

Changes in nutrients, pH, light penetration and heat budget by migrating photosynthetic organisms

Heat budget
Vertical migration
Red tides
Upwelling
Mesodinium

Bilan de chaleur
Migration verticale
Marée rouge
Upwelling
Mesodinium

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ABSTRACT

The possible impact of red tide organisms (*Gymnodinium splendens* in Spring, 1976 and *Mesodinium rubrum* in Spring, 1977) on the oceanography of Peru coastal waters is described. In the upper 1 m of the ocean they can control up to 99 % of the absorption and transport of incoming radiation. These vertically migrating organisms are likely to play a key role in heat transport in eastern boundary systems.

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RÉSUMÉ

Effets des organismes photosynthétiques migrants sur les sels nutritifs, le pH, la pénétration de la lumière et le bilan de chaleur

Les organismes qui forment les marées rouges, *Gymnodinium splendens* au printemps 1976 et *Mesodinium rubrum* au printemps 1977, ont un effet sur les caractéristiques physiques et chimiques des eaux côtières du Pérou. Dans la couche superficielle d'un mètre d'épaisseur, ils peuvent contrôler jusqu'à 99 % de l'absorption et de la propagation du rayonnement incident. Dans leurs migrations verticales, ces organismes photosynthétiques ont probablement un effet important sur le transfert de chaleur par les courants dans l'est de l'océan.

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INTRODUCTION

Motile photosynthetic organisms are able to control their vertical positions in the water column. Certain dinoflagellates and *Mesodinium rubrum* (chlorophyll-containing ciliate), swim to the surface during the daylight period, forming visible concentrations known as red tides or aguajes. Physical processes acting in concert with their swimming activities can create circumstances leading to strong concentrations of

organisms in the near surface regions, e.g. through horizontal advection into convergence zones and input of nutrients by upwelling. Chlorophyll *a* concentrations of up to 425 $\mu\text{g l}^{-1}$ have been reported (Jones, 1978) and represent a standing crop of photosynthetic biomass at least 10 times greater than could have been produced within the local water column. By inference, biological, chemical and physical changes in the environment due to organismal activities can occur very much more rapidly and intensely than

would be the case in unconcentrated populations. Further, these activities and changes occur in the upper few meters rather than being distributed throughout the water column or concentrated in a subsurface chlorophyll maximum as suggested by Lewis *et al.* (1983) and Lewis (this vol.).

In this communication, the effects of these extraordinary concentrations of photosynthetic organisms on the near surface regions of the sea are considered. In the first part of the paper, data from a series of stations, taken on some cruises to the coast of Peru in which red tides were encountered, are presented with the objective of setting upper limits on the changes that may occur under these circumstances. In the second part, estimates are given of the areas over which such changes might be expected. Finally, the consequences of unusually large blooms of red tide forming organisms on local and offshore oceanographic processes is speculated upon.

RED TIDES ALONG THE PERU COAST

Background information on red tides along the coast of Peru can be found in Brongersma-Sanders (1957) and Rojas de Mendiola (1979). The dominant species of many red tides along the Peru coast appears to be *Gymnodinium splendens*, e.g. in the 1976 Aguaje (Rojas de Mendiola, 1979).

In 1977, *Mesodinium rubrum* was seen in abundance off Peru. Its biology and relationship to physical processes was reviewed by Packard *et al.* (1978). It is a single-celled, ciliated animal that contains symbiotic chloroplasts whose symbiotic nature is still a matter of debate. *Mesodinium* functions as a highly mobile phototroph with reported swimming speeds up to 7 m h^{-1} . Individuals range in size from about 20–50 μm . These cells, like diatoms and dinoflagellates, fix inorganic carbon, take up phosphate (Barber *et al.*, 1969), show nitrate reductase activity (Packard *et al.*, 1978) and show a light requirement for uptake of ^{15}N -labelled ammonium and nitrate (Dugdale, MacIsaac, unpublished). The species is found worldwide but confined to bays, fjords and upwelling coasts and has a strong tendency to form patches at the surface under light or moderate wind conditions, often at fronts. Its occurrence in blooms off Ecuador has been documented recently by Jimenez and Intrigao (this vol.).

DAILY CHANGES DURING RED TIDES

A red tide of unusual proportions, the 1976 Aguaje, was observed as the R/V Alpha Helix steamed south from California to Peru to join the CUEA MAM 76 study. Red tide concentrations of organisms were seen starting at 7°S and extending along the coasts of Peru and Ecuador to at least 14°S (Bass, Packard, 1977). Accompanying an El Niño, the 1976 Aguaje was of a magnitude expected to occur only once or twice each century (Dugdale *et al.*, 1977). During the period 22 March to 4 May, 1976, biological measurements were made on the R/V Alpha Helix at stations using water bottle samples and underway samples taken from the ship's intake system at 3 m depth. Bands of very high dinoflagellate concentrations were

commonly encountered during daytime transects made along the "C-line" normal to the coast at 15°S or along a track angled about 45° to the north of the C-line, the latter representing the often observed axis of flow of the upwelling plume at that location. Maximum concentrations of chlorophyll *a* of $300 \mu\text{g l}^{-1}$ were observed both underway and at the C-3 location (near the region of maximum upwelling). Blasco (1979) analyzed the daily changes in data from location C-3. Early in the morning the position of maximum total dinoflagellates oscillated between 1 and 21 m, but by noon they were always at the surface. Blasco concluded that migration towards the surface occurred during the day and estimated that a migratory speed of $1\text{--}2 \text{ m h}^{-1}$ was sufficient to explain the changes.

Patches of *Mesodinium rubrum* were observed frequently at the surface during the March to May 1977 CUEA MAM 77 study at 15°S , Peru. The patches were visible from the air and were often maintained during periods of normal upwelling-favorable winds of 2.5 to 8.5 m s^{-1} (Stuart, 1981). At station 8 (a C-3 station) the surface waters became red in appearance at about 13 00 h. Deck incubators were darkened as a result of the large concentrations of *Mesodinium* pumped into them along with cooling water from the ship's intake at 3 m. Interestingly, at this time, many dead birds were seen, mostly cormorants.

Table 1 shows concentrations of chlorophyll *a* (in $\mu\text{g l}^{-1}$) and particulate nitrogen ($\mu\text{g-at l}^{-1}$) at selected stations taken during 1976 and 1977 along with variables associated with these high chlorophyll *a* stations. Both the chlorophyll concentrations of *Gymnodinium* and *Mesodinium* and their associated activities are spectacular. The transport rate of nitrate uptake (ρ) for *Mesodinium* was about $5 \mu\text{g-at l}^{-1} \text{ h}^{-1}$. This rate would result in complete uptake of the total upwelled nitrate (about $25 \mu\text{g-at l}^{-1}$) in 5 hours. Seawater pH was observed to rise about 0.5 units between regions of few and great populations of either *Mesodinium* or *Gymnodinium*. Oxygen concentrations (in ml l^{-1}) increased as a result of the *Mesodinium* bloom, e.g. double the saturation value was seen at R/V Wecoma station 41. Light penetration at 5 m was reduced by 95 and 97 % of surface irradiance. At R/V Wecoma station 40, at 2 m, the irradiance was only $2 \mu\text{E m}^{-2} \text{ s}^{-1}$ implying an extinction coefficient greater than 0.99 m^{-1} . Temperature increases of 1°C resulting from concentrations of *Gymnodinium* can be inferred from temperature changes observed during underway sampling. A $1\text{--}2^\circ\text{C}$ rise was measured between the outside and inside of a patch of *Mesodinium*. The high values shown in Table 1 are representative of large blooms (60 to $157 \mu\text{g l}^{-1} \text{ chl } a$). Yet these are not the largest changes that migrating organisms can cause, since surface patches with bloom chlorophyll *a* concentrations of $425 \mu\text{g l}^{-1}$ were found in 1976 (Jones, 1978) and $300 \mu\text{g l}^{-1}$ in 1977 (Mickelson, 1978).

SPATIAL CHANGES RELATED TO RED TIDES

Underway data taken during the 1976 Aguaje (MacIsaac *et al.*, 1979) show a relationship between patches of high surface chlorophyll concentration and elevated

Table 1

Comparison of productivity variables at high chlorophyll stations in 1976 and 1977 near 15°S, Peru during the CUEA program.

	Gymnodinium (1976)			Mesodinium (1977)		
	Station		Reference	Station		Reference
chl <i>a</i> ($\mu\text{g l}^{-1}$)	60	27	MacIsaac <i>et al.</i> (1979)	157	11A	CUEA/R/V Wecoma Report (unpublished)
particulate N* ($\mu\text{g-at l}^{-1}$)	59	27	"	127	11A	"
rho NO ₃ * ($\mu\text{g-at l}^{-1} \text{ h}^{-1}$)	0.5	27	"	1.2-5.0	11A	"
pH change (pH units)	0.6	under way	Simpson and Zirino (1980)	0.4	41	Dugdale (unpublished)
O ₂ change (ml l ⁻¹)	nd			7.2	41	CUEA R/V Wecoma Report (unpublished)
Irradiance change (0-5 m)	- 95 %	27	MacIsaac <i>et al.</i> (1979)	- 97 %	11A	Grunseich <i>et al.</i> (unpublished)
Temp. change (°C)	1	27	"	1-2	11A	"

* samples from 1 m depth
nd no data

surface temperatures. A simulated drogue path made on 29 March showed 4 distinct peaks in chlorophyll *a* concentration with accompanying increases in temperature (about 1°C) and phosphate at the first and third peaks (Fig.). One month later, on a path normal to the coast along the C-line, 4 peaks in chlorophyll were seen again, at about 20 km intervals with evident temperature increases associated with the second and third peaks. In both data sets the third peaks had the highest chlorophyll *a* concentration, about 100 $\mu\text{g l}^{-1}$. In the latter data set, the first derivatives (the rate of change of chlorophyll and temperature) were calculated with respect to distance. These also suggested an association between the third peak of chlorophyll and a positive change in temperature. When plotted against distance, the derivative of temperature with respect to chlorophyll concentration, $\delta T/\delta \text{chl } a$, exhibited a flat region associated with peak 3. The mean value, 0.0138°C $\mu\text{g l}^{-1} \text{ chl } a$, may provide an estimate of the temperature rise to be expected over about 1 day for every microgram of chlorophyll. Stevenson *et al.* (1981) estimated from incoming irradiance measurements that a 6 m water column could be heated 0.8°C in 1 day at 15°S, Peru. Multiplying the value obtained in this study by a chlorophyll *a* value of 100 $\mu\text{g l}^{-1}$, a rise of 1.038°C d⁻¹ can be computed. With a chlorophyll *a* concentration of 300 $\mu\text{g l}^{-1}$ (a value seen during 1976 and 1977) the temperature increase would be 4.14°C; both calculations apply to a 1 m thick layer. Extended to fill a 6 m layer, this is almost the same as the estimate of Stevenson *et al.* (1981).

An estimate of the area over which these temperature increases at the surface might occur can be obtained from 1976 ship and 1977 aircraft observations. The 1976 Aguaje was observed by R/V Alpha Helix from 7 to 14°S at a maximum distance offshore of 240 km (Bass, Packard, 1977). A rectangle constructed from these dimensions has an area of $187 \times 10^3 \text{ km}^2$. Another estimate of the affected area can be made from the 15°S underway observations. The mean

distance from the coast to low chlorophyll conditions along 13 of the lines described above was 60 km. Taking the length of coastline affected to extend from

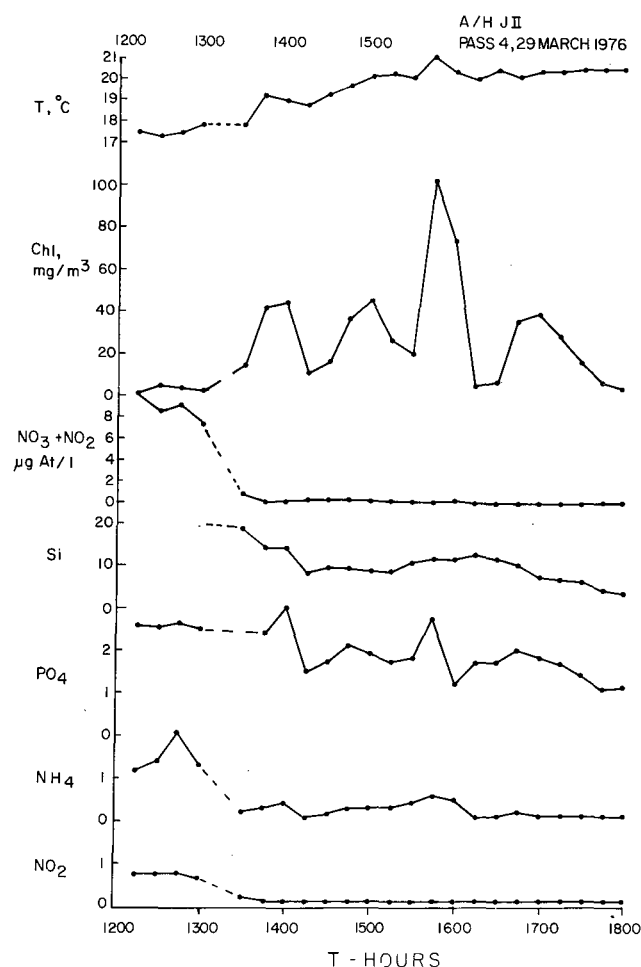


Figure
Changes in properties along a simulated offshore drogue track off 15°S, Peru during Joint II aboard the R/V Alpha Helix (ship speed = 10 knots). Nutrients expressed as $\mu\text{g-at l}^{-1}$.

15 to 5°S, an area of $60 \times 10^3 \text{ km}^2$ can be calculated. Visual observations from an aircraft during surface temperature mapping revealed numerous *Mesodinium* patches on average out to 40 km, maximum 70 km. The width is comparable to that of the *Gymnodinium* bloom of 1976, but no information is available about the longshore extent of the phenomenon.

DISCUSSION

The vertical distribution of heat absorption is an important factor in determining heat transport in eastern boundary current systems where equatorward flow is underlaid by poleward flow as in the Peru coastal upwelling system. During the CUEA studies at 15°S in 1977 the mean depth where surface, offshore flow changed to onshore flow was about 20 m; the depth where surface equatorward flow changed to poleward flow (the level of zero flow) was about 25 m (Brink *et al.*, 1978; Smith, 1981). The mean mixed layer depth was 12–13 m (Codispoti *et al.*, 1982); Stevenson *et al.* (1981) observed the depth of the mixed layer to vary from 0–12 m over a 24 h period in March 1977. From these considerations it is apparent that large concentrations of vertically migrating organisms can affect the manner in which incoming radiation and the heat absorbed is distributed vertically and consequently how it is transported out of the region by current systems. When concentrations are such that virtually all incoming radiation is absorbed in the upper 10 metres, heat will be trapped within the mixed layer and transported equatorward at speeds of about 12.5 cm s^{-1} . Under the extreme conditions described here, when more than 95 % of incoming irradiance is absorbed in the upper 1 or 2 m, the mean equatorward velocity increases to 17.9 cm s^{-1} (Brink *et al.*, 1978) and the equatorward transport of heat must increase also. Radiation absorbed below the mixed layer depth, but above 25 m (where equatorward flow becomes polar) will be transported as heat equatorward at a slower mean speed of 8.2 cm s^{-1} (Brink *et al.*, 1978) with mixing losses across the level of zero flow. Radiation absorbed below this is transported poleward. Also, under these conditions, static stability is enhanced by the organisms through local surface temperature increases of 1–2°C or more.

The effect of photosynthetic organisms on heat transport can be assessed by combining the data on mixed layer depth and level of zero longshore velocity with average light penetration profiles at 15°S and comparing them with a low productivity reference, the Sargasso Sea (Tab. 2). In the Sargasso Sea about 50 %

of the visible incoming radiation is absorbed in the upper 10 m, 70 % in the upper 25 m. When substantial phytoplankton populations ($1.5 \mu\text{g l}^{-1} \text{ chl } a$) are present at 15°S, as at C-3 during Leg 1B of the R/V Wecoma 1977 cruise, 95 and 99 % of the incoming radiation is absorbed in the 10 m and 25 m layer respectively. Under strong red tide conditions, 99 % is absorbed in the upper 10 m, and even in the upper metre during the 1977 *Mesodinium* bloom. Thus, the photosynthetic organisms are involved in determining the depth of absorption of the incoming radiation. They are responsible for a 47 % (99–52 %) increase within the upper 10 m and up to 27 % (99–72 %) within the upper 25 m. Vertically migrating photosynthetic organisms *e.g.* dinoflagellates and *Mesodinium* act as solar collectors, migrating to the surface, trapping heat that is transported with the surface waters equatorward. At the end of the day they move downward and are transported poleward and shoreward if they migrate sufficiently deep (Smith, Barber, this vol.).

The maximum amount of heat transported equatorward above that which would occur in the absence of photosynthetic organisms can be computed by multiplying the 47 % increment in absorption by the areas affected (*see above*). The upper and lower limits of the effect are 220×10^{15} and $70.5 \times 10^{15} \text{ cal d}^{-1}$ and represent the maximum effect of organisms in redirecting heat transfer toward the Equator. A more realistic but still maximal estimate of the effect of extraordinary red tides for Peru waters can be obtained using the increment in absorption in the upper 10 m due to replacement of "normal" phytoplankton by red tide populations (*i.e.* 99–95 % = 4 %). The values obtained, 20.6×10^{15} and $6.6 \times 10^{15} \text{ cal d}^{-1}$, still represent a large amount of heat. That these increased amounts could be delivered rapidly by surface currents into the "cold tongue" area extending offshore from the coast at the Equator (Eriksen, 1975), suggests that warm El Niño-like events may be intensified by the development of strong persistent red tides. In turn, these red tides may initially be triggered to develop by the poorer surface nutrient concentrations associated with El Niño, since the organisms involved, by virtue of their ability to migrate, can use nutrients from deeper water and surface light.

These speculations do not include some important considerations for a serious quantitative study, *e.g.* the increased outward radiation and evaporation resulting from elevated temperatures. These factors will alter the relative effect of mean surface heat concentrations upon the overall ocean-atmosphere heat budget. Nevertheless, it appears that the primary producer segment of an eastern boundary upwelling ecosystem may play a hitherto unsuspected role in the heat budget of nearby equatorial waters.

Table 2

Visible irradiance absorbed in the region above depth indicated.

	% surface irradiance		
	1 m	10 m	25 m
Pure water	1.7	52.0	70.0
Sargasso Sea	1.7	52.0	72.0
Coastal water	5.4	72.0	97.0
Peru, 1977	27.0	95.0	> 99.0
(station 66)			
Peru, 1977	99.9	> 99.0	> 99.0
(<i>Mesodinium</i> bloom)			

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