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Quantitative relationships between phytoplankton, bacteria and heterotrophic microflagellates in shelf waters

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ABSTRACT: Estimates of the numbers and biomass of bacteria as a function of depth in coastal and upwelling waters off the western approaches to the English Channel and in the southern Benguela upwelling region off the Cape Peninsula, South Africa, show that the numbers of bacteria are correlated with the standing stocks of phytoplankton as assessed by chlorophyll *a* concentration. Standing stocks of heterotrophic microflagellates in the size range 3 to 10 μm, amount to some 16.9 % on average, of bacterial standing stocks (mg C m^{-3}) estimated by direct microscopy. Calculations of carbon flow through the microheterotrophic consumer community suggest that approximately 20 to 60 % of primary production, possibly representing the dissolved components leaching out of, and lost from phytoplankton cells during zooplankton grazing, enters the microbial food chain. Much of this appears to be dissipated by bacteria, with some 5.2 to 8.1 % of the photoassimilated carbon being incorporated into bacterial carbon production. At least 66 % of this is exploited by the heterotrophic microflagellates leaving a maximum of 34 % of bacterial production for the larger bactivorous suspension feeders.

INTRODUCTION

Although it is generally recognized that the numbers and biomass of bacteria in the sea are correlated with regions of high primary productivity, and that the heterotrophic flagellates may be significant consumers of marine bacteria (Pomeroy and Johannes, 1968; Sieburth et al., 1978; Haas and Webb, 1979; Hollibaugh et al., 1980), there have been comparatively few attempts to quantify the relationship between the standing stocks of bacteria and phytoplankton, or between the bacteria and heterotrophic microflagellates. Ferguson and Palumbo (1979) have reported that the number of bacteria in neritic waters south of Long Island, USA, is positively correlated with chlorophyll and ammonium concentrations, whilst Fuhrman et al. (1980) have shown that bacterioplankton growth rate is more influenced by the standing stock of phytoplankton than by primary production, suggesting that bacterial growth may be stimulated by leakage of dissolved organic matter from aging, disrupted and incompletely digested phytoplankton cells. Sorokin (1971a, b, 1975, 1977), and Sorokin and Mikheev (1979) in a series of pioneer investigations, studied the partitioning of carbon amongst the standing stocks of heterotrophic microplankton and made some estimates of energy flow through the microplankton compared with the larger zooplankton.

Such estimates have, in the past, been hampered not only by a scarcity of detailed information on the standing stocks of heterotrophic microplankton, including bacteria, flagellates and ciliates, in marine systems but above all by a lack of data on production and consumption requirements of key consumer organisms. Recently, a good deal of information has become available on bacterial production rates (Meyer-Reil, 1977; Sorokin, 1978; Delattre et al., 1979; Hagström et al., 1979; Sieburth, 1979; Karl, 1980; Fuhrman and Azam, 1980; Newell and Christian, 1981; Newell, 1983) and on the carbon conversion efficiency of heterogeneous populations of marine bacteria on natural detrital sources (Linley et al., 1981; Lucas et al., 1981; Newell et al., 1981; Robertson et al., 1982) as well as on the consumption requirements of a variety of marine flagellates (Fenchel 1982a, b, c, d) and ciliates (Fenchel, 1980; Burkill, 1982). It is thus possible to make some realistic estimates of carbon flow through the microheterotrophic consumer organisms in a variety of

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pelagic systems, provided that simultaneous measurements are made of each of the components of the standing stocks in the water column.

The following work was therefore undertaken to measure the standing stocks and primary production of phytoplankton, as well as the standing stocks of bacteria, flagellates and ciliates in several different sea areas. We then used the information which has recently become available for production and carbon requirements of the bacteria and flagellates to estimate carbon flow through the microheterotrophic community as a whole. The results in general conform with previous estimates (see Williams, 1981) and suggest that approximately 20 to 60 % of the carbon fixed by primary production enters the microbial food chain and that at least 66 % of bacterial production is removed by the heterotrophic microflagellates in coastal waters.

MATERIALS AND METHODS

Sampling sites

The data summarized below were obtained on 3 different cruises. The first was the Nimbus G cruise of the Sea Fisheries Institute, Cape Town, between 6. 11. and 14. 11. 78 from the edge of the kelp beds on the west coast of the Cape Peninsula, South Africa, to the edge of the continental shelf in the southern Benguela upwelling region (Lat. 34°S; Long. 18°E; Fig. 1b). During this cruise, samples were taken from 3 depths at 4 stations. The second cruise was aboard R. V. 'Sarsia' (Marine Biological Assoiciation, U.K.) to the central Celtic Sea WSW of the Scilly Isles (Lat. 49°40' N; Long. 07°10' W; see Station P34, Fig. 1a) on 13. 8. 80. The final cruise was aboard the R.V. 'Frederick Russell' (Marine Biological Association, U.K.) between 22. 7. and 2. 8. 81 to 3 main stations in the western approaches to the English Channel. The first station (M) was representative of mixed waters at Lat. 49°19' N; 03°15' W, the second station (F) was at the frontal region at Lat. 49°19' N; 04°34' W and finally the third station (E5) was representative of deeper stratified waters at 49°04' N; 06°37' W. The position of each of these stations is shown in Fig. 1a (see also Holligan et al., 1983). In addition, an inshore station (A1 in Fig. 1a) was sampled at 7 depths on 6. 4., 13. 4., 27. 4. and 4. 5. 82 to establish temporal variability in the standing stocks of microheterotrophic organisms.

Sampling procedure

Pumped samples

Samples were taken over a vertical profile of 60 m depth at the English Channel stations (M, F, E5) and Celtic sea station (P34) with a submersible pump (Flygt Pumps Ltd., Model B2051). The intake hose of 5 cm internal diameter was raised at a rate of 2 m min^{-1} from 60 to 2 m and the average flow rate was 160 l min^{-1}. Water over the depth ranges 60 to 48 m, 48 to 36 m, 36 to 24 m, 24 to 12 m and 12 to 2 m was then allowed to flow into a series of 5 leached 20 l plastic vessels from which samples for subsequent analyses were taken immediately.

N.I.O. bottles

A series of up to 10 1.5 l NIO bottles was also used to collect discrete water samples over the same depth at which the pumped samples were taken in the English

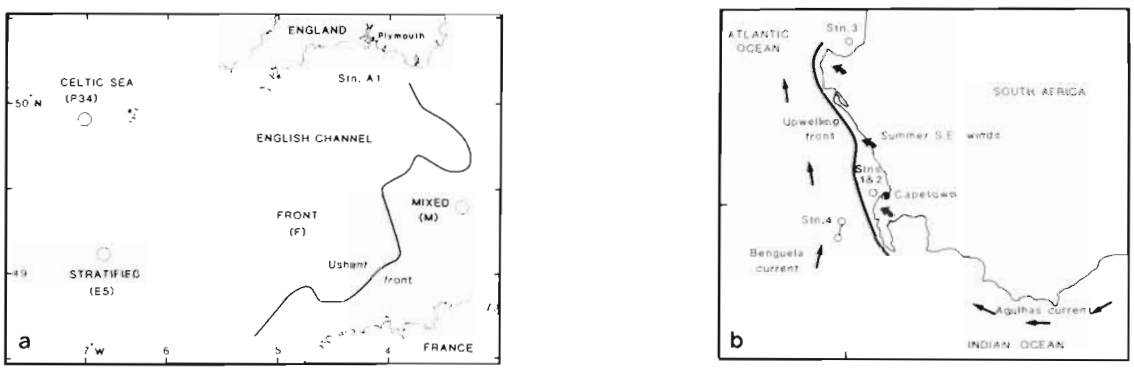

Fig. 1. (a) Sampling stations in nearshore region (Station A1), mixed (Station M) frontal (Station F), stratified waters (Station E5) off the western approaches to the English Channel, and the Celtic Sea (Station P34) sampling site near the Scilly Isles. (b) Sampling sites in the Southern Benguela upwelling region off the western Cape Peninsula, South Africa, sampled during the Nimbus G cruise (Station 1, sampled 11. 11. 78; Station 2, 12. 11 78; Station 3, 13. 11. 78; Station 4, 14. 11. 78). The approximate position of the upwelling frontal system is shown in each area by a line

Channel (M, F, E5). The minimum distance between bottles was 2 m, but in general bottle samples were taken at intervals of 6 to 10 m with somewhat closer spacing over the chlorophyll maximum and thermocline layers. The bottles were subsequently placed on racks on the deck and the water immediately sampled for analysis. Samples were taken at station A1 with 1.5 l NIO bottles at 5 m intervals from the surface to 20 m depth and at 35 and 50 m. Benguela samples (Nimbus G cruise) were taken at the surface, at 50 % of surface light (corresponding with a depth of 10 to 25 m) and at 10 % (corresponding with 20 to 50 m).

Analytical methods

All water used was initially filtered through a 200 µm mesh net to remove large particulate material and zooplankton.

Chlorophyll *a*

A small sample of approximately 5 ml of the filtered seawater was placed in a Turner Model III fluorometer appropriate for chlorophyll *a* fluorescence (Holm-Hansen et al., 1965) and calibrated against chlorophyll *a* (Lorenzen, 1967). This gave an indication of the volume of seawater which was required for subsequent chlorophyll *a* extraction.

Total chlorophyll *a* in the 200 µm fraction was determined following extraction onto a 0.45 µm Nuclepore membrane. The proportion of chlorophyll *a* in the phytoflagellates was determined following filtration through a 10 µm Nuclepore filter, followed by filtration onto a 0.45 µm membrane. The chlorophyll *a* in the 10 µm fraction was then determined by difference. All filtration was carried out using a vacuum of 12 cm Hg. The filters were subsequently homogenized in a small volume of 90 % acetone, centrifuged, rinsed with 90 % acetone, and made up to 20 ml prior to estimation with the fluorometer. Phaeopigments were detected on the same sample following addition of 2 drops of 10 % HCl (Lorenzen, 1966).

Carbon

Depending on the chlorophyll content, 100 to 1000 ml of sample was filtered through a 25 mm Whatman GF/C glass fibre filter which had been pre-ashed for 6 h at 400 °C. The filters were stored at −20 °C and then oven-dried at 55 °C prior to analysis for particulate carbon in a Carlo Erba elemental analyzer (Model 1106) calibrated with cyclohexanone (20.14 % N; 51.79 % C).

The filtrate was used to estimate dissolved organic carbon. Triplicate samples of 8 ml were transferred to precombusted 15 ml glass vials to which 75 µl 1N HCl was added to dispel inorganic carbon as CO_2. The vials were then sealed with Teflon-lined caps and stored at −20 °C. Dissolved organic carbon was then measured as CO_2 by the u/v photo-oxidation method of Collins and Williams (1977) as modified by Gershey et al. (1979). Potassium oxalate (Analar grade) dissolved in carbon-free u/v irradiated distilled water was used as a standard.

Numbers and biomass of micro-organisms

Bacteria

Two separate samples, one of 10 ml and the other of 160 ml, were taken from the NIO bottles and placed in autoclaved vessels together with Analar glutaraldehyde to a final concentration of 2.5 %. The 10 ml sample was used for bacterial counts whilst the larger volume of 160 ml was used as necessary for replicate numbers and biomass estimates.

Bacterial numbers were estimated using an epifluorescence direct counting technique (AODC: Hobbie et al., 1977; Daley, 1979; Linley et al., 1981). The relative frequency and mean volumes of bacteria in enlarged photographs of acridine orange stained cells were obtained from the mean of 100 or more of each cell type for up to 6 cell shape/volume categories (see also Fuhrman, 1981). Carbon:wet biomass ratios for bacteria are known to vary considerably from 0.079 in the heterogeneous populations of small bacteria from natural waters (Ferguson and Rublee, 1976; Bowden, 1977) to 0.121 (Watson et al., 1977) and 0.129 (Krambeck et al., 1981) for cultured bacteria. Bacterial biomass was therefore calculated from the cell volumes using a specific gravity of 1.1 g cm^{-3} (Doetsch and Cook, 1973) and the generally used ratio of carbon:wet biomass of 0.1 (Troitsky and Sorokin, 1967; Straškrabová and Sorokin, 1972), which is the approximate mean of the values cited above.

Replicate bacterial counts and the relative frequencies of different cell types gave maximum standard deviations of ± 4.5 % and 6.7 % respectively, whilst the standard errors of the biovolume estimates ranged from 3.7 % to 9.3 % of the mean values for the various cell types calculated separately.

Protozoa

Samples of 100 ml were taken from the 20 l pumped water bottles and placed in glass bottles together with

1 ml 1% Lugol's iodine solution. Depending on the chlorophyll values, 10 or 100 ml samples were allowed to settle onto counting chambers after which total cell counts were made with a Wild inverted microscope at × 10 magnification. Flagellates were counted from one traverse on × 40 magnification. After species identification, cell volumes were obtained from Larrance and Kovala (1966) and the carbon equivalent was calculated from Eppley et al. (1970).

RESULTS

Standing stocks of bacteria

The mean values and overall range of the numbers of bacteria in relation to dissolved organic carbon, chlorophyll *a* and particulate carbon in the water column from 4 different stations in the western English Channel are shown in Table 1. There is evidently a general correspondence between high bacterial numbers of 12.8×10^5 cells ml^{-1} (range 2.63 to 24.0×10^5 cells ml^{-1}) in regions where the dissolved organic carbon, chlorophyll *a* and particulate carbon are high, as at frontal station (F), declining to only 2.91×10^5 cells ml^{-1} (range 2.28 to 3.94×10^5 cells ml^{-1}) in the stratified waters of station (E5). These values are in agreement with the high numbers of 18.5×10^5 cells ml^{-1} (range 5.0 to 50×10^5 cells ml^{-1}) recorded for productive coastal waters off Long Island, N.Y. by Ferguson and Palumbo (1979), and 19.6×10^5 cells ml^{-1} (range 5.2 to 59.8×10^5 cells ml^{-1}) recorded by Zimmermann (1977) for the Kiel Bight. In contrast, lower values of 0.6 to 6.5×10^5 cells ml^{-1} have been recorded in the oligotrophic waters of McMurdo Sound, Antarctica, by Hodson et al. (1981) and 1.0 to 7.0×10^5 cells ml^{-1} in the Gulf of Mexico (Ferguson, 1981).

The standing stocks of bacteria and the corresponding values for chlorophyll *a*, dissolved organic carbon and particulate carbon are shown in relation to depth for frontal Station (F) in Table 2. The first and most obvious feature is that bacterial numbers decline from 17.6 to 18.8×10^5 cells ml^{-1} in the surface waters to 2.3 to 2.73×10^6 cells ml^{-1} at depths below 20 m. This, and the fact that the surface waters are dominated by large rods with a mean volume of 0.22 μm^3, results in a sharp decline in the bacterial biomass from the surface waters towards the deeper waters below the thermocline where cocci become the dominant morphological types (see also Holligan et al., 1983). The larger size and greater abundance of rod-shaped bacteria in the euphotic zone at Station (F) suggests that the bacteria may be limited by the availability of dissolved organic carbon from the phytoplankton since cocci are generally characteristic of waters with low nutrient availability (see Wiebe and Pomeroy, 1972; Ferguson and Rublee, 1976; Hoppe, 1976; Fuhrman et al., 1980; Fuhrman and Azam, 1982).

The regression equations for bacterial numbers and carbon versus chlorophyll *a*, dissolved organic carbon and particulate carbon are also shown in Table 2. As might be anticipated, despite the fact that availability of dissolved organic carbon could control bacterial numbers and biomass in the water column, it is not correlated well with bacterial abundance since the residual pool of dissolved organic carbon in the water is merely a reflection of the balance between release from phytoplankton and uptake by the bacteria. An inverse correlation could indeed be expected under equilibrium conditions where the bacterial uptake of dissolved organic carbon is equal to the rate of release from the phytoplankton source. In contrast, highly significant correlations are obtained between both bacterial numbers and biomass and the standing stocks of phytoplankton as indicated by chlorophyll *a*. There is also a good correlation with particulate carbon as

Table 1. Summary of mean values and ranges of bacterial numbers ($\times 10^5$ cells ml^{-1}), dissolved organic carbon (DOC mg m^{-3}), particulate carbon (PC mg m^{-3}) and chlorophyll *a* (mg m^{-3}) recorded at 4 stations (0 to 60 m only) in the English Channel. Samples taken between 22. 7. and 2. 8. 81 at Stations (F), (E5) and (M) and between 6. 4. and 4. 5. 82 at Station (A1). For details see p. 78

Station		Bacteria ($\times 10^5$ cells ml^{-1})	DOC (mg m^{-3})	Chlorophyll *a* (mg m^{-3})	PC (mg m^{-3})
(F)	Mean	12.8	1509	10.63	1052
	Range	2.63–24.0	1090–1963	0.58–26.22	127–2471
(E5)	Mean	2.91	1320	0.37	177
	Range	2.28–3.94	933–1520	0.12–1.76	79–404
(M)	Mean	5.18	1350	1.55	207
	Range	3.18–6.80	940–2080	0.10–2.29	154–350
(A1)	Mean	3.49	1195	1.83	323.3
	Range	7.30–11.5	980–1309	0.36–6.75	138–681

Table 2. Vertical profile of bacterial numbers ($\times 10^5$ cells ml^{-1}) and carbon equivalent of bacterial biomass (mg m^{-3}), chlorophyll *a* (mg m^{-3}), dissolved organic carbon (DOC mg m^{-3}) and particulate carbon (PC mg m^{-3}) at frontal Station (F) taken on 2. 8. 81 with N.I.O. bottles. For details, see p. 78. Equations for regressions relating bacterial numbers and bacterial carbon to chlorophyll *a*, dissolved organic carbon and particulate carbon are also shown

Depth (m)	Standing stocks of bacteria: No $\times 10^5$ (cells ml^{-1})	Standing stocks of bacteria: Carbon mg m^{-3}	Chlorophyll *a* (mg m^{-3})	DOC (mg m^{-3})	PC (mg m^{-3})
4	18.8	40.0	26.22	1450	2471
12	17.1	28.1	21.34	1430	2151
14	17.3	20.1	18.91	1936	1592
16	18.3	21.3	12.53	1846	1971
18	17.9	20.8	19.72	1956	1541
20	17.6	20.4	17.56	1963	1963
22	2.63	3.1	1.06	1377	236
25	2.81	2.3	0.82	1333	127
35	2.73	2.2	0.60	1313	142

Equation of regression	Bacterial numbers ($\times 10^5$ cells ml^{-1}) ($Y = b \cdot x + a$)				Bacterial carbon (mg m^{-3}) ($Y = b \cdot x + a$)			
	b	a	r	N				
Chlorophyll *a* (mg m^{-3})	0.713	+ 3.384	0.936***	9	1.243	+1.190	0.957***	9
DOC (mg m^{-3})	0.018	−17.224	0.713*	9	0.015	+7.394	0.348	9
PC (mg m^{-3})	0.008	+ 2.211	0.962***	9	0.014	−3.087	0.881**	9

Table 3. Vertical profile of bacterial numbers ($\times 10^5$ cells ml^{-1}) and corresponding chlorophyll *a* distribution (mg m^{-3}) at 4 separate stations in the Southern Benguela upwelling region (Nimbus G cruise, see text) between 11. 11. and 14. 11. 78. Distribution of bacteria and chlorophyll *a* in relation to depth (m) at Station P34 in the Celtic Sea on 13. 8. 80 is also shown. For details see p. 78. Equations for the regressions ($Y = b \cdot x + a$) are shown

Date	Southern Benguela: Depth (m)	Southern Benguela: Bacteria ($\times 10^5$ cells ml^{-1})	Southern Benguela: Chlorophyll (mg m^{-3})	Celtic Sea: Depth (m)	Celtic Sea: Bacteria ($\times 10^5$ cells ml^{-1})	Celtic Sea: Chlorophyll (mg m^{-3})
11 11. 78	0	6.37	5.00	2	2.94	0.23
(Station 1)	10	6.79	6.25	10	3.50	0.19
	25	2.54	0.43	20	3.21	0.19
12. 11 78	0	6.40	7.35	26	2.75	0.48
(Station 2)	10	6.69	6.60	28	5.08	4.12
	25	2.12	0.57	30	5.88	3.91
13. 11. 78	0	3.86	1.23	35	4.72	2.33
(Station 3)	25	4.82	6.50	40	2.00	0.19
	50	5.13	6.73	50	3.24	0.19
14. 11. 78	0	26.77	25.80			
(Station 4)	10	25.90	20.30			
	20	5.55	2.50			

b	a	r	N	b	a	r	N
1.047	0.788	0.970***	12	0.682	2.806	0.914**	9

might be expected in a water column where the predominant particulate matter is phytoplankton. Significant correlations between bacterial numbers and both chlorophyll *a* and particulate carbon have also been recorded by Fuhrman et al. (1980) and with chlorophyll *a* by Ferguson and Palumbo (1979), although in neither case is the full regression equation given.

Bacterial numbers showed as good a correlation as the carbon equivalent of bacterial biomass in both the productive waters at the frontal station (F) off the

western English Channel as well as in other sea areas. Table 3 shows, for example, the mean values for bacterial numbers and chlorophyll *a* at 3 different depths from 3 separate sample hauls and from 4 different stations along the track of the Nimbus G cruise in the southern Benguela upwelling region off the Cape Peninsula, South Africa (Fig. 1b). Also shown is the depth profile for bacterial numbers and chlorophyll *a* in the Celtic Sea (Station P34, Fig. 1a) from which it will be seen that bacteria again reach their maximum numbers in the chlorophyll *a* maximum zone, which in this case was in the depth range 28 to 30 m. The regression equations for both sites are shown in Table 3 and support the results of Ferguson (1981) who found that the regression relating bacterial numbers ($\times 10^6$ cells ml^{-1}) in the waters of the Gulf of Mexico to chlorophyll *a* (mg l^{-1}) was of the form: bacterial numbers = 0.352 Log_e chlorophyll *a* + 0.697; n = 8, r = 0.968.

Because the regression equations for the 3 sampling sites are apparently similar, it is of interest to compare those obtained for cruises including stratified (Station E5), mixed (Station M) and frontal (Station F) waters off the English Channel, nearshore channel waters (Station A1), Celtic Sea (Station P34), as well as those for the Benguela upwelling region (Nimbus G cruise) and for the Gulf of Mexico (from Ferguson, 1981). These are summarized in Table 4 which yielded the following regression for the pooled data from all our cruises: bacterial Numbers ($\times 10^5$ ml^{-1}) = 0.822 chlorophyll *a* + 2.348 (n = 84; r = 0.935•••).

The common regression, together with the data to which it has been fitted, is shown in Fig. 2, and the regression equations for chlorophyll *a* values 0 to 10 and 10 to 30 mg m^{-3} (calculated separately), are also illustrated for comparison. Although there is some difference in the level of the 2 lines, it is clear that bacterial numbers in a variety of marine waters are correlated with chlorophyll *a* in the water column. This may reflect the availability of dissolved organic matter released either by the living phytoplankton, or following disruption of the cells, even though no good correlation can be established between the residual non-utilized pool of dissolved organic carbon and bacterial numbers in the water column. It is also apparent that despite the similarity of the slopes of regression equations for chlorophyll *a* values 0 to 10 and 10 to 30 mg m^{-3}, the equation for the upper range has a significantly higher intercept value, suggesting that there may be additional organic substrates suitable for

Table 4. Summarized regression equations for bacterial numbers ($B_N \times 10^5$ cells ml^{-1}) versus chlorophyll *a* (mg m^{-3}) for frontal (F), mixed water (M) and stratified (E5) waters off the western approaches of the English Channel (22. 7. to 2. 8. 81). Data for the southern Benguela upwelling region, off the Cape Peninsula, South Africa (11. 11. to 14. 11. 78) and the equation derived by Ferguson (1981) for the Gulf of Mexico are also shown, as well as a series of regressions for coastal waters of the English Channel (Station A1 from 6. 4.to 4. 5. 82) and the Celtic Sea (Station P34 on 13. 8. 80). The regression for the pooled data for all regions including the Gulf of Mexico is also shown

Location	Regression equation	Chlorophyll range	r	n
English Channel				
Station (F)	Y = 0.713X + 3.384	0.58–26.22	0.936•••	9
Station (M)	Y = 3.028 − 0.324X	0.10– 2.29	−0.311	9
Station (E5)	Y = 9.400 − 3.369X	0.12– 1.76	−0.497	9
Pooled Data	Y = 0.739X + 2.867	0.10–26.22	0.965•••	27
Benguela upwelling	Y = 1.047X + 0.788	0.43–25.80	0.970•••	12
Gulf of Mexico (From Ferguson, 1981)	Y = 0.72X + 5.188	0.17–18.00	0.888••	8
English Channel Station (A1)				
6. 4. 82	Y = 1.472X + 1.250	0.36–1.49	0.907••	7
13. 4. 82	Y = 0.514X + 2.456	0.74–1.59	0.421	7
27. 4. 82	Y = 0.301X + 3.044	2.49–6.75	0.610••	7
4. 5. 82	Y = 0.633X + 1.441	2.26–4.37	0.898••	7
Pooled Data	Y = 0.439X + 2.307	0.36–6.75	0.790•••	28
Celtic Sea Station (P34)	Y = 0.682X + 2.806	0.19–4.12	0.914••	9
Total pooled data	Y = 0.822X + 2.348	0.10–26.22	0.935•••	84

bacterial growth associated with the larger standing stocks of phytoplankton, which are not directly related to chlorophyll *a* concentration.

It should be pointed out, however, that where the bacterial numbers exceed 15.0×10^5 cells ml^{-1}, corresponding to a chlorphyll concentration of approximately 10 mg m^{-3}, and a bacterial density suitable for efficient bactivory (Fenchel, 1983), the close cyclic coupling which is likely to occur between heterotrophic microflagellates and their bacterial prey may result in very variable bacterial standing stocks (Fenchel, 1982d). Thus, for most purposes, we regard the relationship as useful in indicating the probable bacterial numbers over the chlorophyll *a* range 2 mg m^{-3} to 7–10 mg m^{-3}, as indicated in Fig. 2.

Standing stocks of Protozoa

The carbon equivalent of the standing stocks of bacteria, flagellates and ciliates as a function of depth at frontal Station (F), mixed water Station (M) and the stratified Station (E5) off the western English Channel is shown in Table 5. The proportion of carbon in the phototrophic microflagellates was estimated from the product of chlorophyll *a* (mg m^{-3}) in the 10 µm fraction (p. 79) and a carbon: chlorophyll *a* ratio of 25.5, which is the mean of a range of 19 to 32 obtained by Parsons et al. (1961) for Chlorophyceae. These values were subtracted from total microflagellate carbon (p. 79) to give estimates of heterotrophic microflagellate carbon.

It is apparent that the proportion of carbon in the standing stocks of heterotrophic microflagellates range from approximately 8 to 45 % of the total flagellates at Stations (F), (M) and (E5). It can also be seen that the ciliates are dominated by tintinnids which may reach a similar biomass to that of the flagellates. The carbon in the standing stock of heterotrophic microflagellates themselves represents 4 to 26 % of the carbon in the bacteria which form their principal prey (with the exception of surface waters of E5, where the figure is 78 % [see Table 5 and Fenchel, 1982d]). We have noted similar proportional relationships consistently in experimental studies on the microbial succession which colonizes plant detritus from a variety of sources (Linley et al., 1981; Linley and Newell, 1981; Newell et al., 1981).

The relation between the carbon in the standing stock of heterotrophic microflagellates and that in the bacteria for the 3 sampling sites is shown in Fig. 3. The regression equation is $\log_{10}$ Flagellate carbon (mg m^{-3}) = 0.717 $\log_{10}$. Bacterial carbon (mg m^{-3}) − 0.675

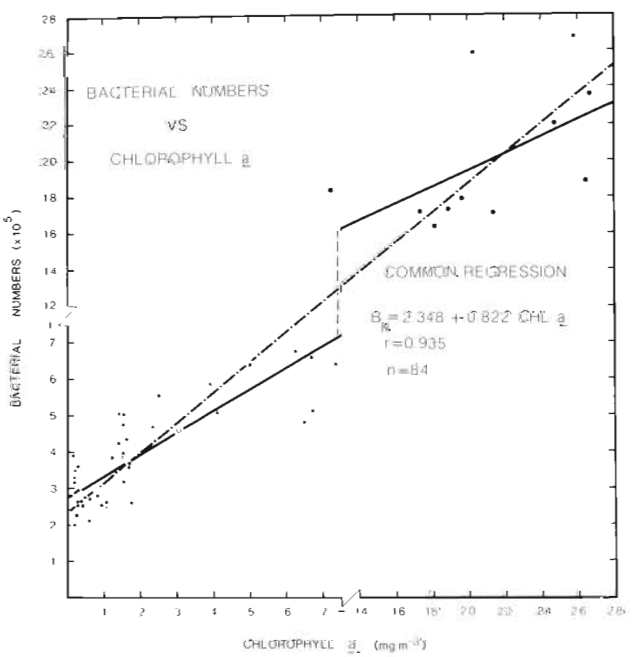

Fig. 2. Regression relating the bacterial numbers (B_N 10^5 cells ml^{-1}) to chlorophyll *a* concentration (mg m^{-3}) for pooled data from English Channel, Celtic Sea and southern Benguela upwelling region (see also Table 4). Regression equations for chlorophyll *a* values of <10 and >10 mg m^{-3} calculated separately, are shown for comparison. Solid dots (English Channel Stations F, M and E5), solid squares (Benguela upwelling stations), open dots (English Channel nearshore Station A1), triangles (Celtic Sea). The regression equations for 0 to 10 and 10 to 30 mg m^{-3} chlorophyll *a* are respectively: $B_N = 2.732 + 0.591$ chl *a* ($n = 73$; $r = 0.636^{***}$) and $B_N = 10.50 + 0.451$ chl *a* ($n = 11$; $r = 0.496$), and that for the pooled data (dotted line) is Bacterial numbers = 0.822. Chlorophyll *a* + 2.348 ($n = 84$; $r = 0.935^{***}$)

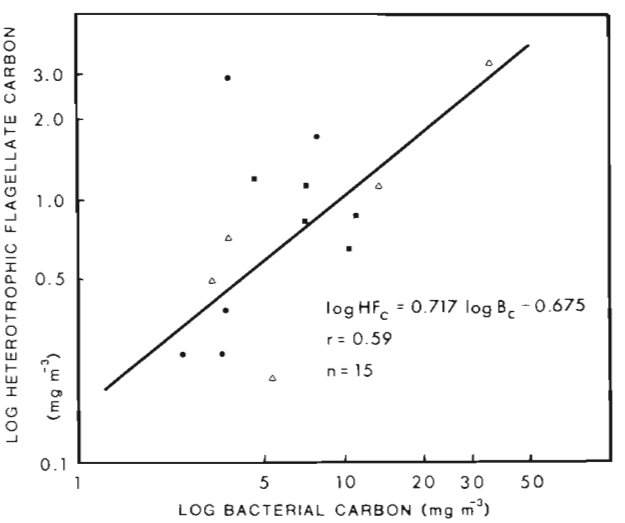

Fig. 3. Regression relating standing stocks of heterotrophic flagellates (Log_{10} HF_C, mg C m^{-3}) to standing stocks of bacteria (Log_{10} B_C, mg C m^{-3}) for pooled data shown in Table 5. Triangles (Station F), solid squares (Station M) and closed circles (Station E5). The regression fitted to data for all 3 channel stations is: Log_{10} $HF_C = 0.717$ Log_{10} $B_C - 0.675$ ($n = 15$; $r = 0.59^{*}$)

Table 5. The standing stocks (mg C m^{-3}) of bacteria, flagellates (total and heterotrophic components) and ciliates (tintinnids and others) at frontal (Station F), mixed (Station M) and stratified waters (Station E5) off the western approaches to the English Channel. Data collected in collaboration with Dr. P. M. Holligan (Marine Biological Association, Plymouth) on R. V 'Frederick Russell cruise 22. 7. to 2. 8. 81, from pumped water profiles (c. f. Table 2 which is for N.I.O. bottle samples).

Station	Depth (m)	Bacteria	Flagellates		Heterotrophic flagellates / Bacteria · 100	Ciliates	
			Total	Heterotrophs		Tintinnids	Others
F	12– 2	35.2	26.06	3.28	9.32	2.28	0.066
	24–12	13.4	14.01	1.26	9.40	2.66	0.350
	36–24	5.4	2.25	0.21	3.89	1.24	0.145
	48–36	3.7	1.99	0.72	19.46	3.26	0.443
	60–48	3.2	1.77	0.49	15.31	2.74	0.400
M	12– 2	10.3	6.43	0.65	6.31	2.66	0.000
	24–12	7.1	6.43	0.82	11.55	5.20	0.010
	36–24	7.2	6.72	1.11	15.42	4.30	0.005
	48–36	10.9	6.48	0.87	7.98	4.12	0.071
	60–48	4.6	6.81	1.20	26.09	3.15	0.000
E5	12– 2	3.8	6.54	2.97	78.16*	2.36	0.000
	24–12	7.9	10.65	1.73	21.90	29.70	0.000
	36–24	3.5	3.32	0.26	7.43	2.88	0.000
	48–36	3.6	2.67	0.38	10.56	1.81	0.000
	60–48	2.5	2.04	0.26	10.40	2.36	0.000

* this value included in the overall mean value of 16.9 %

($n = 15$; $r = 0.59$*) which is similar to the relationships we have obtained from microbial successions on several different sources of phytoplankton debris (Newell et al., 1981). Recalculation of the data presented by Fenchel (1982d) suggests that under natural conditions in the Limfjord, Denmark, the proportion of heterotrophic microflagellates to bacterial prey also ranges from 5.7 to 15.9 % (mean 9.6 %).

DISCUSSION

Because there have been a relatively large number of recent studies on bacterial carbon production in a variety of marine habitats, and because we also have some information on the likely consumption requirements of both the bacteria and the heterotrophic microflagellates, it is now possible to make some estimates on the proportion of phytoplankton carbon which flows through the microheterotrophic consumer community.

The range of values recently reported for bacterial production in a variety of marine systems has been summarized by Newell and Christian (1981) and includes estimates of 2 to 16 mg C m^{-3} d^{-1} for coastal Baltic waters (Hagström et al., 1979), 0.72 to 72 mg C m^{-3} d^{-1} for coastal waters in northwestern USA (Fuhrman and Azam, 1980), 19.2 to 177.6 mg C m^{-3} d^{-1} for nearshore waters in Georgia, USA (Newell and Christian, 1981) and 0 to 78 mg C m^{-3} d^{-1} for the Kiel Fjord and Bight (Meyer-Reil, 1977). Although a great variability exists according to method and area, the mean value for maximal bacterial production (P_{max}) for the data summarized by Newell and Christian (1981) is approximately 75 mg C m^{-3} d^{-1}. This value is very close to that which we have recorded in batch cultures of natural heterogeneous populations of marine bacteria in seawater to which phytoplankton debris was added to a concentration which is similar to that in phytoplankton blooms at Station (F) in the English Channel (Newell et al., 1981).

In these experiments, the results of which have been recalculated in Table 6, we were able to measure concurrently both the increase in the carbon equivalent of bacterial biomass, and thus obtain a measure of bacterial production during the logarithmic growth phase, and also measure carbon utilization from the detrital source. This allows calculation of the carbon equivalent of the 'growth yield' or carbon conversion efficiency (carbon incorporated into bacterial biomass carbon used from the detrital source^{-1} × 100) which, as can be seen from Table 6, was approximately 10 %. Most values for the growth yield of bacteria have been obtained either from continuous cultures in enriched media or from the kinetics of uptake of low concentrations of ^{14}C-labelled simple organic substrates and have generally been found to exceed 50 % (see Payne, 1970; Joint and Morris, 1982). However, as pointed out by Fenchel and Jørgensen (1976), and more recently by Payne and Wiebe (1978), there is now a good deal of

Table 6. Bacterial production (mg C m^{-3} d^{-1}) and carbon conversion efficiency ([mg C incorporated into bacterial biomass. mg C used from detrital source $^{-1}$] × 100) based on phytoplankton cell debris incubated in non-enriched seawater at 10 °C. Data recalculated from Newell et al. (1981)

Detrital source	Detritus concentration (mg C l^{-1})	Bacterial production (mg C m^{-3} d^{-1})	Carbon conversion efficiency (%)
Diatoms			
Thalassiosira angstii	12.12	127	13.48
Chaetoceros tricornutum	13.02	79	8.04
Skeletonema costatum	11.86	79	8.25
Dinoflagellates			
Scrippsiella trochoidea	10.76	61	11.99
Isochrysis galbana	12.0	72	7.60
	$\bar{X}$ = 11.95	$\bar{X}$ = 84	$\bar{X}$ = 9.90

doubt to what extent these data can be applied to the transformation of the relatively high concentrations of complex detrital material which occur following episodic phytoplankton blooms in coastal waters. Quite apart from the fact that carbon conversion is enhanced by the amino acids, vitamins and casamino acids which are usually added to experimental incubation media (Payne and Williams, 1976; see also Newell, 1983), there is some doubt whether the $^{14}CO_2$ respired over a 1 to 2 h incubation period is proportional to the $^{12}CO_2$ respired (Hanson and Wiebe, 1977).

The only data comparable to those cited in Table 6 for the carbon conversion of phytoplankton debris by natural populations of marine bacteria are a series of studies which we have made on kelp detrital material (Linley and Newell, 1981; Lucas et al., 1981; Newell and Lucas, 1981; Stuart et al., 1982), and on detritus from the saltmarsh grasses *Spartina alterniflora* and *Juncus roemerianus* (Newell et al., 1983) which yield carbon conversion efficiency values of 8.8 % to 13.6 %. These values are in good agreement with those recently reported by Robertson et al. (1982) who obtained a carbon equivalent of bacterial biomass of 4 % of the detrital carbon used from the seagrass *Thalassia* and 16.1 % of that from *Syringodium* (i.e. a mean of 10.05 %). It seems unlikely that the low values for carbon conversion of natural detrital material are due to an underestimate of bacterial production resulting from grazing by microflagellates, although apparently, they may consume up to 4.4 % of bacterial production h^{-1} over the first 21 h of incubation (Newell, 1983). In any event, it will be noted from Table 6 that our estimates of bacterial production in the presence of phytoplankton debris concentrations similar to the maximum encountered in a phytoplankton bloom situation are in striking accordance with those obtained by a variety of methods in other sea areas (see p. 84).

Although we have obtained values as high as 37 % for the carbon conversion efficiency of bacterial populations utilizing detrital substrates with low C/N ratio (Newell et al., 1983), it seems likely that a value of 10 % represents the best estimate at the present time for the carbon conversion efficiency of the relatively high concentrations of complex detrital material which occur in phytoplankton blooms under natural conditions. We have therefore used a carbon conversion of 10 % to estimate the consumption requirements of the bacteria in the water column. We recognize, however, that both the kinetics of uptake and the cell yield of heterogeneous populations of bacteria utilizing dissolved components of primary production at low substrate concentrations in oligotrophic waters may be different from that occurring in episodic blooms which characterize shelf waters. Indeed, there is some indirect evidence that a higher cell yield must occur in such waters (see p. 87). Consumption requirements of the microflagellates are now well documented for genera of a variety of sizes from 20 to 200 μm^3 cell volume by Fenchel (1982d). The mean volume of bacteria consumed/volume of flagellate predator 24 h^{-1} is 16.98 ± 3.13 (see also Newell, 1983) and allows some estimates to be made of carbon flow from the bacteria to heterotrophic microflagellates in the pelagic community.

The overall carbon flow for the frontal (F), mixed (M) and stratified (E5) stations off the western approaches to the English Channel is summarized in Table 7. Bacterial production values for Station (F), where the standing stock of phytoplankton and primary production is at its maximum, are available from (1) the mean of the maximum values recorded in the recent literature (see p. 84); (2) direct experimental studies of bacterial growth in batch cultures in the presence of phytoplankton debris at a concentration similar to that at frontal Station (F) (Newell et al., 1981; also Table 6); and (3) an estimate based on the carbon consumption requirements of the heterotrophic microflagellates

(Newell and Christian, 1981). This assumes that (a) heterotrophic microflagellates in the size range 3 to 10 µm are the only consumers of bacteria and (b) bacterial production is in equilibrium with grazing by microflagellates.

From Table 5 it is apparent that the non-tintinnid ciliates are present in insufficient quantity to represent significant bacterial grazers even if, as in the case of *Uronema marinum*, they may be capable of removal of up to 6 times their body weight per day in bacteria (Burkill, 1978). The tintinnids, which are quantitatively the dominant ciliates, in general only consume particles much larger than bacteria and are mainly dependent upon phytoplankton, including the flagellates (Spittler, 1973; Heinbokel, 1978; Fenchel, 1983), and although free-living bacteria may form a substantial portion of the diet of some larvaceans (*Oikopleura dioica*, for example; King et al., 1980), they were not a significant component of the English Channel zooplankton (Holligan et al., 1983). As phagotrophic microflagellates in the size range 3 to 10 µm are the only organisms which can utilize natural concentrations of bacteria efficiently (Fenchel, 1983), they are therefore likely to be the principal, and probably only, bactivores in the present study.

Clearly then, if bacterial production is in equilibrium with grazing by microflagellates, the carbon requirements of the grazers (based on consumption rates of $16.98 \pm 3.14 \times$ their body volume d^{-1} (Fenchel, 1982d; Newell, 1983), approximate to a conservative estimate of bacterial production, i.e. the mean values of 55.8, 12.6, and 40.0 mg Cm^{-3} for F, M and E5

Table 7. Standing stocks (mg C m^{-3}) and estimated consumption requirements (mg Cm^{-3} d^{-1}) of bacteria in the euphotic zone of frontal (F), mixed (M) and stratified (E5) shelf waters off the English Channel. Bacterial production figures for the frontal station are based on: (1) mean of P_{max} from the literature (see text), (2) experimental data for carbon production based on phytoplankton debris at a similar concentration to that at frontal station F (Table 6) and (3) flagellate consumption requirements (see text). The latter value has additionally been used to estimate bacterial production at Stations (M) and (E5). Mean values for primary production were obtained from measurements on 2 (•) or 3 (••) consecutive days, and ranges include estimates from both C^{14} and oxygen method determinations. [+ as % median value.] Data for primary production kindly made available by Dr. P. J. le B. Williams of the University of Southampton, and Dr. P. M. Holligan of the M.B.A., Plymouth

	Water mass		
	Frontal (F)	Mixed (M)	Stratified (E5)
Bacterial biomass (mg C m^{-3})	35.2	8.7	5.9
Bacterial production (mg C m^{-3} d^{-1})			
(1)	75.2		
(2)	84.0		
(3)	55.8		
Mean	71.7	12.6	40.0
P/B Ratio			
(1)	2.14		
(2)	2.39		
(3)	1.59		
Mean	2.04	1.45	6.78
Estimated bacterial Carbon requirements (mg C d^{-1})			
(1)	752		
(2)	840		
(3)	558		
Mean	717	126	400
Primary production (mg C m^{-3} d^{-1})			
Mean (median)	1069•	196•	106•• (495)
Range	828–1500	110–1850	11–1000
Proportion of primary production consumed by bacteria (%)			
(1)	70.3		
(2)	78.6		
(3)	52.2		
Mean	67.0	64.3	80.8+

respectively. This would necessitate generation times of 8 to 19 h, which are well within the range of the 3 to 48 h cited for productive coastal waters by Van Es and Meyer-Reil (1982) in their recent review, and yields bacterial production estimates consistent with the values summarized by Newell and Christian (1981) for a variety of coastal and shelf waters (see also p. 84).

The estimated bacterial carbon requirements at a conversion efficiency of 10 % are thus 10 × the production values or 717 mg C d^{-1} based on all 3 estimations of bacterial production at Station (F), 126 mg C d^{-1} at the mixed water Station (M) and 400 mg C d^{-1} at Station E5. From this it can be seen that carbon consumption by bacteria accounts for 60 to 80 % of the carbon fixed by primary production. This figure is in good agreement with that of Sorokin and Mikheev (1979), who have estimated that as much as 70 to 80 % of total energy flux in the Peruvian upwelling system occurs through the bacteria and microprotozoa. In contrast, by assuming a conversion efficiency of 37 % (obtained on low C : N plant debris, see Newell et al., 1983), the estimated bacterial carbon requirements amount to approximately 14 to 22 % of primary production, which is similar to the results obtained by Wiebe and Smith (1977) who found that uptake of ^{14}C-labelled exudates by bacteria is in equilibrium with its release from phytoplankton and amounts to about 25 % of the carbon originally fixed by the phytoplankton (see also Hagström et al., 1979). It suggests that despite the relatively high dissipation of carbon, which we have measured from complex detrital sources in non-enriched media, carbon fixation by photosynthesis in the euphotic zone of productive coastal waters is well in excess of that required by the microheterotrophic community.

Although there are relatively few detailed studies on the standing stocks of microplankton, including bacteria and heterotrophic microflagellates, in the open oceans, some general comparisons can be made between the results we have obtained for coastal phytoplankton bloom situations and likely carbon flow through the microheterotrophs in oligotrophic waters. The bacterial standing stocks in open oceans is likely to be of the order of 0.05 to 0.15 × 10^6 cells ml^{-1} (Sorokin, 1981). Assuming that a ratio of heterotrophic flagellates: bacterial prey of 0.05 to 0.15 recorded for coastal waters and experimental media occurs in oligotrophic waters (see also Linley and Newell, 1981; Newell et al., 1981; Fenchel, 1982d), and that the flagellates consume approximately 17 times their body volume of bacteria per day (Fenchel, 1982d), the carbon requirements of the flagellates would be 0.6–1.8 mg C m^{-3} d^{-1}. If the bacteria were converting the organic carbon available in oligotrophic waters with an efficiency of only 10 %, as we have recorded in the presence of high concentrations of phytoplankton debris, a primary production of 6.0 to 18 mg C m^{-3} d^{-1} would be required to sustain the consumption requirements of the heterotrophic microflagellates, even if all carbon from primary production entered the microheterotrophic food chain. In fact, primary production is approximately 2.5 to 5.0 mg C m^{-3} d^{-1} (Ryther, 1969), and probably 30 % (but up to 60 %) enters the microbial food chain (Williams, 1981), suggesting that a bacterial carbon conversion of at least 50 % is likely to occur in oligotrophic waters. This accords well with estimates based on experiments with low concentrations of ^{14}C-labelled substrates comparable with oligotrophic waters (see p. 84; Joint and Morris, 1982) and suggests that carbon flow through the microbial community may be different from that in the decomposition phase of phytoplankton blooms in coastal waters. Unfortunately, until there are further studies which simultaneously estimate bacterial and microflagellate biomass and clearly distinguish between heterotrophic and phototrophic flagellates, it is not possible at this stage to make any more detailed comparisons between carbon flow through oligotrophic and coastal communities.

Estimates of carbon flow through the pelagic microheterotrophic community suggest, therefore, that approximately 20 to 60 % of primary production, possibly representing primarily the dissolved components leaching from disrupting phytoplankton cells (Fuhrman and Azam, 1980; Newell et al., 1981) enters the microbial food chain. Much of this is dissipated by the bacteria, only some 5.2 to 8.1 % of the photoassimilated carbon becoming incorporated into bacterial production. At least 66 % of this is exploited by the herotrophic microflagellates leaving a maximum of 34 % of bacterial production for the larger bactivorous suspension feeders.

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