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Biological and Physical Observations

on a Phosphorescent Bay in
Falmouth Harbor, Jamaica, W.I. ¹

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ABSTRACT

A general description of a phosphorescent bay on the northern shore of Jamaica, West Indies, is presented. The brilliant bioluminescence in this embayment is due to the large armored dinoflagellate, Pyrodinium bahamense. It was found in cell densities as high as 200,000 cells/liter. Using a submersible spectrometer, the bioluminescent emission spectrum of these organisms was found to peak at 476 mµ. Simultaneous in situ bioluminescence measurements and cell counts indicate that this dinoflagellate exhibits both a diurnal physiological rhythm in bioluminescence capacity and a diurnal vertical migration. Iron and phosphorus analyses of a small number of water samples suggest that the waters of the embayment are high in inorganic nutrients. However, the rate of photosynthesis by these dinoflagellate populations appears to be quite low.

Introduction. Among the spectacular phenomena encountered in planktonic ecology are the bioluminescent displays by many species of marine dinoflagellates. Dinoflagellate bioluminescence is prevalent at times in many temperate areas, particularly during the warmer seasons, and is encountered in greater frequency and intensity in tropical and semitropical seas. Along the island coasts of the Caribbean Sea, there are several embayments in which the population density of bioluminescent dinoflagellates reaches extremely high levels. Agitation of these waters produces several orders of magnitude more luminescence than is

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found in the open seas. One of these embayments, the famous Bahia Fosforescente, near the city of Mayaguez on the southwestern coast of Puerto Rico, has been the subject of several investigations (Clarke and Breslaw 1960, Burkholder and Burkholder 1958, Odum et al. 1959). A less-publicized bay is located on the northern shore of Jamaica. The purpose of this paper is to present some observations of pertinent environmental and physiological factors along with quantitative measurements of the bioluminescent phenomenon in Oyster Bay. These observations were made in January 1961 and February 1963. Additional data have been previously reported (Seliger et al. 1962).

**General Description.** Falmouth Harbor, on the northern shore of Jamaica about 20 miles east of Montego Bay, lies behind extensive offshore coral reefs and is protected from heavy wave action from the Caribbean Sea. The brilliant bioluminescence is limited to the eastern end of the harbor in an area known locally as Oyster Bay. Fig. 1 shows with fine stippling the approximate limits of the phenomenon and gives the depth contours obtained by hand-line soundings on several transects. Also shown are the stations at which hydrographic

![Figure 1. General topography and location of hydrographic stations, Oyster Bay, Falmouth Harbor, Jamaica, West Indies. Approximate limits of brilliant bioluminescence shown with fine stippling.](image-url)
data, bioluminescence measurements, and chemical and biological samples were collected.

Oyster Bay is a shallow basin with a surface area of approximately 1 km$^2$. It is bordered on the north, east, and south by dense stands of mangrove trees. The small Martha Brae River, which enters the bay along its southwestern perimeter, flows from rugged mountainous country 15 km to the south through a rich valley containing many sugar and banana plantations. Since many of the river’s tributaries are fed by subterranean streams that originate in the mountains, the total drainage area of the river is unknown, but conservatively estimated, it is about 280 km$^2$.

The tide in the harbor is so small that local watermen ignore it. Crude measurements in the bay on 22 January 1961 from a pier extending from “The Rock” showed a difference of about 10 cm between high and low water.

A gently sloping sill with a minimum depth of about 1 m separates Oyster Bay from the remainder of the harbor; the maximum depth of 2 m occurs in a relatively small area of the bay; the average depth is approximately 1 m. The bottom sediments in the bay, where sampled, consisted of soft mud. The bottom surface was brown, fluffy, and aerobic, but at depths greater than a centimeter the mud was anaerobic. Very few stands of attached macroalgae were found, with the exception of several species growing either epiphytically on mangrove roots or attached to artificial fill on the south shore of the bay in the vicinity of “The Rock.” The predominant aquatic plant, turtle grass (Thalassia testudinum), was found in the shallower areas bordering the northern and eastern parts of the bay. When examined in 1961, the turtle-grass beds were dense only in some local areas.

**Methods.** Bioluminescence measurements of the dinoflagellates under stimulation were obtained with underwater photometers whose construction, operation, and calibration have been described (Seliger et al. 1962: figs. 1 b, 1 c). The measurements in 1961 were taken with the instrument diagramed in Fig. 1 b, and those in 1963 with the narrow-intake photometer shown in Fig. 1 c. The spectrum of the dinoflagellate bioluminescence was obtained with an underwater spectrometer designed and built by W. G. Fastie. The instrument has been described by Tyler (1964). For our purposes it was modified by mounting a small impeller pump directly in front of the entrance slit to stimulate the dinoflagellates. Because of the high concentration of organisms and the constant replenishment of the dinoflagellates by the pumping action, the intensity of light emission was essentially constant.

Samples for chemical and biological analyses were collected with a modified Van Dorn plastic sampling bottle. Aliquots used for chemical determinations were returned to the laboratory in polyethylene bottles or in specially treated glass bottles described below.
Salinity was determined by titration with silver nitrate (Knudsen 1901). Temperature was measured in situ with a portable temperature indicator that employs a thermistor with a null point circuit and was calibrated to ±0.02°C (Schiemer 1962).

Phosphate was determined from samples drawn directly into 100-ml borosilicate glass bottles that contained 1 ml of 5% thorium carbonate suspension (neutralized to phenol red) as an adsorbent and a few drops of chloroform as a preservative (Harvey 1960: 194). The samples were acidified at the laboratory with 18 N H₂SO₄ and divided into four aliquots. Two portions were used to determine inorganic orthophosphate by the molybdate-ascorbic acid method of Murphy and Riley (1958). The other aliquots were hydrolyzed in Vycor® flasks (Corning Glass Works, Corning, N. Y.) by autoclaving at 40 psi pressure for five hours (Harvey 1953). Total phosphate was determined on the hydrolysate by the colorimetric method mentioned above. Organic phosphate was taken as the difference between total and inorganic phosphate.

Iron was determined from samples drawn from the Van Dorn sampler into 100-ml borosilicate glass bottles equipped with screw caps lined with Teflon® (E. I. DuPont, Wilmington, Delaware). Before use, these bottles had been thoroughly washed with dilute hydrochloric acid, and 2.5 ml of 6N HCl had been placed in each bottle. When drawing the sample, care was taken not to lose the acid by overflowing. Under these conditions the final pH of the seawater samples was approximately 1. Experience in our laboratories, as well as in others (Armstrong 1957), has demonstrated that immediate acidification of the samples in this manner prevents loss of iron to the walls of the bottle during the interval between collection and analysis. After hydrolysis under conditions similar to those described above for phosphate, total iron was determined by the phenanthroline colorimetric procedure of Armstrong (1957).

For the quantitative phytoplankton survey, aliquots from the sampler were transferred into 150 x 20-mm borosilicate glass test tubes equipped with screw caps. The organisms were fixed by the addition of a few drops of either a potassium iodide-iodine solution (Gray 1954: 255) or an osmic acid-chromic acid fixative (Darlington and LaCour 1950: 114). Both of the fixatives were satisfactory for the examination of these large dinoflagellates. The tubes were sealed and taken to the field laboratory. The total volume of the sample was measured and the organisms were concentrated by centrifugation with a hand-operated centrifuge revolving at approximately 1500 rpm (500 x g). After decantation, the concentrated sample was resuspended in a known volume of membrane-filtered seawater. An aliquot of this concentrated sample was then examined on a haemocytometer slide. Examination of recently obtained whole-water samples under oil immersion at magnifications up to 1250 x did not reveal any dinoflagellates or diatoms that were not also found in the fixed samples.

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<th>1800 Surface</th>
<th>1800 1 Meter</th>
<th>2115 Surface</th>
<th>2115 1 Meter</th>
<th>2230 Surface</th>
<th>2230 1 Meter</th>
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<td>600</td>
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<tr>
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<td>600</td>
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<td>7,200</td>
<td>11,000</td>
<td>14,000</td>
<td>5,600</td>
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<tr>
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<td>156,000</td>
<td>219,000</td>
<td>134,000</td>
<td>190,000</td>
<td>129,000</td>
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<td>1,700</td>
<td>4,400</td>
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<tr>
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<tr>
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<td>6,700</td>
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<tr>
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<td></td>
<td>6,700</td>
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<th>1800 1 Meter</th>
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<th>2115 1 Meter</th>
<th>2230 Surface</th>
<th>2230 1 Meter</th>
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<td>600</td>
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<tr>
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<td></td>
<td></td>
<td>600</td>
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<tr>
<td><em>Nitzschia sp.</em></td>
<td>600</td>
<td></td>
<td></td>
<td>1,100</td>
<td></td>
<td>1,100</td>
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<tr>
<td>Unident. small centrales</td>
<td>14,000</td>
<td>10,000</td>
<td>12,000</td>
<td>14,000</td>
<td>22,000</td>
<td>11,000</td>
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Measurements on the rate of photosynthetic fixation of carbon by the phytoplankton were made by Steeman Nielsen's (1952) carbon\textsuperscript{14} method with modifications recommended by Strickland (1960). All samples were run in triplicate and each series included a dark bottle in order to correct for non-photosynthetic isotope uptake. The dark uptake amounted to 4\% of the maximum photosynthetic carbon fixation. The samples were incubated \textit{in situ}.

\textbf{Observations and Data.} Typical data for one of several quantitative surveys made when there was little or no temperature or salinity stratification are presented in Table I and Fig. 2. These data were obtained at St. B on 19 January 1961 from samples collected at the surface and 1 m at various times from before twilight to well after the occurrence of maximum bioluminescence.

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{figure2.png}
\caption{Vertical distribution of salinity (open circles) and temperature (solid circles) at St. B, Falmouth Harbor, Jamaica, showing homogeneity on 19 January 1961 (broken line) and stratification on 22 January 1961 (solid line).}
\end{figure}
The predominate organism in terms of both cell numbers and biomass was *Pyrodinium bahamense*. Of the other dinoflagellates found, only *Ceratium fusus* has been shown by careful laboratory studies to be bioluminescent (Sweeney 1963); it was present in such small numbers that its contribution to the total luminescence must have been minor. There were approximately twice as many cells of *P. bahamense* in the surface layers after twilight as at 1800. Over the same time interval there was a decrease in cell numbers at 1 m. While other explanations are possible, these data suggest that *P. bahamense* exhibits vertical migration during these early evening hours. Vertical migration of other bioluminescent dinoflagellates has previously been suggested (Seliger et al. 1961, 1962).

Bioluminescence measurements were taken concurrently with the above quantitative samples, and the variation with depth of the luminescent capacity of the dinoflagellate population under stimulation at different times is shown...
in Fig. 3. A diurnal rhythm in the bioluminescence capacity of the population was demonstrated. These data also reflect the vertical migration suggested by the cell-count data.

On 22 January 1961, following two days of rainfall in the drainage basin of the Martha Brae River, both hydrographic and phytoplankton surveys were carried out in conjunction with primary productivity measurements. The twenty-second was a cloudless day with a steady 10 to 15-k wind out of the north-northwest. The hydrographic survey included measurement of the river current (at St. F) with a kite-type drogue, and temperature and salinity measurements at stations on two transects across the bay: one from St. F to St. B', the other from St. A to St. D (see Fig. 1).

Compared with the homogeneous conditions found on 19 January, extreme temperature and salinity stratification was now apparent. The vertical profiles in Fig. 2 show the contrast between the temperature and salinity conditions on these two days at St. B. The drogue measurements showed the river current to be approximately 3 to 4 cm/sec. At the time these studies were made, other river-flow data were not available. The river water did not mix rapidly with the more saline water of the bay, but rather flowed out in a thin tongue over the surface (Fig. 4). The intense halocline and equally strong inverse thermocline are shown in Figs. 5 and 6.

Figure 4. Surface salinity (‰), Falmouth Harbor, Jamaica, 22 January 1961.
Figure 5. Salinity distribution (°/oo), Oyster Bay, Falmouth Harbor, Jamaica, 22 January 1961; top: a section from mouth of Martha Brae River to north shore; bottom: a section from open harbor to head of bay.
Figure 6. Temperature distribution (°C), Oyster Bay, Falmouth Harbor, Jamaica, 22 January 1961; top: a section from mouth of Martha Brae River to north shore; bottom: a section from open harbor to head of bay.
Table II. Dinoflagellates and diatoms in plankton at Sts. B, D, and F in Falmouth Harbor (see Fig. 1), 22 January 1961. Cells/liter.

<table>
<thead>
<tr>
<th></th>
<th>Station B</th>
<th>Station D</th>
<th>Station F</th>
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<tr>
<td></td>
<td>0900</td>
<td>1230</td>
<td>1500</td>
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<tr>
<td><strong>Dinoflagellates</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dinophysis caudata</td>
<td>3,300</td>
<td>6,700</td>
<td>1,200</td>
</tr>
<tr>
<td>Pyrodinium bahamense</td>
<td>17,000</td>
<td>128,000</td>
<td>24,000</td>
</tr>
<tr>
<td>Peridinium breve</td>
<td>3,300</td>
<td>1,100</td>
<td>600</td>
</tr>
<tr>
<td>Peridinium divergens</td>
<td>8,900</td>
<td>2,400</td>
<td>7,400</td>
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<tr>
<td>Ceratium hircus</td>
<td>1,700</td>
<td>5,600</td>
<td>1,200</td>
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<tr>
<td>Ceratium fusus</td>
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<tr>
<td>Unidentified flagellate</td>
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<td><strong>Diatoms</strong></td>
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<tr>
<td>Melosira sp.</td>
<td>-</td>
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<tr>
<td>Rhizosolenia sp.</td>
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<tr>
<td>Lycomophora sp.</td>
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<td>Navicula sp.</td>
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<td>4,600</td>
<td>7,400</td>
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<tr>
<td>Gyrosigma (Pleurosigma?) sp.</td>
<td>-</td>
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<td>-</td>
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<tr>
<td>Nitzschia closterium</td>
<td>1,700</td>
<td>-</td>
<td>1,200</td>
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<tr>
<td>Nitzschia sp.</td>
<td>8,300</td>
<td>-</td>
<td>2,400</td>
</tr>
<tr>
<td>Unident. small centrales</td>
<td>608,000</td>
<td>-</td>
<td>52,000</td>
</tr>
<tr>
<td>Unident. small pennales</td>
<td>-</td>
<td>600</td>
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The results of the phytoplankton survey taken on 22 January are given in Table II. At St. B, surface and 1-m samples were taken at the beginning of each primary productivity run and in the midafternoon.

The species composition at St. B was essentially the same as that on 19 January, but relatively few dinoflagellates were found in the surface waters. Although St. D was outside the area of intense luminescence, the dinoflagellate population at 1 m was relatively high, there being more Dinophysis caudata and Ceratium hircus present than in any other sample. Unexpected also was the number of *P. bahamense* present. St. F had a typical polluted-stream diatom population that was apparently dispersed as the fresh water entered the bay. Remnants of this population were observed in most of the surface samples examined.

Two series of primary productivity measurements were made at St. B on 22 January, one from 0900 to 1100, the other from 1300 to 1500. The data are given in Table III. These observations, preliminary in nature, were undertaken to determine whether the intense bioluminescence was accompanied by an unusually high photosynthetic activity. The morning surface sample contained very few *P. bahamense* (Table II), but it did contain a high concentration of a small, as yet unidentified, centric diatom (diameter 6µ) that was also found in smaller concentrations in many other samples. Except for this sample, the productivity rates were much lower than those usually found in a rich estuarine environment having phytoplankton densities of this order of magnitude.

A limited number of samples for phosphorus and iron analyses were collected at Sts. B and D and in the Falmouth Channel approximately 800 m northwest of St. D, just inside the reef. St. B was sampled on the evening of 19 January 1961; the St. D and harbor samples were collected on 22 January 1961 in conjunction with the productivity measurements. The data are given in Table IV.
No effort was made to distinguish between particulate and dissolved iron, but it is assumed that all of it was particulate.

Fig. 7 is an *in vivo* bioluminescence emission spectrum of *P. bahamense* obtained in Oyster Bay on the evening of 27 February 1963. The values in Fig. 7 have been corrected for the spectral sensitivity of the photomultiplier tube and for the spectrometer transmission.

*Discussion.* *Pyrodinium bahamense* was first described by Plate (1906) from samples collected near Nassau, Bahamas, and identified by him as one of the light-producing dinoflagellates responsible for the “fiery seas” around those islands. The same organism is responsible for the intense bioluminescence in Bahia Fosforescente and Oyster Bay. The species composition of the dinoflagellate population appears to be similar in both bays.

Diurnal vertical migrations of marine dinoflagellates in the surface waters of a Norwegian fjord have been demonstrated by Hasle (1950, 1954). His studies included three species that are known to be bioluminescent, and one of these, *Gonyaulax polyedra*, is similar to *P. bahamense*. The vertical movements
of the dinoflagellates studied by Hasle were phototactic responses, but the direction of the response varied with the species. For the same midsummer conditions, some species showed a positive response to sunlight and others a negative response. Hasle found that *G. polyedra* migrated to the surface in late afternoon. Discussions of diurnal migrations of dinoflagellates in other environments are presented by Seliger et al. (1961) and Yentsch et al. (1964).

Rhythms in the bioluminescent capacity of dinoflagellates have been established by both laboratory studies (Sweeney and Hastings 1957) and field observations (Backus et al. 1961, Seliger et al. 1961, 1962, Yentsch et al. 1964). In Oyster Bay, at a given station and depth, the variation with time of light produced by stimulation of these organisms is the result of this physiological rhythm superimposed on their vertical migration. When these bay waters are homogeneous with depth, *P. bahamense* migrates to the surface and bioluminescence is especially brilliant, particularly if there is no moon. On evenings such as that of 22 January, when the bay waters are stratified, the brilliant luminescence does not appear at the surface but is as bright as at other times below the thermocline. Samples collected above and below the thermocline showed that very few *P. bahamense* were present in the cooler surface waters but were present in the usual population densities just below the thermocline. Thus it would appear that the vertical migration ceases at the depth of sharp temperature and salinity change.

In Falmouth Harbor, *P. bahamense* has been found in high concentrations only to the east of the sill that separates Oyster Bay from the remainder of the harbor and only in water of both high salinity and high temperature. Further study is required to determine whether the bay acts as a basin in which a slowly reproducing population is maintained for a long time or whether the bay provides an environment for a rapidly multiplying population that is in equilibrium with respect to the loss of the organisms from the bay.

*P. bahamense* has been isolated in pure culture by McLaughlin and Zahl (1961), but its specific nutritional requirements are not yet known. Similar dinoflagellates require vitamin B-12 and thiamin. The phosphate and iron analyses indicate that Oyster Bay waters are high in inorganic nutrients. These waters are probably high also in organic nutrients that could be entering the bay from the river, the stands of mangrove, and as a result of benthic bacterial metabolism. Should there be a natural continuous-growth system in operation, it is possible that nutrients from these sources are added to the characteristically warm and highly saline waters of the bay at the same rate that they are being utilized by the phytoplankton and lost from the bay. The data suggest that these large *P. bahamense* populations photosynthesize at a low rate. The same inference was made by Odum et al. (1959) from primary productivity measurements in Bahia Fosforescente.

The temperature and salinity profiles obtained on 22 January (Fig. 2) suggest a mixing mechanism other than those usually associated with estuarine
systems. The lower temperatures from the surface to mid-depths are simply due to the low salinity runoff being colder than the bay waters. However, the waters in the deepest half meter were not only warmer by several degrees than waters of similar salinity outside the bay, but also warmer than the mid-depth water in the bay. Possibly this phenomenon results from absorption of solar radiation by the fine suspended particulate matter just above the bottom. This would be analogous to the situation found in a Norwegian oyster basin where high concentrations of suspended matter at depths of about 2 m resulted in a temperature increase at that depth (Sverdrup et al. 1942: 110). In Oyster Bay, the unstable temperature gradient that develops during the day would result in mixing within that part of the water column having a uniformly high salinity as the amount of solar radiation declines in the evening. This mixing could not penetrate the intense halocline at about 0.5 m, and complete vertical mixing would not occur until the fresh-water runoff decreased considerably. Such a vertical-mixing phenomenon could be a factor in the upward movement of the phytoplankton just after sundown.

The peak value of 476 m\(\mu\) obtained in the emission spectrum of \textit{P. bahamense} agrees with that obtained by Hastings and Sweeney (1957), who used the extracted enzyme system of \textit{G. polyedra}. In fact, the shape of our curve and that obtained by Hastings and Sweeney are nearly identical except for the more rapid decline of our curve below 460 m\(\mu\). Such an asymmetry on the short wavelength side of the emission spectrum has been observed in our laboratories for a few species of luminous bacteria. Possibly there is some self-absorption within the organisms or in the high concentrations of organisms excited within the volume in front of the entrance slit.

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\textbf{Gray, Peter}

\textbf{Harvey, H. W.}
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KNUDSEN, MARTIN

MCLAUGHLIN, J. A., and P. ZAHL

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SELIGER, H. H., W. G. FASTIE, and W. D. MCELROY

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STRICKLAND, J. D. H.

SVERDRUP, H. U., M. W. JOHNSON, and R. H. FLEMING

SWEENEY, B. M.

SWEENEY, B. M., and J. W. HASTINGS

TYLER, J. E.

YENTSCH, C. S., R. H. BACKUS, and A. WING