Respiration and respiratory electron transport activity in plankton from the Northwest African upwelling area[1]

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ABSTRACT

Microplankton and zooplankton respiration were calculated from ETS activity measurements in the upwelled waters off Cape Blanc, Mauritania. The mean respiration was 14.4 mgC $h^{-1}m^{-2}$ for microplankton and 6.4 mgC $h^{-1}m^{-2}$ for zooplankton. Mixing kept the microplankton from accumulating in the surface waters so that vertical profiles were nearly uniform with depth. High levels of ETS activity below the euphotic zone reflected this mixing. Between the bottom of the euphotic zone and the 0.1% light level, the ETS activity averaged 72% of the euphotic zone/ETS activity level. Another 44% of the euphotic zone level could be found even deeper (between the 0.1% and 0.01% light level). Respiration-photosynthesis ratios were calculated from two different assessments of gross productivity. The R/P ratios ranged from 0.07 to 0.15 depending on the method of calculation. The microplankton ETS activity was compared to respiration that was independently calculated by a ^{14}C method (Smith, 1977). The results of the two approaches were correlated (r=0.82, n=10). The microplankton ETS was also correlated with photosynthesis as measured by ^{14}C-uptake (r=0.64, n=16). These correlations support the assumption that phytoplankton dominated the dynamics of microplankton metabolism in the euphotic zone off Cape Blanc. The role of the zooplankton in the regeneration of ammonium in the euphotic zone was investigated by calculating an ammonium excretion rate from zooplankton respiration and comparing this to phytoplankton NH_4^+-uptake rates. From a mean oxygen consumption rate of 17.7 ml O_2 $h^{-1}m^{-2}$ an ammonium excretion rate of 198 μg-at N $h^{-1}m^{-2}$ was calculated. At five stations, the ammonium excretion rate satisfied 55% of the phytoplankton NH_4^+-uptake. The hypothesis that the difference in productivity between the Peru Current and the N.W. African upwelling systems can be explained by the differences in the ratio of the compensation depth to the mixed layer depth was tested. This ratio, D_c/D_m, was 0.7 in the N.W. African upwelling system and 2.4 in the Peru Current system. The threefold difference supports the hypothesis.

1. Introduction

Respiratory oxygen consumption, unlike the assimilatory biological processes of photosynthesis and nitrogen fixation, occurs at all depths and in all regions of the ocean where oxygen is present. In the euphotic zone, this respiration is masked by photosynthesis, but below that zone, it becomes the dominant process. Respiratory

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rates in the euphotic zone fall in the 1 to 20 μl O_2 $h^{-1}l^{-1}$ range, they decrease to 0.10-0.01 μl O_2 $h^{-1}l^{-1}$ between the bottom of the euphotic zone and 100 m, and below 100 m they range from 10 to 0.1×10^{-3} μl O_2 $h^{-1}l^{-1}$ (Riley, 1951; Munk, 1966; Arons and Stommel, 1967; Pomeroy and Johannes, 1968; Wright, 1969; Packard *et al.*, 1971; and Packard *et al.*, 1977). In all cases, this respiration represents the rate at which plankton generate energy for swimming, for growth, and for basal metabolism. This energy is produced during the oxidation of carbohydrates, lipids, and proteins by the reactions of intermediary metabolism and is stored as ATP (Lehninger, 1977). The oxidation process consumes dissolved oxygen from seawater and produces CO_2. If respiration were not balanced against photosynthesis in the euphotic zone and if seawater were not well buffered, the dissolved oxygen would be depleted and the added CO_2 would cause the pH of the seawater to drop below its normal value of 8.2. In the deep sea, the reservoir of dissolved oxygen is large enough to sustain low respiration rates for hundreds of years (Packard *et al.*, 1971 and 1977) and the seawater has enough buffer capacity to accommodate the added CO_2 during this time without a pH shift greater than about 0.3 pH units.

Measurements of respiration are helpful in understanding many oceanic phenomena. They facilitate calculations of the ages and the circulation patterns of deep water masses (Carmack and Aagaard, 1973; Lambert, 1974), they lead to an understanding of the distribution of oxygen and carbon dioxide in the ocean (Craig, 1971; Kroopnick, 1974) and they provide information on the economics of carbon, oxygen, and biologically useable energy in oceanic ecosystems. In the latter case, zooplankton respiration permits the calculation of the animals' minimal food requirements and the minimum primary productivity needed to supply these requirements. Respiration in phytoplankton resting spores in conjunction with the spore's food storage capacity (Anderson, 1975) can be used to calculate the spore's survival time. Respiration of the plankton and benthos in deep sea trenches or fjord bottoms can be used to calculate the minimum turnover time of the deep waters. (Christensen and Packard, 1976).

Respiration also provides the information about the maturity and efficiency of an ecosystem. The ratio of photosynthesis to respiration (P:R) in an ecosystem is an index of the ecosystem's maturity (Odum, 1956; 1967; Margalef, 1974). If the P:R ratio is close to 1, the ecosystem's energy and carbon demands are met by its primary productivity and the ecosystem is said to be mature. In this state, there is no excess productivity to be exported to, or exploited by another ecosystem (Odum, 1956). If the P:R ratio is less than 1, the ecosystem is a consumer system and must be coupled to an exploitable, immature ecosystem with a high P:R ratio. The deep ocean basins are examples of consumer ecosystems, the central ocean gyres are examples of mature ecosystems, and upwelling areas are examples of immature ecosystems.

The Coastal Upwelling Ecosystems Analysis (CUEA) program conducted a com-

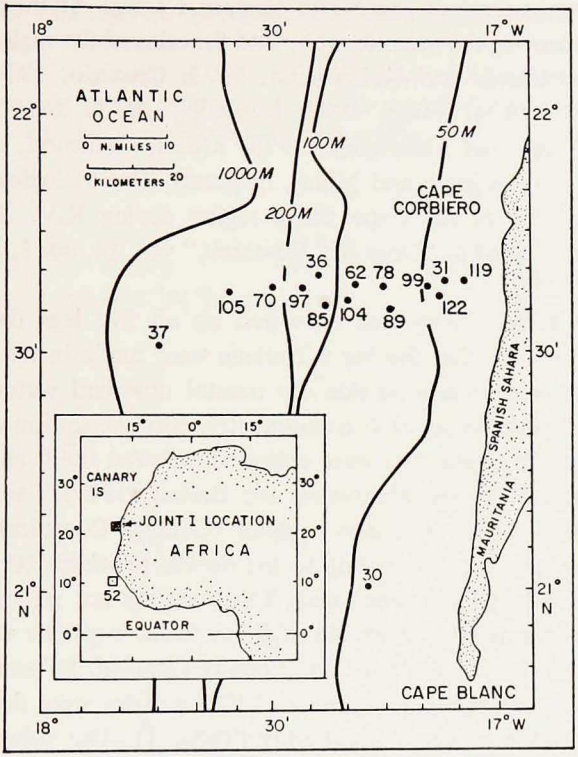

Figure 1. Station locations of R. V. *Atlantis* II, cruise 82 (CUEA expedition, JOINT I) in the Cape Blanc upwelling on the N.W. coast of Africa. The coordinants of station 52 should be read on the larger map.

prehensive study of the upwelling ecosystem off Cape Blanc, Mauritania in March, April, and May 1974 (Barber, 1977). One of the objectives of the expedition was to document the biological processes that contribute to the regulation of the upwelling ecosystem. This contribution describes the plankton respiration, its spatial distribution across the continental shelf and slope off Cape Blanc, and its relation with photosynthesis and with plankton biomass.

2. Methods

This work was done in the upwelled water over the continental shelf and slope off Cape Blanc, Mauritania (Fig. 1). Most stations were made along an east-west transect at 21°40'N latitude, although some stations were made along the coast north and south of the transect. Figure 1 gives the location of the stations that are extensively referred to throughout this report; the station map in Barber and Huntsman (1975) and Huntsman and Barber (1977) gives the location of those stations that are briefly mentioned in this report. The area has been the focus of CINECA

(Cooperative Investigations of the North Eastern Central Atlantic) research since 1970 and descriptions of the oceanography and fisheries of the region have appeared steadily (e.g. Mittelstaedt and Koltermann, 1973; Cruzado, 1974; Fraga, 1974; Coste and Slawyk, 1974; Vives, 1974; Margalef, 1975a and b; Vallespinós y Estrada, 1975; Fraga and Manriquez, 1975; Minas, Codispoti, and Dugdale, in press; and Codispoti, Dugdale and Minas, in press). The biological, chemical, and physical oceanography of the Cape Blanc region during R.V. *Atlantis* II cruise no. 82 has been described in "Deep-Sea Research," vol. 24, no. 1, and in Codispoti and Friederich (1978).

Microplankton ETS activity was measured on all five legs (0-4) of the R.V. *Atlantis* II cruise no. 82, but the leg 0 stations were made in the central Atlantic and leg 4 stations were made outside the coastal upwelled waters along a track from the Canary Islands to Senegal; consequently, only the station data from legs 1, 2, and 3 will be used. These data were collected between 0800 and 0900 h as described by Barber (1977) and Huntsman and Barber (1977). Samples were taken in 30 l Niskin bottles with a rosette sampler (General Oceanics) throughout the euphotic zone at depths corresponding to the depths to which 100, 50, 30, 15, 5, and 1% of the incident light penetrated. These depths are referred to frequently throughout this paper as light levels. In addition to the euphotic zone samples, the 0.1 and the 0.01% light levels were occasionally sampled. Subsamples for chlorophyll, carbon uptake, particulate carbon and ETS activity were drawn immediately from the Niskin bottles without prefiltering (Table 1). The subsamples were not prefiltered because that procedure would have removed the large concentrations of the colonial diatom, *Thalassiosira partheneia,* that were reported at many stations (D. Blasco, personal communication).

Zooplankton were sampled by vertical net hauls towed to the sea surface from either the sea bottom or 200 m, whichever was less. Nonclosing 60 cm Bongo nets with a mesh size of 102 μm were used. The nets were lowered at 40 m/min and raised at 60 m/min. The flow through the net was monitored by a calibrated digital flowmeter. Details of the sampling and additional zooplankton analyses are given by Blackburn (1977).

Carbon productivity was determined by the ^{14}C method outlined by Barber and Huntsman (1975) and Huntsman and Barber (1977). Chlorophyll was measured by the UNESCO (1966) method and particulate organic carbon (PC) was measured by the method of Menzel and Vaccaro (1964) as described by Huntsman and Barber (1977). The PC data have been reported by Barber and Huntsman (1975).

Respiration in both the microplankton and the zooplankton was calculated from ETS activity that was measured by the tetrazolium method (Packard, 1969 and 1971) as modified by Kenner and Ahmed (1975a) for phytoplankton and Owens and King (1975) for zooplankton. Except for the ETS data, all the data discussed in this paper can be found in the CUEA data reports by Barber and Huntsman

Table 1. Biological data from the microplankton in the euphotic zone at 21° 40′ N latitude in the upwelling zone off Mauritania (JOINT I). Each value represents an integration by trapezoidal approximation of 6 values from the sea surface to the 1% light level. The carbon fixation was measured by 6 hr incubation during the period of maximum incident solar radiation. The data for carbon fixation and particulate carbon were taken from Barber and Huntsman (1975).

Station	ETS activity (ml O_2 $h^{-1}m^{-2}$)	Carbon fixation (mg C $h^{-1}m^{-2}$)	Chlorophyll (mg/m^2)	Particulate organic carbon (mg/m^2)
30	52	102	32	1899
31	110	72	22	2320
36	237	231	84	2936
37	154	206	61	1848
52	275	148	132	4389
62	338	649	56	2976
70	160	240	89	3288
78	252	300	97	4220
85	138	306	73	3139
89	140	172	73	3890
97	109	167	60	3857
99	123	153	36	2775
104	186	323	77	3506
105	198	243	66	3255
119	104	96	36	3070
122	308	198	63	2925
Mean	180	225	66	3143
Standard deviation	81	136	28	735

(1975) and Friebertshauser *et al.* (1975), and in the technical report by Codispoti *et al.* (1976).

3. Results

Conditions of the upwelling system. ETS activity was measured at 16 stations along a 75 km strip off the Mauritanian coast between 21N and 21°40′N latitude (Table 1). The stations were taken between 10 and 98 km from the coast between 17W and 17°44′W longitude. All but three of the stations were situated on a line across the continental shelf at 21°40′N latitude at depths ranging from 42 m (station 119) to 694 m (station 105). Stations 30 and 52 were taken south of the main line at 21N in 48 and 1372 m of water, respectively. Station 37 was taken 10 km south of the main line in continental slope waters 512 m deep. Stations 30 through 52 were occupied between 14 and 21 March (leg 1). Stations 62 through 97 were occupied

between 1 and 14 April (leg 2), and stations 99 through 122 were occupied between 22 and 28 April 1974. The wind speeds during the 14-21 March period had a mean and standard deviation of 29 ± 15 km h^{-1} (Fig. 2). During the 1-14 April period, the wind averaged 24 ± 14 km h^{-1}, and during the 22-28 April period, it averaged 39 ± 9 km h^{-1}. The wind blew from the north or north-northeast during the entire period except for three days between 7-9 April. On these days, the wind reversed direction and blew from the west-southwest. Given the generally north-south alignment of the Cape Blanc coast, the north-northeast winds were blowing in the correct direction for upwelling except during the reversal period. Barton, Huyer, and Smith (1977) reported that wind speeds in excess of 29 km h^{-1} (8m/sec) induce subsurface waters colder than 17°C to upwell. The time periods when the winds could induce upwelling have been hatched out in Figure 2. The high wind periods of 14-16 March, 21 March, and 1-5 April, coincided with observed upwelling of 16°C seawater as reported by Barton, Huyer, and Smith (1977). Their record stops at 9 April, so the strong upwelling on leg 3 (Fig. 2) was not independently verified. In spite of the variations in the upwelling, the waters on the shelf and over the continental slope were conducive to plankton growth. The seawater was largely North Atlantic Central Water with a small amount of South Atlantic Central Water according to Codispoti and Friederich (1978). In the euphotic zone, the sigma-*t* varied between 26.6 and 26.8 and the temperature varied between 15 and 18°C. The average nitrate levels across the shelf at 21°40′N varied from 1 to 11 μg-at l^{-1}, the silicate from 1 to 6 μg-at l^{-1} and the ammonium from 0.5 to 2 μg-at l^{-1} (Huntsman and Barber, 1977; Friederich and Codispoti, 1979). High levels of ammonium were always found close to shore. The incident light averaged 538 ± 77 ly d^{-1} for leg 1, 627 ± 41 ly d^{-1} for leg 2, and 640 ly d^{-1} for leg 3. At these levels, the phytoplankton at the sea surface were not light limited. However, along the inshore edge of the upwelling, the suspended particle load became as high as 1 mg l^{-1} (Milliman, 1977), the secchi disk depth decreased to 2 m and the extinction coefficient became as high as 0.979 (station 14, Barber and Huntsman, 1975). Huntsman and Barber (1977) report that these conditions induced shade adaption in the inshore phytoplankton and suppressed their photosynthetic capacity. Thus, although light and nutrients were ample for plankton growth, suspended sediment and mixing suppressed water column productivity on the inshore edge of the upwelling zone. (Huntsman and Barber, 1977).

ETS activity. The ETS activity in the euphotic zone (1-100% light levels) along the 21°40′N line ranged from 104 to 338 ml O_2 $h^{-1}m^{-2}$. The mean of all 16 stations including those to the south of the line, was 180 ± 81 ml O_2 $h^{-1}m^{-2}$ (Table 1). On the inshore edge of the upwelling where the depth was less than 50 m and where chalky, detritus laden seawater was observed, the ETS activity was less than the mean (Table 2). The activity was higher than the mean value at the mid-shelf

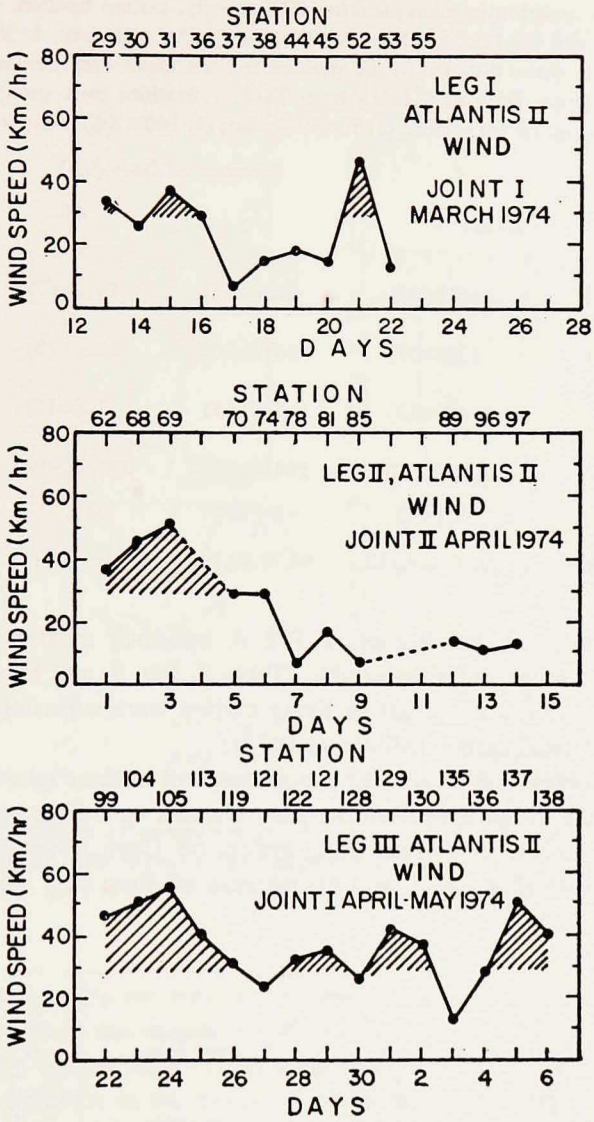

Figure 2. Wind speed as recorded on the *Atlantis* II during the JOINT I expedition (Frieberts-hauser *et al.*, 1975). The periods when the wind blew stronger than 29 km/hr (8 m/sec) are the periods favorable to upwelling.

where the depth was between 50 and 100 m (Fig. 3). Further offshore, over the shelf edge and slope, the activity was lower again, as it was inshore (Table 2). The cross-shelf profiles of carbon fixation and phytoplankton biomass (chlorophyll-*a*) were similar to the ETS profiles in that all three profiles had mid-shelf maxima

Table 2. Offshore variation in microplankton ETS activity, carbon fixation, chlorophyll *a*, particulate carbon, and the 1% light level depth along the 21°40'N latitude line off the coast of N.W. Africa. The mean distance of the stations and the mean and standard deviation of the parameters are given. Data were taken from Table 1. Stations were grouped according to 4 depth intervals (Fig. 1): (1) <50m; (2) 50≤Z≤100m; (3) 100≤Z≤200m; (4) >200m.

	Distance offshore (km)			
	15	31	45	70
ETS activity ($ml\ O_2\ h^{-1}m^{-2}$)	161(±98)	229(±86)	161(±67)	170(±24)
Carbon fixation ($mg\ C\ h^{-1}m^{-2}$)	130(±57)	361(±203)	235(±70)	230(±21)
Chlorophyll (mg/m^2)	40(±17)	76(±17)	72(±12)	72(±15)
Particulate carbon (mg/m^2)	2773(±325)	3648(±535)	3310(±484)	2797(±822)
1% light level (m)	22(±4)	21(±5)	22(±4)	21(±4)
Stations included	31,99,119,122	62,78,89,104	36,85,97	37,70,105

(Fig. 3 and Huntsman and Barber, 1977). A mid-shelf maximum in particulate carbon (PC) was only faintly discernible (Table 2, Fig. 3, and Huntsman and Barber, 1977) because the variations in living carbon were superimposed on a large background of detrital carbon (Milliman, 1977).

The depth profiles of ETS activity and chlorophyll in the euphotic zone off Cape Blanc were unlike the profiles from the Peru Current upwelling system (Fig. 4 and Packard *et al.*, 1971). In the upwelling system off Cape Blanc, the profiles were uniform with depth (Figs. 4, 5, and 6), whereas off Peru they were often sigmoid

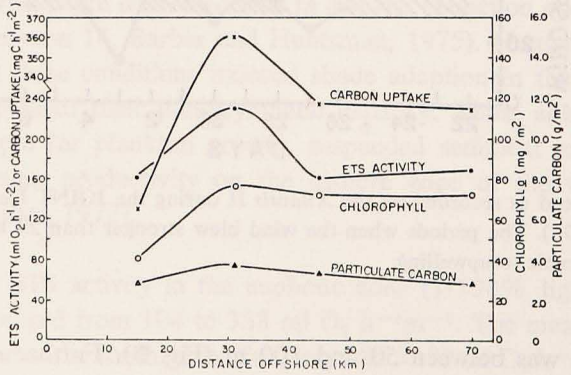

Figure 3. Offshore changes in ETS activity, carbon fixation, chlorophyll-*a*, and particulate carbon in the euphotic zone along the 21°40'N latitude line off Cape Blanc. Standard deviations are given in Table 2.

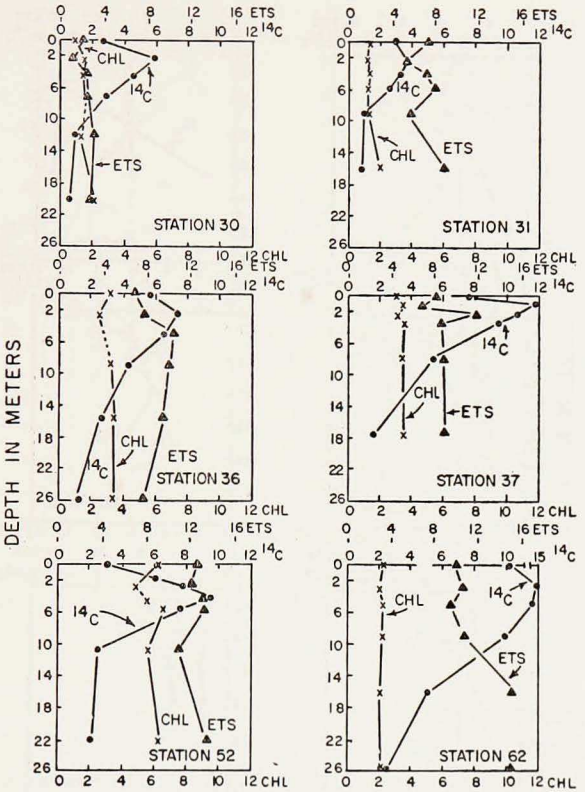

Figure 4. Vertical profiles of carbon-uptake (^{14}C), chlorophyll (Chl) and ETS activity in the euphotic zone of the N.W. African upwelling system. The units are: μg C day^{-1}l^{-1} for carbon-uptake; μg l^{-1} for chlorophyll; and μl O_2 h^{-1}l^{-1} for ETS activity.

with high values near the sea surface and low values at the bottom of the 1% light level. The difference in the shapes of the profiles from the two areas was caused by differences in the mixing depth (Huntsman and Barber, 1977). These differences will be investigated later in this paper under the Compensation Depth section. Regardless of causality, the uniformity of the Cape Blanc profiles plus the relatively high values of chlorophyll and ETS activity at the 1% light levels suggest the presence of large populations of metabolically active microplankton below the euphotic zone. When sub-euphotic zone samples were taken, these populations were found. Table 3 shows that the metabolism of these populations was nearly as great as, and sometimes greater than, the metabolism of the euphotic zone microplankton. The euphotic zone averaged 21 m in depth (1% light level). Below that depth, to 36 m, the ETS activity averaged 72 ± 25% of the activity in the upper 21 m (on a m^{-2} basis). At another three stations, where the ETS activity was measured below

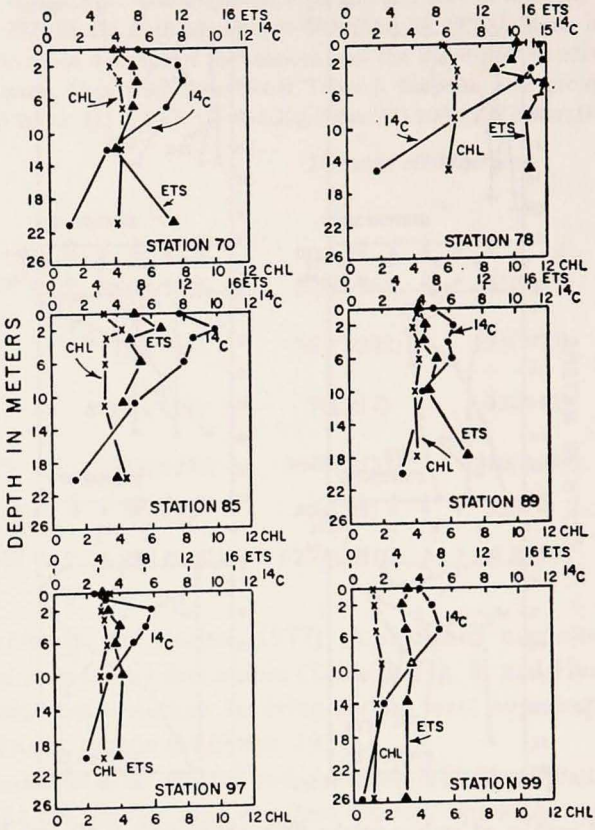

Figure 5. Vertical profiles of ETS activity, chlorophyll (Chl) and carbon uptake (^{14}C) in the N.W. African upwelling system. The units are: $\mu l\ O_2\ h^{-1}l^{-1}$ for ETS activity, $\mu g\ l^{-1}$ for chlorophyll, and $\mu g\ C\ day^{-1}l^{-1}$ for carbon uptake.

36 m (0.1% light level), it represented 44 ± 3% of the euphotic zone activity. Measurements deeper than the 0.1% light level (47 m) were not made, although significant activity probably would have been found. None of this sub-euphotic zone activity was considered in the subsequent calculations because the ETS data suite at these depths was incomplete and because there were few chlorophyll and ^{14}C-uptake data to accompany it. Nevertheless, the ETS data in Table 3 suggest that the sub-euphotic zone populations should not be excluded in models or budgets of the Cape Blanc upwelling system.

The zooplankton ETS activity, wet weight, and dry weight were measured at the same stations as was the microplankton ETS activity. These measurements are given in Tables 4 and 5. The zooplankton ETS activity was five-fold lower than the microplankton ETS activity, averaging 36 ± 28 ml $O_2\ h^{-1}m^{-2}$ as compared to a mean

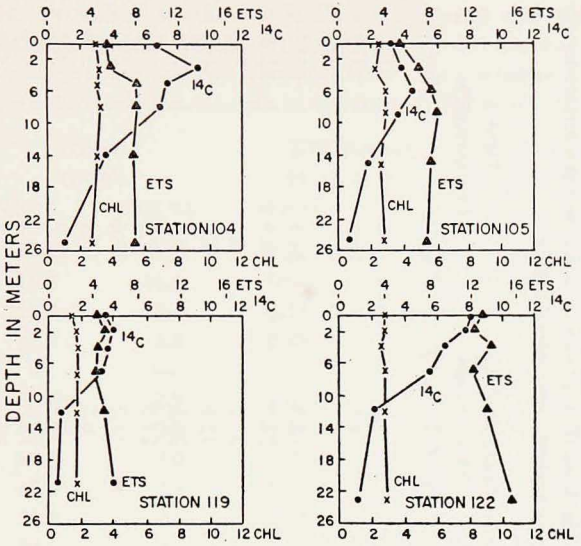

Figure 6. Vertical profiles of ETS activity, carbon uptake (^{14}C) and chlorophyll (Chl) in the N.W. African microplankton. The units are: $\mu l\ O_2\ h^{-1}l^{-1}$ for ETS activity, $\mu g\ l^{-1}$ for chlorophyll, and $\mu g\ C\ day^{-1}l^{-1}$ for carbon uptake.

of 180 ± 81 ml $O_2\ h^{-1}m^{-2}$ for the microplankton. When the value from station 52 value was excluded, the mean zooplankton ETS activity was only 29 ± 11 ml $O_2\ h^{-1}m^{-2}$. The frequency distribution of both the zooplankton and microplankton ETS activity is given in Figure 7. For the zooplankton, 81% of the measurements

Table 3. Microplankton ETS activity at depths below the 1% light level in the surface water off the N.W. African upwelling system.

Station	ETS activity (A) 100–1% I_o	ETS activity 1–0.1% I_o		ETS activity 0.1–0.01%	
	(ml $O_2\ h^{-1}m^{-2}$)	(ml $O_2\ h^{-1}m^{-2}$)	(% of A)	(ml $O_2\ h^{-1}m^{-2}$)	(% of A)
62	338	182	54	—	—
70	160	117	73	73	46
78	252	168	67	103	41
85	138	64	46	—	—
89	140	158	112	—	—
97	109	109	99	—	—
99	123	63	52	56	46
104	186	103	55	—	—
Mean and Standard deviation			72(±25)		44

Table 4. CO_2 evolution of the microplankton and zooplankton from the N.W. African upwelling system. Microplankton CO_2 evolution was calculated from microplankton ETS activity by the equation: $\Delta CO_2 = ETS \times 0.15 \times 1 \times 12/22.4$; where 0.15 converts ETS activity in phytoplankton to O_2 consumption (Kenner and Ahmed, 1975b), 1 is the R.Q., 12 the atomic weight of carbon, and 22.4 the molar volume of O_2. Zooplankton CO_2 evolution was calculated from zooplankton ETS activity by the equation: $\Delta CO_2 = ETS \times 0.50 \times 0.85 \times 12/22.4$; where 0.50 converts ETS activity in zooplankton to O_2 consumption (Owens and King, 1975) 0.85 is the R.Q., and the factor, (12/22.4) converts O_2 consumption to CO_2 evolution as in the microplankton. The zooplankton ETS activity is based on a sea-surface to sea-bottom net haul while the microplankton ETS activity is based on euphotic zone samples only.

Station	Zooplankton ETS activity (ml O_2 $h^{-1}m^{-2}$)	Zooplankton CO_2 evolution (mg C $h^{-1}m^{-2}$)	Microplankton ETS activity (ml O_2 $h^{-1}m^{-2}$)	Microplankton CO_2 evolution (mg C $h^{-1}m^{-2}$)	Total CO_2 evolution (h^{-1})	Total CO_2 evolution (day^{-1})
30	16.0	3.6	52	4.2	7.8	187
31	30.1	6.9	110	8.8	15.6	374
36	42.7	9.7	237	19.0	28.7	689
37	39.6	9.0	154	12.3	21.4	514
52	133.0	30.3	275	22.0	52.3	1255
62	27.2	6.2	338	27.1	33.3	794
70	29.5	6.7	160	12.8	19.5	468
78	53.9	12.3	252	20.2	32.4	778
85	31.2	7.1	138	11.0	18.1	434
89	36.8	8.4	140	11.2	19.6	470
97	19.1	4.4	109	8.7	13.1	314
99	26.6	6.1	123	9.8	15.9	382
104	19.1	4.4	186	14.9	19.2	466
105	17.4	4.0	198	15.8	19.8	475
119	12.5	2.9	104	8.3	11.2	269
122	33.0	7.5	308	24.7	32.2	772
Mean	35.5	8.1	180	14.4	22.5	540
Standard deviation	28.2	6.4	81	6.5	11.0	264

fall in the range of 13-40 ml O_2 $h^{-1}m^{-2}$, the principal mode of the frequency distribution. The microplankton distribution was more skewed; only 62% of the measurements fall in the principal mode. The relationship between the zooplankton ETS activity and biomass was investigated. If the age and species composition of the zooplankton were constant throughout the area and if ETS were a constitutive en-

Table 5. Wet weight, dry weight, weight specific ETS activity and weight specific respiration of the zooplankton from the 21° 40′ N latitude line off the Mauritanian coast (JOINT I). The specific ETS activities and specific respiration rates were calculated from data in Table 4. The weights were calculated from the data of R. Clutter (Blackburn, 1977).

	Weight (g/m^2)		ETS Activity ($ml\ O_2\ h^{-1}g^{-1}$)		Respiration ($mg\ C\ h^{-1}g^{-2}$)	
Station	Wet wt.	Dry wt.	Wet wt.	Dry wt.	Wet wt.	Dry wt.
30	60.0	5.2	0.27	3.08	0.061	0.700
31	75.4	11.8	0.04	2.55	0.091	0.581
36	122.8	6.4	0.35	6.67	0.079	1.519
37	81.6	3.9	0.49	10.15	0.111	2.313
52	—	—	—	—	—	—
62	32.7	2.9	0.83	9.38	0.189	2.134
70	30.0	2.6	0.98	11.35	0.224	2.585
78	90.9	4.0	0.59	13.48	0.135	3.068
85	42.5	2.3	0.73	13.57	0.167	3.087
89	35.5	2.9	1.04	12.69	0.236	2.890
97	34.2	3.9	0.56	4.90	0.127	1.115
99	42.6	1.0	0.62	26.60	0.142	6.060
104	25.4	2.2	0.75	8.68	0.171	1.977
105	50.3	1.9	0.35	9.16	0.079	2.084
119	23.3	2.6	0.54	4.81	0.122	1.096
122	44.2	3.6	0.75	9.17	0.170	2.086
Average	52.8	3.8	0.62	9.75	0.140	2.220
Standard deviation	28.3	2.6	0.23	5.85	0.053	1.333

zyme system, then the relationship should be described by a straight line passing through the origin. Regression analysis yielded the following equation: ETS = 0.26 × wet weight + 15.01 ($r = 0.66$, $n = 15$). The large intercept indicates that some of the assumptions are not valid. Most likely the zooplankton age and species composition were not constant.

The wet weight and dry weight specific ETS activity and respiration are presented in Table 5. The wet weight specific activity averaged 0.62 ± 0.23 ml $O_2\ h^{-1}g^{-1}$ and the dry weight specific activity averaged 9.8 ± 5.9 ml $O_2\ h^{-1}g^{-1}$. The variations across the upwelling system of the dry weight specific ETS activity, the ETS activity per unit area and the dry weight are shown in Table 6. Regardless of how the ETS activity was normalized, it did not change from the inshore to the offshore edge of the upwelling system.

ETS, carbon, chlorophyll, and ^{14}C-uptake relationships. Carbon, chlorophyll, and ^{14}C-uptake measurements yield different information about microplankton assemblages. Carbon represents total sestonic particulate carbon including the living and

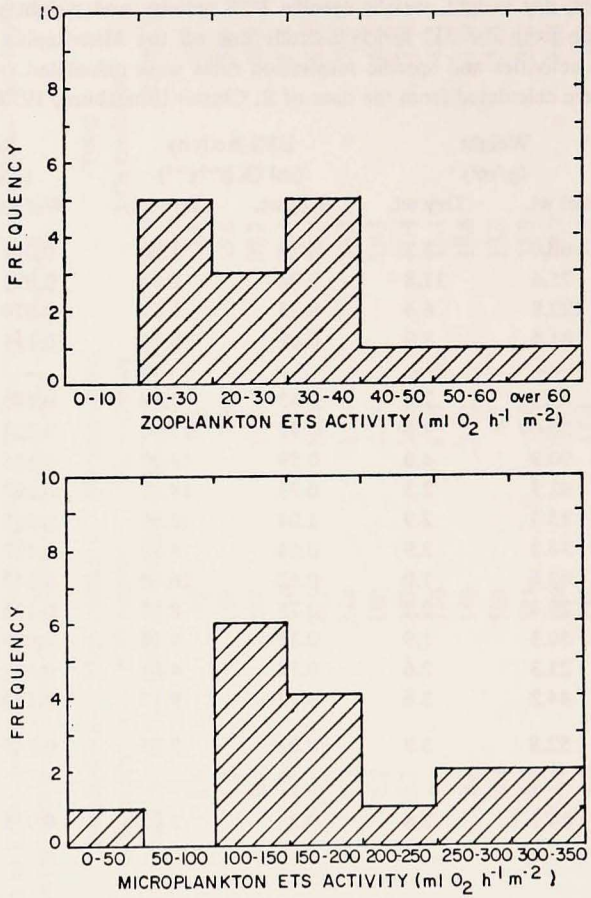

Figure 7. The frequency distribution of the ETS activity in the zooplankton (panel A) and microplankton (panel B) along 21°40'N latitude off Cape Blanc. The microplankton data represents the integrated activity throughout the euphotic zone water column. The zooplankton data represent activity from the sea bottom to the sea surface. Frequency is expressed as the number of stations with ETS activity within the specified range.

nonliving fractions. Chlorophyll, being a prerequisite of algal photosynthesis, serves as an index of phytoplankton biomass. Both carbon and chlorophyll are static properties, concentrations of mass. C-uptake, like ETS activity, is a dynamic property, the rate at which a concentration (C liter^{-1}) changes. However, unlike ETS, it is associated exclusively with the phytoplankton and not with microzooplankton or bacteria. Thus, when the phytoplankton dominate the microplankton one would expect a close correlation between ETS and C-uptake and to a lesser degree between ETS and chlorophyll. Should either the bacterial or the microplankton fractions be large, then the correlation between ETS and C-uptake, and between ETS

Table 6. Offshore variation in dry-weight specific ETS activity and dry-weight in the zooplankton along the 21°40′N latitude line off the coast of N.W. Africa. The depth intervals for each group of stations is given in Table 2.

	Distance offshore (km)			
	15	31	45	70
Dry weight (g/m^2)	4.8(±4.8)	3.0(±0.7)	4.2(±2.1)	2.8(±1.0)
ETS activity ($ml\ O_2\ h^{-1}m^{-2}$)	22(±10)	34(±15)	31(±12)	29(±11)
ETS activity ($ml\ O_2\ h^{-1}g^{-1}$)	10.8(±10.9)	11.1(±2.4)	8.4(±4.6)	10.2(±1.1)
Stations included	31,99,119,122	62,78,89,104	36,85,97	37,70,105

and chlorophyll would be weak. Unless the detritus concentrations were exceptionally low, the ETS-particulate carbon couple should always be weak.

In the Baja California upwelling system, at a time when the phytoplankton population was dominated by *Gonyaulax polyedra* (Blasco, 1978), the microplankton ETS activity was closely associated with C-uptake, chlorophyll and particulate carbon (Packard *et al.*, 1974). The close couple with chlorophyll and C-uptake suggested that the microzooplankton and bacteria played a minor role, compared to the phytoplankton, in the plankton dynamics of that ecosystem. A similar analysis with the ETS, carbon, chlorophyll, and carbon uptake data from N.W. Africa (Table 1) did not yield the same results. ETS activity was not as closely coupled with C-uptake and chlorophyll as expected; however, ETS activity was unexpectedly better coupled with chlorophyll and even with particulate carbon than C-uptake was coupled with these two variables (Table 7). Between ETS and C-uptake, there was a slightly better relationship than between ETS and chlorophyll; $r = 0.64$ for ETS $= f$ (C-uptake) as compared to $r = 0.55$ for ETS $= f$ (chlorophyll).

Cross-self variations in the microplankton. If microplankton ETS were largely associated with phytoplankton respiration, then the ratios of microplankton ETS to

Table 7. Regression equations between ETS activity and C-uptake (^{14}C) and chlorophyll (UNESCO method) for the microplankton along 21°40′N latitude. The data were taken from Table 1. Correlation was tested at the 5% level and found significant for the ETS-C-uptake and ETS-chlorophyll regressions, but not for the ETS-particulate carbon regression.

Equation	N	r	r^2
ETS = 0.385 ^{14}C+93	16	0.64	0.41
ETS = 1.62 Chl+73	16	0.55	0.30
ETS = 0.04 PC+53	16	0.37	0.14
^{14}C = 1.07 Chl+155	16	0.22	0.05
^{14}C = 0.03 PC+141	16	0.14	0.02

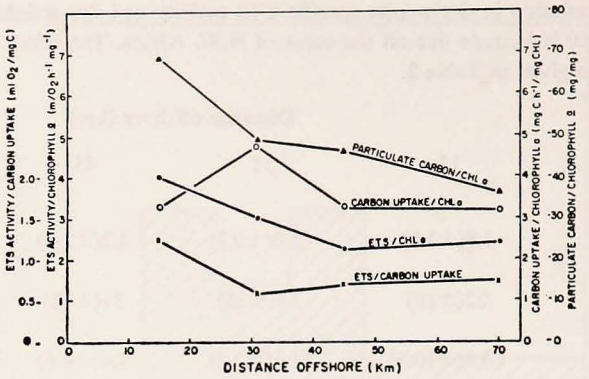

Figure 8. Cross-shelf profiles of ETS/Chl, ETS/carbon-uptake, the assimilation number, and the carbon/chlorophyll ratio at 21°40'N latitude off Cape Blanc.

chlorophyll and microplankton ETS to C-uptake would be indices of phytoplankton respiration to phytoplankton biomass (R/B) and phytoplankton respiration to phytoplankton productivity (R/P). To determine whether the metabolic efficiency or the photosynthetic efficiency varied in a cross-section through the upwelling system, these ratios were calculated from the data in Table 1 for the groups of stations outlined in Table 2 and plotted against the mean distance from shore for each group of stations (Fig. 8).

The photosynthetic efficiency has a maximum value at 30 km off the coast where Barton *et al.* (1977) show persistent upwelling throughout the period of 23 February to 7 April 1974. The metabolic efficiency indices, R/B and R/P, increase at the inshore edge of the shelf suggesting the influence of bacteria and/or microzooplankton, or the depression of photosynthesis in this zone. Either of these effects could cause the elevated seawater NH_4^+ values that Codispoti *et al.* (1976) observed on the inshore edge of the upwelling system.

Carbon Losses through respiration. The respiratory carbon losses of the microplankton and the zooplankton can be calculated from the ETS activity by first calculating oxygen consumption and converting the O_2 consumption into CO_2 evolution using a respiratory quotient. The equation to do this is:

$$R = \text{ETS} \times F \times Q \times 0.54$$

where F is the respiration/ETS ratio (0.15 for microplankton, Kenner and Ahmed, 1975b; and 0.5 for zooplankton, Owens and King, 1975), Q is the respiratory quotient (1 for phytoplankton, Strickland, 1965, and 0.85 for zooplankton), and 0.54 provides the volume to mass conversion. These calculations were made for the microplankton in the euphotic zone (Table 1) and for the zooplankton in the water column between the sea surface and the sea bottom (Tables 4 and 5). The zooplank-

Table 8. Respiratory carbon evolution from the microplankton and the zooplankton, together, and from the microplankton alone. The calculations are presented as percentages of the phytoplankton carbon fixation. The hourly carbon fixation data represents results from 6 h incubation experiments (Barber and Huntsman, 1975) or the results from the 24 h incubation experiments divided by (1.72 × 6) as described in Huntsman and Barber (1977). All rates are expressed as mg C m^{-2} for their respective times.

Station	Carbon fixation (h^{-1})	Carbon fixation (day^{-1})	Total carbon evolution as percent of carbon fixed (h^{-1})	Total carbon evolution as percent of carbon fixed (day^{-1})	Microplankton carbon evolution as percent of carbon fixed (day-light period)
30	102	1137	8	16	4.1
31	72	763	22	49	12.2
36	231	2423	12	28	8.2
37	206	2512	10	20	6.0
52	148	2237	35	56	14.9
62	649	5005	5	16	4.2
70	240	2436	8	19	5.3
78	300	3098	11	25	6.7
85	306	2732	6	16	3.6
89	172	2112	11	22	6.5
97	167	1719	8	18	5.2
99	153	1677	10	23	6.4
104	323	4163	6	11	4.6
105	243	2179	8	22	6.5
119	96	1004	12	27	8.7
122	198	2049	16	38	12.5
Mean	225	2328	12	25	7.2
Standard deviation	136	1093	7	12	3.3

ton CO_2 evolution ranged from 2.9 to 30.3 mg C $h^{-1}m^{-2}$ and averaged 8.1 ± 6.4 mg C $h^{-1}m^{-2}$. However, the value at station 52 is nearly four times the mean value and thus is not representative. If it is excluded, the range falls to 2.9 to 12.3 mg C $h^{-1}m^{-2}$ and the mean falls to 6.6 ± 2.6 mg C $h^{-1}m^{-2}$. The microplankton CO_2 evolution was twice as great. The range for all 16 stations was 4.2 to 27.1 mg C $h^{-1}m^{-2}$ and the mean was 14.4 ± 6.5 mg C $h^{-1}m^{-2}$. There were no extreme values.

The significance of the CO_2 evolution by both plankton fractions can be evaluated by comparison with the carbon fixation data (Table 1 and Barber and Huntsman, 1975). In Table 8, the carbon losses by the microplankton and by the microplankton and zooplankton combined, are calculated as a percentage of the net carbon fixation during (1) mid-day and (2) a 24 hr day-night period. During mid-day, when photosynthesis is at a maximum, microplankton and zooplankton respiration amounts to 12% of net photosynthesis. The microplankton alone accounts for 7% of this. Dur-

Table 9. Net productivity (Barber and Huntsman, 1975, Smith *et al.*, 1977) gross productivity and respiratory loss in the microplankton at 14 stations from the JOINT-I cruise. Net productivity is the carbon fixation during a 24 h incubation (column 1). Gross productivity was calculated in 2 ways: (1) by adding the night respiration (Table 2 of Smith, 1977) to the net productivity (column 2) and (2) by adding the ETS-derived respiration on a 24 h basis (Table 4), to the net productivity (column 3). The respiratory loss simply represents the difference between the gross and net productivity divided by gross productivity × 100. Thus columns 4 and 5 were calculated from the gross productivity values in columns 2 and 3, respectively.

	Net productivity ($gC\ day^{-1}m^{-2}$)	Gross productivity ($gC\ day^{-1}m^{-2}$)		Respiration loss (%)	
Station	(1)	(2)	(3)	(4)	(5)
30	1.14	1.24	1.24	8	8
31	0.76	0.86	0.97	12	22
36	2.42	2.95	2.88	18	16
62	5.01	6.10	5.66	18	11
70	2.44	2.91	2.75	16	11
85	2.73	3.44	2.99	21	9
89	2.11	2.75	2.38	23	11
99	1.68	1.85	1.92	9	13
105	2.18	2.73	2.56	20	15
119	1.00	1.07	1.20	7	17
Mean	2.15	2.59	2.45	15	13
Standard deviation	1.21	1.53	1.35	6	4

ing a complete day when dark respiration by the phytoplankton reduces the 24 hr photosynthesis measurement, the respiration of the 2 plankton assemblages accounts for 25% of net photosynthesis.

It would be theoretically more meaningful if the respiration could be compared to gross photosynthesis (Dugdale, 1975), but gross photosynthesis is technically difficult to measure and rarely reported; consequently, it must be calculated. For the JOINT I productivity data, this can be done from the results of Smith (1977). He calculated the nocturnal carbon loss from the difference between the 6 hr and 24 hr productivity measurements (Barber and Huntsman, 1975) in a modified version of the method used by Eppley and Sharp (1976). The gross productivity is the sum of this nocturnal carbon loss and the net productivity (Table 2 of Smith, 1977). This calculation is presented in Table 9. For ten stations, the gross productivity averaged 2.6 ± 1.5 g C $d^{-1}m^{-2}$. A similar calculation can be made from the ETS-derived respiration (Table 4). It assumes that mitochondrial respiration is constant over a 24 hr period whereas the calculation from Smith's data assumed either non-measurable or negligible daytime respiration. Gross productivity by this approach is 2.5 ± 1.4 g C $d^{-1}m^{-2}$, nearly the same as the previous calculation. Column 5 of

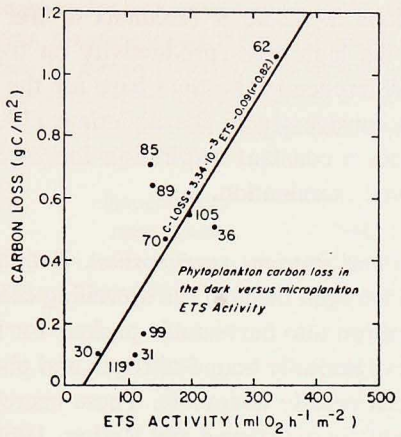

Figure 9. A comparison of two measures of respiratory losses, phytoplankton carbon loss in the dark (Smith, 1977) and microplankton ETS activity (Table 5). The regression is significant at the 1% level. The data pair from station 122 were not included in the regression analysis because the carbon loss appeared unusually low in comparison with the other biological data from that station (Table 1).

Table 9 gives a reevaluation of the magnitude of the microplankton respiration as compared to gross photosynthesis; the average is 13 ± 4%. Column 4 (Table 9) gives a comparable respiratory loss, 15 ± 6%, but calculated from Smith's (1977) data. The respiration of the microplankton and the zooplankton (last column, Table 4) represents a 21% loss from the gross photosynthesis (column 2, Table 9); the zooplankton are responsible for 8% of this loss.

The calculations of respiration from ETS activity measurements (Tables 4, 8, and 9) are highly dependent on the experimental results of Kenner and Ahmed (1975b). The respiration calculations of Smith (1977) provide an opportunity to evaluate the relationship between ETS activity and respiration that Kenner and Ahmed (1975b) observed. Not all of Smith's calculations can be used because 20% of his calculations yield unrealistically low values of respiration; nevertheless, 10 of his calculations can be directly compared with the ETS-derived microplankton respiration as given in Table 4. A plot of the paired data is shown in Figure 9. The regression equation is: $L = 3.34 \times 10^{-3} \times \text{ETS} - 0.09$ ($r = 0.82$), where L is the carbon loss in a 10.6 h night (the average dark period during the R.V. *Atlantis* II phase of the JOINT I expedition). This regression is significant ($P > 0.99$), but when the two indices of respiration are compared directly, the ^{14}C method gives higher values. The mean for the nighttime carbon loss for the ten stations considered in the regression analysis was 0.41 gm C m^{-2}. The ETS-derived respiration rate for the same stations was 0.15 g C m^{-2}, a third of the ^{14}C-derived respiration. The large difference between these calculations and the small difference between the

respiratory loss calculations in Table 9 (columns 4 and 5) is explained by (1) the dampening effect of the high gross productivity on the percentage calculation in Table 9, and (2) the difference in the time base for the two respiration calculations. The ^{14}C approach considers only the nighttime (10.6 hr) respiration, while the ETS approach assumes a constant respiration for 24 hr. The validity of both approaches needs additional examination.

Zooplankton metabolism and nutrient regeneration. Zooplankton play a dual role in the flow of carbon and nitrogen through the upwelling ecosystem. As grazers, they concentrate the phytoplankton into harvestable packets for the higher trophic levels. As excreters, they reduce organically bound nitrogen and phosphorus to ionic species that the phytoplankton can readily assimilate. These excreted nutrients greatly enhance phytoplankton productivity (Menzel and Ryther, 1960; Dugdale and Goering, 1967) and their regeneration by zooplankton is a major factor in regulating the nitrogen flow through an aquatic ecosystem (O'Brien and Wroblewski, 1976). Smith and Whitledge (1977) have recently reported that the zooplankton in the Cape Blanc region supply 44% of the phytoplankton ammonium demand and 25% of their total nitrogen demand. Since their data and the ETS data in Table 4 were obtained from the same zooplankton samples, their results can be directly compared to ammonium regeneration rates calculated from the ETS data.

The method for calculating ammonium regeneration is described in Packard (1969), Whitledge and Packard (1971), and Packard *et al.* (1974). Respiratory oxygen consumption was calculated first from the ETS activity and the respiration was then converted to ammonium excretion. In the calculation, the respiration-ETS activity ratio of 0.5 (Owens and King, 1975) and the respiration-excretion ratio of 8:1 (Smith and Whitledge, 1977) were used. Both the respiratory oxygen consumption and the ammonium excretion calculations for the 16 stations are shown in Table 10. The ammonium excretion rates range from 70 μg-at N $h^{-1}m^{-2}$ at station 119 to 742 μg-at N $h^{-1}m^{-2}$ at station 52. The mean was 198 $\pm$ 157 μg-at N $h^{-1}m^{-2}$ for all 16 stations. If stations 30 and 52 are excluded (they are not on the 21°40′N line), then the range is 70 to 301 μg-at N $h^{-1}m^{-2}$ and the mean is 167 $\pm$ 62 μg-at N $h^{-1}m^{-2}$. These values are much higher than excretion rates measured earlier in the Peru Current and in the Costa Rica Dome. For seven stations in the Costa Rica Dome upwelling system (Packard, 1969), the ammonium excretion rate ranged from 1 to 47 μg-at N $h^{-1}m^{-2}$ ($\bar{x} = 14 \pm 15$) and for six stations in the Peru Current (Packard, 1969) at 15S latitude, the rate ranged from 1 to 17 μg-at N $h^{-1}m^{-2}$ ($\bar{x} = 8 \pm 6$). These calculations were made on a similar basis as those in Table 10.

The influence of this excretion on water column chemistry can be evaluated by considering the *in situ* NH_4^+ concentration and calculating the accumulation time for this concentration if the NH_4^+-uptake by phytoplankton were to cease. The

Table 10. Rates of oxygen consumption and ammonium excretion in zooplankton from the upwelled waters off Cape Blanc, Mauritania and the time required, at these rates, to build up the ammonium concentration to measured levels. The oxygen consumption was calculated from the ETS activity (Table 4) using an R/ETS ratio of 0.5 (Owen and King, 1975). The ammonium excretion was calculated from the oxygen consumption rates using an atomic ratio (O:N) of 8:1 (Smith and Whitledge, 1977).

Station	Zooplankton oxygen consumption (ml O_2 $h^{-1}m^{-2}$)	Zooplankton ammonium excretion (μg-at N $h^{-1}m^{-2}$)	NH_4^+ in water column (mg-at m^{-2})	Build-up time assuming no uptake (days)
30	8.0	90	17.1	7.9
31	15.0	168	41.6	10.3
36	21.3	239	10.1	1.8
37	19.8	221	4.2	0.8
52	66.5	742	5.0	0.3
62	13.6	152	14.6	4.0
70	14.7	165	5.2	1.3
78	27.0	301	3.4	0.5
85	15.6	174	3.8	0.9
89	18.4	206	3.2	0.7
97	9.5	107	3.2	1.3
99	13.3	149	15.6	4.4
104	9.5	107	5.4	2.1
105	8.7	97	7.3	3.1
119	6.2	70	15.4	9.2
122	16.5	184	7.5	1.7
Mean	17.7	198	10.2	3.1
Standard deviation	14.1	157	9.7	3.2

ammonium concentrations at each station are required for this calculation. These were extracted from Friebertshauser *et al.* (1975) and are presented in Table 10. Based on these values and the ammonium excretion rates, the build-up time ranged from 0.3 to 10.3 days and averaged 3.1 days. Three stations had uncharacteristically high build-up times ($\bar{x} = 9$ days) which skewed the mean from 1.8 ($\pm$ 1.3 days) to 3.1 ($\pm$ 3.2 days).

The significance of zooplankton NH_4^+ excretion to phytoplankton nitrogen metabolism can be determined by considering the phytoplankton NH_4^+-uptake rate and calculating the fraction of this rate that can be sustained by zooplankton NH_4^+ excretion. The NH_4^+-uptake rates for five stations in the JOINT I study area are given in Table 11 (MacIsaac and Dugdale, personal communication). These rates range from 175 to 280 μg-at N $h^{-1}m^{-2}$ with a mean of 221 $\pm$ 39 μg-at N $h^{-1}m^{-2}$. The zooplankton NH_4^+ excretion (Table 10) can sustain 56 $\pm$ 20% of this uptake.

Table 11. The NH_4^+ uptake by phytoplankton that can be accounted for by the rate of NH_4^+ excretion by zooplankton. From the CUEA cruise, JOINT I, off N.W. Africa.

Station	Phytoplankton NH_4^+ uptake (μg-at N $h^{-1}m^{-2}$)	% of NH_4^+ uptake accounted for by zooplankton NH_4^+ excretion
30	175	52
37	280	80
99	208	72
104	212	50
119	230	30
Mean	221	56
Standard deviation	39	20

This is remarkably close to the 44% that Smith and Whitledge (1977) calculated considering that independent methods were used for determining the excretion.

Compensation depth. The compensation depth for phytoplankton is that depth in the water column at which photosynthesis and respiration are equal for the phytoplankton assemblage. The depth will vary with time of day, extinction coefficient, cloud cover, wave action and the species composition of the phytoplankton assemblage. The ratio of this compensation depth to the mixed layer depth (D_c/D_m) is called the production ratio and is thought to control primary productivity in nutrient-rich waters (Gran and Braarud, 1935; Sverdrup, 1953; Cushing, 1975). Low production ratios ($D_c/D_m < 1$) indicate poor conditions for phytoplankton growth and high ratios ($D_c/D_m > 1$) indicate favorable bloom conditions.

Off Cape Blanc in 1974 the mixing depth was deep and the turbidity was high. Both factors would suppress the production ratio and may have suppressed phytoplankton production (Huntsman and Barber, 1977). This suppression can be re-

Table 12. Maximum and minimum productivity in the euphotic zone of the Peru Current (28 March-1 May 1969) and the upwelled waters off Cape Blanc, N.W. Africa (8 March-25 May 1974). The Peru data were taken by R. T. Barber (Anonymous, 1970). The N.W. African data were taken by Barber and Huntsman (1975). The productivity measurements were based on 24 h incubations under simulated *in situ* conditions.

Upwelling area	Maximum productivity (P_{max}) (μg C $day^{-1}l^{-1}$)	Productivity at the 1% light level (P_{min}) (μg C $day^{-1}l^{-1}$)	P_{max}/P_{min}
Peru Current	496 ($\pm$226, n=31)	10 ($\pm$11, n=30)	47
Cape Blanc N.W. Africa	195 ($\pm$107, n=41)	28 (17, n=41)	7

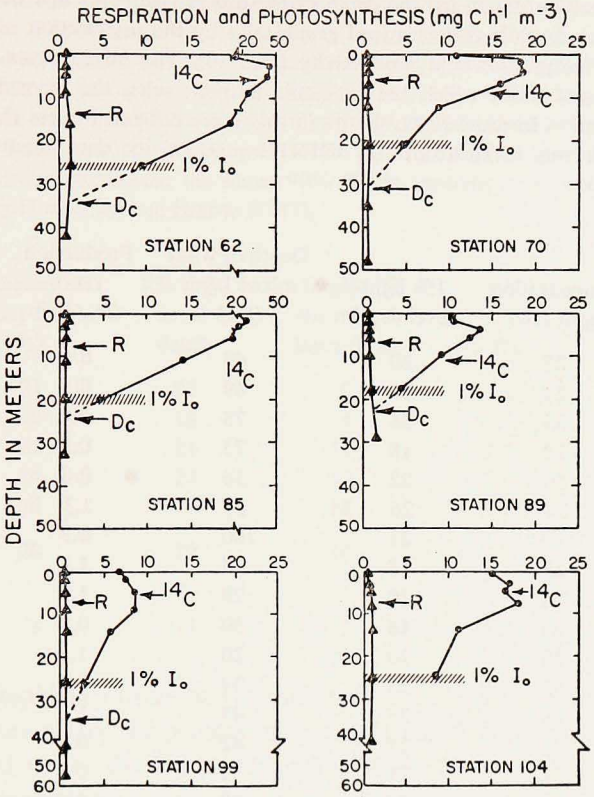

Figure 10. Respiration, photosynthesis, compensation depth, and the 1% light depth for stations along 21°40'N, off Cape Blanc. Respiration was calculated from ETS activity using the conversion factor 0.08 mg C/ml O_2; photosynthesis was taken from Barber and Huntsman's (1975) carbon productivity data.

vealed by comparing the productivity maxima and minima as well as the ratios between these extremes in the Peru Current and in the Cape Blanc upwelling systems (Table 12). The data for this comparison may be found in Barber and Huntsman (1975) and in Anonymous (1970). The latter summarizes the ^{14}C-uptake work of R. T. Barber from the R.V. *Thompson* Cruise (TT-036) to the Peru Current. In the Peru Current, the ratio of the productivity maximum to the productivity minimum was 47 while off Cape Blanc it was only 7 (Table 12). Enhanced turbidity off the N.W. African coast does not explain this difference because the extinction coefficient of incident radiation was not unusually high off Cape Blanc except for the near-shore area value at R.V. *Atlantis* II station 14. The mean value of the extinction coefficient (k) for the 16 stations discussed here was 0.22 m^{-1}. In the Peru

Table 13. Compensation depth and the depth of the mixed layer off Cape Blanc, N.W. Africa. The compensation depth was determined graphically by the intersection of the extrapolated depth profiles of respiration and productivity (Fig. 10). The mixed layer depth was determined as the depth above which the inorganic nutrient salts, the oxygen and chlorophyll displayed uniformity. In most cases, the σ_t in this layer differed by less than 0.02. The 1% light level depth was taken from the JOINT-I productivity data report of Barber and Huntsman (1975).

Station	Compensation depth (D_c)	1% light-level depth	Depth of wind mixed layer (D_m)	Production ratio (D_c/D_m)	Assimilation number (mg C day^{-1}/ μg Chl)
30	25	20	40	0.6	38
31	24	16	49	0.5	43
36	33	26	75	0.4	24
37	22	18	75	0.3	29
52	30	22	50	0.6	22
62	34	26	26	1.3	81
70	31	21	100	0.3	24
78	16	15	15	1.1	25
85	24	20	20	1.2	36
89	23	18	30	0.8	22
97	30	20	20	1.5	20
99	35	26	39	0.9	21
104	58	25	43	1.4	25
105	39	25	42	0.9	24
119	24	21	35	0.7	22
122	25	23	29	0.9	20
Mean	30	21	46	0.7	26
Standard deviation	10	4	23	0.4 (n=15)	7 (n=15)

Current and Baja California upwelling systems, k was not markedly different (Barber *et al.*, 1976). These authors found values ranging from 0.22 m^{-1} to 0.43 m^{-1} ($\bar{x} = 0.34$, $n = 4$) for the Peru Current (El Nino Watch Expedition) and from 0.09^{-1} to 0.30 m^{-1} ($\bar{x} = 0.21$, $n = 33$) for the Baja California upwelling area (MESCAL II Expedition). Since turbidity alone does not explain the large differences between the productivity in the two upwelling regions, other factors such as compensation depth (D_c) or mixing depth (D_m) must be considered. The low ratio between productivity maxima and minima in the water column off the N.W. African coast suggests strong mixing. The effect of this mixing in repressing the phytoplankton productivity can be assessed by comparing D_c with D_m. To do this D_m was determined by inspection from the chemistry, hydrographic and productivity data (Friebertshauser *et al.*, 1975; Barber and Huntsman, 1975; Barton *et al.*, 1975). D_c

Table 14. Compensation depth, depth of the mixed layer, and carbon assimilation number in the Peru Current, 1969. The compensation depth was determined as in Table 13 (Packard, 1969). The mixed layer depth and the 1% light-level depth were determined as in Table 13 but from the data of R. T. Barber and R. C. Dugdale (Anonymous, 1970). The assimilation number was calculated from the productivity and chlorophyll data integrated from the sea surface to the 1% light-level. These data were taken by R. T. Barber (Anonymous, 1970). Assimilation numbers calculated for the upper 90% of the euphotic zone are much higher than those reported by Huntsman and Barber (1977).

Station	Compensation depth (D_c)	1% light level depth	Depth of the mixed layer (D_m)	D_c/D_m	Assimilation number (μg C day^{-1}/ μg Chl)
30	21	21	5	4.2	32
36	18	18	6	3.0	24
46	21	21	12	1.8	51
58	24	23	12	2.0	41
62	18	16	16	1.1	20
Mean	20	20	10	2.4	34
Standard deviation	3	3	5	1.2	13

was calculated graphically from the vertical profiles of respiration and photosynthesis (Fig. 10). It occurs where the profiles intersect. In the N.W. African upwelling system, D_c occurred below the 1% light level (Table 13), suggesting shade adapted phytoplankton assemblages. In the Peru Current in 1969, the 1% light level and D_c coincided (Table 14). In both upwelling regions, the 1% light level occurred at 20 to 21 m. D_m and the production ratio differ markedly in the two upwelling areas. Off N.W. Africa, the D_m averaged 46 m, while off Peru it averaged only 10 m (Table 14). The production ratio off Cape Blanc averaged only 0.7 while off Peru it averaged 2.4. Thus, the weak mixing off Peru enabled the phytoplankton to bloom in the upper part of the euphotic zone whereas off Cape Blanc the strong mixing suppressed blooms by cycling the phytoplankton deep into the light-impoverished dysphotic zone.

4. Discussion

The objective of this research was to determine the respiration in the phytoplankton and zooplankton in the upwelled waters off Cape Blanc, N.W. Africa. Since phytoplankton cannot be separated from the total microplankton, which includes bacteria, microzooplankton, as well as phytoplankton, the ETS activities on the filtered material were reported as microplankton ETS. In spite of the uncertainty, much of the microplankton ETS activity was traceable to the phytoplankton as shown by the correlation between ETS activity and C-uptake (Table 7). On this

basis, phytoplankton respiration was calculated (Table 4) from the ETS measurements (Table 1) using the respiration-ETS ratios of Kenner and Ahmed (1975b). The respiration was reported throughout the paper in carbon units rather than oxygen units because it facilitated comparison with photosynthetic carbon uptake. Both the respiration and the ETS values are difficult to evaluate because few reports of either variable can be found in the literature and furthermore, when they are reported, the use of different methodologies precludes direct comparison. The methods part of this problem has recently been addressed by comparing the results of six different ETS assays (Christensen and Packard, 1979). The activity ratios obtained from that exercise can now be used to compare recent observations with older ones. This was done in Table 15. The results show that the ETS activities in the N.W. African region were the same in 1971 and 1974. The activities from the Peru Current and Baja California upwelling systems vary too much to rank the three systems. The activities from the other areas (Costa Rica Dome, Eastern Tropical North Pacific, Saanich Inlet, and the Mediterranean Sea) are much lower than the activities from the upwelling areas.

The zooplankton respiration measurements can be compared with the measurements made in the same region in 1971 (Groupe Mediprod, 1974; Packard, *et al.*, 1974) and with measurements made in the Northeast Tropical Pacific (Codispoti and Lowman, 1973; King, *et al.*, 1978). The respiration of the zooplankton in the upper 50 m of the water column off the N.W. African coast averaged 23 ml O_2 $h^{-1}m^{-2}$ which converts to 10.5 mg C $h^{-1}m^{-2}$. The average from Table 4 was 8.1 mg C $h^{-1}m^{-2}$, so the two different studies in the same area agree well in spite of the three year separation of the studies. In the Northeast Tropical Pacific, the respiration was 5.7 mg C $h^{-1}m^{-2}$ which, as expected, is lower than the N.W. African data, but not as low as one might expect for an area reported to be oligotrophic.

The calculations of respiration made throughout this paper have been based on (1) the assumption that the ETS is the chemical basis of respiration, and (2) the correlations between ETS activity and respiration (Kenner and Ahmed, 1975b; King and Packard, 1975; Owens and King, 1975). With the exception of the phytoplankton respiration calculations of Smith (1977), there are no other synoptic respiration data from the JOINT I expedition that could serve to verify the ETS-derived rates. Nevertheless, some evaluation of the microplankton respiration can be accomplished by consideration of the results of Steemann-Nielsen and Hansen's (1959) study of North Atlantic phytoplankton respiration and Platt and Jassby's (1976) study of the phytoplankton respiration in Nova Scotian coastal waters. Steemann-Nielsen and Hansen (1959) found that 90% of their respiration measurements on North Atlantic plankton assemblages fell below 15% of the photosynthesis; the mean fell in the 6-10% range. Platt and Jassby (1976) found that Nova Scotian coastal phytoplankton respired between 0 and 40% of the photosynthesis. The mean respiration under optimal conditions was 4% of photosynthesis. I found

Table 15. ETS activities in different oceanic regions.

Region	Data from the original measurement: Method	Activity† (ml O_2 $h^{-1}m^{-2}$)	Reference	ETS activities at levels comparable with those obtained by the Kenner & Ahmed (1975a) method (ml O_2 $h^{-1}m^{-2}$)
Upwelling Systems				
N.W. African (1971)	Packard (1971)	59(5)	Packard *et al.* (1974)	179*
N.W. African (1974)	Kenner & Ahmed (1975a)	180(16)	This paper	180
Baja Californian (1972)	Packard (1971)	368(19)	Packard *et al.* (1973)	1112*
Baja Californian (1973)	Kenner & Ahmed (1975a)	147(29)	Packard (unpubl. data)	147
Peru Current (1969)	Packard (1969)	124(5)	Packard (1969)	552**
Peru Current (1977)	Kenner & Ahmed (1975a)	150(47)	Setchell and Packard (1978)	150
Other Systems				
Costa Rica Dome January 1973	Packard (1971)	22(15)	Kuntz *et al.* (1975)	67*
Eastern Tropical North Pacific Ocean	Packard (1971)	34(14)	King *et al.* (1978)	102*
Mediterranean Sea (western basin)	Packard (1971)	438(2)	Slawyk *et al.* (1976)	55*
Saanich Inlet (British Columbian fjord)	Packard (1971)	26(2)	Packard *et al.* (1973)	78*

† The number of samples is given in parenthesis.

* A factor, 3.02, relates ETS activities measured by the Packard (1971) method to the activities measured by the Kenner and Ahmed (1975a) method (Table 3 of Christensen and Packard, 1979).

** A factor, 4.45, relates ETS activities measured by the Packard (1969) method to the activities measured by the Kenner and Ahmed (1975a) method (Table 3 of Christensen and Packard, 1979).

a value of 7% (Table 8, column 6) which is higher than Platt and Jassby's, but in the middle of the range observed by Steemann-Nielsen and Hansen (1959). Using R/P values as a basis for comparing respiration measurements permits results from diverse areas to be compared, but since the high level of photosynthesis dampens the effect of respiration fluctuations, only large differences in respiration are detectable. Thus, direct comparison of simultaneous but independent observations is desirable. Smith (1977) calculated a mean respiration rate of 262 mgC m^{-2} during the night in the waters off Cape Blanc. I calculated a rate of 144 mgC m^{-2} at the same time and place. The 45% discrepancy indicates that the measurement of microplankton respiration requires refinement.

The results of the zooplankton respiration can be compared to the measurements of Smith and Whitledge (1977). The results are not calculated on an areal basis, but on a dry weight-specific basis for certain size fractions. Their results for the 102-223 μm and the 223-505 μm size fractions are the most comparable to the results in Table 5. The average respiration for these two sizes was 0.61 μg-at O h^{-1} (g dry wt)$^{-1}$ (Table 2 of Smith and Whitledge, 1977). In carbon units, the equivalent rate is 3.11 mg C h^{-1} (g dry wt)$^{-1}$. The average ETS-derived respiration was 2.2 mg C h^{-1} (g dry wt)$^{-1}$ which is 30% lower. Thus, the independent zooplankton respiration measurements are in better agreement than are the independent phytoplankton measurements.

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REFERENCES

Anderson, O. R. 1975. The ultrastructure and cytochemistry of resting cell formation in *Amphora coffaeformia* (Bacillariophyceae). J. Phycol., *11,* 272–281.

Anonymous. 1970. R/V *T.G. Thompson* cruise 36 (PISCO). Part I: Hydrography and productivity. Special Report. Dept. Oceanogr., Univ. Washington Data Report 42, 97 pp.

Arons, A. B. and H. Stommel. 1967. On the abyssal circulation of the world ocean—III. An advection—lateral mixing model of the distribution of a tracer property in an ocean basin. Deep-Sea Res., *14,* 441–457.

Barber, R. T. 1977. The JOINT I expedition of the Coastal Upwelling Ecosystems Analysis program. Deep-Sea Res., *24,* 1–6.

Barber, R. T., S. A. Huntsman, and J. E. Kogelschatz. 1976. CUEA Data Report 32, 173 pp.

Barber, R. T. and S. A. Huntsman. 1975. JOINT I carbon, chlorophyll, and light extinction—R.V. *Atlantis* II cruise 82. CUEA Data Report 14, 165 pp.

Barton, E. D., A. Huyer, and R. L. Smith. 1977. Primary production off the coast of northwest

Africa: excretion of dissolved organic matter and its heterotrophic uptake. Deep-Sea Res., *24,* 35–47.

Barton, E. D., R. D. Pillsbury, and R. L. Smith. 1975. A compendium of physical observations from JOINT I. Vertical sections of temperature, salinity, and sigma -t from R/V Gillis data and low-pass filtered measurements of wind and currents. CUEA Data Report 16, 60 pp.

Blackburn, M. 1977. JOINT I zooplankton measurements R.V. *Atlantis* II cruise 82. Coastal Upwelling Ecosystems Analysis Data Report 43, 49 pp.

Blasco, D. 1978. Observations on the diel migration of marine dinoflagellates off the Baja California coast. Mar. Biol., *46,* 41–47.

Carmack, E. and K. Aagaard. 1973. On the deep water of the Greenland Sea. Deep-Sea Res., *20,* 687–715.

Christensen, J. P. and T. T. Packard. 1979. Respiratory electron transport activities in phytoplankton and bacteria: Comparison of Methods. Limnol. Oceanogr., *24,* 576–583.

—— 1976. Oxygen utilization and plankton metabolism in a Washington fjord. Estuar. and Coast. Mar. Sci., *4,* 339–347.

Codispoti, L. A., D. D. Bishop, and M. A. Friebertshauser. 1976. JOINT-I, the *Atlantis* II sections: R.V. *Atlantis* II cruise 82. CUEA Technical Report No. 20, 76 pp.

Codispoti, L. A. and G. E. Friederich. 1978. Local and mesoscale influences on nutrient variability in the Northwest African upwelling region near Cabo Corbeiro. Deep-Sea Res. *25,* 751–770.

Codispoti, L. A. and D. Lowman. 1973. R.V. *Thomas G. Thompson* cruises 35, 37, 46, and 66. Technical Report 284. Univ. Washington, Dept. Oceanogr., 15 pp.

Codispoti, L. A., R. C. Dugdale, and H. J. Minas. A comparison of the nutrient regime off northwest Africa, Peru, and Baja California. CINECA Symposium on the Canary Current, Los Palmas, April 1978. (in press).

Coste, B. and G. Slawyk. 1974. Structures de répartition superficielles des sels nutritifs dans une zone d'upwelling (Cap Corveiro, Sahara Espagnol). Tethys, *6,* 123–132.

Craig, H. 1971. The deep metabolism: Oxygen consumption in abyssal ocean water. J. Geophys. Res., *76,* 5078–5086.

Cruzado, A. 1974. Coastal upwelling between Cape Bojador and Point Durnford (Spanish Sahara). Tethys, *6,* 133–142.

Cushing, D. H. 1975. Marine Ecology and Fisheries. Cambridge Univ. Press, Cambridge, 278 pp.

Dugdale, R. C. 1975. Biological Modelling I. *In* J. C. J. Nihoul, ed., Modelling of Marine Systems. Elsevier Oceanography Series 10, Elsevier, New York, 272 pp.

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

Eppley, R. W. and J. H. Sharp. 1976. Photosynthetic measurements in the central North Pacific. The dark loss of carbon in 24-h incubations. Limnol. Oceanogr., *20,* 981–987.

Fraga, F. 1974. Distribution des masses d'eau dans l'upwelling de Mauritanie. Tethys, *6,* 5–10.

Fraga, F. and M. Manríquez. 1975. Oceanografía química de la región de afloramiento del noroeste de Africa. II Campaña << Atlor II >>, Marzo 1973. Invest. Pesq. Res. Exp. Cient. B/O Cornide, *4,* 185–218.

Friebertshauser, M. A., L. A. Codispoti, D. D. Bishop, G. E. Friederich, and A. A. Westhagen. 1975. JOINT I hyrographic station data, R.V. *Atlantis* II cruise 82. CUEA Data Report 18, 243 pp.

Friederich, G. E. and L. A. Codispoti. 1979. On some factors influencing dissolved silicon distribution over the Northwest African shelf. J. Mar. Res., *37,* 337–353.

Gran, H. H. and T. Braarud. 1935. A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf of Maine (including observations on hydrography, chemistry, and turbidity). J. Biol. Bd. Can., *1,* 279–467.

Groupe MEDIPROD. 1974. Généralités sur la campagne CINECA-CHARCOT-II (15 Mars-29 Avril 1971). Tethys, *6,* 33–42.

Huntsman, S. A. and R. T. Barber. 1977. Primary production off Northwest Africa: the relationship to wind and nutrient conditions. Deep-Sea Res., *24,* 25–33.

Kenner, R. A. and S. I. Ahmed. 1975a. Measurement of electron transport activities in marine phytoplankton. Mar. Biol., *33,* 119–127.

—— 1975b. Correlation between oxygen utilization and electron transport activity in marine phytoplankton. Mar. Biol., *33,* 129–133.

King, F. D., A. H. Devol, and T. T. Packard. 1978. On plankton biomass and metabolic activity from the eastern tropical North Pacific. Deep-Sea Res., *25,* 689–704.

King, F. D., and T. T. Packard. 1975. Respiration and the activity of the respiratory electron transport system in marine zooplankton. Limnol. Oceanogr., *20,* 849–854.

Kroopnick, P. 1974. The dissolved O_2–CO_2–^{13}C system in the eastern equatorial Pacific. Deep-Sea Res., *21,* 211–227.

Kuntz, D., T. T. Packard, A. Devol and J. Anderson. 1975. Chemical, physical, and biological observations in the vicinity of the Costa Rica Dome (January-February, 1973). Tech. Rep. No. 321, Dept. Oceanogr., Univ. of Wash., 187 pp.

Lambert, R. B., Jr. 1974. Small-scale dissolved oxygen variations and the dynamics of Gulf Stream eddies. Deep-Sea Res., *21,* 529–546.

Lehninger. A. L. 1977. Biochemistry, Worth Publishers, New York, 1104 pp.

Margalef, R. 1974. Ecologia. Ediciones Omega, Barcelona, Spain. 951 pp.

—— 1975a. Composición y distribución del fitoplancton marino en la region de afloramiento del NW de Africa, en marzo de 1973 (Campana << Atlor II >> del << Cornide de Saavedra >>). Invest. Pesq. Res. Exp. Cient. B/O Cornide, *4,* 145–170.

—— 1975b. Ciliados planctónicos de la región de afloramiento del NW de África segun datos de la compaña << Atlor II >>. Invest. Pesq. Res. Exp. Cient. B/O Cornide, *4,* 171–174.

Menzel, D. W. and J. H. Ryther. 1960. The annual cycle of primary production in the Sargasso Sea off Bermuda. Deep-Sea Res., *6,* 351–357.

Menzel, D. W. and R. F. Vaccaro. 1964. The measurement of dissolved organic and particulate carbon in seawater. Limnol. Oceanogr., *9,* 138–142.

Milliman, J. D. 1977. Effects of arid climate and upwelling upon the sedimentary regime off southern Spanish Sahara. Deep-Sea Res., *24,* 95–103.

Minas, H. J., L. A. Codispoti, and R. C. Dugdale. Nutrients and primary production in the N.W. African upwelling region. Symposium on the Canary Current Upwelling and Living Resources. Las Palmas, April 1978 (in press).

Mittelstaedt, E. and K. P. Koltermann. 1973. On the currents over the shelf off Cape Blanc in the northwest African upwelling area. Deutsche Hydrographische Zeit-Schnift, *26,* 195–215.

Munk, W. H. 1966. Abyssal recipes. Deep-Sea Res., *13,* 707–730.

O'Brien, J. J. and J. S. Wroblewski. 1976. A simulation of the mesoscale distribution of the lower marine trophic levels off west Florida, *in* B. C. Patten, ed., Systems Analysis and Simulation in Ecology. Academic Press, New York, 607 pp.

Odum, H. T. 1956. Primary production in flowing waters. Limnol. Oceanogr., *1,* 102–117.

—— 1967. Biological circuits and the marine systems of Texas, *in* T. A. Olson and F. J. Burgess, eds., Pollution and Marine Ecology. Wiley Interscience Publishers, New York, 364 pp.

Owens, T. G. and F. D. King. 1975. The measurement of respiratory electron–transport–system activity in marine zooplankton. Mar. Biol., *30,* 27–36.

Packard, T. T. 1969. The estimation of the oxygen utilization rate in seawater from the activity of the respiratory electron transport system in plankton. Ph.D. thesis, Univ. Washington, Seattle, 115 pp.

—— 1971. The measurement of respiratory electron transport activity in marine phytoplankton. J. Mar. Res., *29,* 235–244.

Packard, T. T., M. L. Healy, and F. A. Richards. 1971. Vertical distribution of the respiratory electron transport system in marine phytoplankton. Limnol. Oceanogr., *16,* 60–70.

Packard, T. T., D. Harmon, and J. Boucher. 1974. Respiratory electron transport activity in plankton from upwelled waters. Tethys, *6,* 213–222.

Packard, T. T., H. J. Minas, T. Owens, and A. Devol. 1977. Deep-sea metabolism in the eastern tropical North Pacific Ocean, *in* Oceanic Sound Scattering Prediction, N. R. Andersen and B. J. Zahuranec, eds., Plenum Press, New York, 859 pp.

Packard, T. T., T. Moore, D. Harmon, A. Devol, and F. D. King. 1973. Respiratory electron transport activity in the euphotic zone plankton of the western Mediterranean Sea, North Atlantic Ocean, and the North Pacific Ocean, *in* Report of the working conference on a systems approach to eutrophication problems in the eastern Mediterranean, J. J. MacIsaac, ed., Special Report No. 53 of the Dept. Oceanogr., Univ. Washington, Seattle, 270 pp.

Platt, T. and A. D. Jassby. 1976. The relationship between photosynthesis and light for natural assemblages of coastal marine phytoplankton. J. Phycol., *12,* 421–430.

Pomeroy, L. R. and R. E. Johannes. 1968. Occurrence and respiration of ultraplankton in the upper 500 meters of the ocean. Deep-Sea Res., *15,* 381–391.

Riley, G. A. 1951. Oxygen, phosphate, and nitrate in the Atlantic Ocean. Bingham Oceanogr. Collect. Bull., *13,* 1–169.

Setchell, F. W. and T. T. Packard. 1978. ETS and nitrate reductase activities in the Peru Current, March, April and May 1977. CUEA Data Report No. 54.

Slawyk, G. H. J., J. Minas, and T. T. Packard. 1976. A further investigation on the primary productivity in the divergence zone near the French Mediterranean coast. Int. Revue ges. Hydrobiol., *61,* 373–381.

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

Smith, W. O., Jr. 1977. The respiration of photosynthetic carbon in eutrophic areas of the ocean. J. Mar. Res., *35,* 557–565.

Smith, W. O., Jr., R. T. Barber, and S. A. Huntsman. 1977. Primary production off the coast of northwest Africa: excretion of dissolved organic matter and its heterotrophic uptake. Deep-Sea Res., *24,* 35–47.

Steemann-Nielsen and V. K. Hansen. 1959. Measurements with carbon-14 technique of the respiration rates in natural populations of phytoplankton. Deep-Sea Res., *5,* 223–233.

Strickland, J. D. H. 1965. Production of organic matter in the primary stages of the marine food chain, *in* Chemical Oceanography, J. P. Riley and G. Skirrow, eds., Academic Press, New York, 606 pp.

Sverdrup, H. U. 1953. On conditions for vernal blooming of phytoplankton. J. Cons. Int. Explor. Mer., *18,* 287–295.

UNESCO. 1966. Determination of photosynthetic pigments in seawater. Monogr. Oceanogr. Methodol., *1,* 1–69.

Vallespinós, F. and M. Estrada. 1975. Nitrógeno particulado en la región del NW de Africa.

Distribución y relación con otros parámetros. Invest. Pesq. Res. Exp. Cient. B/O Cornide, *4,* 131–144.

Vives, F. 1974. Le zooplankton el les masses d'eau des environs du Cap Blanc. Tethys., *6,* 313–318.

Whitledge, T. E. and T. T. Packard. 1971. Nutrient excretion by anchovies and zooplankton in Pacific upwelling regions. Invest. Pesq., *35,* 243–250.

Wright, R. 1969. Deep water movement in the western Atlantic as determined by use of a box model. Deep-Sea Res., *16* (suppl.), 433–446.

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