.0	0.36	21.0
04.89	7.0	1.6	0.03	0.015	12.0	0.45	5.5
04.89	8.4	1.6	0.18	0.115	9.5	0.97	18.5
04.89	8.7	2.9	0.07	0.025	12.4	3.19	2.2
04.89	8.7	3.5	0.11	0.031	12.2	4.10	2.7
04.89	8.7	5.8	0.10	0.017	5.0	-	-
04.89	8.7	5.8	0.14	0.025	9.0	-	-
04.89	8.7	5.6	0.07	0.022	12.0	3.20	2.3
04.89	7.0	1.5	0.19	0.123	3.0	-	-
04.89	7.0	1.4	0.12	0.086	3.0	-	-
04.89	7.3	1.7	0.26	0.149	3.0	-	-
04.89	7.1	1.6	0.18	0.114	3.0	-	-
04.89	7.0	1.8	0.22	0.123	3.0	-	-
04.89	8.7	3.8	0.44	0.117	3.0	-	-
05.89	10.7	0.6	0.19	0.308	10.8	0.27	71.0
05.89	10.6	0.8	0.14	0.169	12.0	0.21	67.6
05.89	10.7	0.9	0.18	0.208	12.0	0.23	75.9
05.89	11.2	0.7	0.24	0.334	6.5	-	-
05.89	8.3	2.6	0.11	0.041	11.5	1.16	9.3
05.89	8.8	2.8	0.15	0.053	13.0	1.27	11.5
05.89	11.1	1.2	0.15	0.122	9.5	0.35	42.8
05.89	10.2	0.6	0.12	0.204	12.0	0.27	47.9
06.89	15.4	5.1	0.16	0.031	17.0	0.73	21.9
06.89	15.8	1.7	0.14	0.085	16.5	0.72	19.4
06.89	14.3	1.4	0.21	0.150	18.0	0.36	58.3
06.89	14.7	2.4	0.31	0.131	10.5	0.76	40.8
06.89	15.4	5.1	0.12	0.024	6.0	-	-
06.89	15.8	1.7	0.16	0.097	8.5	-	-
06.89	14.3	1.4	0.25	0.178	10.3	-	-
06.89	12.0	2.8	0.32	0.115	10.8	-	-
06.89	14.7	2.4	0.16	0.067	10.5	-	-
07.89	13.0	1.3	0.17	0.129	8.0	-	-
07.89	13.5	0.6	0.10	0.178	16.3	0.25	40.0
07.89	12.5	0.8	0.18	0.220	17.0	0.40	45.0
07.89	14.4	0.5	0.10	0.217	15.5	0.17	58.8
07.89	13.0	0.5	0.09	0.169	16.5	0.21	42.8
10.89	16.8	2.9	0.20	0.068	8.0	-	-
10.89	16.2	2.8	0.15	0.054	12.0	2.41	6.2
10.89	16.1	2.8	0.09	2.032	7.0	-	-
10.89	16.1	2.8	0.09	0.032	7.0	-	-
10.89	15.8	3.2	0.13	0.041	10.0	1.72	7.6
10.89	15.8	3.3	0.13	0.040	5.0	-	-
10.89	15.8	3.5	0.13	0.037	11.0	2.09	6.2
10.89	15.5	2.2	0.11	0.050	9.5	0.72	15.3
10.89	15.2	2.5	0.19	0.076	5.0	1.29	14.7

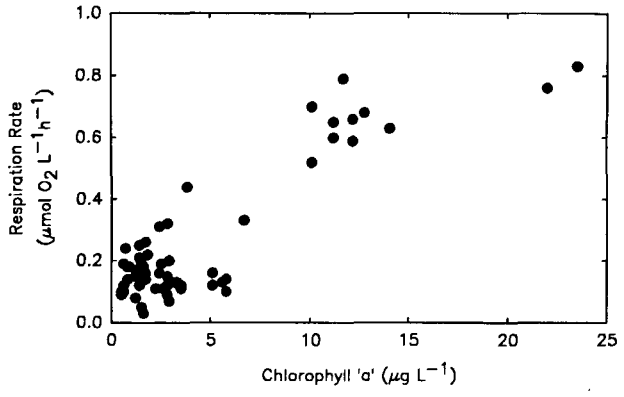

Figure 1

Relationship between chlorophyll a *concentration and plankton community respiration rate.*

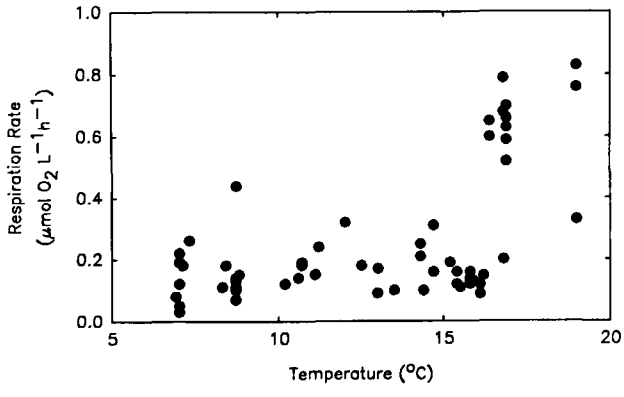

Figure 2

Relationship between water temperature and plankton community respiration rate.

1982) and microheterotrophs (Antai,1990) as might be expected from thermodynamic considerations. In natural waters, however , other factors co-vary with temperature *i.e.* insolation increases and surface mixed layer depth can decrease if a pycnocline develops. In temperate seas an increase in water temperature throughout the surface mixed layer is usually associated with increased organic production by the algae as the incident radiation increases and the water column stabilizes. Thus greater availability of organic carbon to the microbial community (including both autotrophic and heterotrophic populations) is probably more important in determining absolute respiration rates than the direct physiological effect of fluctuations in sea temperature.

Plankton respiration rates have been shown to correlate with chlorophyll *a* concentration by a number of authors *e.g.* Packard (1979), Setchell and Packard (1979) Packard and Williams (1981), Holligan *et al.* (1984) and Laanbroek *et al.* (1985), although some other data have shown little correlation (Packard, 1979; Harrison, 1986). A more detailed analysis of our results suggests that the correlation between chlorophyll *a* and respiration is influenced by the level of chlorophyll *a* present in the samples. If data expressed in Table 1 where respiration rates were determined at low to moderate chlorophyll a concentrations (0.46 to 5 μg l^{-1}) are analyzed separately from those at higher concentrations, the correlation between absolute respiration rate (μmolO_2 l^{-1} h^{-1}) and chlorophyll *a* concentration is statistically insignificant. Respiration rates determined in waters containing low levels of chlorophyll *a* were obtained over a wide range of seawater temperatures and so, correlation of respiration rate with chlorophyll *a* concentration in this low to moderate concentration range was re-determined by separating the data into two groups, a low temperature (< 12°C) and a high temperature (> 12°C). In neither of the two data sets was the correlation significant. This analysis further indicates that seawater temperature was not a dominant factor controlling rates of respiration in the water column. Packard (1979) suggests that at low algal biomass levels, the correlation between chlorophyll *a* concentration and respiration rate will be weak, since under these conditions, and given that zooplankton respiration is often reported as a minor component of total plankton respiration (Andersen and Jacobsen, 1979; Baars and Fransz, 1984; Bell and Kuparinen, 1984; Harrison *et al.*, 1987; Williams, 1981 *b*), microheterotrophs should make up a major proportion of plankton community respiration. Our results support this observation, since chlorophyll *a* specific respiration rate regressed against chlorophyll *a* concentration significantly deviates from a constant relationship at low chlorophyll *a* levels *i.e.* below 5 μg l^{-1} (Fig. 3). Martinez *et al.* (1990) have recently reported similar results from a study in the Mediterranean Sea. In general, good agreement was found between chlorophyll *a* levels and plankton community ETS activity in their study. The enhanced ETS activity at high chlorophyll *a* concentration was mainly attributed to high phytoplankton metabolic activity in frontal boundary regions. However, the authors also noted a high variability in ETS activity, with some relatively high values in low chlorophyll *a* (< 0.2 μg l^{-1}) waters, suggesting an important microheterotrophic contribution to the rates of respiration. Fractionation respiration experiments we conducted in the North Sea in June and July 1989 (chlorophyll *a* levels of 1.4 to 2.8 μg l^{-1}) further substantiate this point. Rates of respiration determined for the fraction passing a 3 μm filter ranged from 70 to 100 % (mean 80 %) of the rates determined for the unfractionated sample, whereas in

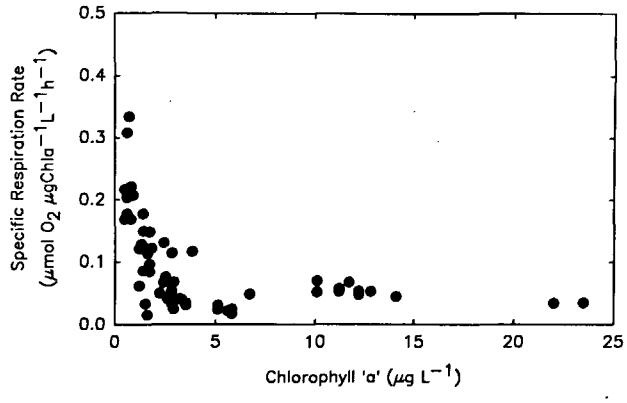

Figure 3

Relationship between chlorophyll a *concentration and chlorophyll* a *specific respiration rate.*

Table 2

Contribution of the fraction passing 3 µm Nuclepore filters to overall community chlorophyll a concentration and respiration rate measured in June/July, 1989 in the North Sea.

Exp	* Chlorophyll *a* TOT	< 3 µm	%	** Respiration rate TOT	< 3 µm	%
2	1.65	0.126	7.6	0.16	0.13	83
3	1.40	0.245	17.5	0.25	0.17	70
4	2.78	0.214	7.7	0.32	0.25	80
5	2.36	0.300	12.7	0.16	0.16	100

* µg Chl *a* l^{-1}.
** µmol O_2 l^{-1} h^{-1}.
% percentage contribution of the smaller than 3 µm fraction to the total sample.

terms of chlorophyll *a* concentration, the small size fraction made up between 7 and 17 % of the unfractionated sample (Tab. 2). Although Salonen and Kononen (1984) have shown that some caution should be taken in interpreting rates of respiraton activity in filtrates, data from size-fractionation measurements reported by Harrison (1986) in Arctic waters also showed microheterotrophs to be responsible for a substantial part of the plankton community respiration at low chlorophyll *a* concentrations, (mean chlorophyll *a* level of 4.12 µg l^{-1}). Similar fractionation results are reported by Williams (1981 *b*), though the chlorophyll *a* levels were not specified in this study.

A close coupling between plankton respiration activity and chlorophyll *a* concentration can be interpreted in two ways: either a) photosynthetic organisms are the major contributors to plankton community respiration rates (Packard, 1979); or b) the growth and/or standing stock of phytoplankton populations significantly enhances the presence and/or activity of microheterotrophs, the latter being the most important contributors to overall respiration even under conditions of high chlorophyll *a* concentration. It has been shown that bacteria numbers are often positively correlated with phytoplankton standing stock (Antai, 1990; Bird and Kalff, 1984; Ferguson and Palumbo, 1979; Fuhrman *et al.*, 1980; Linley *et al.*, 1983) and sometimes also with primary production (Derenbach and Williams, 1974; Larsson and Hagstrom, 1982; Lancelot and Billen, 1984). What proportion of the respiration can be attributed to microheterotrophs and how much to phytoplankton is still a matter of debate. Holligan *et al.* (1984) considered that under conditions of high chlorophyll *a* concentration, during a developing bloom of *Gyrodinium aureolum* in the English Channel, most of the respiratory activity could be attributed to the dominant microalgae. Soulsby *et al.* (1984) reported that in Southampton water dense aggregations of the phototrophic ciliate *Mesodinium rubrum* can lead to a severe depletion of oxygen in the lower part of the water column. This was attributed to night time oxygen demand of the ciliate. Williams (1981 *b*), however, from measurements of respiration in coastal waters using size-fractionation techniques, showed that a substantial proportion of the respiratory activity could be attributed to the < 1 µm fraction, even during diatom blooms, although levels of chlorophyll *a* at the time of the bloom were not specified. Kuparinen (1984) reported that microheterotrophs were the major contributors to overall respiration in surface waters off the coast of Finland on an annual basis, but only 20 % of the respiration during the spring diatom

Table 3

A summary of plankton community respiration rates, maximum rates of photosynthesis and ratios of respiration to maximum photosynthesis measured over a few days in water bodies containing phytoplankton populations in different states of development during 1989 in the North sea and 1987 in the western English Channel (a: µmolO_2 $l^{-1}h^{-1}$, b: µmolO_2 µg Chl $a^{-1}h^{-1}$, n: number of measurements).

n	Chl *a* µg l^{-1}	Respiration a	Respiration b	P_{max} a	P_{max} b	R/P_{max} %	Comments
3	2.9-5.6	0.07-0.11	0.022-0.031	3.19-4.10	0.57-1.17	2.2-2.7	High net production April *Phaeocystis* bloom southern NS
3	2.8-3.5	0.12-0.15	0.037-054	1.72-2.41	0.54-0.86	6.2-7.6	Low net production October *Rhizosolenia* population southern NS
3	0.6-0.9	0.14-0.19	0.169-0.308	0.21-0.27	0.26-0.45	67.6-75.9	Scenescent May *Phaeocystis* bloom southern NS
2	2.6-2.8	0.11-0.15	0.041-053	1.16-1.27	0.45	9.3-11.5	May 14-16 *Nitzschia* population central NS unstratif.
2	0.6-1.2	0.12-0.15	0.122-0.204	0.27-0.35	0.29-0.45	42.8-47.8	May 18-20 low diatom concentration central NS stratif.
5	10.1-12.8	0.59-0.79	0.048-0.070	1.80-4.01	0.16-0.31	16.9-35.7	July *G. aureolum* bloom English Channel

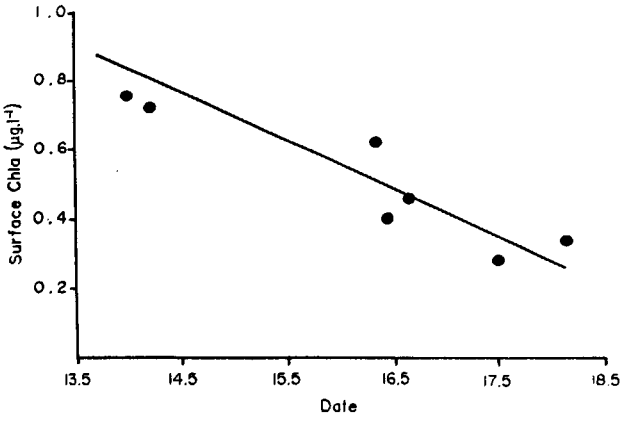

Figure 4

Variation of chlorophyll a *concentration in surface waters during a scenescent bloom of* Phaeocystis *sp in May 1989 in the southern North Sea.*

bloom (chlorophyll *a* levels of 10 to 22 µg l^{-1}) could be attributed to the < 3 µm fraction. Data from freshwater environments show a similar pattern: bacterial respiration accounted for only 30 % of the community respiration during the spring diatom bloom (chlorophyll levels up to 23 µg l^{-1}) in Lake Erken, Sweden (Bell and Kuparinen, 1984). Schwaerter *et al.* (1988) determined from lake studies that bacterial contribution to community respiration could be up to 60 to 70 % at low algal biomass, decreasing to 20 % under conditions of high algal biomass.

Table 3 summarizes rates of respiration, light saturated photosynthesis and ratios of respiration to light saturated photosynthesis (R/P_{max}) from waters in which phytoplankton populations were sampled over a period of a few days. Lowest values of R/P_{max} (2.2 to 2.7 %) were obtained during April 1989 in a bloom patch of *Phaeocystis* sp. in Dutch coastal waters. Values of light saturated photosynthesis normalized to chlorophyll *a* were high (0.57-1.17 µmolO_2 µg chl a^{-1} h^{-1}) and chlorophyll *a* specific respiration rates were low (0.022-0.031 µmolO_2 µg chl a^{-1} h^{-1}), indicating efficient growth of the microalgae. Water samples were collected over a period of four days from a coherent water body sampled in the vicinity of a drogued buoy; high values of net water column production were indicated over the four days from increases in oxygen saturation (110-120 %), chlorophyll *a* concentration (2.9-5.8 µg l^{-1}) and total *Phaeocystis* cell number (3.9-14 x 10^6 cell l^{-1}; Daneri and Purdie, 1990 *b*). Low chlorophyll *a* specific respiration rates were also measured while following the development of a small autumn diatom bloom dominated by *Rhizosolenia stolterfothii* in a coherent water body during October 1989 in the southern bight (Tab. 3; Daneri and Purdie 1990 *a*). The range of community respiration was somewhat higher than that measured during the *Phaeocystis* bloom, 0.12-0.15 µmolO_2 $l^{-1}h^{-1}$ and 0.07-0.11 µmolO_2 $l^{-1}h^{-1}$ respectively, and the range of P_{max} (1.72-2.41 µmolO_2 $l^{-1}h^{-1}$) was lower than during the *Phaeocystis* bloom (3.19-4.1 µmolO_2 $l^{-1}h^{-1}$). As a result, the range of the ratio R/P_{max} measured during the autumn diatom bloom (6.2-7.6 %) was more than double that of

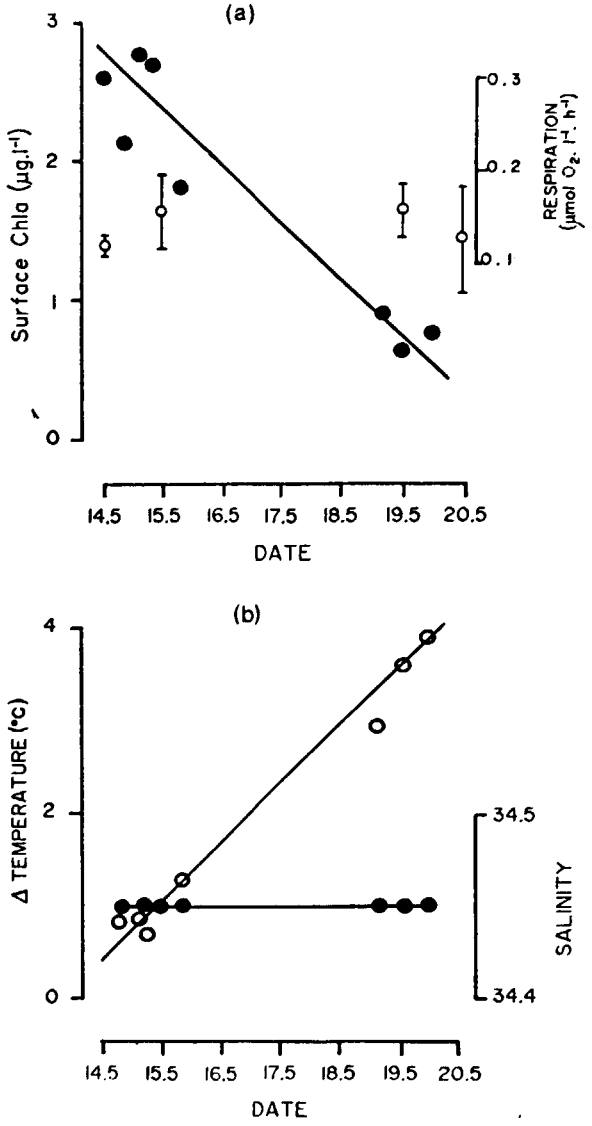

Figure 5

a) variation of chlorophyll a *concentration (•) and respiration rate (± S.E.) (o) in surface water during a bloom of* Nitzschia pseudoseriata *during May 1989 in the central North Sea; b) variation of the temperature difference between the surface and the bottom of the water column (o), showing the development of a thermocline, and variation of salinity (•), indicating that sampling was performed from a coherent water body.*

the spring *Phaeocystis* bloom (2.2-2.7). The values of chlorophyll *a* specific respiration determined during the autumn diatom bloom were higher than during the April *Phaeocystis* bloom and P_{max} normalized to chlorophyll *a* was lower in the autumn than in the April samples, reflecting the lower net rate of increase in the algal population determined from changes in diatom cell numbers (Daneri and Purdie, 1990 *a*). During May 1989 two locations were sampled in the North Sea. The first location was in the southern bight where *Phaeocystis* sp. was the dominant microalgae (over 90 % by cell count). However, the colonies were in a scenescent state, as revealed by microscopic examination, and decreasing levels of chlorophyll *a* were recorded over a period of five days in this region (Fig. 4). Chlorophyll *a* specific rates of respiration were high, P_{max} normalized to chlorophyll *a* was low and R/P_{max} was high

(above 65 %), indicating little potential for positive net community production (Tab. 3). In accordance with these features, levels of oxygen saturation were close to or slightly below 100 % in surface waters, showing an increased biological oxygen demand by the plankton community. The second location visited during May 1989 was in the central area of the North Sea and a population of *Nitzschia pseudoseriata* dominated the phytoplankton when the water column was well mixed on the 14th and 15th of May 1989. The region was sampled again on the 19th and 20th of May when a temperature difference of up to 3°C had established between surface and bottom waters. The phytoplankton were now concentrated below the thermocline and levels of chlorophyll *a* had dropped significantly in surface waters over the six day period (Fig. 5). Absolute respiration rates in surface waters, however, remained at a similar level to that prior to stratification (Fig. 5) and chlorophyll *a* specific respiration rates were consequently increased. This observation is further circumstantial evidence supporting the contention that plankton community respiration is often dominated by non-photosynthetic organisms. Data is also presented in Table 3 of respiration rates determined in samples collected from a *Gyrodinium aureolum* bloom in the English Channel during July 1987. Respiration rates were high but little *in situ* net growth in the population was detected from cell counts determined over a period of 5 days (Garcia and Purdie, 1991). R/P_{max} values were high (16.9 to 35.7) and specific respiration rates were higher than those determined for actively growing blooms in the North Sea. The dinoflagellate population P_{max} values normalized to chlorophyll *a* were relatively low (0.16-0.31 $\mu molO_2\ \mu g\ chl\ a^{-1}h^{-1}$) and other parameters measured over the five days of observations *i.e.* increase in the percentage of phaeopigments and decrease in the percentage oxygen saturation, suggest the bloom was in an early phase of scenescence due to nutrient limitation (Garcia and Purdie, 1991). Water column gross primary production was approximately in balance with the respiratory oxygen demand (Garcia and Purdie, 1991).

In general, results from Table 3 show that low values of chlorophyll *a* specific respiration rates together with high values of P_{max} % normalized to chlorophyll *a* and lowest values of R/P_{max} % were determined in water masses where the phytoplankton was showing high rates of net growth *i.e.* water masses with high rates of net community production, as indicated by independent methods. We, therefore, suggest R/P_{max} % as being a useful indicator of the trophic balance of the plankton community, lowest values (*i.e.* 2-10 %) being found in photosynthetically active algal dominated plankton populations and values greater than 20 % occurring in plankton populations where heterotrophic oxygen consumption is dominant or the phytoplankton population is in a scenescent state. In agreement with these conclusions, Grande *et al.* (1991) found that light intensity had a less marked effect on respiration rates in plankton communities with higher ratios of dark respiration to P_{max} (%). This result also suggests that heterotrophic organisms make a greater contribution to the overall plankton community respiration rate when the R/P_{max} ratio is high.

CONCLUSIONS

The range of plankton community respiration rates presented is in agreement with data from the literature for coastal waters. Results suggest that at low and moderate chlorophyll levels microheterotrophs play a major role in the overall rates of respiration, however, under conditions of exceptionally high phytoplankton biomass the microalgae can dominate the plankton community respiration rates. The ratio of R/P_{max} is regarded as a good index of the trophic balance of the plankton community. Lowest values of R/P_{max} were measured in water masses where high rates of net community production were occurring *i.e.* water masses with high rates of net algal population growth.

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