

# NET PHYTOPLANKTON AND THE GREATER THAN 20-MICRON PHYTOPLANKTON SIZE FRACTION IN UPWELLING WATERS OFF BAJA CALIFORNIA

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## ABSTRACT

Between 26 March and 6 April 1973 various phytoplankton studies were carried out during the MESCAL II survey in an area measuring circa 105 km × 30 km, and centered approximately at Punta San Hipolito, Baja California. Upwelling was then in its early stages. The composition of 22 collections of net phytoplankton (No. 20 net), and the composition and abundance of the non-setose (i.e., excluding *Chaetoceros*, *Bacteriastrum*) size fraction >20 μm collected at various depths at 13 stations are reported here. The mean carbon content in the upper 50 m contained in the >20 μm non-setose size fraction was 533.5 mg C/m<sup>2</sup> for all stations, and ranged from 306 to 1,022 mg C/m<sup>2</sup> at individual stations. Based on a C/Chl *a* ratio of 40:1, the mean concentration in the euphotic zone represents circa 12% of the total phytoplankton carbon present. *Lauderia annulata* (28%) and several *Coscinodiscus* species (33%) accounted for most of the carbon found in the >20-μm size fraction, even though the latter comprised only about 10% of the mean population expressed as cell number. The mass occurrence of *Coscinodiscus* reported previously for Magdalena Bay during summer upwelling was not observed. The *Coscinodiscus* population and the non-setose component of the >20-μm size fraction contributed only 1.2% and 4%, respectively, of the daily caloric ingestion estimated for the crab, *Pleuroncodes planipes*, previously reported to graze heavily on *Coscinodiscus*. Sinking rates (61 to 144 m/h) of *Pleuroncodes* fecal material exceeded by onefold to fourfold those rates estimated for the various sizes of *Coscinodiscus* and zooplankton fecal pellets sampled during the survey. The abundant crab population is, thus, important in causing an exceptionally rapid deposition of unassimilated phytoplankton frustules and organic material onto the sea floor. Floristic changes accompanying upwelling were detectable. The occurrence of the unique diatoms *Coscinodiscus (Brenneckella) eccentricus* and *Planktoniella muriformis* in these waters is apparently reported for the first time. The present data together with earlier observations suggest that the net diatom community is similar in the coastal waters extending from San Diego, Calif., to the Gulf of Panama. The data do not support the idea that the abundance of *Pleuroncodes* in this upwelling system is causally linked to that of *Coscinodiscus*.

There is little information on the composition and abundance of the phytoplankton community in the upwelling waters off Baja California. The available data are mostly qualitative (Allen 1924, 1934, 1938; Balech 1960; Cupp 1930, 1934), aside from recent, cursory observations on phytoplankton cells >25 μm which are grazed by the red crab, *Pleuroncodes planipes* (Longhurst et al. 1967).

Unique mass blooms of *Coscinodiscus* have been observed by Longhurst et al. in the upwelled waters of Magdalena Bay. This phenomenon and the great abundance of *Pleuroncodes*, which grazes on *Coscinodiscus* cells, may be distinctive characteristics of this upwelling system. Smith et al.<sup>2</sup> have concluded that this crab is an impor-

tant herbivore in the California Current upwelling system, where its role is comparable to that of the anchovy, *Engraulis ringens*, in the Peru Current. Longhurst (1968) has evaluated the potential fishery for this galatheid crab, which occurs in both the benthic and pelagic zones; some crabs exhibit diurnal migrations (Longhurst et al. 1967).

*Pleuroncodes* is generally distributed throughout this region (Blackburn 1969), while information on the regional distribution and abundance of *Coscinodiscus* is lacking. It is therefore unknown whether *Coscinodiscus* indeed generally characterizes the phytoplankton community in these upwelled waters. Clarification of this is relevant

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Clifford. Respiration and chemical composition of *Pleuroncodes planipes* (Decapoda: Galatheidae): Energetic significance in an upwelling system. Manuscr., 22 p. Woods Hole Oceanogr. Inst., Woods Hole, Mass.

to the question of whether *Pleuroncodes*' occurrence is causally linked to that of *Coscinodiscus*.

*Coscinodiscus* and other heavily silicified diatoms sink to the sea floor, as documented for the Gulf of California (Round 1967, 1968). This deposition contributes skeletal remains (i.e., to the thanatocoenosis) and organic matter to the sediments. The abundance and sinking characteristics of this diatom population are also of interest, since *Pleuroncodes* also occurs in the benthos. During this benthic residence, when population densities up to 250 individuals/m<sup>2</sup> have been found (Smith et al. footnote 2), it may feed on detrital material (Longhurst et al. 1967).

Various studies on phytoplankton were carried out during the Mescal II expedition of the RV *Thomas G. Thompson* in 1973 to study upwelling off Baja California, as a continuation of 1972 activities in this area (Walsh et al. 1974). These included the routine, shipboard examination of both net phytoplankton and the >20- $\mu$ m size fraction filtered from quantitative samples. The discovery that natural populations of a *Ditylum brightwelli* and, possibly, *Biddulphia mobiliensis* exhibited diel cell division has been reported (Smayda in press a).

Examination of the >20- $\mu$ m size fraction was partly motivated by the need to know its composition and abundance, particularly that for *Coscinodiscus*. This was to evaluate the aforementioned relationship possibly occurring between *Pleuroncodes* and *Coscinodiscus*, and to establish the latter's importance during the initial stages of upwelling. This latter objective was prompted by the remarkable bloom found in Magdalena Bay during a later stage of the upwelling cycle. Finally, such data are needed to evaluate the sinking and turnover rates of the more heavily silicified and dissolution-resistant components of this size fraction which sink faster and represent an energy source for benthic secondary production.

## METHODS

Between 26 March and 6 April 1973, 22 collections of net phytoplankton were made at 15 stations (multiple sampling on different days at some). A No. 20 (mesh opening of 69  $\mu$ m) net 30 cm in diameter sampled the upper 50 to 100 m (depending on depth) for 30 min by repeated vertical oscillations, during which the net was lowered at a rate of ca. 30 m/min and retrieved at a rate of 10 m/min. The samples were examined microscopi-

cally soon after collection, after placing onto a slide an aliquot of the unpreserved, sedimented material from an unagitated sample.

Of the 15 stations sampled, 13 were located in a sampling block measuring about 105 km long and 30 km wide centered approximately at Punta San Hipolito off the coast of Baja California (Figure 1). The coordinates of the northern- and southern-most stations are lat. 27°6.7'N, long. 114°21.2'W and lat. 26°28.5'N, long. 113°45.5'W, respectively. The stations extended offshore from within sight of land to within, or near, the California Current; the inner- and outermost stations were at lat. 26°55.2'N, long. 114°02.2'W and lat. 26°51.2'N, long. 114°10.7'W, respectively. Stations 1 and 2 (not shown in Figure 1) were located about 460 km north of this main sampling area at lat. 30°57.8'N, long. 116°32'W and lat. 28°8.2'N, long. 115°39.2'W, respectively.

Quantitative samples were also collected at 13 stations from the surface to 50 m at 10-m intervals, and at 75 m with 5-liter Niskin Bottles. Seven stations (18 to 24) were sampled at 6-h intervals while following a drogue. From samples collected in the upper 30 m, 2 liters were usually filtered through a 20- $\mu$ m mesh net, and 3 liters from greater depths. The apparatus used is illustrated in Durbin et al. (in press). The material

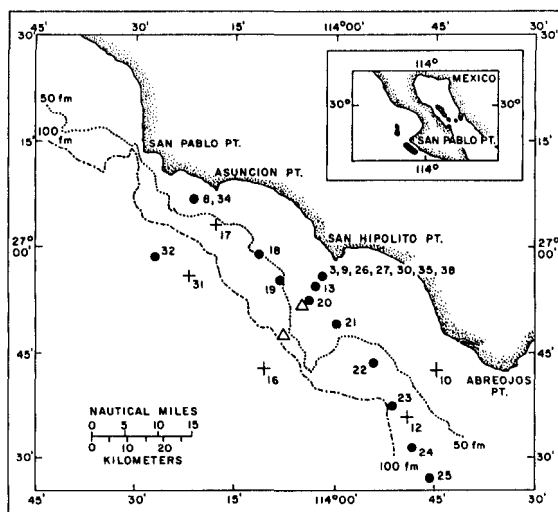


FIGURE 1.—Location of stations where collections of net phytoplankton (+) and net and water bottle samples (●) were made from 26 March to 6 April 1973 (except that net and water bottle collections were made only at Stations 26 and 38 at the frequently sampled station located off Punta San Hipolito).  $\Delta$  represents stations, along with Station 27, used to illustrate the occurrence of upwelling in Table 1; the outermost station is Station 29.

retained by the net was concentrated to 30 ml, preserved with hexamine + Formalin<sup>3</sup> and 1 ml of the concentrate then enumerated on board ship using a Sedgwick Rafter Counting Chamber. The concentrate was obtained by stopping filtration to leave about 1 cm of water above the filter.

As stated in the Introduction, cells in the size class  $>20 \mu\text{m}$  are frequently heavily silicified and sink to the sea bed. *Chaetoceros* and *Bacteriastrium* are usually not represented in the latter (Round 1968), presumably because of rapid dissolution of their silicon frustules. The various objectives of the present and other, ongoing studies during MESCAL II emphasized the *Coscinodiscus* and other non-setose genera, and also required real-time data for proper execution of the program. Shipboard enumeration of phytoplankton was therefore necessary. Quantitative shipboard enumeration of specimens belonging to genera characterized by setae is difficult; their setose nature makes them prone to movement within the counting chamber in response to the ship's vibrations and movement. For these various reasons, during the numerical census representatives of the genera *Chaetoceros* and *Bacteriastrium* and a species similar in general appearance to (but probably not) *Nitzschia frigida* were not enumerated.

Numerical abundance was transformed into carbon equivalents. From 10 to 40 cells of each species (depending on abundance) were measured to obtain the mean dimensions required to calculate cell volume using appropriate mensuration formulae. The carbon content was then calculated from Strathmann's (1967) equation

$$\log C = 0.758 (\log V) - 0.352$$

where  $V$  is the cell volume in  $\mu\text{m}^3$ . From this cellular estimate (pg per cell), the population carbon was computed. The constant 0.352 differs slightly from Strathmann's given value, and is based on additional diatom analyses (Eppley, pers. commun.).

The mean population per liter ( $\bar{C}$ ) in the upper 50 m was calculated from:

$$\bar{C} = \frac{1}{2Z_5} [(C_0 + C_1)(Z_1 - Z_0) + (C_1 + C_2)(Z_2 - Z_1) + \dots + (C_4 + C_5)(Z_5 + Z_4)]$$

where  $C_0, C_1$ , etc. are the observed cell (carbon) concentrations per liter at the surface ( $Z_0$ ) and 10 m ( $Z_1$ ), etc., down to 50 m ( $Z_5$ ). Concentrations per square meter of sea surface down to 50 m were obtained from ( $\bar{C}$ ) ( $5 \times 10^4$ ). Samples were collected at 75 m at only 9 of the 13 quantitative stations because of depth. This, together with the sparse populations usually found there, accounts for the emphasis on the upper 50 m.

## RESULTS

Upwelling occurred during the field program. Table 1 presents some representative physical and chemical parameters along a transect of three stations sampled on 3 and 4 April near Punta San Hipolito (Figure 1). The inflow and upwelling of cold, nutrient-rich water at the nearshore station (27) is evident. Upwelling was usually more pronounced near and shorewards of the 50-fathom isobath. Details of this upwelling, which was in its early stages, and associated biotic responses will be presented elsewhere (Walsh, Kelley, Whitledge, Huntsman, and Pillsbury in prep.).

### Net Phytoplankton

The species identified in the net material are listed in Appendix Table 1. Throughout the ship's track of ca. 700 km the No. 20 net phytoplankton was characterized by the genus *Chaetoceros*

TABLE 1.—Hydrographic conditions along a transect off Punta San Hipolito showing the occurrence of upwelling during 3 and 4 April 1973 (Stations shown in Figure 1).

Depth (m)	°C	‰	$\sigma_t$	$\mu\text{g at/liter}$		
				PO <sub>4</sub>	NO <sub>3</sub>	SiO <sub>2</sub>
Station 29 (lat. 26°48'N, long. 114°07.5'W) 0220						
0	16.04	34.122	25.08	0.47	0.98	1.23
10	16.04	34.119	25.08	0.54	0.98	1.10
20	15.67	34.127	25.17	0.55	0.98	0.98
30	15.65	34.112	25.16	0.63	1.31	1.53
40	13.68	33.957	25.47	1.05	3.94	7.52
50	11.87	33.736	25.65	1.40	9.18	13.34
75	11.51	33.821	25.79	1.65	14.43	18.83
Station 28 (lat. 26°51.5'N, long. 114°04.8'W) 0100						
0	15.69	34.044	25.10	0.51	0.66	1.75
10	15.25	34.002	25.17	0.63	0.66	2.48
20	14.35	33.912	25.29	0.82	1.31	4.91
30	13.64	33.930	25.45	1.06	3.94	8.52
40	11.94	33.690	25.60	1.22	8.20	11.29
50	11.84	33.922	25.80	1.67	14.43	16.95
Station 27 (lat. 26°55.2'N, long. 114°02.2'W) 1720						
0	13.53	34.080	25.59	1.15	7.03	11.87
10	13.26	34.086	25.65	1.32	7.91	12.39
20	13.04	34.092	25.70	1.57	10.94	15.36
30	12.26	34.063	25.83	1.83	14.28	18.85
40	11.81	34.141	25.98	2.12	20.08	22.68
50	11.36	34.243	26.14	2.34	23.72	27.05

<sup>3</sup>Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

(*affinis*, *curvisetus*, *debilis*, *didymus*, *socialis*) in species and abundance. The genus *Coscinodiscus* was a conspicuous co-dominant, but varied in relative abundance from station to station. The remarkable colonial diatom *Planktoniella muriformis* (Loeblich et al. 1968; Round 1972) was also prominent throughout this region. Nonetheless, some apparent regional differences are noteworthy.

At Station 1 located near Punta Kolnett a very rich, diverse net plankton community occurred on 26 March dominated by *Chaetoceros* and *Nitzschia* spp. and *Thalassiothrix frauenfeldii*. *Asterionella japonica*, *Eucampia cornuta*, and *Lithodesmium undulatum* were other abundant diatoms. This community stands out from others in the importance of *Asterionella* (many small pennate diatoms were attached to the colonies), which was not found in subsequent net tows. Also unlike subsequent stations, *Phaeocystis* cf. *pouchetii* was common while *Coscinodiscus* spp. were not. Allen (1945) has reported extensive blooms of *Phaeocystis* off southern California. This colonial haptophycean is well known for its apparent adverse effects on certain fisheries in the North Sea during mass blooms.

The lack of nutrient data at Stations 1 and 2 prevents assessment of possible upwelling. However, when sampled on 27 March the upper 50 m of the latter station was considerably warmer (15.29°C at 0 m, 14.94°C at 50 m) than at Station 1 (14.53°C at 0 m, 11.42°C at 40 m). The net phytoplankton community was considerably poorer and dominated by *Ceratium* spp.; peridinians were frequent, and the diatoms *Biddulphia mobilensis*, *Coscinodiscus* spp., and *Planktoniella sol* were common. This community suggests that upwelling was weak, if occurring.

The principal features of the net collections ( $n = 20$ ) made in the intensive survey area (Figure 1) are: 1) the community at the deepwater stations (16, 31, 32) located seaward of the 50-fathom isobath was less abundant and differed somewhat relative to the shallower stations; 2) the composition at the latter stations was generally similar; and 3) a slight change in apparent species dominance occurred by the end of the 12-day sampling period.

At the outer, deepwater Station 16 (30 March) *Chaetoceros affinis* and *curvisetus* dominated; *Ceratium* and *Peridinium* spp. were also common. At Stations 31 and 32 (4 April), *Bacteriastrium* dominated together with the above *Chaetoceros*

species and *decipiens* and *socialis*. *Coscinodiscus* spp. were subordinate; *Asterolampra marylandica* and cf. *Pyrocystis lunula* were frequent. The lower relative abundance and the difference in dominant species at these outer stations are also reflected in the quantitative samples (Table 2). The lowest mean concentration occurred at Station 32 (quantitative samples were not collected at Stations 16 and 31). The physical-chemical data indicate that upwelling was not occurring at Station 16 and was insignificant, if taking place, at Stations 31 and 32.

At the nearshore Station 34 (4 April), where the hydrographic conditions were similar to Station 27 (Table 1), the *Bacteriastrium* component important at Stations 31 and 32 was absent and *Thalassiosira rotula* dominated along with the *Chaetoceros* spp. This increased importance of *Thalassiosira rotula* relative to samples collected a week earlier is also noted in the series collected near Punta San Hipolito (Stations 3 to 38) (Figure 1). The nearshore communities were otherwise dominated by different proportions of *Chaetoceros* and *Coscinodiscus* spp. The *Coscinodiscus* component was especially prominent at Stations 10, 17, and 19, for example. (The net tows frequently contained pennate diatoms which might have been scoured from bottom sediments during upwelling.)

The apparent differences in net community composition, abundance, and species succession during the 10-day sampling period in the intensive survey area probably reflect variations in intensity of upwelling, which was just beginning based on aerial reconnaissance of sea-surface temperatures prior to the ship's arrival in the survey area. Between 28 March (Station 3) and 30 March (Station 13) cold water ascended 10 m at the fixed station near Punta San Hipolito (Figure 1; Pillsbury, pers. commun.).

## Quantitative Samples

### Numerical Abundance

The results of the quantitative census of the non-setose species in the  $>20\text{-}\mu\text{m}$  size fraction are presented in Table 2. The mean population level in the upper 50 m ranged from about 2,110 to 9,800 cells/liter. *Lauderia annulata* dominated numerically (from 35 to 60% of total abundance) throughout the area, except at the last station (38) sampled (3%) where *Thalassiosira rotula* dominated

TABLE 2.—The mean, non-setose population (cells/liter and  $\mu\text{g C/liter}$ ) in the  $>20\text{-}\mu\text{m}$  size class in the upper 50 m. Lower value in cell abundance (i.e.  $n/n$ ) represents number of dead cells.

Station	Time	$\Sigma$ cells/carbon	<i>Actinocyclus undulatus</i>	<i>Biddulphia mobilensis</i>	<i>Ceratium</i> spp.	<i>Coscinodiscus</i> ( <i>Brennekeella</i> ) <i>eccentricus</i>	$\Sigma$ <i>Coscinodiscus</i> spp.	<i>Ditylum brightwellii</i>	<i>Eucampia cornuta</i>	<i>Guinardia flaccida</i>	<i>Lauderia annulata</i>	<i>Lithodesmium undulatum</i>	<i>Planktoniella muriformis</i>	<i>Planktoniella sol</i>	<i>Rhizosolenia</i> spp.	<i>Schroederella delicatula</i>	<i>Thalassiosira rotula</i>	OTHERS	% dead cells of <i>Coscinodiscus</i> spp.	
13	1145	4,067 11.05	29/5 0.07	115/1 0.72	119 0.25	33 0.08	630/54 4.83	198/7 1.49	24 0.01	3 0.01	2,015/2 2.68	330 0.48	32 0.20	308/25 0.20	5/1	173 0.17	48 0.06	5	8.5	
18	1800	3,995 13.85	47/6 0.11	254/15 1.58	29 0.06	35 0.09	631/49 6.61	284/6 2.14	57 0.02	16 0.07	1,396 1.86	589 0.85	87 0.22	335 0.22	3 0.18	177 0.18	48 0.06	7	7.8	
19	0000	4,576 16.13	94 0.23	171 1.06	12 0.02	30 0.08	520/63 7.26	267 2.01	14 0.004	43 0.18	2,942 3.92	508 0.74	31 0.15	220 0.15	6 0.45	448/17 0.45	24 0.03	5	11.5	
20	0600	3,321 7.38	22/3 0.05	59/2 0.37	12 0.02	7/1 0.02	309/27 2.38	125 0.94	2 0	22 0.09	2,008 2.67	306 0.44	20 0.13	197/3 0.13	5 0.12	116/34 0.12	114 0.15	3	8.7	
21	1200	2,456 8.31	29/2 0.09	68/2 0.42	5 0.01	29 0.07	332/35 4.37	137 1.03	— —	37 0.15	1,171/2 1.56	181/18 0.26	28 0.13	194/5 0.13	36/2	168 0.17	37 0.05	4	10.5	
22	1800	9,806 20.44	45 0.11	232 1.44	10 0.02	55 0.14	479/29 3.96	552/15 4.16	123 0.04	91 0.38	5,665 7.55	719 1.04	37 0.50	746 0.50	11 0.85	841/19 0.85	190 0.25	10	6.1	
23	0000	4,476 8.96	26/1 0.06	76/2 0.47	10 0.02	40 0.10	318/50 2.27	148/2 1.16	77 0.02	94 0.39	2,512 3.35	425 0.62	36 0.19	288/12 0.19	130/2	236/50 0.24	56 0.07	4	15.7	
24	0600	3,595 7.11	21/1 0.05	80/2 0.50	17 0.04	97 0.24	191/17 1.79	64 0.48	— —	101 0.42	1,957/10 2.61	314 0.46	7 0.36	538/13 0.36	52	113 0.11	38/5 0.05	5	8.9	
25	1200	4,915 9.13	48 0.12	76 0.47	36 0.07	44 0.11	257/42 1.90	179 1.35	190 0.06	42 0.18	2,616 3.48	461 0.67	30 0.38	569 0.38	28	276 0.28	46 0.06	17	16.3	
26	1800	3,248 7.75	26/2 0.06	88 0.55	0 0	12 0.03	508/50 3.23	78/2 0.59	10 0.003	8 0.03	1,526 2.03	148 0.21	6 0.03	46 0.03	—	170 0.17	618 0.82	3	9.8	
32	1800	2,110 6.12	8 0.02	59 0.37	43 0.09	101/1 0.25	230/43 2.88	53/1 0.40	— —	109 0.46	819 1.09	120 0.17	6 0.37	552 0.37	29	7 0.01	10 0.01	7	18.7	
34	2140	8,653 15.00	10/2 0.02	54/1 0.34	12 0.02	11 0.03	406/16 2.47	272 2.05	46 0.01	43 0.18	3,835 5.11	486 0.70	12 0.10	151/2 0.10	7	1,318 1.33	1,990 2.64	—	3.9	
38	0720	4,926 9.03	53/2 0.13	6 0.04	49 0.10	4 0.01	623/65 3.10	40 0.30	18/60 0.005	26 0.11	136/7 0.18	602/19 0.87	8 0.05	82 0.05	5	618 0.62	2,639/2 3.51	17	10.4	
																			$\bar{x}$	10.5

(54%). The latter was also important at Station 34 (23%); the maximum, mean abundance of *Schroederella delicatula* (1,318 cells/liter) was also found here. *Coscinodiscus* spp. were usually next to *Lauderia* in numerical importance, and composed a maximum of 10 to 15% of the mean population. Table 3 lists the species of *Coscinodiscus* found. (*Coscinodiscus* "large species" may represent several species difficult to identify properly in the counting chamber.) *Planktoniella sol* contributed from about 2 to 25% of the mean population, and *Lithodesmium undulatum* usually around 7 to 12%.

The absolute abundance of the unique colonial aggregate, *Planktoniella muriformis*, which can have up to at least 530 cells/colony (Loeblich et al. 1968), is unknown; individual cells in the colonies were not counted. The mean number of colonies per liter in the upper 50 m ranged from 6 to 92, with the low levels (6 to 10) persistent at stations made after Station 25 (Table 2). The mean vertical

distribution of this species shows a similar abundance (22 to 30 colonies/liter) in the upper 40 m (Table 4; Figure 2), contrary to expectations, and will be reconsidered later.

Species of *Rhizosolenia*  $>20\ \mu\text{m}$  were not abundant, and included: *bergoni*, *calcar avis*, *imbricata* var. *shrubsolei*, *stolterfothii*. Diatoms which are included in OTHERS in Table 2, and their maximum abundance (cells per liter) are:

- Asteromphalus heptactis* (12)
- Corethron pelagicum* (19)
- Dactyliosolen* sp. (72)
- Hemidiscus cuneiformis* (84)
- Leptocylindrus danicus* (228)
- Paralia sulcata* (79)
- Skeletonema costatum* (152)
- Stephanopyxis* cf. *turris* (192)
- Thalassionema nitzschioides* (126)
- Thalassiothrix* cf. *mediterranea* var. *pacifica* (16)

TABLE 3.—The mean population as cells/liter (a) and  $\mu\text{g C/liter}$  (b) of the different *Coscinodiscus* species  $>20\ \mu\text{m}$  in the upper 50 m.

Station	( <i>Brenneckella</i> ) eccentricus	cf. <i>asteromphalus</i>	? <i>concinus</i>	eccentricus	cf. <i>granii</i>	"large species"	$\Sigma$
13 a	33	118	3	465	3	41	663
b	0.082	0.568	0.015	1.361	0.061	2.822	4.91
18 a	35	209	95	262	2	63	666
b	.087	1.005	.467	.767	.041	4.337	6.70
19 a	30	202	103	135	4	77	551
b	.075	.972	.506	.395	.082	5.300	7.33
20 a	7	152	36	104	0	17	316
b	.017	.731	.177	.304	0	1.170	2.40
21 a	29	182	18	94	5	44	372
b	.072	.876	.088	.275	.102	3.029	4.44
22 a	55	204	57	184	5	30	535
b	.137	.981	.280	.539	.102	2.065	4.10
23 a	40	144	28	116	10	13	351
b	.100	.692	.138	.340	.205	.895	2.37
24 a	97	64	51	64	4	14	294
b	.241	.308	.251	.187	.082	.964	2.03
25 a	44	167	13	64	1	12	301
b	.109	.803	.064	.187	.020	.826	2.01
26 a	12	176	18	283	11	18	518
b	.030	.847	.088	.828	.225	1.239	3.26
32 a	101	125	17	42	34	20	339
b	.251	.601	.084	.123	.696	1.377	3.13
34 a	11	95	24	271	0	16	417
b	.027	.457	.118	.793	0	1.101	2.50
38 a	4	60	19	528	0	17	628
b	.009	.289	.093	1.545	0	1.170	3.11

These species are listed only to indicate their presence; their actual abundance is probably greater, since most of these would routinely pass through a  $20\text{-}\mu\text{m}$  mesh net depending on orientation of the cells during filtration.

*Ceratium furca* usually dominated the dinoflagellates  $>20\text{-}\mu\text{m}$ ; populations of *Ceratium fusus* were persistent. Reproductive stages similar to those depicted by von Stosch (1964) for some ceratians were frequent. *Pyrocystis* was present, including an organism quite reminiscent of *Pyrocystis lunula* (vide Figure 559 in Schiller 1937) in shape and stages found. Maximum abundance was 60 cells/liter in the upper 10 m at Station 38 ( $13.96^\circ$  to  $14.31^\circ\text{C}$ , otherwise similar to Station 27 (Table 1)). Various stages of the cf. *Pyrocystis lunula* cycle were also found during growth experiments carried out with mixed, natural populations. The dinoflagellate population was usually sparse, however, with no indication of red tide in the  $>20\text{-}\mu\text{m}$  size fraction either visually or microscopically. However, several weeks later, following temporary subsidence of upwelling, a red-

tide outbreak occurred in these waters (Walsh, pers. commun.) similar to pre-upwelling blooms encountered during MESCAL I in March 1972 (Walsh et al. 1974).

A coccolithophorid similar to *Syracosphaera apsteini* (15 cells/liter) was found occasionally.

*Noctiluca scintillans* was frequently encountered in the samples, especially at Station 38, with evidence of active predation of the phytoplankton by *Noctiluca*.

### Carbon Abundance

The mean carbon content in the upper 50 m for the dominant non-setose diatom component  $>20\ \mu\text{m}$ , exclusive of *Planktoniella muriformis*, *Rhizosolenia* spp., and OTHERS is given in Table 2. The reason for excluding *Planktoniella muriformis* is because of the great difficulty to enumerate the cells within the colonies, whose size varied considerably. Insufficient specimens of the rarer *Rhizosolenia* and "other" species prevented reliable cell sizing to calculate cell volume.

The mean carbon content in the upper 50 m ranged from 6.12 to 20.44  $\mu\text{g C/liter}$  at the various stations; the overall mean was 10.67  $\mu\text{g C/liter}$  (Tables 2 to 4). Comparison of the percent of the total population represented by a species on a numerical and carbon basis shows an inherent inadequacy of the numerical census as a population monitor. For example, the *Coscinodiscus* spp. as carbon contributed from 16.7 to 53.4% of that in the  $>20\text{-}\mu\text{m}$  size fraction (exclusive of the non-setose species which were not monitored), while numerically they composed only from 4.8 to 16.7%. The corresponding means for all stations were about 36% and 11%, respectively. The six most abundant species as carbon ( $\bar{x} = 10.67\ \mu\text{g C/liter}$ ) compared to their numerical ( $\bar{x} = 4,732$  cells/liter) importance in the upper 50 m are:

	$\mu\text{g C/liter}$	%	cells/liter	%
<i>Lauderia annulata</i>	2.97	27.8	2,227	47
<i>Coscinodiscus</i> "large species"	1.84	17.2	27	0.6
<i>Ditylum brightwelli</i>	1.38	12.9	184	3.9
<i>Coscinodiscus</i> cf. <i>asteromphalus</i>	0.71	6.7	148	3.1
<i>Biddulphia mobiliensis</i>	0.64	6.0	103	2.2
<i>Thalassiosira rotula</i>	0.61	5.7	454	9.6

For *Coscinodiscus* (*Brenneckella*) spp., the means are 3.53  $\mu\text{g C/liter}$  (33.1%) and 458 cells/liter (9.7%). The *Coscinodiscus* (*Brenneckella*) spp. and the four other species given above compose 9.13

TABLE 4.—Mean vertical distribution as cells/liter and as equivalent carbon ( $\mu\text{g C/liter}$ ) of the  $>20\text{-}\mu\text{m}$  non-setose size fraction at all stations between 30 March and 6 April 1973 in MESCAL II survey area ( $n = 12$  (0 m),  $n = 13$  (10-50 m),  $n = 9$  (75 m))

Species	Depth (m)							$\bar{x}$ upper 50 m
	0	10	20	30	40	50	75	
<i>Actinoptychus undulatus</i>	36	41	48	36	18	13	8	34
<i>Biddulphia mobilensis</i>	0.08	0.10	0.12	0.09	0.04	0.03	0.02	0.081
<i>Ceratium spp.</i>	177	185	121	66	47	19	5	103
	1.10	1.15	0.75	0.41	0.29	0.12	0.03	0.64
	66	68	28	5	0	2	0	27
	0.14	0.14	0.06	0.01	0	0.005	0	0.057
<i>Coscinodiscus (Brenneckella) eccentricus</i>	73	67	43	22	17	9	2	38
	0.16	0.17	0.11	0.05	0.04	0.02	0.005	0.092
<i>Coscinodiscus cf. asteromphalus</i>	286	228	150	96	112	18	33	148
	1.38	1.10	0.72	0.46	0.54	0.09	0.16	0.709
<i>Coscinodiscus ? concinnus</i>	49	64	46	13	30	17	16	37
	0.24	0.31	0.23	0.06	0.15	0.08	0.08	0.182
<i>Coscinodiscus eccentricus</i>	296	346	254	151	85	62	15	203
	0.87	1.01	0.74	0.44	0.25	0.18	0.04	0.593
<i>Coscinodiscus cf. granii</i>	11	8	3	10	2	2	0	6
	0.23	0.16	0.06	0.20	0.04	0.04	0	0.119
<i>Coscinodiscus</i> ("large species")	26	28	60	16	15	3	5	27
	1.79	1.93	4.13	1.10	1.03	0.21	0.34	1.838
$\Sigma$ <i>Coscinodiscus</i> ( <i>Brenneckella</i> )	741	741	556	308	261	111	71	458
	4.67	4.68	5.99	2.31	2.05	0.62	0.63	3.53
<i>Ditylum brightwellii</i>	304	346	247	98	73	3	4	184
	2.29	2.61	1.86	0.74	0.55	0.02	0.03	1.38
<i>Eucampia cornuta</i>	85	24	28	85	33	6	0	43
	0.03	0.01	0.01	0.03	0.01	0	0	0.015
<i>Guinardia flaccida</i>	69	109	66	24	17	2	0	50
	0.29	0.46	0.28	0.10	0.07	0.008	0	0.211
<i>Lauderia annulata</i>	3,393	3,761	3,597	1,479	580	46	30	2,227
	4.52	5.01	4.79	1.97	0.77	0.06	0.04	2.97
<i>Lithodesmium undulatum</i>	584	667	589	259	211	42	8	408
	0.85	0.97	0.85	0.38	0.31	0.06	0.01	0.59
<i>Planktoniella muriformis</i> (colonies)	24	24	27	32	30	12	11	26
<i>Planktoniella sol</i>	506	664	406	195	113	26	11	329
	0.34	0.44	0.27	0.13	0.08	0.02	0.007	0.22
<i>Rhizosolenia</i> spp.	24	29	64	11	6	1	1	25
<i>Schroederella delicatula</i>	601	456	705	220	116	47	0	364
	0.61	0.46	0.71	0.22	0.12	0.05	0	0.37
<i>Thalassiosira rotula</i>	442	420	969	585	57	34	0	454
	0.59	0.56	1.29	0.78	0.08	0.05	0	0.61
$\Sigma$ cells/liter	7,028	7,100	7,424	3,403	1,532	352	138	4,732
$\Sigma$ $\mu\text{g C/liter}$	15.51	16.59	16.98	7.17	4.37	1.04	0.77	10.67

$\mu\text{g C/liter}$ , or 86% of the mean, and 3,426 cells/liter (72%).

### Vertical Distribution

The mean vertical distribution of the species numerically and as carbon is given in Table 4. Selected examples of the types of vertical distribution characterizing certain species are given in Figure 2.

The standing stock declined sharply between 20 and 30 m; a uniform abundance characterized the upper 20 m. Both numerically and as biomass, the mean population at 30 m was about 45% of that at 20 m (Table 4). Expressed as carbon, and relative to the populations at 20 m, the mean populations at greater depths were only 25% (40 m), 6% (50 m) and 4.5% (75 m). About 62% of the mean carbon content of 533.5 mg C/m<sup>2</sup> in the upper 50 m occurred in the upper 20 m, where a mean of 16.42  $\mu\text{g C/liter}$  is calculated. This pattern in vertical distribution is consistent with the mean compensation depth of about 23 m determined from Secchi

disc measurements at 17 stations during this cruise leg.

The mean vertical carbon distribution of certain species (Figure 2) illustrates that peak abundance usually occurred in the upper 20 m. The phototactic ceratians are most concentrated in the upper 10 m, with a rapid decrease (as percent of mean maximum abundance) with depth. The possibility that the "working distance" vertically within the water column varies between species is suggested by the representative distributions illustrated in Figure 2. The depth at which 50% of the mean maximum abundance occurred ranged from about 20 to 35 m between species, and from 25 to 55 m for the 25% level. Differences in light requirements, particularly that of growth at low intensities, might account for the observed distributions, if a physiological explanation can be applied. However, such distributions can also reflect differences in sinking rates, differential grazing, etc. Thus, while the underlying reasons are obscure, it is evident that the biomass distribution within and

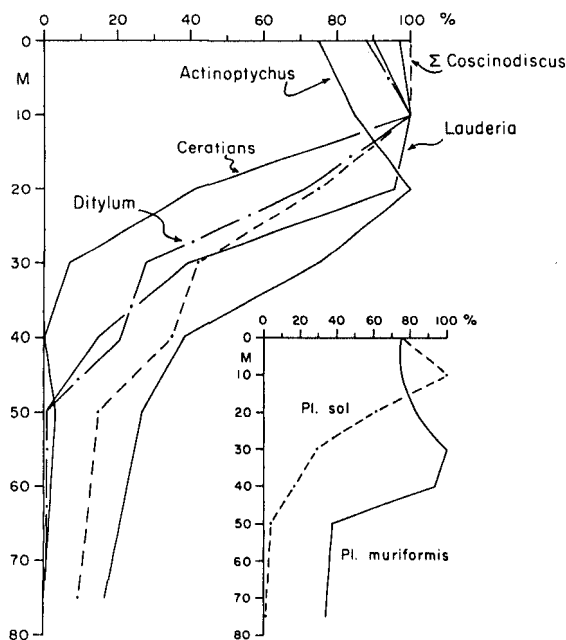


FIGURE 2.—The mean vertical distribution at all stations of *Actinopterychus undulatus*, *Ditylum brightwelli*, *Lauderia annulata*, *Planktoniella muriformis*, and *P. sol*, and for the combined *Ceratium* and *Coscinodiscus* species. Abundance is given as percent of the maximum mean abundance for each species presented in Table 4.

below the euphotic zone differs between species of phytoplankton.

## BIOGEOGRAPHICAL COMMENTS

### *Planktoniella muriformis*

Loeblich et al. (1968) described *Coenobiodiscus muriformis* as a new genus and species from north San Diego Bay, Calif., where blooms occur, and where it was reported to be in every sample collected since its first sighting in July 1966. Cultures were also established at 23° to 25°C. This unique, colonial diatom comprised up to 530 cells embedded in a one-cell thick gelatinous matrix which linked the cells in the girdle region. The circular to subcircular colonies have concave-convex shape and can be at least 500  $\mu$ m in diameter. Round (1972) recently described a similar organism from the harbor at Tema in Ghana, Africa. (Environmental data were not given.) It differed from the San Diego population in the presence of considerably fewer cells per colony and slight microstructural variations. Nonetheless, Round

concluded that these taxa were similar, and transferred this species to the genus *Planktoniella*.

This unique organism was conspicuous in the present survey, both in the vertical net tows and quantitative samples along the approximately 700-km track at temperatures ranging from about 11.5° to 16°C. In experiments to be described elsewhere in greater detail (Smayda in press b), the growth rate for colony increase was 2.9 and 2.0 "doublings" per day at ca. 15° to 18°C. These compare with daily colony doubling rates of 1.3 to 1.6 for cultured populations at 23° to 25°C calculated from data presented in Loeblich et al. (1968). The principal value of these data is the indication that active growth occurred under the upwelling conditions. Loeblich et al. and Round disagree as to whether all cells in the colony divide to produce a new colony, or whether growth without new colony formation can also occur.

The maximum recorded abundance of *Planktoniella muriformis* was 205 colonies/liter at the surface at Station 18. It was very common in the net tows. Thus, given its relative abundance at this time, its noteworthy appearance, and the long-term program of frequent net collections (especially during this time of year) in the coastal waters of southern and Baja California (including this survey area), carried out by Allen and Cupp, their failure to comment in any fashion on its presence is puzzling. Nor is it cited in any way in their periodic species lists for these waters (Cupp 1934; Allen 1938), or for the Gulf of California (Cupp and Allen 1938; Gilbert and Allen 1943), where floristic similarities are evident. Neither does Round (1967) mention it in his recent report on the net phytoplankton in the Gulf of California. Further, only this species and *Thalassiosira rotula*, of those found during this survey, were not found in the Gulf of Panama (Smayda 1966). Thus, the present observations suggest that *Planktoniella muriformis* is presently distributed in the Pacific Ocean from San Diego south to Punta Abreojos. But it is uncertain whether its presence and/or distribution in these coastal waters are relatively recent phenomena. Its apparent general rarity in nature and intriguing global distribution (off Baja California and Ghana) are also puzzling, although possibly an artifact of sampling. (The recent discovery of another remarkable colonial diatom, *Thalassiosira partheneia*, in the upwelling waters off Cape Blanc, Africa may also illustrate this latter problem (Schrader



## DISCUSSION

1972.) It is also possible that differences in habitus account for this enigma. Loeblich et al. (1968) report that solitary cells present in cultures were unable to form colonies, and under certain conditions colonies reproduced themselves as "clusters of cells" or "a solitary pattern of growth" occurred. If the occurrence of variations in habitus correctly explains these biogeographical issues, then the factors triggering colony formation become of interest. Upwelling does not appear to be detrimental in this regard, at least during its initial stages in the survey area.

From its size, thickness, and concave-convex shape, it might a priori be presumed that *Planktoniella muriformis* is particularly well adapted for flotation and has a near-surface niche. However, the equal distribution in colony abundance in the upper 40 m is noteworthy, and contrasts to *Planktoniella sol*'s concentration in the upper 20 m (Figure 2; Table 4).

### *Coscinodiscus (Brenneckella) eccentricus*

In the Gulf of Panama a unique centric diatom was found identified as *Brenneckella* sp. (Smayda 1966). It was characterized by an "outer, gelatinous" ring surrounding the girdle region in or on which coccolithophorids and other particulate matter were embedded. This organism was also commonplace in the present material (Tables 1, 4), and grew actively in one experiment when 2.9 divisions/day were measured (Smayda in press b). Gaarder and Hasle (1961) have reviewed its taxonomic history, the limited information on its distribution, and the potential relationships between the attached organisms and the host diatom. Based on electron microscopy, they concluded that the two species of *Brenneckella* described earlier are conspecific with *Coscinodiscus eccentricus*, a synonymy which is followed here. Nonetheless, it is listed separately as *Coscinodiscus (Brenneckella) eccentricus* in Tables 2 and 4 where mean values for the *Coscinodiscus* spp. are given.

Gaarder and Hasle suggest that the attachment of coccolithophorid cells to this diatom is a mere agglutination without any symbiotic significance. While this may be so, the relationship still remains intriguing. One may ask why other *Coscinodiscus* species, or centric diatoms, including *Planktoniella sol* characterized by an outer membrane, seemingly are invariably devoid of such epibionts.

Allen (1924, 1934, 1938) and Cupp (1930, 1934; Cupp and Allen 1938) carried out a long-term survey (approximately 1921 to 1937) of the net phytoplankton in the coastal, surface waters of southern and Baja California. These data are valuable principally in their suggestion that the net diatom community in these waters from San Diego to the Gulf of Panama is similar, inclusive of the Gulf of California (Cupp and Allen 1938; Gilbert and Allen 1943). Subsequent quantitative observations in the Gulf of Panama (Smayda 1963, 1966), net collections in the Gulf of California (Round 1967), and the present survey generally support this.

Diatoms dominated the net community (Table 4) in response to upwelling, then in its early stages. A red-tide outbreak occurred during mid-April in the survey area following a temporary subsidence of upwelling (Walsh pers. commun.). During the MESCAL I survey of 1972 in this same region the dinoflagellate *Gonyaulax polyedra* was dominant in March (Walsh et al. 1974). Its abundance then also probably reflects the occurrence of limited, if any, upwelling. Thus, annual variations in time of inception of upwelling in these waters, as well as variations within a given upwelling cycle, are reflected in the relative importance of dinoflagellates vis-à-vis that of diatoms. An abundance of diatoms will be an indication of nutrient enrichment, as is generally observed in upwelled waters.

The species composition of the diatom community is of considerable interest, given the observations of Longhurst et al. (1967). They reported that *Coscinodiscus* species, especially *C. eccentricus*, were important dominants of the upwelling communities in June and August 1964 near Magdalena Bay, lying south of the present survey area. Blooms of this genus are of exceptional interest. *Coscinodiscus*, a priori, is not generally expected to occur in great abundance pelagically in unmodified coastal and oceanic water masses. This is generally confirmed by worldwide observations, as reported in the extensive literature on phytoplankton surveys. The periodic, enormous spring blooms of *Coscinodiscus concinnus* in the North Sea are noteworthy and puzzling (Grøntved 1952).

This interest in local species composition is sustained, given the remarkable occurrence and abundance of the red crab, *Pleuroncodes planipes*,

(Longhurst 1968) in these waters. Although it is omnivorous, while herbivorous it grazes on phytoplankton cells  $>25 \mu\text{m}$  (Longhurst et al. 1967), i.e., the size class of *Coscinodiscus*. Indeed, these authors report active grazing on this genus under experimental conditions, and confirmed during the present study (unpubl.). Therefore, is an abundant *Coscinodiscus* community significant causally to *Pleuroncodes*, whose occurrence is a major biotic characteristic of the Baja California upwelling system? Some calculations will be made to evaluate this relationship, and to examine the other questions posed in the Introduction.

The maximum observed abundance of all *Coscinodiscus* (*Brenneckella*) spp. was 2,243 cells/liter; the mean abundance for all stations in the upper 50 m was 458 cells/liter (Table 4). This meager abundance contrasts with a mean of  $4.3 \times 10^6$  cells/liter reported for *Coscinodiscus eccentricus* by Longhurst et al. (1967). In their study, this concentration represented only 8% of the total community, which was dominated by several *Nitzschia* species. *Coscinodiscus* cells of  $<20 \mu\text{m}$  diameter were also not present in bloom concentrations in the present material. Therefore, unlike in Magdalena Bay, this genus was not important numerically, at least during the initial stages of upwelling in the survey area.

It remains obscure whether a regional patchiness characterizes the abundance of *Coscinodiscus* during upwelling along the coast of Baja California, as for *Coscinodiscus asteromphalus* in the Gulf of California (Round 1967). Allen and Cupp referred repeatedly to such patchiness in other species in these waters. It is also possible that the *Coscinodiscus* bloom reported by Longhurst et al. represents a later state in a species succession. Finally, it might have represented an episodic bloom in response to local, unique factors, rather than reflect a general regional or successional phenomenon. Nonetheless, the reported summer abundance of *Coscinodiscus eccentricus* during upwelling in 1964 remains intriguing. The dynamics of *Coscinodiscus* populations in these waters warrant further study.

The dominant (non-setose) species numerically in the  $>20\text{-}\mu\text{m}$  fraction was *Lauderia annulata*, although blooms of *Schroederella delicatula* and *Thalassiosira rotula* characterized individual stations (Table 2). The total *Coscinodiscus* (*Brenneckella*) spp. represented only about 10% of the mean population numerically, but this represented 33% of the mean carbon; corresponding

values for *Lauderia annulata* are 47% and 28%, respectively. Thus, although *Coscinodiscus* was not as abundant as in the Longhurst et al. survey it dominated the  $>20\text{-}\mu\text{m}$  biomass fraction during MESCAL II.

The percent of the total phytoplankton community represented by the  $>20\text{-}\mu\text{m}$  fraction can be established indirectly from chlorophyll determinations made at 10 of the stations for which quantitative  $>20\text{-}\mu\text{m}$  phytoplankton counts were also made. The mean concentration (based on 5 depths) in the upper 20 m was  $3.46 \mu\text{g Chl } a/\text{liter}$ . This depth is near the compensation depth; chlorophyll determinations were not made at depths greater than this 1% level. The significant decrease in mean phytoplankton abundance between 20 and 30 m was pointed out previously (Table 4). The mean carbon content of the non-setose fraction  $>20 \mu\text{m}$  in the upper 20 m is  $16.4 \mu\text{g}/\text{liter}$ .

Longhurst et al. (1967) give a mean carbon/chlorophyll *a* ratio of 258:1 for their material. This is exceptionally high, and contrasts with a mean ( $n = 17$ ) of 110:1 characterizing the community dominated by *Gonyaulax polyedra* during the 1972 MESCAL I survey (Walsh et al. 1974). A mean ratio of 40:1 characterized diatom-dominated communities found throughout the euphotic zone in the Peru Current (Lorenzen 1968). Applying this conversion factor yields a mean carbon content of  $138 \mu\text{g C}/\text{liter}$  in the upper 20 m in the present survey. If a similar carbon/chlorophyll ratio characterizes the  $>20\text{-}\mu\text{m}$  fraction (it may differ with cell size), then this size group (exclusive of setose species) contributes at least 12% of the viable phytoplankton carbon in the euphotic zone. *Lauderia annulata* and the *Coscinodiscus* (*Brenneckella*) species each contribute 3.5%. The non-setose component of this size grouping would appear to represent only a modest portion of the phytoplankton biomass in the euphotic zone. However, significant diel variations in this component occur, which indicate a high turnover rate. The fluxes and kinetics of this response are considered elsewhere (Smayda in press b).

Longhurst et al. (1967) estimated that the grazing rate of *Pleuroncodes* on phytoplankton was 540 liters/day per animal. Its mean abundance during MESCAL II was 1 animal/ $\text{m}^3$  (Whitledge, pers. commun.), threefold greater than that during Longhurst and coworkers' study. The total phytoplankton population in the upper 20 m was

276 mg/m<sup>3</sup>, assuming a dry weight : carbon ratio of 2. Smith et al. (footnote 2) report a mean caloric content of 1,699 cal for *Pleuroncodes* during MESCAL II, and cite a caloric value of 3,814 cal/g dry wt for diatoms. From these data, a daily caloric ingestion of phytoplankton of 568 cal/m<sup>3</sup> within the euphotic zone is calculated, which represents 33% of the total caloric content of the crab. *Coscinodiscus* would contribute only 1.2% of this daily caloric ingestion and the non-setose component of the >20- $\mu$ m size fraction 4%, based on their contributions of 3.5 and 12%, respectively, to the phytoplankton standing stock in the upper 20 m. Even at the maximum growth rates of 3 divisions/day for *Coscinodiscus* observed during the survey (Smayda in press b) this genus would provide a negligible fraction of the daily caloric intake estimated for *Pleuroncodes*. This suggests that the *Coscinodiscus* population could not then support the *Pleuroncodes* population; other food sources were necessary.

Smith et al. (footnote 2) demonstrated that the respiration rate (as oxycaloric equivalents) of *Pleuroncodes* is only 3% of the ingestion rates calculated using the grazing rate proposed by Longhurst et al. (1967). Other calculations made by them support their notion that the grazing rate of 540 liters/day is too high, and partly accounts for the discrepancy between rates. Other factors which might contribute to the apparent feeding inefficiency of *Pleuroncodes* would be high energy losses as fecal material. Longhurst et al. observed the copious production of fecal material packed with *Coscinodiscus*. While the magnitude of this waste production during MESCAL II can not yet be evaluated, the relative rates of deposition of frustules and organic matter to the sediments when contained in fecal pellets and as free cells can be put into perspective.

The sinking rates ( $n = 24$ ) of fecal pellets produced by freshly collected crabs, and determined on board ship (unpubl.), ranged from 61 to 144 m/h. These rates exceed by 1 to 4 orders of magnitude those calculated (Smayda 1970) for the different sizes of *Coscinodiscus* encountered, and that (5.2 m/hr) estimated (Smayda 1969) for the mean zooplankton fecal pellet size (320,000  $\mu$ m<sup>3</sup>) collected routinely in the >20- $\mu$ m fraction. Thus, while *Coscinodiscus* apparently contributed only a negligible fraction of the daily caloric ingestion of *Pleuroncodes*, the latter's ingestion and avoidance in fecal material of this genus and other heavily silicified diatoms >20  $\mu$ m represent a

means of exceptionally rapid deposition onto the sea floor.

The mean carbon content of 138  $\mu$ g/liter during the initial stages of upwelling compares with a mean standing stock of 566  $\mu$ g C/liter at 20 stations reported for this region during the *Gonyaulax polyedra* bloom in March 1972 (from Table 1 in Walsh et al. 1974). The mean carbon content ranged from 23 to 100  $\mu$ g/liter at three stations sampled over a 5-mo period off La Jolla, Calif. (Eppley et al. 1970). The mean concentration during upwelling south of the survey region during June 1964 ranged from 48  $\mu$ g C/liter (from C/Chl *a* of 40:1) to 308  $\mu$ g C/liter using data given by Longhurst et al. (1967). However, the data are too limited as yet for any meaningful comparison of regional or seasonal variations in apparent productivity in these coastal waters. They also indicated that the net plankton was usually more abundant in April (upwelling) between Punta Abreojos and Punta Eugenia, i.e., in the present survey area (Figure 1). However, quantitative data are needed to confirm this.

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APPENDIX TABLE 1.—List of phytoplankton taxa identified to species found in net tows and in >20- $\mu$ m size fraction.

## BACILLARIOPHYCEAE

*Actinocyclus octonarius* Ehrenberg  
*Actinocyclus undulatus* (Bailey) Ralfs  
*Asterionella japonica* Castracane  
*Asterolampra marylandica* Ehrenberg  
*Asteromphalus heptactis* (Br bisson) Ralfs  
*Bacteriastrium hyalinum* Lauder  
*Biddulphia mobilensis* Bailey  
*Biddulphia cf. sinensis* Greville  
*Cerataulina pelagica* (Cleve) Hendey  
*Chaetoceros affinis* Lauder  
*Ch. cf. costatus* Pavillard  
*Ch. curvisetus* Cleve  
*Ch. debilis* Cleve  
*Ch. decipiens* Cleve  
*Ch. didymus* Ehrenberg  
*Ch. peruvianus* Brightwell  
*Ch. socialis* Lauder  
*Ch. subsecundus* (Grunow) Hustedt  
*Corethron pelagicum* Brun  
*Coscinodiscus cf. asteromphalus* Ehrenberg  
*C. centralis* var. *pacifica* Gran et Angst  
*C. concinnus* W. Smith  
*C. curvatulus* Grunow  
*C. eccentricus* Ehrenberg  
*C. granii* Gough  
*C. perforatus* var. *pavillardi* (Forti) Hustedt  
*C. radiatus* Ehrenberg  
*Coscinodiscus (Brenneckella) eccentricus*  
(Lohmann) Gaarder et Hasle  
*Ditylum brightwelli* (West) Grunow  
cf. *Ethmodiscus rex* (Rattray) Hendey  
*Eucampia cornuta* (Cleve) Grunow  
*Guinardia flaccida* (Castracane) Peragallo  
*Hemidiscus cuneiformis* Wallich  
*Lauderia annulata* Cleve  
*Leptocylindrus danicus* Cleve

## BACILLARIOPHYCEAE—Cont.

*Lithodesmium undulatum* Ehrenberg  
*Paralia sulcata* (Ehrenberg) Cleve  
*Planktoniella muriformis* (Loeblich III, Wight et  
Darley) Round  
*Planktoniella sol* (Wallich) Sch tt  
*Rhizosolenia alata* Brightwell  
*R. bergoni* H. Peragallo  
*R. calcar avis* M. Schultze  
*R. delicatula* Cleve  
*R. imbricata* var. *shrubsolei* (Cleve) Schr der  
*R. robustum* Norman  
*R. stolterfothii* H. Peragallo  
*Roperia tessellata* (Roper) Grunow  
*Shroederella delicatula* (Peragallo) Pavillard  
*Skeletonema costatum* (Greville) Cleve  
*Stephanopyxis turris* (Greville) Ralfs  
*Thalassionema nitzschioides* (Grunow) Hustedt  
*Thalassiosira rotula* Meunier  
*Thalassiothrix frauenfeldii* Grunow  
*T. longissima* Cleve et Grunow  
*T. mediterranea* var. *pacifica* Cupp

DINOPHYCEAE

*Ceratium furca* (Ehrenberg) Claparede et Lachmann  
*Ceratium lusus* (Ehrenberg) Dujardin  
*Dinophysis miles* Cleve  
*Gonyaulax cf. polyedra* Stein  
*Noctiluca scintillans* (Macartney) Kofoid et Swezy  
*Pyrocystis cf. lunula* Sch tt  
*Pyrophacus horologicum* Stein

CHRYSOPHYCEAE

*Distephanus speculum* (Ehrenberg) Haeckel

HAPTOPHYCEAE

*Phaeocystis poucheti* (Hariot) Lagerheim

PRASINOPHYCEAE

cf. *Halosphaera viridis* Schmitz