PLANKTON POPULATIONS AND UPWELLING OFF THE COAST OF PERU, JUNE 1969

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ABSTRACT

Plankton populations associated with upwelling areas and the changes with time of upwelled patches were studied off the coast of Peru near Supe in June 1969. Two patches, detected by their higher nutrient levels, greater chlorophyll pigment concentrations, and lower surface temperatures than surrounding waters, were each monitored for several days, during which time they gradually lost their identity. Actively photosynthesizing phytoplankton crops (doubling time ca. 1.4 days) of predominantly small monads and other flagellates were found in both patches. The zooplankton populations in the patch areas were estimated to be consuming no more than about 25% of the daily phytoplankton production. Direct determination of physical mechanisms affecting the patches showed a relatively high level of vertical instability in Patch 1 which would allow for turbulent mixing and the carrying of phytoplankters below the compensation depth. A horizontal divergence was associated with Patch 2 and would also have the effect of dissipating the patch. Approximate estimates of upwelling suggested vertical velocities of about 2×10^{-2} cm/sec in both patches.

Interest in biological production in Peruvian coastal waters has been high in recent years. The prosperous fish-meal industry developed around the anchovy, *Engraulis ringens*, has stimulated numerous investigations by Peruvian scientists of the food chain leading to this commercially valuable fish (see, for example: Guillén and Izaguirre de Rondan, 1968; Zuta and Guillén, 1970; and various "Informes" of the Instituto del Mar del Perú). In addition, massive upwelling and its associated biological activities along the Peru coast has been of concern to investigators from other countries and has resulted in several international cruises which have added to our knowledge of the pelagic ecology of the area.

The distribution of upwelled water at the surface is often in somewhat discrete "patches," perhaps the result of dynamic physical forces such as currents and/or eddies acting in the area. In March-April 1966, Strickland, Eppley, and Rojas de Mendiola (1969) observed low standing crops of phytoplankton (chlorophyll a, <2 μg/liter) in high-nutrient patches (e.g., surface NO_3-N, 20 μg at./liter or higher). In other similarly rich water phytoplankton abundance was high (chlorophyll a, 15 μg/liter). Barber et al. (1971) reported the surface water in an area of recent upwelling showed a lack of the "organic conditioning compounds" which may be needed for phytoplankton growth. However, in the nutrient-rich but low-chlorophyll patches examined by Strickland et al. (1969) relatively high growth rates (ca. 0.8 doubling/day averaged over the euphotic zone) were found for the phytoplankton. Similar rates (ca. 0.6 doubling/day) can be calculated from the ^{15}N (nitrate and ammonium) assimilation studies done in this area by Dugdale and co-workers (University of Washington Department of Oceanography, 1970).

A high grazing pressure exerted by the pelagic animal populations was considered by Strickland et al. (1969) as a possible underlying cause for the low standing crops in the nutrient-rich patches with active phytoplankton populations. Ryther et al. (1970) also proposed grazing as an important mechanism for the reduction of the

phytoplankton stock in a patch of upwelled water they observed continuously for 5 days in April 1966, south of Callao. Both zooplankton and the anchovy must be considered as potentially important direct grazers of the phytoplankton. Rojas de Mendiola et al. (1969) found the stomach contents of anchovies collected in February-March of 1968 in the area of this study (i.e., off Supe) to be predominantly phytoplankton whereas those from the south (Tambo de Mora) were mainly zooplankton remains. At that time the phytoplankton crop off Supe was principally diatoms while diatoms were of much less importance in the phytoplankton populations off Tambo de Mora. Rojas de Mendiola et al. (1969) also reported they had some evidence that adult anchovies may prefer phytoplankton while animal plankters are the choice of juveniles (65-70 mm anchoveta).

In May-June of 1969 the Food Chain Research Group of the Institute of Marine Resources, University of California, in cooperation with the Instituto del Mar del Perú studied various aspects of the physical processes and biological populations associated with upwelling along the Peruvian coast during austral fall. This work was carried out as Leg 7 of the PIQUERO Cruise of the RV *Thomas Washington*. A complete description of these studies is recorded in two "unpublished" data records on file with the University of California, Institute of Marine Resources (1970,[3] 1971[4]). From these studies the coastal current system along Peru was also described (Stevenson, 1971). During PIQUERO Leg 8 the work was extended north to the Equator where the zonal circulation was studied (Stevenson and Taft, 1971). Anchovy studies (abundance, schooling, stomach contents, etc.) were carried out by Villanueva, Jordán, and

Burd (1969) on board the Peruvian research vessel *SNP-1* during the first week of PIQUERO 7 in an area south of Callao.

Since neither Strickland et al. (1969) nor Ryther et al. (1970) provided quantitative evidence to support the hypothesis that grazing may be an important means of regulating the phytoplankton crop in these waters, one purpose of our present studies was to determine the abundance of the zooplankton—both microzooplankters (see Beers and Stewart, 1970) and larger forms—and to relate this to observations on phytoplankton abundance, growth rates, and taxonomic composition. In addition, we were interested in the "disappearance" of the patches with time. Evidence is examined for a suggestion that patches may dissipate through physical mechanisms such as horizontal and vertical mixing. The detailed study of physical variables has provided insight into factors affecting biological production in the waters off Peru which would not have been appreciated by the biologist working independently.

MATERIALS AND METHODS

Studies were conducted between 13 and 22 June 1969, in the approximate area bounded by lat 10° and 12° S and long 78° and 79° W off Supe. Extensive "surface" mapping operations at various times throughout this period with underway continuous analysis of inorganic nutrients, phytoplankton pigment fluorescence, and temperature allowed for the detection and surveillance of two patches of upwelled water in this area. Water for the mapping as well as for other "surface" sampling described below was taken with a pump fitted into the ship's hull about 3 m below the sea surface. This unit delivered 10 to 11 liters/min through plastic piping. A series of 57 discrete stations were made during the period of observing the patches for sampling the microzooplankton and macrozooplankton populations, obtaining water for primary production measurements and phytoplankton enumeration, and for determining temperature and salinity profiles. These were taken from various depths in and below the euphotic zone within and outside of the patches.

Our purpose was to return to the same patch of water, sampling it on successive days as it "evolved." In general, the temperature and fluorescence of the surface water were used to determine the desired location of sampling after the navigational capabilities of the ship had been used to locate the general area.

Physical measurements, i.e., temperature and salinity, were either by continuous vertical profiles generally from the surface to the bottom, or 500 m, using a STD (Salinity-Temperature-Depth Measuring System, The Bissett-Berman Corp. Model 940)* or at the surface (3 m) using a thermo-salinograph (The Bissett-Berman Corp. Model 6600T). Both systems were electronically interfaced to a shipboard IBM 1800 computer.

Vertical profiles of current velocity were made at Stations 99 and 101 using a Hydro Products, Model 502, meter having a precision Savonius rotor to sense current speed and a direction vane coupled with a magnetic compass. The instrument, lowered on the hydrowire, measured the currents for 15 min at each of a series of depths through the upper 200 or 500 m. At each station the current direction and speed were referenced to the deepest observation. The lower practical current threshold is considered to be about 2.5 cm/sec.

Phytoplankton nutrient concentrations (i.e., PO_4, $NO_3 + NO_2$, and SiO_3) in water from the surface pump or taken by water bottles from various depths were determined using an Autoanalyzer and methods described in Strickland and Parsons (1968). A Turner fluorometer with a continuous flow-through cell (Lorenzen, 1966) was used for mapping surface phytoplankton pigment distribution. Vertical profiles of extracted chlorophyll and phaeophytin were done following the procedure of Holm-Hansen et al. (1965).

Levels of primary production through the euphotic zone were measured by the radiocarbonate uptake method at seven stations (see Table 3). Stations 59, 68, 77, and 87 were associated with Patch 1 while Stations 88, 93, and

99 were in the second mass of upwelled water (Patch 2) followed. Water was collected by Van Dorn bottles from depths corresponding to 80, 30, 20, 15, 5, and 1.5% of the surface irradiance at each location. These depths were estimated from Secchi disc depths. Incubation of samples in deck incubators cooled by surface seawater was for 6 (noon to sunset) or 24 hr.

At each site where primary production was measured, water samples were taken for analysis by the inverted microscope method of Utermöhl (1958) of the phytoplankton species composition, numerical abundance, and estimates of biomass (volume and organic carbon). Generally aliquots from the several depths sampled at each site were integrated to provide a composite sample over the euphotic zone, preserved with 5% Formalin (pH 8.2 ± 0.2), and studied as described in University of California, Institute of Marine Resources (1971, see footnote 4) and Reid, Fuglister, and Jordan (1970).

Unconcentrated samples for study of the ciliate populations were taken along with the phytoplankton as above. In addition, the ciliates of the euphotic zone were studied at eight additional sites where the larger zooplankton abundance was measured and they were also determined in integrated samples from depth intervals, generally 20 to 30 m sampled at 5-m intervals, below the photosynthetic compensation point (1.5% surface irradiance) at 10 stations.

Samples of the microzooplankton populations concentrated on 35-μ mesh cloth after excluding larger material on 202-μ mesh filters were collected from the surface (3 m) using the intake in the ship's hull at most stations where biological sampling was carried out and during certain of the mapping operations. These samples provided material for study of all microzooplankton groups other than the ciliates, many of which are too small to be retained by this size mesh. An unconcentrated pump sample taken for total ciliates is not considered here as there were indications the pump was damaging the non-loricate forms. Methods of analysis of the total microzooplankton and ciliate populations including conversion from a volume estimate to organic carbon are given in Beers and Stewart

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* The use of trade names is merely to facilitate descriptions; no endorsement is implied.

(1970) and University of California, Institute of Marine Resources (1971, see footnote 4).

Larger zooplankton abundance was studied at 21 sites including the four stations associated with Patch 1 but only at one location, Station 93, where productivity was measured in Patch 2. Samples were taken by vertical tows from approximately 100 m to the surface using paired 0.5 m nets having 103 μ mesh. The volume of water filtered was determined by a flowmeter mounted in the mouth of one of the nets. At some stations wire angles of 10° to 25° developed during the sampling. The numerical abundance and biomass of all developmental stages of the copepod *Calanus chilensis* Brodsky were determined. An estimate of the biomass of the total Formalin-preserved net material divided into fractions of >505 μ and <505 μ was obtained as dry weight and converted to organic carbon by multiplying by 0.40. For the discussion the total material is considered to be zooplankton although there was undoubtedly a small fraction of phytoplankton and detritus associated with the net sample.

RESULTS

UPWELLING PATCHES

Periodic changes in position and configuration of the two patches as determined from surface mapping of phytoplankton pigments is shown in Figures 1 and 2. Patch 1, when detected on 13 June, appeared relatively compact and had a maximum surface pigment (Chl a and "phaeopigments") concentration of 6 to 8 μg/liter. Surrounding waters showed 1 to 2 μg/liter. The patch was bounded on the south and west by a well-defined front. Surface temperature and salinity within the patch were 19.5° C and 35.15‰, respectively, while values reached 21.0° C and 35.25‰ on moving out of the patch. The levels of temperature and salinity at the surface of the patch were similar to those found at depths of 35 to 45 m and 50 m, respectively. Surface nitrate and silicate concentrations of 16 and 13 μM, respectively, were found in the patch, dropping abruptly to about 10 and 7 μM on crossing the thermal front bordering the patch. A decline of surface pigment and nutrient levels was observed over the period 13 to 21 June. By June 17 it was apparent that this patch was disappearing and a more extensive mapping operation revealed a clearly defined patch, Patch 2, about 16 miles (25 km) south of Patch 1 (Figure 2). Patch 2 surface parameters included: maximum pigment concentration of 6 μg/liter; temperature, 19.5° C; salinity, 35.15‰; nitrate, 10 μM; and silicate, 13 μM. A distinct front bordered the patch on the west. Somewhat colder water (19.0° C) but with a lower pigment concentration ($\sim$3 μg/liter) was on the eastern side. A transect from east to west across Patch 2 passed through water with temperatures from 19° to 21.5° C. Variations of surface chlorophyll with temperature for Patch 2 are shown diagrammatically in Figure 3. This patch was no longer recognizable by 21 June. Mapping operations late in the cruise period revealed the presence of additional patches in the area but time did not allow for their study.

WATER MOVEMENT IN AND AROUND PATCHES

Calculations of dynamic topography suggested that Patch 1 occurred in a cyclonic eddy of the Peru Coastal Current (Figure 4). Based on the displacement of the chlorophyll pigments at the surface, the patch was being shifted to the west at about 23 cm/sec. Beneath the surface the dynamic computations suggested a poleward flow of about 15 cm/sec at 50 m (Table 1, Stations 54, 59, and 78). Cool surface water of relatively low salinity (35.15‰) was found on the nearshore side of the meander.

The limited data available for calculation of the dynamic topography around the second patch (Patch 2) suggested a northward flow of surface water along the western boundary of the front (Figure 4). Direct measurements with a current meter at Stations 99 and 101 in this patch showed a flow of 18 cm/sec to the ENE at 10 m, a stronger southerly flow of 30 cm/sec at 50 m and little current, i.e., less than 5 cm/sec, below 100 m (Table 2). Beyond the temperature-salinity front on the west of the patch, the velocity of the water was about 5 cm/sec toward the ENE

FIGURE 1.—The time sequence of changes in the config-
uration of Patch 1 as shown by the mapping of the total
chlorophyll *a* and phaeopigments concentration (μg)
liter) in the surface (i.e., 3 m) waters. In Figures 1
and 2, all chlorophyll pigment values are less than
10 μg/liter and are shown with one figure to the right
of the decimal point. The decimal point is often difficult
to see.

FIGURE 3.—Variation in total chlorophyll a and phaeo-pigments concentration with temperature noted in an east to west transect across Patch 2.
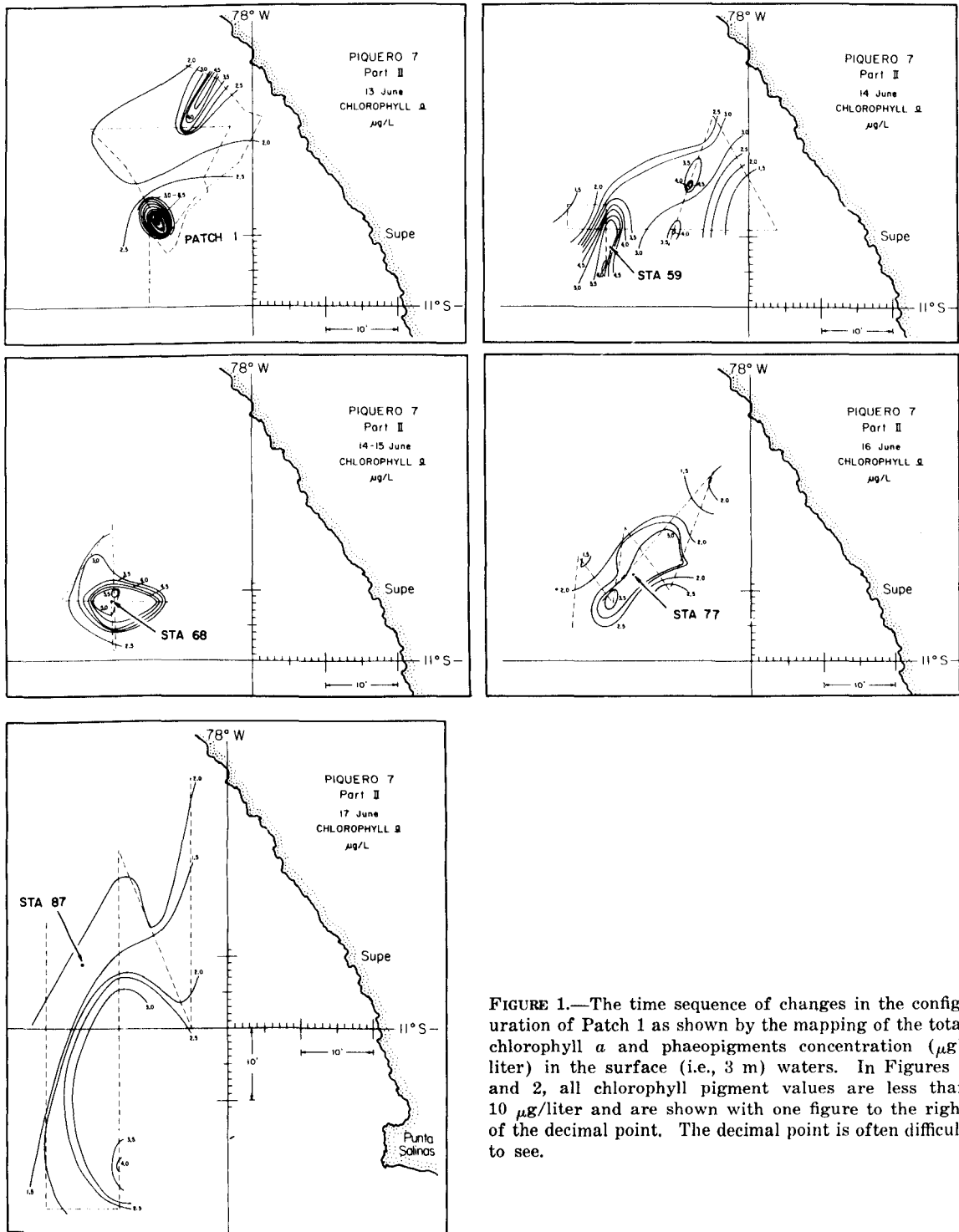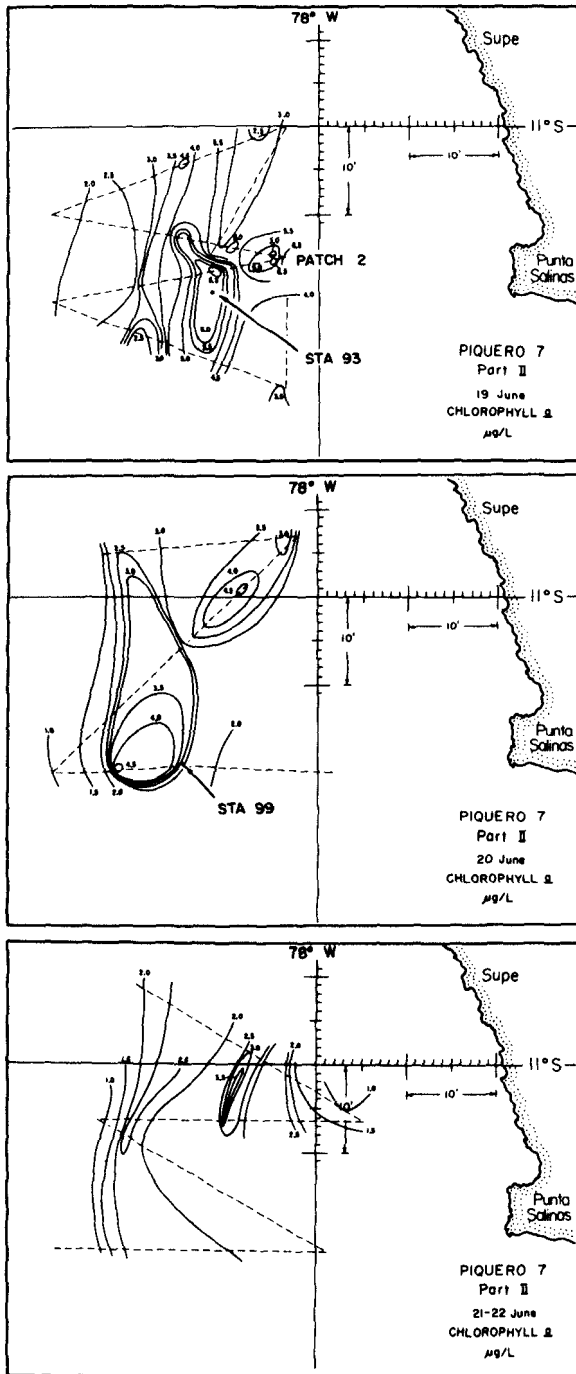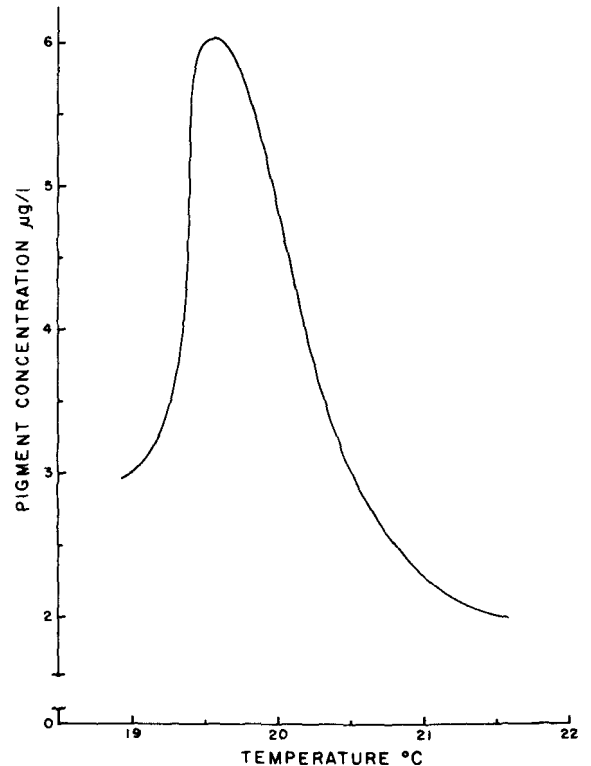

FIGURE 2.—The time sequence of changes in the config-uration of Patch 2 as shown by the mapping of the total chlorophyll a and phaeopigments concentration (μg/liter) in the surface (i.e., 3 m) waters.

at 10 m (Figure 4). At greater depths at this location flow was generally eastward at velocities up to 4 cm/sec. A small northerly component was seen at 50 m. A horizontal divergence was apparent between the two stations from the zonal components of the velocity measured at 10 m.

In addition to indicating the horizontal direc-tion of water flow, measurements from current meters can be used to estimate vertical shear (Table 2). Shear on the west side of Patch 2 was generally low because of fairly uniform flow toward the east. Maximum vertical shear in-side the patch and to the east of the front was up to seven times greater than the maximum to the west of the patch. The large negative meridional (north-south) shear in the patch sig-nified a change from weak northerly flow to strong southerly flow at 49 m.
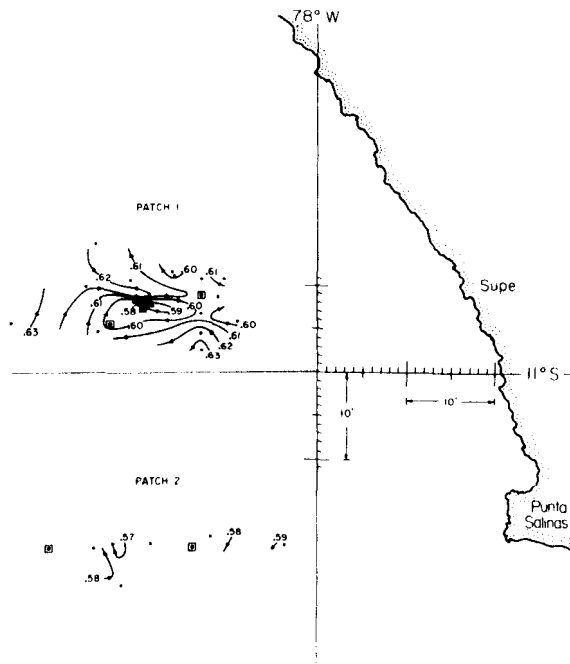
FIGURE 4.—Dynamic topography (in dynamic meters) of the sea surface referenced to the 300 db surface. Patch 1 was observed 13-21 June 1969; Patch 2, 18-21 June 1969. Data from a detailed analysis of stations designated by a square (▣) are given in Tables 1 and 2.

In order to obtain information on the turbulent activity of the water in the vicinity of each patch, the Väsäilä frequency, N, an indicator of static instability, and the Richardson number, Ri (Phillips, 1966), an indicator of dynamic instability, were calculated at various depths for the three stations in Patch 1 and the two current meter stations associated with Patch 2 (Table 1 and 2). The Väsäilä frequency, based on the vertical density gradient, is often used as an indication of the vertical stability in a water column assuming static conditions, i.e., no vertical shear. Small positive values for N imply the possibility of weak vertical mixing and negative values indicate the probable overturn of the water layer being studied. For the purpose of comparison it was assumed a Väsäilä number less than 1×10^{-3} sec^{-1} signified the start of static instability. Since the effects of a possible vertical shear are not considered, this measure will give an inaccurate estimate of the

likelihood of significant turbulence in the presence of nonuniform horizontal currents. The Richardson number, Ri, is generally used to estimate whether turbulent mixing is an important factor for consideration. A Richardson number less than 0.25 is considered indicative of dynamic instability and the development of turbulent mixing. Owing to a lack of current meter data for Patch 1 it was necessary to estimate the shear used for determination of Ri from geostrophic currents.

In Patch 1 conditions of static instability are specifically indicated at a depth of 30 to 50 m for Station 54 (Table 1). The water columns at the other two stations associated with this patch were weakly stable. Dynamic instability was also indicated between 30 and 50 m at Station 54. In addition, the upper 10 m of Station 59 showed dynamic instability. Although static stability was greater at Station 78 than at the other two stations, the water column was dynamically unstable from the surface to 50 m because of the larger vertical shear present.

Conditions in Patch 2 (Table 2) contrasted with those in Patch 1. Vertical shear was generally much less than in Patch 1. This, however, may be partly attributable to differences arising between direct measurements of currents (Patch 2) and estimates of currents based on the horizontal distribution of mass (Patch 1). Compared with Patch 1, the water column in Patch 2 was more stable. The Richardson numbers from the west side of the front on Patch 2 are all very high and indicate conditions that are not favorable for vertical turbulent mixing. In Patch 2 the meridional component of Ri is smaller and suggests that, while the water column is not dynamically unstable in the upper 50 m, turbulent mixing might not subside as quickly as if the water column was highly stratified.

Direct current measurements to the east and west of the front (Patch 2) were made to 200 m and 500 m, respectively. If water motion within the patch at 200 m, however, was similar to the measurements at that depth on the west side of the front, the change in current velocity would be to increase the velocity in the eastward direction by about 4 cm/sec and thereby increase

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TABLE 1.—Vertical shear and stability in Patch 1.

Stations	Depth (m)	Väsäilä frequency, [1] N (10^{-3} sec^{-1})	Velocity, [2] V (cm sec^{-1})	Vertical shear, $\dfrac{\partial v}{\partial z}$ (10^{-3} sec^{-1})	Richardson number,[3] Ri
Station 54	0		−20		
10°51.0′ S		2.5		2.0	1.53
78°13.0′ W	10		−22		
13 June 1969		4.0		3.0	1.74
	20		−25		
		2.5		−1.0	6.10
	30		−24		
		[4]__		−3.5	−1.69
	50		−17		
		12.0		−3.6	10.95
	75		− 8		
		8.3		3.6	5.34
	100		−17		
Station 59	0		18		
10°52.5′ S		2.5		7.0	0.124
78°19.6′ W	10		12		
14 June 1969		5.0		2.0	6.30
	20		10		
		14.0		3.0	21.9
	30		7		
		14.0		6.0	5.08
	50		− 6		
		8.1		8.4	0.921
	75		−28		
		8.3		−1.6	27.0
	100		−24		
Station 78	0		134		
10°54.2′ S		11.0		31.0	0.116
78°23.1′ W	10		103		
16 June 1969		10.0		29.0	0.120
	20		74		
		9.1		37.0	0.060
	30		37		
		13.0		30.0	0.205
	50		−23		
		9.8		7.2	1.85
	75		−40		
		8.3		−5.2	2.56
	100		−27		

[1] The Väsäilä frequency, $N = \left(\dfrac{g\partial\rho}{\rho\partial z} - \dfrac{g^2}{c^2}\right)^{1/2}$ (Phillips 1966) where g = acceleration of gravity, ρ = density of sea water, c = velocity of sound, and z = distance below sea surface.

[2] Velocities in this column represent component velocities in the NW-SE direction and are based on geostrophic computations between the individual stations and the adjacent station to the west.

[3] The Richardson number, $Ri = N^2 / \left(\dfrac{\partial v}{\partial z}\right)^2$ (Phillips (1966) where N = Väsäilä frequency and $\dfrac{\partial v}{\partial z}$ = vertical shear using the component of horizontal velocity, V.

[4] The argument of the Väsäilä equation was negative for this layer and signifies static instability.

the difference in zonal (east-west) velocities across the patch. Water motion in the vicinity of the patch suggests a divergent front with greater eastward water motion found on the nearshore side. The lower surface temperatures and salinity values, relative to offshore salinity, are evidence for localized upwelling and such a mechanism could provide the water needed for replacement owing to horizontal divergence near the surface.

The source for the upwelled water in the two patches we studied appears to be a poleward flow associated with a high-salinity core found at 50 m depth (Stevenson, 1971). Some of the transport from this Coastal Undercurrent is lost through upwelling as the water moves down the coastline. The undercurrent has been traced southward to lat 15°30′ S where it was still present at 50 m. The salinity in the core, however, had decreased to about 35.12‰ and the

TABLE 2.—Vertical shear and stability in Patch 2.

Stations	Depth (m)	Väsäilä frequency, N (10^{-3} sec^{-1})	Velocity (cm sec^{-1})		Vertical shear (10^{-3} sec^{-1})		Richardson number[2]	
			^1u	^1v	$\frac{\partial u}{\partial z}$	$\frac{\partial v}{\partial z}$	Ri_u	Ri_v
Station 99	10		17	5				
11°20.0′ S		12.2			—0.266	7.69	2,100	2.5
78°14.8′ W	49		18	—25				
20 June 1969		10.9			3.80	—4.20	8.2	6.7
	99		—1	—4				
		5.2			—0.101	—0.404	2,681	168
	198		^{3}0	^{3}0				
Station 101	10		5	1				
11°20.0′ S		14.3			1.00	—0.250	205	3,280
78°30.0′ W	50		1	2				
20 June 1969		11.8			—0.612	0.408	368	829
	99		4	0				
		5.7			0.200	0.000	822	--
	149		3	0				
		4.6			—0.204	—0.204	514	514
	198		4	1				
		4.2			0.100	0.100	1,950	1,952
	298		3	0				
		4.7			0.150	0.000	995	--
	498		^{3}0	^{3}0				

[1] Component velocities, u and v, are from current meter measurements and are positive to the east and north, respectively.

[2] Ri_u, Ri_v = Richardson numbers using the east and north velocity components, respectively.

[3] The deepest observations are used for reference and are shown with zero velocity.

measured velocity of about 15 cm/sec was about half that seen in this study around lat 11° S. From the PISCO Cruise of the University of Washington, April-May 1969, Smith et al. (1971) were able to estimate upwelling in a narrow coastal region near lat 15° S. They determined the vertical velocity to average 2×10^{-2} cm/sec over the period of the investigation and estimated it to decrease with increased distance from shore so as to become zero at 20 km offshore.

PHYTOPLANKTON DYNAMICS IN THE PATCHES

Photosynthetic carbon assimilation measurements (Table 3) showed that the phytoplankton crop was physiologically active in both patches throughout the periods of observation even though the patches, as defined by their surface characteristics, were gradually becoming more difficult to recognize (see Figure 5). The decline in the abundance of phytoplankters at the

TABLE 3.—Phytoplankton standing crop as carbon, photosynthetic rate, specific growth rate, chlorophyll a and carbon/chlorophyll a ratio for plankton patches off Peru, June 1969. (See Table 4 for positions of stations.)

| Station	Date	Patch	Euphotic zone depth (m)	Phytoplankton standing crop (g C/m²)	Photosynthetic rate (g C/m²/day)	Specific growth rate (μ) (doublings/day)	Chlorophyll a (mg/m²)	Ratio carbon/chl a (g/g)
59	14 June 1969	1	18	2.16	1.19	0.64	50.3	42.8
68	15 June 1969	1	28	1.39	0.83	0.68	45.7	30.4
77	16 June 1969	1	30	1.40	1.09	0.83	39	36
87	18 June 1969	1	42	1.91	1.01	0.61	40.8	46.7
88	18 June 1969	2	20	2.56	1.26	0.58	46.8	55
93	19 June 1969	2	27	[1]1.33	1.79	1.23	60.3	22.0
99	20 June 1969	2	30	2.27	1.03	0.54	52.9	42.9

[1] Value probably low, judged from the high μ or low C/chl a ratio.

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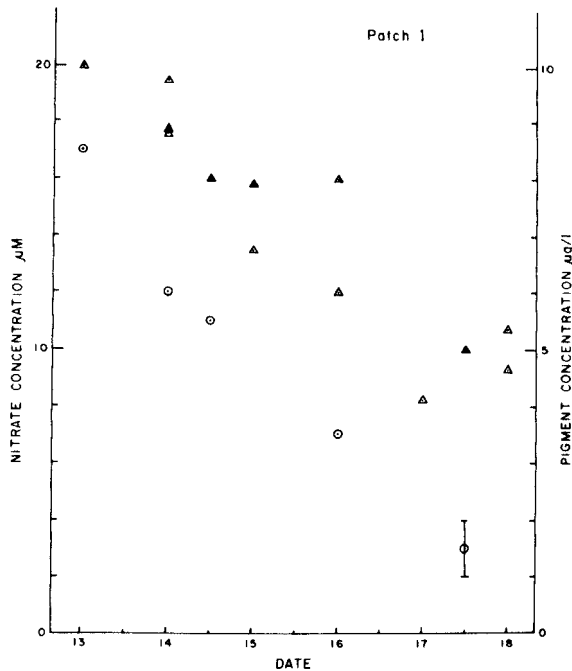
FIGURE 5.—Decline with time in surface nitrate (▲) and chlorophyll pigments concentration (⊙) in Patch 1. Solid triangles (▲) are maximum nitrate values found by automatic analysis (Autoanalyzer) during underway mapping. Open triangles (△) are discrete nitrate samples collected on station. Pigment values are maxima of fluorescence found in the mapping area.

surface was compensated for by a deepening of the euphotic zone such that chlorophyll a, standing crop as carbon, and photosynthesis showed little variation (<twofold) when integrated over the increasing euphotic zone depth. The specific growth rate, μ, of the crop averaged 0.7 doubling/day over the euphotic zone indicating it should double in 1.4 days if grazers could be eliminated. Similar measurements of μ in March-April 1966 off Peru (Strickland et al., 1969) averaged 0.8 doubling/day for four stations.

The ratio of phytoplankton carbon/chlorophyll a (Table 3) averaged 40:1 and was similar to that reported by Lorenzen (1968), using different methods, for a phytoplankton bloom off Peru. The ratio of photosynthetic rate (g C/m²/day) to chlorophyll a (g/m²) averaged 28 day⁻¹,

about one-half that observed by Lorenzen (1968).

As the phytoplankton crop decreased the ratio of phaeopigments to chlorophyll a also declined.

SPECIES COMPOSITION OF THE PHYTOPLANKTON CROPS

Taxa with volumes less than that of 10 μ spheres accounted for an average 73% (range: 46%, Station 68 to 93%, Station 59) of the total plant carbon. The dominant forms in both patches were small (2-4 μ and 5-7 μ) cells, often flagellates, and probably cryptomonads or chrysophytes although positive identification was impossible in the Formalin-preserved material. Diatoms never contributed more than 10 to 12% (average pennates + centrics, 5.2%) of the carbon content of the crop. Of the diatoms two species, Corethron hystrix and Nitzschia delicatissima curva, were the most abundant at all sites. The Corethron was one of the very few large taxa that would be retained by phytoplankton nets (35 μ mesh). The "photosynthetic" ciliate, Mesodinium rubrum (Taylor, Blackbourn, and Blackbourn, 1969), occurred at all stations but was relatively more abundant in Patch 1 where numbers reached 3000/liter at Station 68. Dinoflagellates contributed 5 to 21% of the total phytoplankton carbon. Unidentified naked forms of cell size <15 μ (equivalent sphere) were the most common of the dinoflagellates. Coccolithophorids (e.g., Coccolithus huxleyi and Syracosphaera quadricornum) were quite numerous when the patches were disappearing, totaling up to 11 to 14 μg C/liter or 31% (Station 87, Patch 1) and 15% (Station 99, Patch 2) of the plant carbon.

MICROZOOPLANKTON POPULATIONS

Ciliates dominated the microzooplankton populations of the two patches in terms of both numbers and biomass. No marked differences in the abundance of ciliates were noted between the patches. Their standing stock was greatest early in our sampling of each patch (i.e., Station 59, Patch 1; Station 88, Patch 2) owing to relatively large numbers of nonsheathed oligo-

trichs, and was correlated with the generally highest chlorophyll a and/or phytoplankton organic carbon level observed. The relatively small number of samples obtained, however, did not allow us to determine the variability within the patch at any given time.

Average ciliate abundance over the euphotic zone at the 15 stations studied ranged from 2400 to 18,000/liter (average, 6200/liter) (Table 4). Oligotrichous forms were at least 75% of the average numbers. Small (10-20 μ) oligotrichs without well-developed sheaths, e.g., *Lohmanniella oviformis,* were generally in much greater number than larger sheathed species, e.g., *Strombidium conicum.* Tintinnid ciliates, of which *Acanthostomella obtusa, Craterella urceolata,*

Codonellopsis contracta, and *Epiplocylis brandti* were common, composed an averaged of 7% of the total numbers. Estimated total ciliate organic carbon levels (Table 4) ranged from 0.7 to 4.8 μg/liter (average, 1.9 μg/liter) of which 17% and 78%, at least, were accounted for by the tintinnids and oligotrichs, respectively.

The abundance of ciliates dropped significantly below the euphotic zone. In the approximately 20-m depth interval beneath the compensation point (10 stations observed, Table 4) ciliate organic carbon was an average 16% of that in the upper waters whereas the average chlorophyll level was still 43% of the average concentration within the euphotic zone. Ciliate abundance over the upper 100 m comparable to the water

TABLE 4.—Ciliate standing stock abundance.

Station	Date	Position	Ciliate standing stock numbers, euphotic zone (no./liter)	Ciliate standing stock biomass, euphotic zone (μg C/liter)	Ciliate standing stock biomass, below (20-m depth interval) euphotic zone (μg C/liter)
[1]59	14 June 1969	10°52.5' S 78°19.6' W	10,000	3.3	--
[1]77	16 June 1969	10°48.1' S 78°16.2' W	5,300	2.0	0.27
[1]87	18 June 1969	10°51.2' S 78°20.4' W	3,800	1.9	--
[1]88	18 June 1969	11°19.5' S 78°18.6' W	18,000	4.8	0.25
89	18 June 1969	11°19.8' S 78°03.6' W	5,600	1.2	0.16
[1]93	19 June 1969	11°18.8' S 78°11.8' W	2,900	0.9	0.38
94	19 June 1969	11°18.8' S 78°11.8' W	2,400	0.7	0.38
95	19 June 1969	11°20' S 78°12' W	3,800	1.2	0.52
96	20 June 1969	11°20' S 78°12' W	4,300	1.0	0.49
97	20 June 1969	11°20' S 78°12' W	4,000	1.3	0.43
[1]99	20 June 1969	11°20' S 78°14.8' W	6,500	2.0	--
100	20 June 1969	11°20' S 78°25' W	11,000	4.0	--
[2]102	21 June 1969	10°55.0' S 78°24.6' W	3,300	0.9	0.09
103	21 June 1969	10°54.2' S 78°19.8' W	4,700	0.9	--
104	21 June 1969	10°51.2' S 78°20.4' W	6,700	2.4	0.31

[1] Stations with primary productivity and phytoplankton crop taxonomic composition data.
[2] Surface chlorophyll a level <1.5 μg/liter.

column sampled for the "net" zooplankton was examined at Station 77. Expressed as a percentage of the average ciliate organic carbon concentration within the euphotic zone, the vertical distribution was 30 to 50 m, 14%; 55 to 75 m, 7%; and 80 to 100 m, 6%. Chlorophyll levels over the same depth intervals were 20%, 8%, and 1% of the euphotic zone average. Ciliate organic carbon estimate for the 100-m column was more than 20% of that of the total 103-μ net sample.

The numbers of small shelled sarcodinan protozoa, i.e., Foraminifera and Radiolaria, were relatively low. Numbers counted in the samples integrated over the euphotic zone were too small to provide a good estimate but suggested less than 10 foraminiferans and radiolarians/liter. At the surface, the average abundance of Sarcodina for the 12 stations was low—5.3 organisms/liter or 0.032 μg C/liter.

The metazoan microzooplankters, principally juvenile copepods, were also few in numbers. Less than one metazoan/liter was found, on the average, in +35 sample from the surface. Average numbers in the unconcentrated samples over the euphotic zone were higher (up to 40/liter) but the very few counted puts wide confidence limits on the figure. The size of the "average" individual copepod, both naupliar and post-naupliar, was significantly greater than seen previously (Beers and Stewart, 1970) and this suggests the relative absence, at least at this time of year, of the smaller species and their developmental stages compared with nutrient-rich coastal areas off California.

LARGER (+ 103 μ) ZOOPLANKTON

Standing stock zooplankton at five stations where productivity was measured (Station 59, 68, 77, 87, and 93) averaged 2.4 mgC/m³ over the upper 100 m and showed less than a twofold difference between sites (Table 5). For the twenty-one 103-μ net samples collected, average zooplankton organic carbon was calculated to be 4.9 mg/m³. Zooplankters small enough to pass 505 μ mesh were 30% of the total at the "productivity" sites and 25% overall. *Calanus chilensis* (NVI-adults) constituted approximately

TABLE 5.—The standing stock biomass, as dry weight, of the 103 μ net zooplankton samples, 100 m to surface tows.

Station	Date	+103 μ zooplankton dry weight (mg/m³)		
		<505 μ	>505 μ	Total
58	13-14 June 1969	228	789	1,017
59	14 June 1969	155	273	428
65	15 June 1969	420	933	1,353
66	15 June 1969	384	886	1,270
67	15 June 1969	142	147	289
68	15 June 1969	254	586	840
70	15 June 1969	594	2,410	3,004
73	15 June 1969	433	1,284	1,717
74	16 June 1969	459	1,740	2,199
75	16 June 1969	249	756	1,005
76	16 June 1969	538	1,030	1,568
77	16 June 1969	275	503	778
85	18 June 1969	399	896	1,295
86	18 June 1969	473	911	1,384
87	18 June 1969	83	351	434
93	19 June 1969	130	398	528
95	19 June 1969	145	1,169	1,314
97	20 June 1969	106	685	791

25% of total net organic carbon at the productivity sites. At other stations its estimated abundance as a percentage of the total ranged from <4% to more than 100%. It appeared as though the *Calanus* population associated with Patch 1 was staying with the patch and growing as evidenced by following a cohort of NV and NVI individuals into CI at Day 3 (June 15) and CII at Day 6 (June 18) (see University of California, Institute of Marine Resources, 1971; footnote 4).

DISCUSSION

Many of the specialized studies of biological populations and production in Peruvian coastal waters have been done during the late summer or early fall months of the southern hemisphere, i.e., February to April. The relatively large amount of data available from the Instituto del Mar del Perú provides seasonal coverage of the important food chain variables and allows us to place the conditions we found in this study during austral late fall-early winter in their proper perspective. The transport of nutrient-rich water to the surface through upwelling occurs throughout the year but it is generally most intense in winter (see Wooster and Reid, 1963; Zuta and Guillén, 1970). However, biological production, mainly as evidenced by standing crop

and stock abundance, and primary production levels (Guillén and Izaguirre de Rondan, 1968), appears to be highest during the summer period. Anchovy abundance near the coast is greatest during spring and summer, the time of the most active fishing (Sanchez, 1966).

Strickland et al. (1969) and Ryther et al. (1970) as well as others have pointed out the relatively large variation in upwelled patches at the surface. During the present cruise extensive mapping both to the north and south of Callao failed to show the very high pigment patches (chlorophyll a, >10 μg/liter) reported by Strickland et al. (1969) in March-April 1966. Further, the two patches we followed did not have the visually brown coloration described by Strickland et al. (1969) for patches with phytoplankton in bloom conditions. The phytoplankton population of high-chlorophyll, brown-water patches has been found to be principally diatoms whereas the dominant forms in "blue" water areas were generally small flagellates (coccolithophorids and "monads"). In the regions where Rojas de Mendiola et al. (1969) reported the diet of anchovies to be phytoplankton, the crop was principally diatoms and these were the main forms, although not necessarily the same species, recognized in the gut contents of the fish. Even though the cell size of many of the diatom species reported from the brown-water patches is small they are often chain-formers which would provide a size and/or configuration that could be more easily retained on the gill rakers of the anchovy.

The size of most plant cells in the populations found during the present study is relatively small compared with the chain-forming diatoms and, therefore, these may not be efficiently utilized by the anchovy if they pass through their filtering mouthparts. If this size limitation is important, then it is plausible to suggest the anchovy will prey on larger organisms such as many of the zooplankters which in turn have grazed the small algal cells. At the time of year of this study juvenile anchovies (i.e., peladilla) of length 65 to 70 mm and of age 4 to 6 months are generally abundant, having been spawned during the spring and early summer months (see Sanchez, 1966). Rojas de Mendiola

(1959)[a] and Rojas de Mendiola et al. (1969) have shown the stomach content of this size class of fish to be mainly zooplankton and have suggested a preference for this food. It would appear this could possibly be due to a lack of the diatoms or other appropriate-sized plant cells. At such times as this when the diatoms are not abundant the food chain leading to the anchovy would necessarily be lengthened by at least one extra trophic level and therefore "efficiency" of utilization of primary production in terms of production of anchovy carbon would be lessened. Growth rate (i.e., increase in length) of anchovies during these winter months is less than half that at other times of the year (Sanchez, 1966). This may be a reflection of the lower abundance of their "food" at this time of year and the need for expending a greater amount of energy to obtain the same or a lesser amount of food.

While some of the diatoms that have been reported in bloom proportions at other times of the year (e.g., Ryther et al., 1970) were present during this study, the absolute abundance of diatoms was low and they were a relatively unimportant component of the total phytoplankton crop. This could be the result of a low rate of production for these forms or may suggest they are being kept down by grazing.

Obvious possible limiting variables of the chemical and physical environment to diatom production do not seem to be relevant here. Even though these observations were made at the winter solstice, light at a location so near the Equator is probably not limiting to production, although at the time of this study the nearcoastal region of Peru was often obscured by a persistent cloud cover. And, in fact, photosynthesis was saturated at an irradiance about 20% of that at the surface. Basic nutrient requirements of the diatoms should be met with the levels present. Silicate-Si at four of the five stations where productivity was measured was 8 to 10 μg at./liter or greater through the euphotic zone. Nitrate + nitrite-N levels were

[a] Rojas de Mendiola, B. 1959. Breve informe los hábitos alimenticios de la anchoveta (*Engraulis ringens* Jennys) en los años 1954-1958. A report presented to the Cia. Administradora del Guano, 30 April 1959. (Unpublished manuscript.)

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generally in excess of 12 to 15 μM and PO_4-P above 1 μM. It is possible, however, that a nutrient requirement of the diatoms may not be met because of the lack of "conditioning compounds" or some similar mechanism as postulated by Barber et al. (1970). Temperature is of doubtful significance as many of the abundant species in the "blooms" enumerated by Ryther et al. (1970) and Strickland et al. (1969) might be expected to grow equally well at both winter and summer surface temperatures.

Thus, at this time of year the food chain leading to the anchovy probably consists of an intermediate zooplankton step. Villanueva et al. (1969) found stomach contents of anchovies collected 6 to 8 June during this study in an area off Punta San Juan and San Nicholas to be primarily zooplankton. Since no measure of the anchovy standing stock was made, it is not possible to estimate the predation of the anchovy on the zooplankton, but it is possible with our data to evaluate the importance of zooplankton grazing on phytoplankton as a mechanism for preventing their "blooming." The standing stock of zooplankton in the Peruvian coastal waters is generally high (Reid, 1962) although, as pointed out by Gulland (1970), there is probably a marked degree of seasonal and geographical variation in their abundance. Cushing (1969) noted an inverse correlation marked by a short lag between anchovy egg numbers and zooplankton abundance off the Peru coast during the spawning season. He implicated the spawning fish as either the direct or indirect causative agent for this. In either case it was suggested that the low zooplankton stocks and hence their reduced grazing pressure at the end of the spawning season allows for another cycle of biological production. Initially this would be of principally primary production during late summer-early fall followed by an increase in secondary production in the fall. The latter would be available to the juvenile anchovies. While this is simply speculation at the moment, hopefully it will become clearer when more data on the seasonal variation, including small-scale variations, of plankton populations are tabulated (see Gulland, 1970).

A striking feature of the zooplankton popula-tions we observed off Peru was the great absolute and relative abundance of ciliates. The ciliates may be essential elements for the utilization of the small phytoplankton species present, and, if preyed upon in turn by the zooplankton, may represent still an additional trophic level and lengthening of the "food chain" between the primary producers and the harvestable anchovy. The average ciliate organic carbon level over the euphotic zone was about an order of magnitude greater than that found for 12 equidistantly spaced stations from lat 10° N to 12° S along long 105° W in the eastern tropical Pacific (Beers and Stewart, 1971). Ciliate abundance off Peru was similar to the average estimated for a site 1 mile off the coast of La Jolla, Calif., from weekly samples over a 5-month period in the spring and summer of 1967 (Beers and Stewart, 1970). However, off La Jolla the tintinnids accounted for almost three-quarters of the ciliate biomass. Also, just 5 to 6 miles off the California coast the average ciliate abundance (as organic carbon) over the same period had decreased to a level about one-quarter of that recorded for the present set of stations which were generally between 10 and 20 miles off the coast.

Despite their prominence in the zooplankton populations the standing stock of ciliates as organic carbon in the euphotic zone was an average of only 3.2% of the phytoplankton standing crop (6 stations with productivity data). The average daily phytoplankton production over the euphotic zone at these six sites was 49 mg C/m³. The ciliate carbon was only approximately 5% of the new phytoplankton crop being added daily. An estimate of the fraction of the daily primary production that might be consumed by the ciliates can be made assuming the ciliates require three times their bodily carbon per day. Laboratory culture studies of pelagic ciliates (unpublished) have suggested that tintinnids may be dividing every 1 or 2 days and that the doubling time may be even shorter for the oligotrichs (see also Beers and Stewart, 1970). Values for possible ciliate consumption of new phytoplankton production ranged from 5% (Station 93) to 24% (Station 87), averaging 15%. Other microzooplankton consumption would, on the

average, be a very small addition to the total. If the ciliate populations found off Peru with their dominance of oligotrichous forms receive much of their nutritional requirements through functional chloroplasts in their endoplasm, their direct consumption of phytoplankton would probably be lower than assumed. The gymnostome ciliate, *Mesodinium rubrum*, for which good evidence of endocellular chloroplasts exists (Taylor, Blackbourn, and Blackbourn, 1969) was not included in this calculation.

The *Calanus* standing stocks at the four stations associated with Patch 1 (0-100 m) were estimated to be consuming an average of 22 mg C/m²/day. These estimates were derived using the data of Mullin and Brooks (1970) on ingestion by the various developmental stages of *Calanus helgolandicus*. The average net primary production over the euphotic zone at these four stations was found to be 1035 mg C/m₂/day. Thus the *Calanus* population, which was an average of 27% of the total 103 μ net biomass was consuming only a little more than 2% of the plant production. Even if the remaining 73% of the zooplankton population were migrating to the euphotic zone and consuming phytoplankton at the same rate as *Calanus* the total consumption estimate would still be less than 10% of the daily production. Of course, a significant number of the zooplankters may not be herbivores and also many are much larger forms than *Calanus* and it is probable that their daily ingestion as a percentage of their bodily carbon would be lower than that of *Calanus*. The zooplankton populations below 100 m which might migrate vertically to feed have not been considered here. The majority of tows taken on this cruise were during daylight hours but no significantly greater abundance was evident in the few tows taken during the hours of darkness. The level of dissolved oxygen at 100 m and below in Peruvian coastal waters is low (usually <1 ml/liter). However, Mullin (1966)[7] found

[7] Mullin, M. M. 1966. Vertical distribution of zooplankton occurring in the oxygen minimum layer off Peru. *In* University of California, Institute of Marine Resources, Research on the marine food chain, Progress report, January 1966 - December 1966, p. 359-369. (Unpublished manuscript.)

numerous zooplankton species inhabiting the oxygen-poor waters off Peru, and some species even showed their greatest abundance at these depths. Nevertheless, in terms of total zooplankton biomass the upper 100 m would probably be of much greater importance than lower depths.

In summary, our estimates call for no greater consumption by the zooplankton than about 25% of the daily primary production. Coupling this with the fact there was no indication that the actively photosynthesizing phytoplankton crop in either patch was increasing with time but, in fact, was actually disappearing, indicates some mechanism other than grazing must be at least partly responsible. Likewise, the fact that there was no significant increase in the phaeophytin level or in the chlorophyll/phaeophytin ratio as the patch was monitored with time argues against zooplankton grazing as a principal cause. Dugdale and Goering (1970) in their study of biological production in the Peru Current during a period of high diatom levels indicated grazing was not the principal source of "loss" of phytoplankton and that the combined anchovy and zooplankton grazing was at a daily level of about 20% of the standing crop. It was further suggested that, of these, the anchovy were a quantitatively more important grazer than the zooplankters.

Strickland et al. (1969) suggested three alternate hypotheses to grazing which implicated physical factors as mechanisms for patch disappearance. In the present study, estimates of vertical shear and stability indicated that turbulent mixing was occurring in the upper 50 m in Patch 1.

Although a lack of current measurements limits our ability to accurately determine local motion within Patch 1, an order of magnitude estimate for the rate of upwelling in the patch is possible from a consideration of the size of the patch and associated biological productivity. From Figure 4 the patch size was found to be 10 km by 5 km by 50 m, in the east-west, north-south and vertical dimensions, respectively. The corresponding volume of the patch is 25×10^{14} cm³. The patch is assumed to be 50 m thick, below which a subsurface poleward flow is

present. If the doubling rate for plankton is 1.4 days, then to maintain a constant concentration level requires that the water in the patch is removed at a rate of 2.1×10^{10} cm³/sec. The southward transport of the undercurrent beneath the patch is estimated at 20.2×10^{10} cm³/sec, or about 10 times the flow required for replacement of water in the patch. Upwelled water is required to replace the water being removed along the outer boundary of the patch. Since we assume that most, if not all of the water used to replace water lost from the patch, passes through the bottom of the patch at 50 m, the ascending velocity of water at 50 m is estimated to be 4.1×10^{-2} cm/sec for the patch. This is probably an upper limit since other processes also act to reduce the biomass. Unfortunately, only one sub-euphotic zone sample (30-50 m) from Patch 1 is available, and it shows a chlorophyll level only 20% of the average in the upper layer. However, if the ciliate and other zooplankton populations were grazing this material in which no new organic carbon was being produced, it would only be a relatively short time before a marked diminution of the chlorophyll level would be expected. In addition, chlorophyll levels above and below the compensation depth may not be a comparable index to phytoplankton abundance as there is an apparent decrease in chlorophyll level in many phytoplankters when kept in the dark for any period of time. Thus, the plant cell population in the sub-euphotic waters may be underestimated. The phytoplankton cells near to the compensation depth had a lower photosynthetic rate, g C/g Chl a/hour (University of California, Institute of Marine Resources, 1970, see footnote 3), than those higher in the water column. Eppley, Holmes, and Strickland (1967) showed that cells in such a physiological state sink at a more rapid rate than faster growing phytoplankters. While sinking or upwelling alone may not result in moving material out of the euphotic zone and preventing a "bloom" from developing, this combined with the turbulence may be a significant contributing factor. Dugdale and Goering (1970) following a high chlorophyll patch of water over 5 days, concluded that approximately 85% of the phytoplankton production at that

time was being lost through sinking and mixing processes. At one site examined more closely, 16% of the standing crop was lost daily.

Continued upwelling with the consequent spreading out and/or sinking of the surface waters is another mechanism which would result in masking any bloom that might have developed had the upwelled water mass remained more localized. This was suggested as a means of "preventing" blooms in regions of divergences in the Antarctic (Beklemishev, 1958). Horizontal divergence of Patch 2 with a relatively greater eastward water motion of the nearshore side was indicated by our current measurements. Water on the nearshore side would appear to "stretch" in the horizontal plane and be supplemented by ascending subsurface water. Examination of the graphic reconstruction of chlorophyll distribution (Figures 1 and 2) suggests a spreading out of the chlorophyll patches, becoming diluted in the surrounding area with time. Since dynamic vertical mixing is not indicated by the Richardson numbers for Patch 2, the decrease in chlorophyll may be largely attributed to the divergence and associated upwelling. Horizontal mixing, however, is undoubtedly an important dispersing mechanism in both patches. A rough estimate of upwelling based on the horizontal divergence was made by using the current measurements from Patch 2. Upwelling in the patch is assumed to be confined to a surface layer 50 m thick, where the vertical velocity is a maximum at 50 m (the same depth as the poleward flow of the coastal undercurrent). The resulting estimate of vertical velocity at 50 m is 2.5×10^{-2} cm/sec and compares favorably with the upwelling rate computed with greater accuracy for a nearby coastal zone (Smith et al., 1971). The surface concentration of nitrate declined in the patches over time as did the total chlorophyll pigments concentration (Patch 1, Figure 5). Nitrate consumption by the phytoplankton was calculated, assuming 1 g nitrate assimilated per 6 g of carbon fixed in photosynthesis, and the indicated plant consumption was only about one-third of the observed nitrate decline. This observation again suggests mixing of water in the patches with surrounding less rich water.

We are left with a system that is undoubtedly the result of a combination of interacting factors —both biological and physical—which can be sorted out only semiquantitatively. Apparently a loss equivalent to about 25% of the phytoplankton production may have been due to grazing by zooplankters. As measured here, diffusive mixing of the patches with adjacent waters and sinking of the phytoplankton would account for considerable additional loss of phytoplankton material. In addition other avenues of possible loss such as the direct consumption by the anchovies exist but were not evaluated here. That the relative significance of the different variables may change on a very small scale in time and location at this time of year can be suggested. Such complexity would lead to the variety of conditions that have been described from the coast of Peru.

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