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Occurrence and respiration of ultraplankton in the upper 500 meters of the ocean

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Abstract—By gentle concentration the ultraplankton of the open ocean were prepared for estimation of their rate of respiration and for microscopic examination while still alive. Except in coastal waters the predominant organisms of the upper 500 m in the western North Atlantic and Southeast Pacific were generally μ flagellates (2–10 μ). Most bacteria and many flagellates were associated with flocculent organic aggregates. Below 25–50 m most of the flagellates were non-pigmented. Evidence is presented that much of the energy fixed by photosynthesis is utilized by Protista. Organic aggregates appear to be the locus of much of the metabolic activity in the ocean.

INTRODUCTION

PLANT production often is used as the basic index of biological activity in the sea. Since all energy fixed by phytoplankton is not utilized by consumers at the same time or in the same place it is produced, primary production is a somewhat uncertain index of energy utilization by the plankton community. Temporal and spatial imbalances between respiration and photosynthesis must occur in the ocean owing to the sinking and horizontal transport of organic matter. Community respiration should be a more accurate index of the energy being utilized by consumers at a given time and place.

There is considerable evidence that the very small components of the plankton (1–10 μ) are important in the food chain of the open sea (BERNARD, 1963; WOOD, 1963; JOHANNES, 1964; ANDERSON, 1965; FOURNIER, 1966). There is no standard nomenclature for small marine organisms, and most size classifications have reference to phytoplankton only. RAYMONT (1963) specifically excludes zooplankton from the term, nannoplankton. Bacteria generally are excluded. We have chosen to use the term, ultraplankton, to describe all living organisms in the size range $< 10\,\mu$, according to the usage of STRICKLAND (1965a and b), without other taxonomic or trophic distinctions. We find organisms in this size range to be accountable for most of the total respiration (POMEROY and JOHANNES, 1966), as others have found them to dominate photosynthesis and sometimes biomass. This report presents further observations on respiration in the upper 500 m, on the kinds of organisms making up the ultraplankton, and on their relation to non-living particulate organic matter, including organic aggregates.

Lack of sensitive techniques has hindered progress in measuring oxygen consumption by the ultraplankton. Dark-bottle incubations are not sensitive enough for water of the open sea, and ^{18}O does not promise to be a sensitive tracer. These methods can be improved by gently concentrating the plankton to the point where respiration

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per unit volume of water is rapid enough to be measured quickly and accurately. Here we give details of a method for estimating respiration of the ultraplankton and some tests of the correctness of the results.

MATERIALS AND METHODS

We have modified the method of DODSON and THOMAS (1964) to concentrate plankton gently, with a minimum of manipulation (Fig. 1). By using 8 concentrators at once, it is possible to concentrate up to 200 litre of water to a final volume of 10 ml in 2–3 hr, while keeping most of the ultraplankton in suspension. While water from the reservoir is flowing through the system, there is no depletion of oxygen and no build-up of excretory products in the concentrate. In the final stages, after the reservoir is empty, dissolved oxygen remains near saturation, but phosphate analyses show that there is some buildup of excretory products.

When concentration is completed, the filter is turned on its side and washed down with a few ml of membrane-filtered sea water. A small sample is removed for immediate microscopy, and the remainder is transferred quantitatively to a graduated cylinder. A measured amount is then placed in a 14 ml respirometer which is equipped with AgO–Pt electrodes (CARRITT and KANWISHER, 1959; TEAL and HALCROW, 1962) and paddle-stirred at 60 rev/min. Change in oxygen tension is recorded continuously on a recording potentiometer. A good record can be obtained in 1 hr, but the rate remains linear for several hours or until the oxygen has been reduced to 25% of

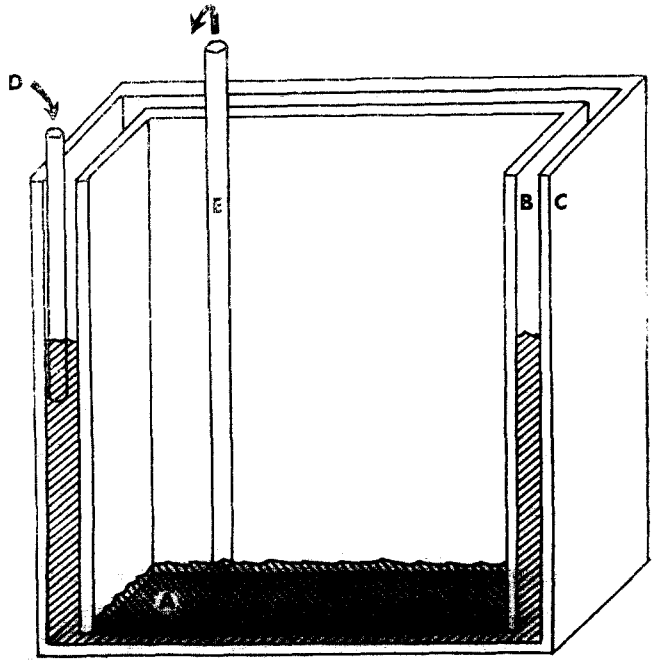

Fig. 1. Section through a plankton concentrator. A membrane filter (A), 15 × 15 cm, of 0·8 μ porosity, is attached with epoxy resin to the bottom of an acrylic plastic box (B), which nests inside another one (C). Water is introduced between the boxes (D) from a carboy to maintain a head of 5 cm of water. As water passes through the filter, it is aspirated away (E) to maintain the pressure.

saturation or less. When the process is completed, a sample is taken for microscopic examination.

The membrane filter is back-washed after use by filling the inner box partially with fresh water and gently rubbing the outside of the filter, so it may be used again. When the filtration time becomes too long, the old filter is scraped off with a knife, and a new one is put on.

The respirometers are calibrated using Winkler titrations. They are sterilized before each use with 70% ethyl alcohol, followed by several rinses with freshly membrane-filtered sea water. Frequent checks on the rate of drift are run with freshly filtered water, and the results corrected for drift.

Samples are examined with a fluorescence microscope, using both blue and white light and medium and high-dry objectives. Acridine orange proves helpful in resolving small organisms with fluorescence, but it also stains a variety of non-living organic particles. We do not find it useful for discriminating between living and dead material. Living bacteria are identified by adding a drop of 3-*o*-methyl fluorescein phosphate in sea-water solution. Those with phosphatase enzymes on their surfaces quickly develop a fluorescent yellow halo. While this may not reveal them all, it is helpful in finding many that otherwise might be overlooked under conditions at sea.

Sea water is collected either in a 25-litre Menzel dazzler or a 200-litre Gerard–Ewing (1961) bottle. In either case the water is drawn into carboys at once by gravity. The dazzler is positioned by reading wire out on the hydrographic winch. Wire-angle corrections have not been necessary, because the casts are so shallow. The G–E bottle is positioned by observing it on the precision echo sounder. This is particularly useful in taking samples located precisely in the scattering layer.

OBSERVATIONS

Respiration of the larger zooplankton may change by a factor of 2 or 3 when they are concentrated (cf. SATOMI and POMEROY, 1965). To test for a similar effect on ultraplankton, we took single, large samples of surface water, filled all eight concentrators with the water, and prepared aliquots that contained varying densities of plankton. Because of the limited equipment available to us, it was necessary to use water that contained a moderate amount of plankton to begin with, and we could only produce 3 or 4 different plankton densities from a single initial water sample. Since each sample of water had its intrinsic respiration rate, we could expect each to have a different slope (Fig. 2). However, we found in all cases that the lines regress toward zero, except at very high concentration factors. These were therefore avoided in practice. Some of our observations show rates of respiration as high as those of dense concentrates, but they were prepared from water initially containing dense plankton populations. It appears that concentration has little effect on the respiration rate of ultraplankton. Since the lines regress toward zero, it is reasonable to calculate the respiration in the original water sample from measurements made on the concentrates.

It was our intention to process samples as rapidly as possible, on the supposition that the metabolism of small, delicate organisms could not be expected to remain normal for long periods under experimental conditions. Moreover, the build-up of soluble metabolites in the respirometer might be inhibiting after some time. Metabolites could be expected to stimulate the growth of bacteria, which would then con-

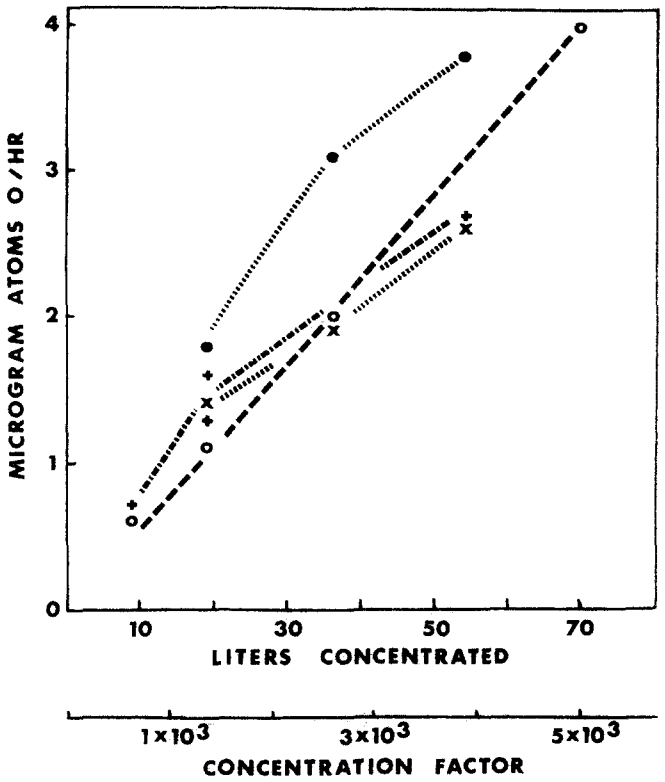

Fig. 2. Relation of respiration rate observed to concentration factor of plankton concentrates. Each symbol represents a different water sample. See text.

tribute more than normal to oxygen demand. However, when we have held concentrates in the respirometer for several hours, the observed rates have been linear with time until oxygen tension became low. We have been unable to detect any influence of metabolites or of the initial stress of handling on these rates.

Substantial differences in respiration were found in several water types of the Western North Atlantic (Table 1). The slope-water station appeared to be at the height of the spring bloom. Large diatoms, as well as ultraplankton, were abundant in the water. The respiration at 5 m was the highest we have observed. The Gulf Stream station showed irregular differences at the depths sampled. Since the respiratory rates were reproducible to within 0·1 mg atoms O m^{-3} day^{-1}, these were real differences. Probably they reflected a layering of ultraplankton populations. There are precedents for such fine structuring in the chemical observations of HOLM-HANSEN *et al.* (1966). One station in the Western Sargasso Sea was occupied for 4 days. Replicates at a single depth represent different water samples taken on successive days, and give some idea of local variation in space and time. The samples at 300 and 400 m on that station were in the scattering layer, where on this occasion respiration seemed to be significantly higher at adjacent depths, although still quite low. On other occasions, however, it was not higher there.

The stations off the coast of Peru were occupied over a period of 6 weeks (Table 2, Figs. 3 and 4). In both sections aerobic respiration is high where dissolved oxygen in

Table 1. *Respiration at stations in the Western North Atlantic*, mg atoms O m^{-3} day^{-1}. (*Bold numbers are in the scattering layer*).

Sample depth, m	May, 23–26, 1966 33°30′N 72°00′W Sargasso Sea	Aug 13–17, 1966 33-32°N 71°20′W Sargasso Sea	Aug. 18–19, 1966 33°N 75°W Sargasso Sea	Apr. 4, 1966 35°55′N 73°32′W Gulf Stream	Apr. 2–3, 1966 36°10′N 74°38′W slope water
0·1	1·3, 1·9, 1·3	0·9, 0·8	0·9, 0·7	2·4	3·8
5					15·5
10		0·5			
15			2·6		5·4
20		0·2			
25	0·9, 0·2				
30			0·4		
50	0·9, 0·6	0·2		3·1	0·5
75	0·6				
100	0·3	0·3		0·7	0·7
150	0·3				
200	0·3	0·5			
250	0·3	0·1		0·3	0·9
300	**0·5**				
400	**0·5**	**0·3**			
500	0·2	**0·3**	**0·5**	0·5	0·8
550		0·3			
700		0·3			
750				0·05	
800	0·1	0·05			

the water is sufficient to support it. Total respiration amounts to from 200 to nearly 900 mg atoms O m^{-3} day^{-1} (Table 2). Below the first 100 meters or so, where dissolved oxygen is very low, aerobic respiration is lower by an order of magnitude, in spite of the fact that the samples became fully aerated during the process of concentration. An exception to this occurred in the vicinity of 82°W (Fig. 3) at a depth of

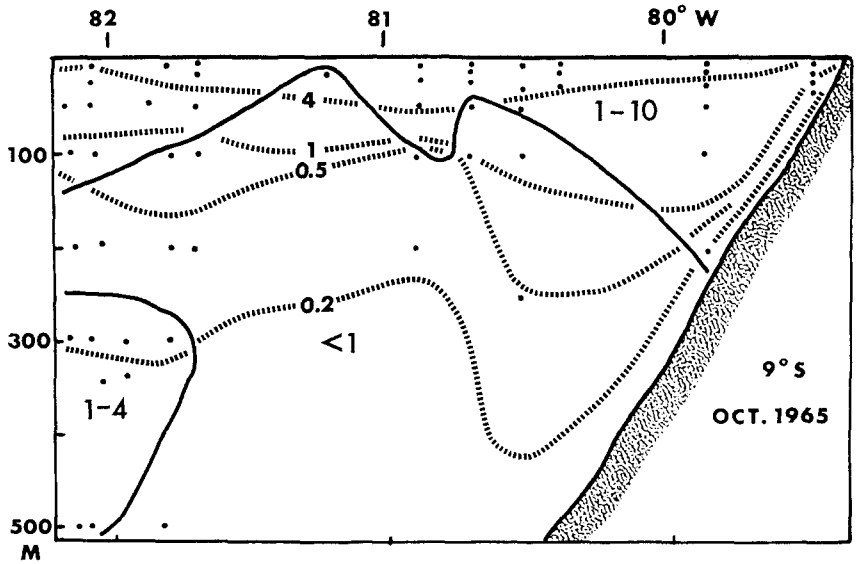

Fig. 3. East–west section off the coast of Peru at 9°S, showing respiration rate, estimated from plankton concentrates (solid lines), in mg atoms O m^{-3} day^{-1} and dissolved oxygen content of the water (dotted lines) in ml l^{-1}. Positions of water samples are indicated by dots.

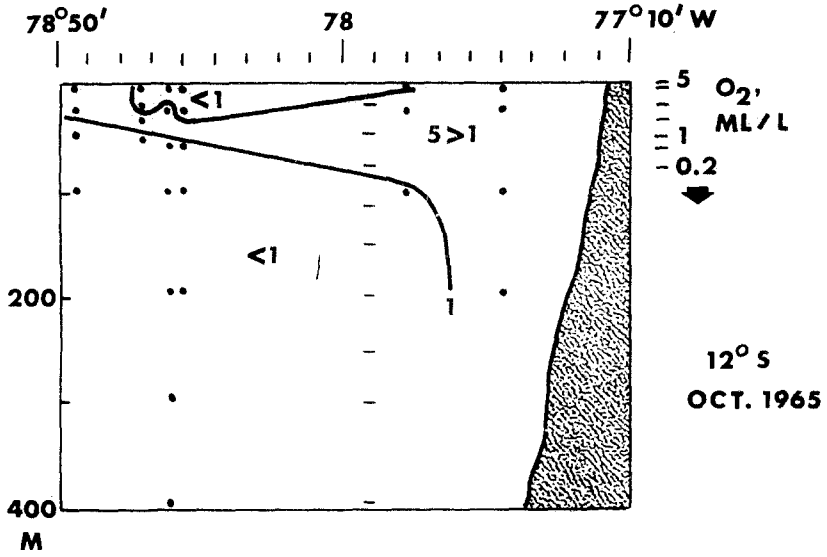

Fig. 4. East-west section off the coast of Peru at 12°S, showing respiration rate, estimated from plankton concentrates, in mg atoms O m^{-3} day^{-1}. A single set of measurements of dissolved oxygen, taken at 77° 51'W is shown at the right.

300–400 m. Here the rates indicated the presence of viable aerobic ultraplankton which responded to aeration. This was in all probability not representative of the normal rate of respiration at that depth *in situ*, because oxygen would be insufficient to support it. Therefore we omitted it from calculations in Tables 2 and 3. While most upwelled water is supplied by the Peru Countercurrent, some moves in from offshore at depths greater than 100 m (WYRTKI, 1966). Such movement could bring viable aerobic organisms into the oxygen-depleted water. Whatever their source, it

Table 3. Respiration in the upper 500 meters, and P/R ratios at stations in the Southeast Pacific off Peru. Photosynthesis estimates are from MENZIES *and* CHIN (1966).

Sta.	*Total depth* (m)	*Location*	*Respiration* (mg atoms O m^{-2} day^{-1})	*P/R*
40	41	07° 58'S 79° 21'W	375	1·6
127	80	08° 20'S 79° 33'W	400	
118	200	08° 17'S 79° 52'W	520	0·9
84	520	07° 57'S 80° 32'W	568	5·3
138	568	11° 51'S 77° 33'W	878	1·0
132-4	600	08° 34'S 80° 00'W	216	1·3
103	1900	08° 16'S 80° 52'W	469	
111	3100	08° 22'S 80° 45'W	250	1·0
96	4500	08° 24'S 81° 40'W	315	1·3
62-8	4500	06° 22'S 81° 47'W	169	1·1
33	4900	05° 49'S 82° 05'W	319	0·7

seems probable that they cannot respire aerobically at the observed rates in water largely depleted of oxygen.

In addition to measuring respiration, we routinely examined each concentrate immediately at sea and recorded qualitative observations. The great advantage of our method is that organisms, detritus, and aggregates retain their normal three-dimensional form. The dominant organisms in the Western North Atlantic were flagellated cells of the order of 5 μ in size. Most of them were not pigmented except near the sea surface. In the Gulf Stream and Sargasso Sea small (2–10 μ), naked flagellates which showed green fluorescence in blue light dominated many samples. Similar forms frequently were dominant in the Southeast Pacific. Their frequent occurrence in surface water leads us to suspect that these cells are autotrophic and that some accessory pigment masks the red fluorescence of chlorophyll. Atlantic slope water in spring and some samples from regions of most active upwelling off Peru were populated predominantly by diatoms. At depths below the euphotic zone in both oceans pigmented cells were rare but always present. Bacteria were seen, but not in large numbers.

Other organisms were present in decreasing abundance as their size increased. There seldom were more than one or two copepods or other microplankton per sample. Of course, our sampling method did not collect microplankton efficiently, but we have given evidence previously (POMEROY and JOHANNES, 1966) that net plankton account for only a small fraction of total plankton respiration. By measuring separately the respiration of larger plankters, we find that their contribution to the total is insignificant, ordinarily less than 5%.

Most of the mass of the concentrates was made up of non-living materials. These included crystals of several kinds, animal tests, plant fibers, and flat blade-like objects. All of these occurred both singly and adhering to aggregates. Some variation in the distribution of non-living materials has been noted. Near-surface samples contained the greatest variety. At depths of 300 m or more in the Western Sargasso Sea flat, blade-like crystals, frequently twinned, were sometimes an important component. They are readily distinguishable from organic aggregates. A sample from 800 m, near the oxygen minimum, was turbid and contained a large amount of fine detritus which appeared to be organic when examined under the microscope. The sample clogged the membrane and was concentrated with great difficulty. It proved to have a barely measurable rate of respiration. A much higher percentage of the detritus in areas of high production was visibly of plant origin (e.g. decomposing diatoms).

Copepod fecal pellets were observed frequently, particularly in the Southeast Pacific. Although some of them were green under white light, they fluoresced only very faintly or, more often, not at all under blue light. No more than 5 or 6 discrete phytoplankton cells were ever seen in any one fecal pellet. These observations suggest that superfluous feeding by zooplankton (BEKLEMISHEV, 1962) probably was not an important process in these waters.

More significant than the variations from place to place was the uniformity of the presence of detrital aggregates with their resident populations of flagellates and bacteria. They contained much open space and were colonized by many of the μ-flagellates and bacteria. The flagellates could be seen swimming about inside, adhering to them, or swimming near their external surface. Bacteria adhered to the mucus-like substance of the aggregates.

DISCUSSION AND CONCLUSIONS

Several approaches have been made to the estimation of total respiration in the sea. Long-term changes in oxygen *in situ* (RILEY, 1951; 1957) offer the great advantage of dealing with an undisturbed system, neither concentrated nor bottled. However, the changes *in situ* have such long time constants that they can be interpreted only by including in the calculation terms for eddy diffusion and advection. These terms introduce uncertainty into the calculation (REDFIELD *et al.*, 1963). RILEY's (1951) estimate of respiration in the Sargasso Sea is much lower than ours, for example. Changes in oxygen in bottles of sea water are very slow and are subject to errors arising from the growth of bacteria on the surface of the bottles and from the death of other populations. For this reason, bottle methods are not used in the open sea. Methods such as ours also present difficulties (p. 383). There is no evidence, however, that the respiration in the concentrates is greater than it would be in the volume of water from which they were taken. In fact, at very high concentration factors there is a slight depression. This may be because the organisms in nature are already very localized in and around aggregates, so their distribution in space is not so greatly affected by the concentration process. It is difficult to ascertain whether a significant number of organisms is destroyed by manipulation. We do find many small, naked flagellates. Tintinnids were rare in our samples, but we have no reason to believe that they were selectively destroyed. Further examination of the method and comparisons with other methods are needed, but the results to date are consistent, and tests of the effect of concentration are encouraging.

On the basis of our results thus far, we can make some inferences about the metabolism of the sea. In general, high rates of respiration are found in regions where photosynthesis is high: in the spring bloom of the Atlantic slope water and in upwellings off Peru. It is low where photosynthesis is relatively low: the Sargasso Sea. Temperature is not as important as available organic matter, since respiration was higher in the slope water at 6°C and in upwelled water at 15°C than in the Sargasso Sea at 19–22°C. Varied P/R ratios (Table 2) and significant respiration below the euphotic zone indicate that photosynthesis and respiration are not completely coupled. Presumably this is owing to a lag between production and consumption, to the transport of organic matter by advective processes, and to the sinking of particulate matter.

In the Western North Atlantic respiration decreases in the first 500 m to a rate that we cannot distinguish from zero with our present technique. This leaves 90% of the mean water column still to be considered, and even if the rate per unit volume below 500 m were an order of magnitude less than that near the surface, it would involve half the total energy fixed by photosynthesis (assuming it to be the only significant energy source). It is reasonable to suppose that respiration below 500 m is lower than that near the surface by perhaps several orders of magnitude. Otherwise, we should find the oxygen to have been totally depleted in the deep water.

It would be helpful to have absolutely correct estimates of photosynthesis with which respiration could be compared. However, there is still reason to doubt that the ^{14}C method as ordinarily used is absolutely correct. Several authors have presented evidence that it is too low by perhaps a factor of 2 or 3 (VERDUIN, 1959; VALLENTYNE, 1965; ARTHUR and RIGLER, 1967; ODUM, 1967).

Table 2. Respiration at stations in the Southeast Pacific, mg ato

Sample depth (m)	4, 5 Oct. 05° 50′S 82° 04′W (27, 31, 33)	7 Oct. 06° 21′S 82° 14′W (45, 48)	10, 11 Oct. 06° 21′S 81° 46′W (52, 65, 67)	14 Oct. 07° 57′S 81° 40′W (84, 86)	15 Oct. 08° 24′S 81° 04′W (96)	17 Oct. 08° 16′S 80° 52′W (103)	17 Oct. 08° 22′S 80° 43′W (109)	18 Oc 08° 22′ 80° 45′ (111)
0·1	0·61		13·9, 0·89, 0·71, 0·63	9·11	2·80	6·3, 8·6	2·35	2·46
10							3·12	2·17
20								
25	1·31		1·80	6·60	0·80	7·4	2·86	0·91
30								
50	1·04		1·96, 0·85	1·04	0·95	3·51	0·28	0·83
60								
75						0·00	0·00	1·13
100	0·45	0·73	0·05	0·67	0·34			
175								
200	0·21	0·00	0·24		0·09	0·68		
250				0·22				
300	1·90	0·00	0·00		0·99			
400								
500	0·66	0·00	0·00					

ıst Pacific, mg atoms O m^{-3} day^{-1}. *Numbers in parentheses are station numbers of R.V.* Anton Bruun *Cruise*

17 Oct. 08° 22′S 80° 43′W (109)	18 Oct. 08° 22′S 80° 45′W (111)	19 Oct. 08° 17′S 79° 52′W (118)	19 Oct. 07° 58′S 79° 21′W (123)	20 Oct. 08° 20′S 79° 33′W (127)	20 Oct. 08° 34′S 80° 00′W (132)	25 Oct. 11° 51′S 77° 33′W (138)	25 Oct. 11° 53′S 77° 49′W (142)	26 Oct. 12° 01′S 78° 30′W (148)	27 Oct. 11° 58′S 78° 35′W (149)	28 Oct. 12° 00′S 78° 46′W (154)
2·35	2·46	4·00	5·46	12·24	4·16	4·50	0·00	0·32	0·82	1·60, 0·60
3·12	2·17	7·66	13·32	6·56						
			7·05							
2·86	0·91	4·93		6·44	3·48	3·65		2·80		1·65
			6·50						0·10	
0·28	0·83	3·40		2·40	1·33, 1·46	2·66	2·06	0·67	1·10	0·22
				2·40					0·70	
0·00	1·13	2·31			0·04					
						3·20		0·00		0·20
		1·33								
						4·00	0·80	0·13		0·10
					0·27			0·22		
								0·12		

We do not have concurrent estimates of photosynthesis for our stations in the Western North Atlantic, but it was estimated at many of our stations off Peru. This was done by John Hall of the permanent scientific party of R.V. *Anton Bruun*, and is published elsewhere (MENZIES and CHIN, 1966). We can make some comments on the relation of photosynthesis (P) to respiration (R), within the limits expressed above. Photosynthesis data also were used in calculating the P/R ratios in Table 2. Since it is reasonable to expect that P and R will be out of phase some of the time, the P/R ratio in the sea may vary considerably. A mean of the ratios at many stations probably is more meaningful than the individual values. If both P and R are taken without correction factors, the mean P/R for our series of observations is 1·5. This seems low, considering that neither the larger zooplankton nor the anchovetas are not represented in our respiration values. If the requirements of the whole food chain off Peru are taken into account, either the true P should be higher or the true R lower.

Since we do not have concurrent ^{14}C estimates of photosynthesis for our estimates of respiration in the Western North Atlantic, we cannot even provisionally calculate P/R. Uncorrected ^{14}C data in the literature suggest that P/R would be near 1. Our Sargasso Sea stations are in the extreme western portion, where productivity is higher than in the Bermuda area. Therefore, Bermuda data are not a valid basis for comparison, and it should not be assumed that respiration near Bermuda can be estimated from our data.

It has been suggested that respiration in the dark is much lower than in the light in situations where most of the organisms are very small (ODUM *et al.*, 1963). If this is so, then our estimates of respiration, which were made in darkness, are underestimates for the euphotic zone. The true P/R is lower, if heterotrophic respiration does in fact decrease at night.

It is striking that many of the bacteria and protozoa, as well as considerable numbers of phytoplankton, are associated with organic aggregates. These conform to the description of the organic aggregates found throughout the water column by other methods (RILEY, 1963; RILEY *et al.*, 1964; 1965). Riley describes them as sheet-like or flake-like when seen on membrane filters. When seen in suspension, they are fluffy, loose, and nearly transparent, with much interior open space. Their size, adherent materials, and associated organisms are as Riley described them.

The aggregates appear to be centers of metabolic activity in the sea. They also are likely sites of adsorption of soluble material, as others have suggested (RILEY, 1963; BAYLOR and SUTCLIFFE, 1963). At the same time they must be substrates for the bacteria we see in them. Probably the bacteria serve as food for the Protozoa. There is evidence that this also is the food chain in benthic detritus (MARE, 1942; JOHANNES, 1965). If such a food chain does exist within the aggregates, then probably the concentration of materials excreted by animals, and plants as well, is high inside them. This means that there may be local concentrations of dissolved materials in the sea where conditions are much more favorable than in the water generally for the adsorption of dissolved organic matter and its degradation by bacteria. Such localized concentrations would also be favorable sites for the direct uptake of dissolved organic materials by protists of all kinds. The biological availability of dissolved materials in the sea may depend not on their concentration in the open water but on their concentration within and on surfaces of aggregates.

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