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Studies at Oyster Bay in Jamaica, West Indies.
II. Effects of Flow Patterns and Exchange
on Bioluminescent Distributions¹

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ABSTRACT

From July 1966 to July 1967, regular observations and some experiments were carried out in Oyster Bay at the eastern end of Falmouth Harbor, Jamaica, W. I. This paper gives a general description of the area; it reports observations on the tidal movement, the density currents, the wind force and direction, and the water discharge by the Martha Brae River; and it correlates the flow patterns in Oyster Bay with observed bioluminescent distributions. A fluorescent pigment, Rhodamine WT, was used in two experiments to measure the exchange rate of Oyster Bay waters with Falmouth Harbor.

The results indicate that: (i) large variations in bioluminescence observed at a fixed point are produced by the flow patterns rather than by the previously supposed vertical migration of *Pyrodinium bahamense*; (ii) the exchange rate of Oyster Bay waters is high, so that a doubling time of 1 to 2 days must occur to maintain the dinoflagellate populations.

Introduction. The occurrence of high concentrations of the bioluminescent dinoflagellate, *Pyrodinium bahamense*, in Oyster Bay at the eastern end of Falmouth Harbor in Jamaica has already been described on the basis of some short-term field observations in that area (Seliger et al. 1962, Soli 1966, Taylor et al. 1966). Beginning in 1966, a program of regular observations has been carried out to obtain a more complete picture of the phenomenon of bioluminescence and the physical oceanographic features of Falmouth Harbor. Some results of these investigations are reported in this issue (see Seliger and McElroy 1968, Seliger and Fastie 1968).

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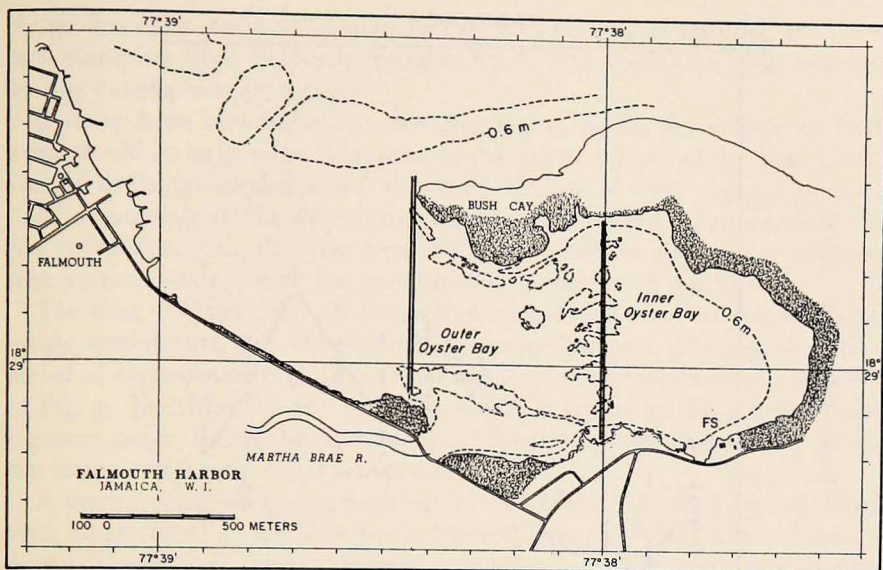


Figure 1. Chart of Falmouth Harbor, revised from British Admiralty chart 451 on the basis of aerial photographs; major changes are along the northern and eastern shores. The double solid lines indicate an arbitrary division of Oyster Bay into two parts. The dashed lines indicate the 0.6-m contour. The location of the fixed station observation position is shown as FS.

This paper gives a general description of the Bay and its oceanographic and meteorological features, correlates the resulting flow patterns with bioluminescent distributions, and reports the results of two dye-tracer experiments used to observe the exchange rate of water between Oyster Bay and western Falmouth Harbor.

Physical Features of Falmouth Harbor. Taylor et al. (1966) have already presented a general description of Falmouth Harbor. Additional information gathered during this extended study allows us to give a more precise description. The revised chart in Fig. 1, based on recent aerial photographs, shows the Falmouth Harbor area, with Oyster Bay at the eastern end divided for convenience into two parts: the inner and outer bays. The surface area of the entire Harbor is approximately $29.4 \times 10^5 \text{ m}^2$; the area of the inner bay is $7.5 \times 10^5 \text{ m}^2$, that of the outer bay, $8.9 \times 10^5 \text{ m}^2$.

The shallows between the two bays were visible on aerial photographs, and their locations were confirmed by lead-line soundings along north-south transects. The channels between the shallows are 1 m deep. Eastward from the shallows, the depth increases to 1.7 m at approximately 100 m from the shallows and then gradually decreases to an extensive area having depths of less than 0.6 m. This large shallow area of soft sediments has developed as a result

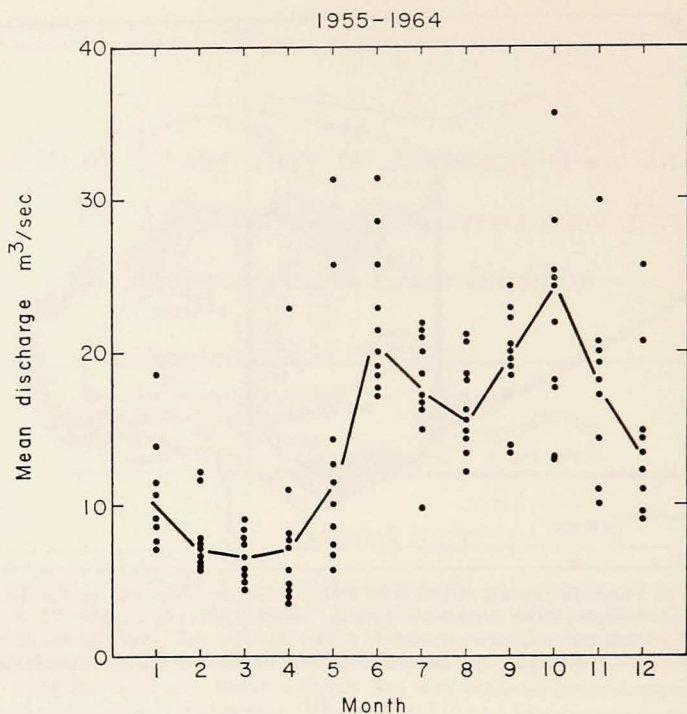


Figure 2. Plot of the mean monthly discharge rate of the Martha Brae River for the years 1955-1964 from records supplied by the Groundwater Research Unit, United Nations Special Fund and the Food and Agriculture Organization, Kingston, Jamaica, W. I.

of protection from the predominant ENE winds by the large mangrove trees along the eastern shore.

The Martha Brae River (hereafter referred to as the River) enters the southern part of the outer Bay. The depth of the extensive shoal at its mouth is only 0.3 m, but the fresh water can pass over the shoal without much restriction, since the vertical section over the shoal is 150 m² and the velocities even at high flow are only 30 cm/sec. While the shoal appears to direct the discharge toward the inner Bay, its effect is minor compared to the other flow-directing factors of tide and wind. Thus, the inner Bay is an unusual estuary with a fresh-water supply that is some variable fraction of the total river discharge.

River Water Discharge, Tide and Wind Observations. While Taylor et al. (1966) described the river as "small" on the basis of visual inspection during a period of low flow, data provided to us by the Groundwater Research Unit of the United Nations Special Fund and by the Food and Agricultural Organization show that the discharge is substantial. The mean monthly rates of dis-

charge for 1955-1964 are shown in Fig. 2. The flow is seasonal, with low flow occurring from February through April. The maximum flow recorded for 1955-1964 was 43 m³/sec.

If these flows accumulated in the Bay for 24 hours, the volume of fresh water would be large when compared to the size and depth of the Bay. Under average discharge conditions of 18 m³/sec, a layer of fresh water 1 m thick could accumulate in the Bay during 24 hours. Since the mean depth of the Bay is less than 1 m, the flow from the river would be adequate to produce, with vertical mixing, very low salinities in the waters of the Bay.

The tides in Oyster Bay, as determined by our own observations, are dominantly semidiurnal, but the diurnal inequality becomes pronounced with a period of approximately 14 days. Two segments of our tidal record are shown in Fig. 3. The March 1967 segment, which is typical of the records, shows a greater range during the dominance of the diurnal components than during the interval of nearly equal semidiurnal tides.

A vertical range of 30 cm, as shown by our March record, is typical. However, ranges up to 45 cm have been observed by us, as shown in the February record. Taylor et al. (1966) observed only a 10-cm range, apparently on a day when a diurnal tide occurred. Although the tidal ranges here are negligible in terms of ordinary navigation, ranges of 30 to 40 cm are large if we consider a mean depth of only 1 m for the inner Bay; this area is so small and shallow that the tidal displacements are nearly simultaneous (travel time, 12 minutes). However, during midtide, the surface elevation may be changing at a rate of 10 cm/hr, so that a 2-cm difference in elevation may exist between the ocean at the Harbor entrance and the eastern end of inner Oyster Bay. The horizontal flows of the saline water associated with the tides are not large. For example, with a surface-elevation change of 35 cm in six hours, the mean speed of flow through the section dividing the two bays would be 0.03 knots and the horizontal displacement during the tide would amount to approximately 350 m.

The wind in the Falmouth area is predominantly diurnal, as shown in Fig. 3. From January 1, 1967 through May 10, 1967, speeds greater than 5 mph throughout the night occurred on only three occasions. The direction of the wind is remarkably uniform, with the most frequent direction being ENE and varying only from NE to E, except during the infrequent storms, which produce N or NW winds that may persist through a night.

The fresh water discharged into the outer Bay by the River may be distributed as a brackish surface layer in various patterns, depending on the tide and wind. While the ENE wind is blowing, the surface brackish layer is forced westward out of the Bay.

Correlation of Flow Patterns and Bioluminescence. To illustrate the effects of various combinations of wind and tide and the resulting flow patterns on

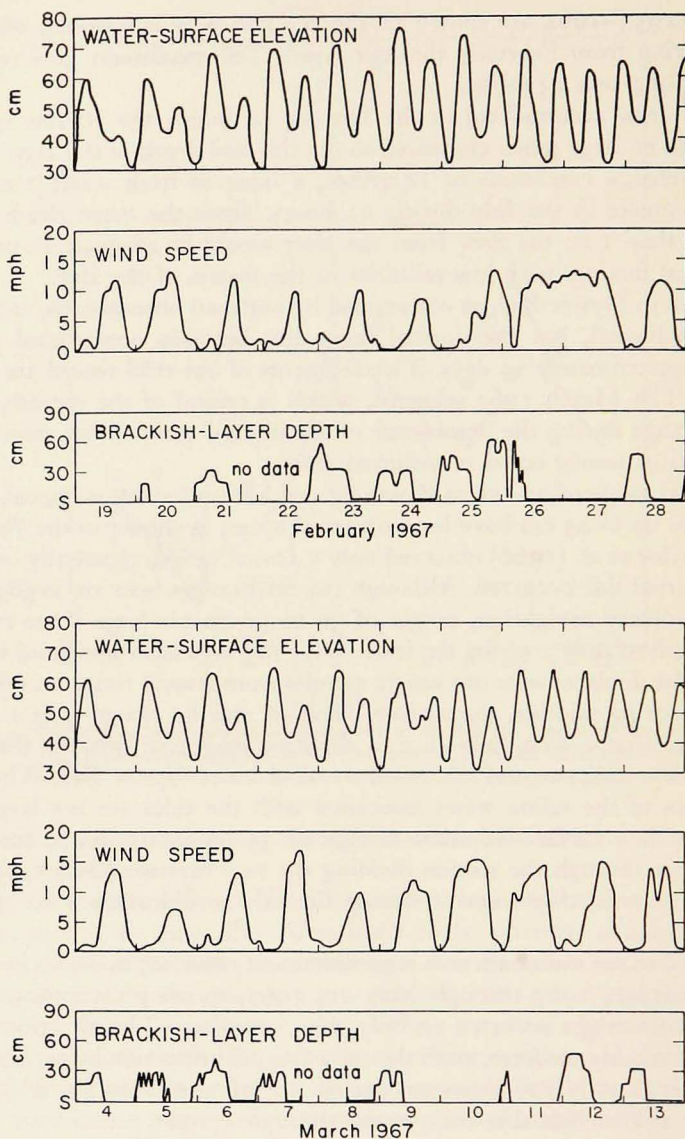


Figure 3. Samples of records of water-surface elevation, wind speed, and brackish-layer depth (salinity of 30‰ or less) for Oyster Bay, February and March 1967, showing the variation in the brackish-layer depth at the fixed station in relation to the wind and tide.

the observed stimulated bioluminescence, we have used data obtained at the fixed station, described by Seliger and McElroy (1968). Figs. 4-7 show plots of data selected to cover the various combinations.

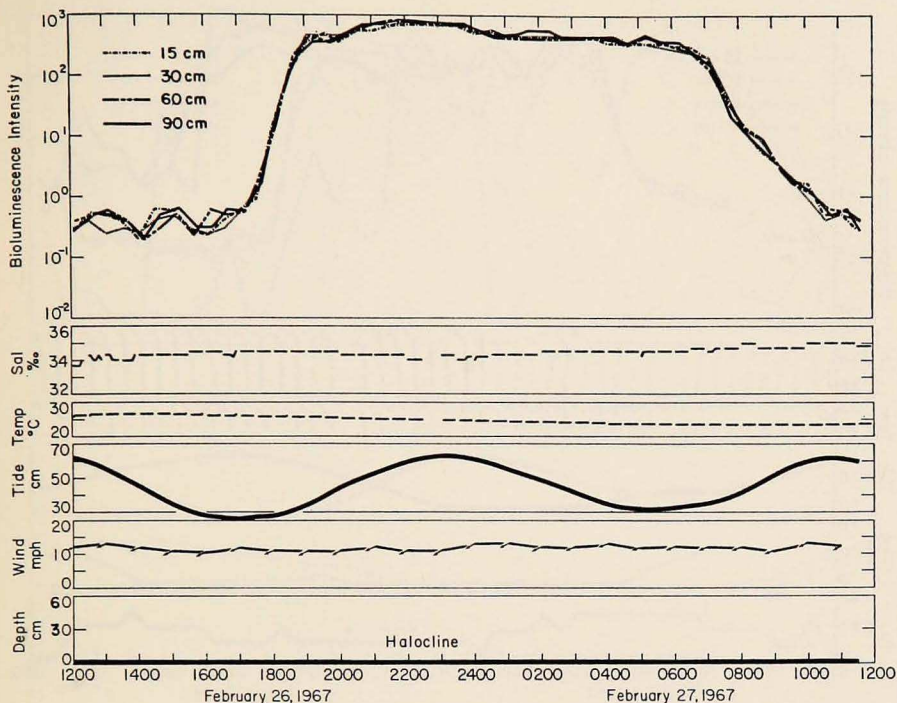


Figure 4. Data for February 26 and 27, 1967. The following observations have been plotted: (i) logarithms of the intensity of stimulated bioluminescence observed at depths of 15, 30, 60, and 90 cm at half-hour intervals; (ii) profiles of salinity versus depth prepared from observations taken at half-hour intervals from 15 to 150 cm; each profile originates at a point on the time axis that corresponds to the time of observation, and the time interval between observations has been divided into six portions, each representing 30 cm of depth; (iii) profiles of temperature versus depth, from the surface to 150 cm; (iv) water-surface elevation; (v) wind speed averaged over one hour; the arrows are dimensionless vectors showing mean direction; (vi) depth of water having salinities of 30‰ or less.

In Fig. 4 are shown the conditions on February 26 and 27, 1967, that produced a rare example of a completely mixed Bay that led to a period of "perfect" diurnal bioluminescence without fluctuations due to variations in the concentration of organisms at the observation point. Since water was flowing constantly past the fixed station, the observed constancy of temperature, salinity, and bioluminescence indicates large-scale lateral uniformity under the observed conditions of persistent wind. The ENE wind throughout the night kept the fresh water out and maintained lateral homogeneity. These data illustrate the dominant role played by the wind in removing or preventing the layering of fresh low-salinity water across the surface of the inner Bay. Usually, by 1800 h the wind had died down and the flooding tide had directed a layer of low-salinity river water (free of *P. bahamense*) toward and across the inner Bay; and by 2000 h, the usual time of peak stimu-

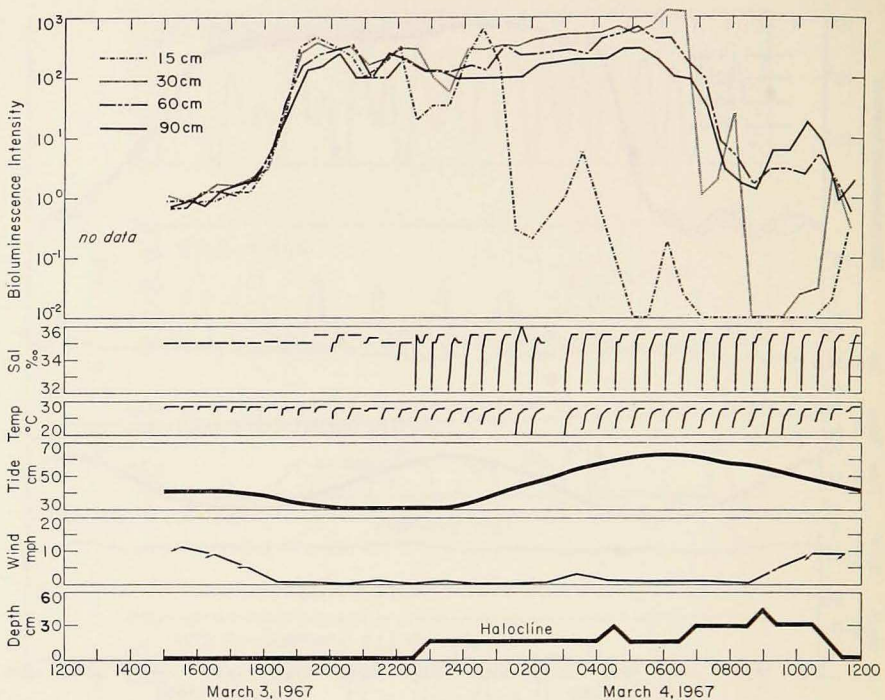


Figure 5. Data for March 3 and 4, 1967. Bioluminescent intensity, salinity and temperature vertical profiles, tide, wind, and halocline depth plotted against time. See Fig. 4 legend for further explanation.

lable bioluminescence per organism, there would be no bioluminescence at the surface.

In Figs. 5-7 are shown progressively deteriorating conditions in the uniformity demonstrated in Fig. 5. Fig. 5 shows that the wind had stopped at 1800 h on March 3, 1967, during an ebbing tide, and that the flooding tide did not begin until approximately 2200 h, after which time fresh water began to layer over the inner Bay. In the salinity-depth profile, the arrows pointing downward indicate that at this depth the salinity had dropped below 32‰. The large fluctuations in stimulated bioluminescence reveal large lateral gradients in the concentrations of *P. bahamense* that flowed past the fixed station during the night. By 0100 h, the low-salinity layer caused the 15-cm reading of stimulated bioluminescence to drop by a factor of more than 1000. By 1700 h, the low-salinity layer was deep enough to cause a decrease in the bioluminescence at 30 cm. By 0900 h, the ENE wind had picked up again, and this, together with the ebbing tide, removed the low-salinity layer. The 30-cm reading and then the 15-cm reading of bioluminescence again increased to the usual daylight value.

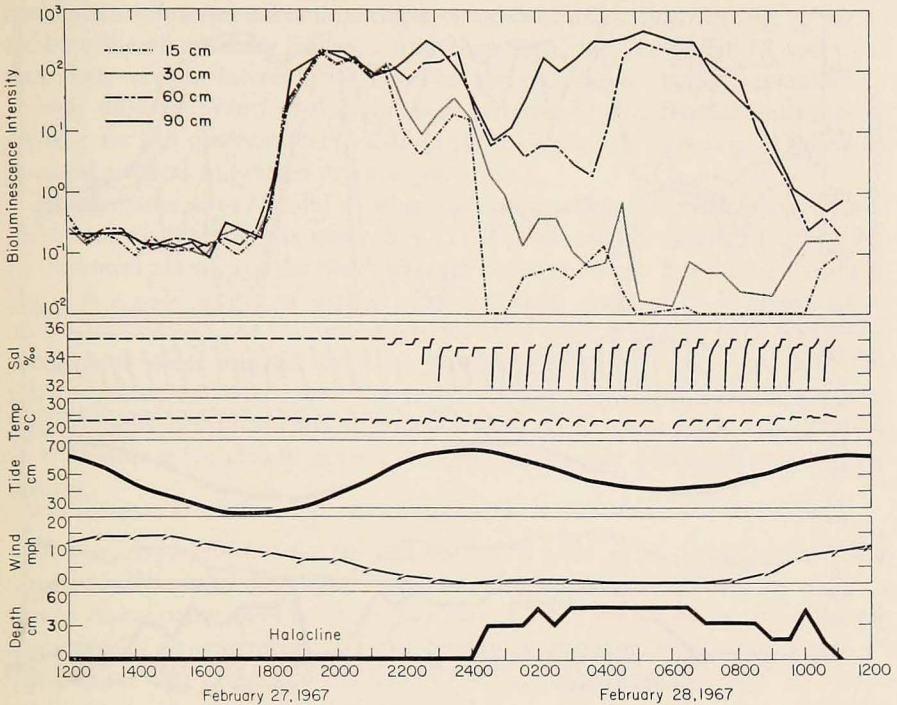


Figure 6. Data for February 27 and 28, 1967. Bioluminescent intensity, salinity and temperature vertical profiles, tide, wind, and halocline depth plotted against time. See Fig. 4 legend for further explanation.

Fig. 6 shows that the flooding tide began at 1800 h on February 27, 1967, but that the ENE wind did not die down until approximately 2000 h, thus effectively keeping the fresh-water layer out of the inner Bay until 2000 h in spite of the flooding tide. Subsequent to 2200 h, the 15-cm and 30-cm readings decreased, and the 60-cm and 90-cm readings were perturbed as well. At 1000 h on February 28, 1967, the ENE wind came up, fresh water was forced out of the inner Bay, and the Bay water approached the well-mixed conditions that we obtained from 1200 to 2200 h on the previous afternoon.

Fig. 7 shows some unusual conditions. On the morning of February 25, 1967, there was a flooding tide and an unusually light ENE wind. It is not clear whether the wind speed was sufficient to prevent a fresh-water layer from spreading across the inner Bay, but we have assumed, on the basis of the slight salinity gradients at 1200 h and 1230 h, that a small amount of fresh water did enter the inner Bay during the flooding tide. Then the wind, instead of dying, changed direction at 1230 h and blew from the north (as the result of an offshore storm). In concert with the flooding tide, this N wind directed

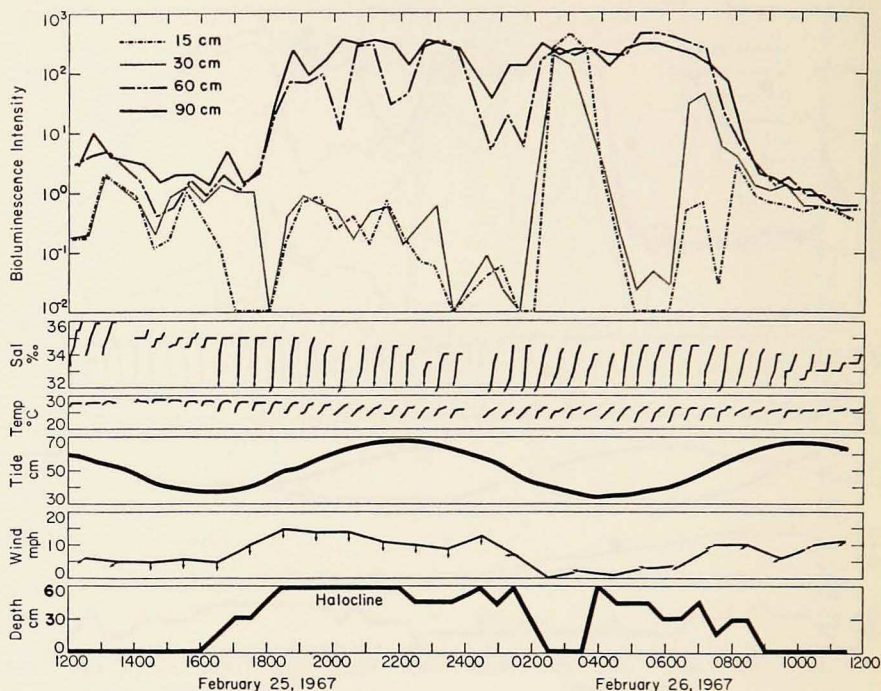


Figure 7. Data for February 25 and 26, 1967. Bioluminescent intensity, salinity and temperature vertical profiles, tide, wind, and halocline depth plotted against time. See Fig. 4 legend for further explanation.

a fresh-water layer across the inner Bay prior to the evening rise in stimulative bioluminescence. The large fluctuations in the intensities of observed bioluminescence resulted from the patchy concentrations in the lateral distribution of *P. bahamense*. At 0030 h, a temporary change in wind direction from north to east and an ebbing tide produced a temporary removal of the fresh-water layer; the bioluminescence at intensities of 15 and 30 cm increased. By 0230 h, the wind had died down completely and the fresh-water layer returned. By 0700 h the normal ENE wind had returned, and by 0900 h the fresh-water layer had again been removed from the inner bay, despite a flooding tide.

The rate of water discharge from the river has little effect on the depth of fresh water in the inner Bay. For the conditions shown in Fig. 7, the daily average river flow was only 4.8 m³/sec; for the conditions in Fig. 4, the river flow was 13.6 m³/sec, nearly three times greater.

It may be seen in Figs. 5-7 that accumulations of low-salinity *P. bahamense*-free river water in a surface layer could be incorrectly interpreted as downward vertical migration of organisms. Fluctuations due to horizontal gradients in the concentration of organisms in the water that passed by the fixed station

could also be interpreted as downward or upward migrations. In Fig. 4, where we have shown ancillary evidence from data on salinity, temperature, and wind that there are no lateral gradients, the observations on bioluminescence are entirely uniform. We feel that the flow patterns for this Bay are sufficient to account for the observations by Soli (1966) without the necessity of invoking nocturnal vertical migration as an explanation.

In the course of our study, we observed on numerous occasions a luminescent band advancing across the inner Bay. This phenomenon usually accompanied the eastward advance of the brackish layer across the inner Bay during darkness. Fig. 8 is a photograph of such a luminous band observed in February 1966 on a calm evening. At the time there was low river flow, the band was a few centimeters wide, and the brackish layer was approximately 1 cm thick; its rate of movement was approximately 20 cm/sec. On other occasions a less-brilliant band, several meters wide and several centimeters thick, was observed as it moved more slowly against a light breeze that produced some vertical mixing.

Tracer Experiments. As pointed out by Taylor et al. (1966), their data were insufficient 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." We have made direct measurements of the exchange rate of Bay water with the ocean water in western Falmouth Harbor by releasing dye in the inner Bay and following its distribution with time. One tracer experiment was performed under conditions of high river-discharge rate (November 1966) and another was performed under conditions of low river-discharge rate (February 1967).

PROCEDURE. Rhodamine WT (Du Pont de Nemours Co., Inc.), a fluorescent water-soluble pigment that can be excited by green light to emit an orange fluorescence, was used in all tracer experiments. Standard solutions of Rhodamine WT, prepared in distilled water and in Bay water, showed identical intensities of fluorescence. The tracer was introduced into the Bay waters as a 20% w/w solution in methanol and ethylene glycol. Late afternoon was chosen as the time of introduction because the brackish-water layer was absent and only the high-salinity water would be tagged. The solution was discharged 0.8 m below the surface along continuous lines; within 10 minutes, vertical mixing had brought part of the tracer to the surface; this action created essentially a vertical plane of water containing the dye.

Dye concentrations were determined by pumping water through a flow cuvet in a Turner Model III fluorometer (Turner Associates, Palo Alto, California) on board the survey boat. A continuous recording of the concen-



Figure 8. Photograph of a luminescent band—3 cm wide—that moved eastward across Oyster Bay from 1900 h to 2000 h on February 26, 1966. Photograph taken by Beatrice Sweeney.

tration at a particular depth along a prescribed transect was obtained by positioning the intake of the sampling hose in a faired strut that could be towed at that depth at speeds up to 10 knots. Vertical profiles at a fixed location were obtained by raising and lowering the intake.

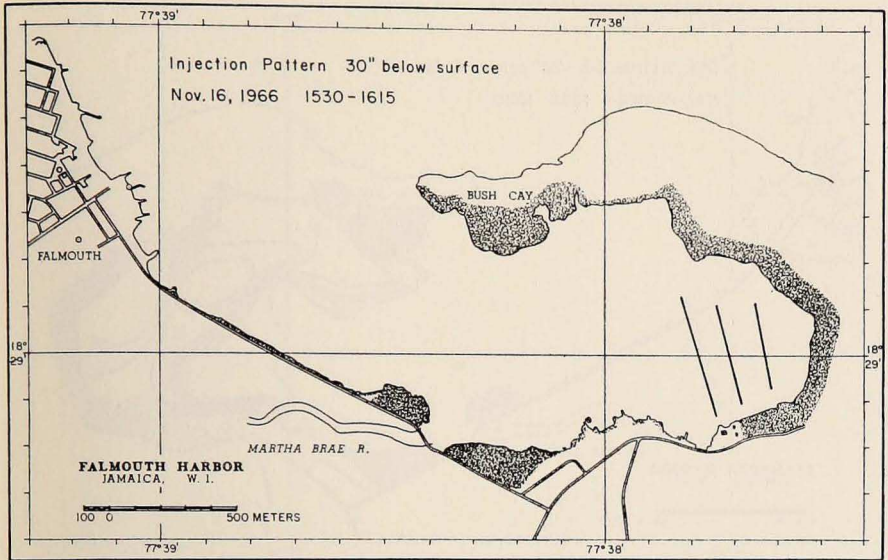


Figure 9. Courses along which dye was released at the beginning of Expt. 1.

EXPERIMENT 1. In this study the dye was discharged in the central and eastern parts of the inner Bay when the flow from the river was high (31–33 m³/sec). The tracer was discharged from 1515 h to 1545 h on 16 November 1966 along three transects in the inner Bay (Fig. 9); a total of 306 g of dye was released.

By noon on November 17 (18 hours after discharge), circulation and turbulent diffusion had distributed the tracer as shown in Fig. 10. This distribution was determined at the end of flood tide, hence the observed displacement seaward was not caused by the most recent tide. At this time there was no evidence of the tracer beyond Oyster Bay as defined in Fig. 1. The low concentration found in the southern half of the inner Bay suggests that inflow occurs primarily in this area. Although high concentrations of the tracer were retained around the perimeter of the Bay, particularly along the southern shore, the bulk of the dye was in the northern half of the Bay.

At 0800 h on November 18 (39 hours after discharge), measurable concentrations of the dye, at the end of ebb tide, were present in western Falmouth Harbor beyond Oyster Bay (Fig. 11). The previous pattern of drift, establishing the higher concentrations in the northern area of Oyster Bay, had persisted. At 1400 h on November 18 (45 hours after discharge), the pattern was similar to that observed at 0800 h on this same day (Fig. 11), but detectable concentrations were not present in Falmouth Harbor beyond Oyster Bay, and in the inner Bay the concentration was uniformly 0.20–0.23 ppb.

On November 19 at 0900 h (64 hours after discharge), the observable dye

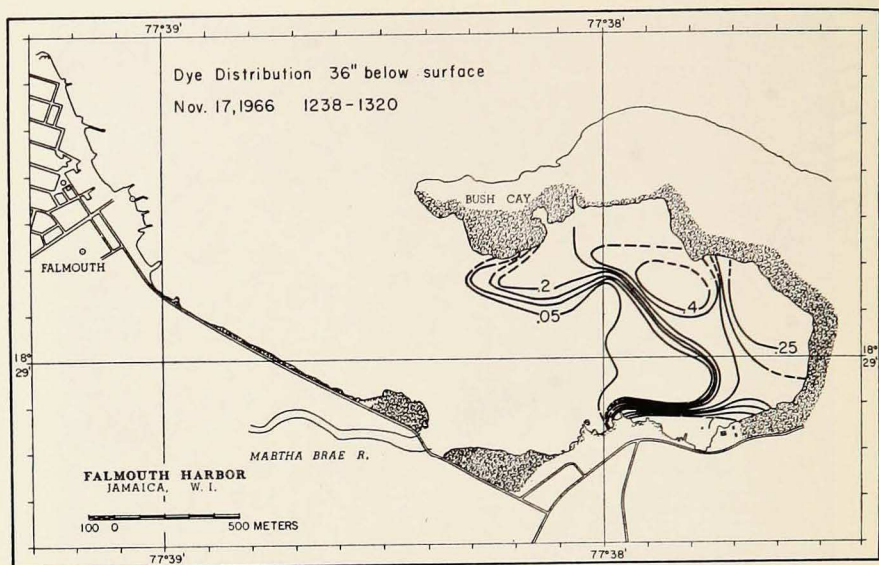


Figure 10. Contours of the dye distribution interpolated from the observed concentrations along continuous transects—approximately 18 h after release of the dye in Expt. 1.

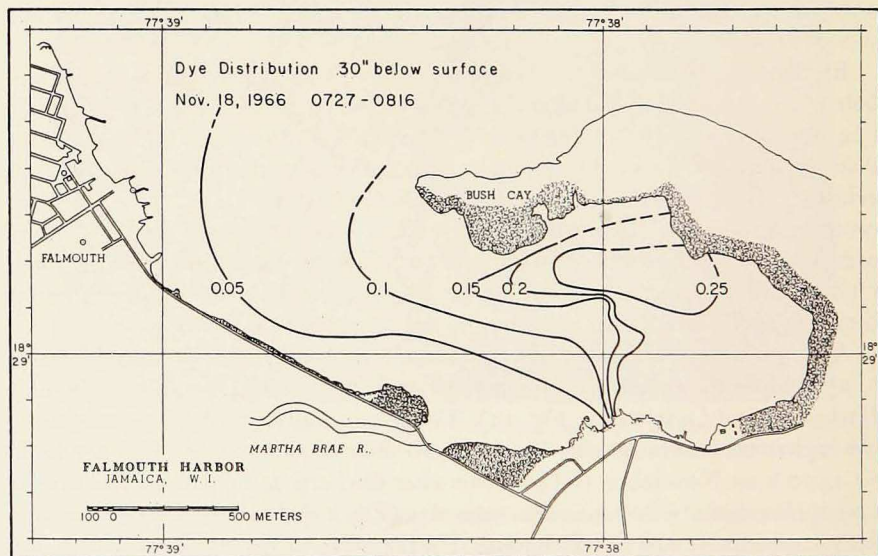


Figure 11. Contours of the dye distribution interpolated from the observed concentrations along continuous transects—approximately 39 h after release of the dye in Expt. 1.

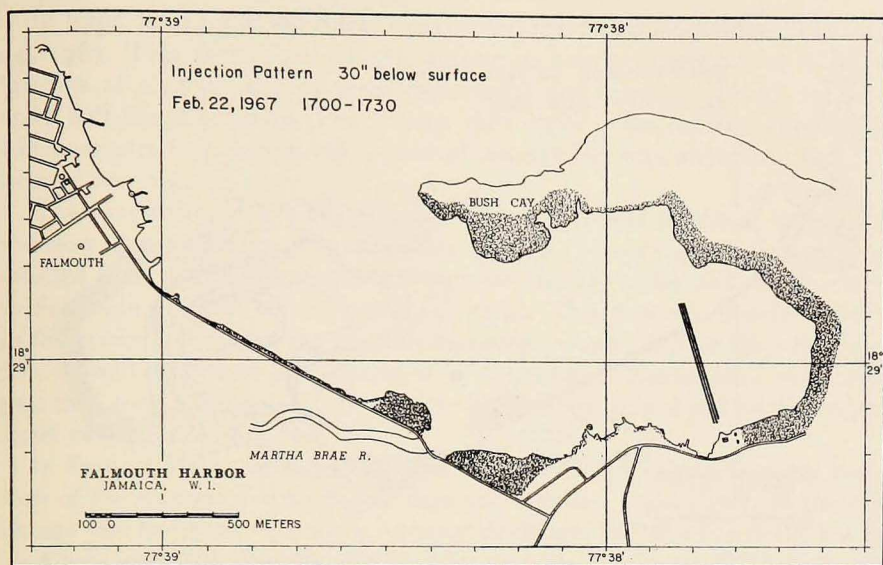


Figure 12. Courses along which dye was released at the beginning of Expt. 2.

was uniformly distributed throughout the inner Bay at concentrations of 0.10–0.12 ppb and in the outer Bay at concentrations of 0.05–0.07; the concentration transition occurred in the shoal area between the two bays.

EXPERIMENT 2. The dye was distributed along three closely spaced transects, approximately in the center of the inner Bay, on February 22, 1967, at 1500–1530 h during low river discharge (Fig. 12); 400 g of Rhodamine WT were released. The horizontal distributions on February 23 and 24 are shown in Figs. 13 and 14.

DISCUSSION. We have estimated that, of the 306 g of dye originally discharged in Expt. 1, 135 g of the tracer remained in Oyster Bay at 0900 h on November 19, 1966—44% of the dye discharged. If this loss of 56% during 64 hours took place by movement of discrete layers or zones, without recirculation, then a linear decrease in the dye inventory with time would be expected, and the observed inventory would correspond to a loss rate of 0.21 per day. If the loss were produced entirely by turbulent diffusion, with no large-scale flows, an exponential decrease in the dye inventory would be expected and the observed inventory would correspond to a loss-rate constant at 0.31 per day and to a half-life of 2.2 days. The actual process includes both large-scale flow and turbulent diffusion; we estimate from the above that the fractional loss of dye is 0.25 per day and that the doubling time of the dinoflagellate population must be roughly two days to offset the loss of cells from Oyster Bay.

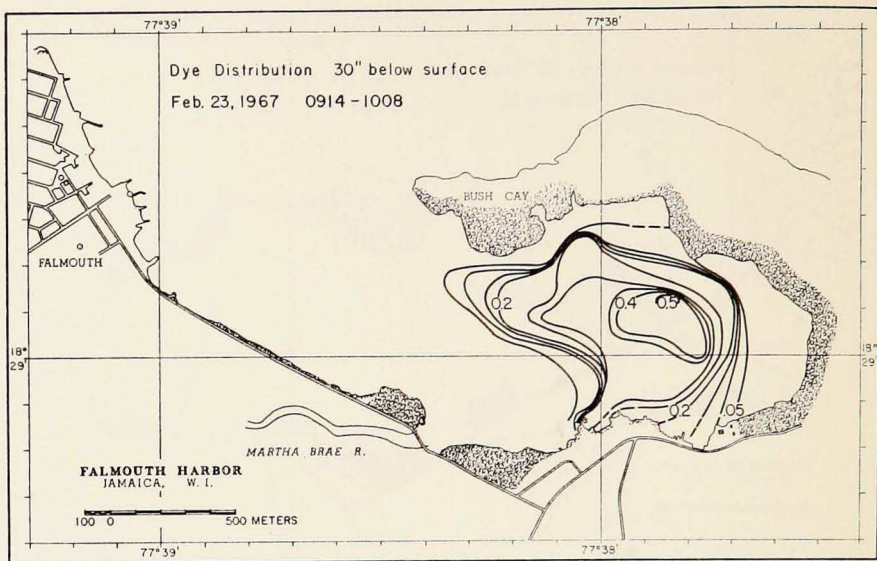


Figure 13. Contours of the dye distribution interpolated from the observed concentrations along continuous transects—approximately 17 h after release of the dye in Expt. 2.

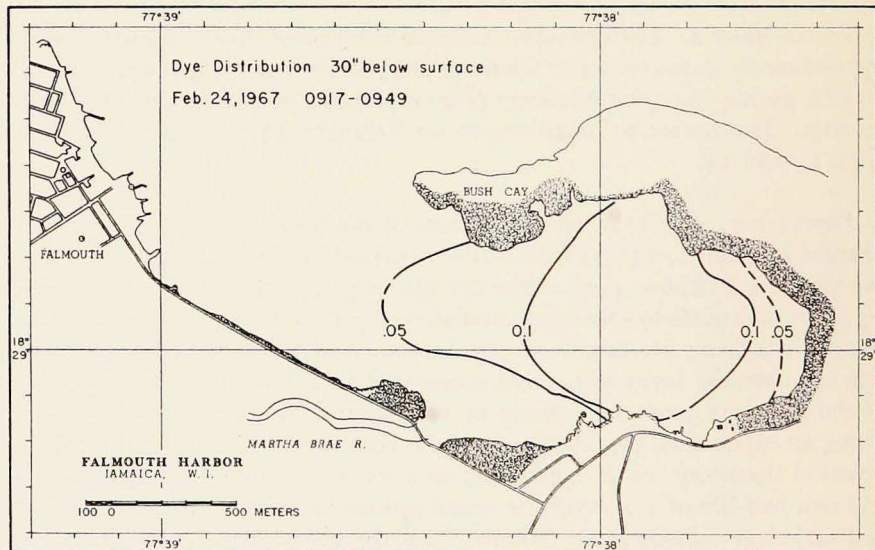


Figure 14. Contours of the dye distribution interpolated from the observed concentrations along continuous transects—approximately 40 h after release of the dye in Expt. 2.

In Expt. 2, 114 g of the tracer remained in the Bay at 0930 h on February 24, 1967. This decrease of 71.5% during 40 hours corresponds to a linear loss rate of 0.42 per day or to an exponential rate constant of 0.55 per day and a half-life of 1.3 days. The division time required for constant dinoflagellate concentrations during this period of observation was, therefore, approximately one day.

The movement of dye out of inner Oyster Bay was produced largely by the slow flow of water of intermediate salinity (33–34‰); this movement resulted from the density differences between the bay water and the seawater in Falmouth Harbor (salinities 36.0–36.5‰). This flow was clearly evident in the vertical profiles of the dye concentration in outer Oyster Bay; the profiles showed maximum concentrations at intermediate depths, with very little (less than 0.02 ppb) at the surface in the low-salinity waters and in the deeper water of higher salinity.

In Expts. 1 and 2, with high and low river discharge, respectively, the half-lives of the released dye were two days and one day, respectively. If the exchange rate had been dependent on river discharge, the opposite result might have been obtained. But the results show that the density flow, which is primarily responsible for the exchange, may be produced during periods of low river discharge to an extent that is equal to, or greater than, the density flow produced under high river discharge. The intensity of the density flow should vary with salinity differences between the Bay and oceanic waters, and these differences appear to depend on the intensity of vertical mixing in the inner Bay rather than on the rate of fresh-water supply.

During Expt. 1 on November 17, 1966, a considerable quantity of the released dye remained along the south shore of the inner Bay (Fig. 10) and then passed into the central portion of the inner Bay on November 18, 1966. This sequence did not occur during experiment 2. The delay during Expt. 1 between discharge and relatively uniform distribution throughout the inner Bay led to a longer residence time of the dye than would occur in the absence of this sequence; and the results of Expt. 1 may be biased toward longer apparent retention than is typical.

Our "best" estimate of the half-life of planktonic organisms in the inner Bay is 1.5 days—considering only the losses produced by physical processes. The observed steady dinoflagellate-population levels can be maintained only if the division time of *P. bahamense* in the inner Bay is frequently 1 to 2 days. This inferred division rate is in contrast to the division times of three days or more observed in our laboratory cultures.

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