YALE PEABODY MUSEUM

P.O. BOX 208118 | NEW HAVEN CT 06520-8118 USA | PEABODY.YALE. EDU

JOURNAL OF MARINE RESEARCH

The *Journal of Marine Research*, one of the oldest journals in American marine science, published important peer-reviewed original research on a broad array of topics in physical, biological, and chemical oceanography vital to the academic oceanographic community in the long and rich tradition of the Sears Foundation for Marine Research at Yale University.

An archive of all issues from 1937 to 2021 (Volume 1–79) are available through EliScholar, a digital platform for scholarly publishing provided by Yale University Library at https://elischolar.library.yale.edu/.

Requests for permission to clear rights for use of this content should be directed to the authors, their estates, or other representatives. The *Journal of Marine Research* has no contact information beyond the affiliations listed in the published articles. We ask that you provide attribution to the *Journal of Marine Research*.

Yale University provides access to these materials for educational and research purposes only. Copyright or other proprietary rights to content contained in this document may be held by individuals or entities other than, or in addition to, Yale University. You are solely responsible for determining the ownership of the copyright, and for obtaining permission for your intended use. Yale University makes no warranty that your distribution, reproduction, or other use of these materials will not infringe the rights of third parties.



This work is licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License. https://creativecommons.org/licenses/by-nc-sa/4.0/



SPRING CHANGES IN PHYTOPLANKTON ABUNDANCE IN A DEEP ESTUARY, HOOD CANAL, WASHINGTON¹

By

JOHN P. BARLOW

Department of Conservation, Cornell University Ithaca, New York

ABSTRACT

Spring changes in abundance of plankton pigments (Jan.-May, 1953) in Hood Canal, a deep estuary on the coast of the State of Washington, are described. Since there was a less dense brackish surface layer throughout the period of observation, these changes in plankton abundance are not a result of changes in the stability of the water column such as those that initiate spring flowering in temperate coastal waters. Rather, they appear to have been brought about by seasonal changes in solar radiation and transparency which caused marked differences in the depth of the euphotic zone and in the mean illumination in the mixed surface layer. As a result there were great seasonal changes in the rate of photosynthesis of the population in the mixed surface layer with which the general changes in phytoplankton abundance were related.

INTRODUCTION

The spring diatom flowering in temperate waters offers an outstanding illustration of the significance of a stable water column for the development of abundant phytoplankton populations. In positive estuaries, stability is almost wholly a result of dilution rather than warming. Since the occurrence and characteristics of a stable surface layer in deep estuaries will depend much more on seasonal changes in salinity than on temperature, we may anticipate some distinct and interesting differences in the development of phytoplankton populations in estuaries as compared to open coastal and offshore regions. These differences are generally most apparent in the spring of the year when the populations are changing most rapidly. The purpose of the present paper is to demonstrate

¹ Contribution No. 223 from the Department of Oceanography, University of Washington, Seattle 5, Washington. This work was supported in part by Contract N8ONR - 520/111, Project NRO83-012, with the Office of Naval Research. Publication was supported in part by the Agnes H. Anderson Fund of the University of Washington.

Journal of Marine Research

the significance of physical and chemical changes in the surface layer to changes in phytoplankton abundance in the spring of the year in a deep estuary, Hood Canal, Washington.

METHODS

Hood Canal is one of the deep natural channels in the Washington coastline (Fig. 1). From its connection with Admiralty Inlet in the north to its southern extremity the entire canal is about 50 miles long. However, this study is concerned principally with the 30-mile portion south from Quatsap Point, south of which the Canal is nearly straight for a stretch of 20 miles, with a width of about a



Figure 1. Hood Canal, Washington. Numbers indicate locations of stations.

mile and uniform depths of 75-90 m. As it bends abruptly to the east it begins to shoal, reaching depths of 5 or 6 m in the last two or three miles.

This southern half of the Canal receives fresh water from a number of rivers and small streams draining the surrounding mountainous country. The largest of these is the Skokomish River (drainage area, 230 mi²) which originates at elevations of 4,600 to 5,000 ft. in the western Olympic Mountains and empties into the southwestern angle of the Canal. Two other rather large streams enter the Canal's western shores: the Duckabush (drainage area, 65 mi²) at a point three miles north of St. 5 and the Hamma Hamma (drainage area, 50 mi²) about three miles south of St. 5. The remainder of the fresh water enters through a number of smaller streams along both shores and by direct runoff.

During the period of this study, the Water Resources Division of the U.S. Department of the Interior maintained gages on five of the rivers in this area: the Union, Tahuya, Skokomish, Dewatto and Hamma Hamma, accounting for about $68 \, ^{0}/_{0}$ of the total drainage area of around 620 mi². Total stream flow into the Canal below Quatsap Point was estimated by dividing the drainage area of that part of the Canal (as determined from U.S. Geological Survey topographic maps) into four sections, each containing one or more gaged streams. The areas in each section drained by ungaged and gaged streams were determined with a planimeter, and the total drainage was estimated from the stream flow records and from the proportion of gaged to ungaged areas. No attempt was made to account for direct runoff or seepage.

Daily solar radiation measured at the Seattle-Tacoma airport about 30 miles east of the Canal has been published in U. S. Weather Bureau Climatological Summaries. This Weather Bureau Office has also provided unpublished hourly radiation measurements for each sampling day.

Observations were made during regular monthly hydrographic surveys of Puget Sound by the R. V. BROWN BEAR, operated by the Department of Oceanography, University of Washington. After a preliminary study in November 1952, surveys were made January 22, February 18–19, March 17–18, April 17–18 and May 20–21, 1953. Phytoplankton, salinity, temperature and transparency were measured at a number of stations along the entire north-south axis of the Canal, including the five that were regularly occupied in the southern portion, as indicated in Fig. 1. Salinity and temperature were sampled with Nansen bottles and reversing thermometers at standard depths from surface to bottom. Separate casts with 2.5 liter Atlas bottles sampled the phytoplankton at from four to six depths in the upper 50 to 75 m, with four samples usually being taken in the upper 25 m. From 25 to 40 phytoplankton samples were taken on each of the 1953 cruises.

Salinity was determined by titration with silver nitrate. The mean salinity in various sections of the region was estimated with a planimeter from plots of the vertical distribution of salinity. The fraction of fresh water in each section was estimated (Ketchum, *et al.*, 1951) by assuming that fresh water had mixed with sea water of the maximum salinity found in the region during each cruise. This base salinity varied from 30.80 to $31.87 \,^{\circ}/_{00}$. Total fresh water was estimated from this fraction and from the total volume of each section as determined from bathymetric charts (U.S.C. & G.S. # 6450 and # 6460) of the region. The flushing time in days was determined by summing cumulatively the daily total river flow preceding each survey until it equaled the total accumulated fresh water.

Phytoplankton abundance was estimated from one or two liter samples concentrated with a Foerst continuous centrifuge. After drying, pigments were extracted with 90 $^{0}/_{0}$ acetone and stored in the dark in a freezing locker until the ship returned to Seattle. Concentrations of chlorophyll *a* were then determined spectrophotometrically with a Beckman DU Spectrophotometer after the method of Richards with Thompson (1952). Mean concentrations of chlorophyll *a*, determined with a planimeter from plots of the vertical distribution, were weighted according to the volume of each section.

Samples for phosphate determinations were taken at standard depths during the April and May cruises. Soon after collecting, determinations of inorganic phosphate were made by the colorimetric method of Robinson and Thompson (1948).

Transparency was measured from January through April with a hydrophotometer in which an unfiltered photocell was exposed to an incandescent light source through a fixed light path. This instrument was unavailable for the May cruise, when transparency had to be determined by the Secchi disc. Secchi disc depths (D) were converted to extinction coefficients (k) by the relation k = 1.7/D (Poole and Atkins, 1929).

RESULTS

SEASONAL CHANGE IN PHYTOPLANKTON ABUNDANCE

The principal features of the seasonal changes in abundance as indicated by chlorophyll a concentrations are shown in Fig. 2. The low abundance that had been observed in the preliminary survey



Figure 2. Vertical distribution of Chlorophyll $a (mg/m^3)$ in upper 50 m. Depth in meters. Numbers on abscissa indicate stations; QP = Quatsap Point.

in November continued in January when the weighted mean concentration in the upper 20 m was about 0.5 mg/m^3 . A slight increase in February, confined to a thin surface layer in the southern end, brought the mean to 1.1 mg/m^3 . By March, however, there had been a general increase to maximum values of over 10 mg/m^3 , resulting in a mean concentration of 8.8 mg/m^3 in the upper 20 m. In April, abundance was reduced to less than a quarter of that in the previous month, with the mean concentration falling to 1.9 mg/m^3 . Subsequently the population again increased throughout the surveyed region and attained a mean concentration of 18.8 mg/m^3 . The most striking feature of these seasonal changes is certainly the decrease in population between March and April. This decrease was much greater in the region from Skokomish River seaward than in the region east of this River (Sts. 1 and 2).

SEASONAL CHANGES IN ENVIRONMENTAL FACTORS

Salinity. Fig. 3 shows that there was always a mixed brackish surface layer which varied in depth from about 5 to 20 m. Below this layer the salinities were so much higher that nearly all of the fresh water was evidently confined to this upper layer. The maximum amount of fresh water was observed in the mid-February survey (Table I), some three weeks after the peak river flow of the year. Although runoff decreased from 36×10^6 to 7×10^6 m³/day during the month of February, the fresh water had not yet fallen much by March 17. The continued decrease in April, despite the relatively small changes in runoff, evidently represents a continuing adjustment to the larger change in runoff that took place earlier. Thus, during the first four months there was a rapid increase in



Figure 3. Vertical distribution of salinity $(^{0}/_{00})$ in upper 50 m. Depth in meters. Numbers on abscissa indicate stations; QP = Quatsap Point.

Date	Wgtd. Mean Salinity (º/00)	Aver. River Flow for Pre- ceeding 30 Days (10 ⁶ m ³ /day)	Accumula- ted Fresh Water (10 ^e m ³)	Flushing Time, Days River Flow Accumulated	Mean S.R. of Week Preceeding (g cal/cm²/ day)	S.R. for Day of Ob- servations (g cal/cm ² / day)
January 21–22	28.31	27	525	15	34	42
February 18-19	27.24	23	700	30	113	144
March 17-18	28.56	9	610	46	231	322
April 17-18	28.83	7	390	59	347	407
May 20-21	28.47	9	440	67	374	455

TABLE I. SALINITY, RIVER FLOW, AND FLUSHING TIME IN UPPER 20 M OF HOOD CANAL, WASHINGTON IN 1953, AND SOLAR RADIATION TAKEN AT SEATTLE-TACOMA AIRPORT BY U.S. WEATHER BUREAU OFFICE

flushing time. Between the April and May observations there was an increase in accumulated fresh water which resulted in another somewhat smaller increase in flushing time.

In contrast to the surface layer, the deep water changed so little in salinity from February through May that the fresh water content is considered to have been practically constant. Examination of temperature-salinity relations in various parts of the Canal indicates that small decreases in salinity of the bottom water were due to intrusion of colder and more dilute water from the north.

Temperature. The temperature of the surface water varied from a minimum of about 8° C in January to a maximum of about 12.5° C in May while the deeper water showed some small decreases in the same period. These seasonal changes in temperature were so small when compared to the seasonal changes in radiation and transparency that it seems unlikely that they could have had important effects on the seasonal changes in growth and photosynthesis of the phytoplankton. They will not, therefore, be considered further.

Phosphate. At the time of the April cruise, inorganic phosphate was everywhere greater than $1.0 \ \mu g$ -at/l, except at the surface at Sts. 1, 2 and 3, where minimum values of 0.7 to 0.9 may be accounted for on the basis of dilution with nutrient-poor river water. In May, at the time of maximum observed populations, there was some evidence of increasing nutrient depletion above 5 m, but even then the minimum phosphate values were mostly above $0.4 \ \mu g$ -at/l.

1958]

Radiation and Transparency. Weekly mean solar radiation is shown in Fig. 4. Since radiation on the principal sampling day of each survey did not differ markedly from mean daily radiation in the week preceding (Table I), radiation measurements on those days



Figure 4. Solar radiation, November 1952-May 1953. Weekly means at Seattle-Tacoma Airport. Arrows indicate time of surveys.

have been taken to represent both total radiation and hourly changes in radiation to which the phytoplankton had been exposed in the period immediately preceding each sampling.

During the first months of the year the water was exceptionally turbid, with greatest extinction coefficients at the surface in the southernmost portion (Table II). It was obvious, when sampling during periods of peak river flow in January and February, that this turbidity in the early part of the year was due to suspended matter brought in by river water. Maximum transparency occurred in April during a period of low river flow and of relatively small phytoplankton populations. It is probable that the subsequent increase in extinction coefficients in May was due to the greatly increased phytoplankton population. Riley (1956) has recently shown that in nonturbid offshore waters the relation between extinction coefficients, k, and the plant population may be given by

$$k = 0.04 + 0.0088 C + 0.054 C^{*/3}$$

in which C is the concentration of chlorophyll a in mg/m³. This relation has been used here to estimate the extinction by the phyto-

8] Barlow: Spring Changes in Phytoplankton

 TABLE II. EXTINCTION COEFFICIENTS AND DEPTH OF EUPHOTIC ZONE OF HOOD

 CANAL, WASHINGTON. INDIVIDUAL VALUES GIVEN FOR STS. 1, 3 AND 5; MEANS

 INCLUDE ALL STS. 1-5 (SEE FIG. 1). DEPTHS BASED ON RADIATION VALUES IN

 TABLE I. SEE TEXT FOR FURTHER EXPLANATION

Month	Station	Measured Extinction Coefficient, k.	Estimated Extinction by Phytoplankton,	h ().	Depth of Euphotic Zone
Tanuany			~p	^k p ^{/k} t	(<i>m</i>)
January	1	_	STREET, STREET	-	1.2*
	3	1.45	0.09	0.06	2.0
	5	1.06	0.11	0.10	1.7
Mean, Sts. 1–5		1.06	0.10	0.09	1.8
February	1	2.25	0.16	0.07	1.4
	3	0.81	0.14	0.17	4.0
	5	0.39	0.10	0.25	5.0
Mean, Sts. 1-5		1.16	0.14	0.16	3.5
March	1	1.50	0.20	0.13	2.4
	3	1.08	0.16	0.15	3.4
	5	0.93	0.41	0.44	3.7
Mean, Sts. 1-5		1.17	0.25	0.22	3.3
April	1	0.36	0.16	0.44	12
	3	0.41	0.19	0.46	18
	5	0.30	0.14	0.47	16
Mean, Sts. 1-5		0.35	0.18	0.51	16
May	1	0.49	0.28	0.57	8
	3	0.68	0.41	0.60	6
	5	_	0.52	_	6**
Mean, Sts. 1-5		0.55	0.41	0.61	7

* Surface transparency from St. 3 was used to supply missing value.

** Assuming transparency to be the same as at St. 3.

plankton, k_p , from January through April at all depths for which hydrophotometer measurements of total extinction, k_i , were available. In May the approximate extinction coefficients of populations in the upper 5 m were determined. These were compared with Secchi disc measurements which gave the extinction in about the upper 5 m also. These estimated extinction coefficients are shown in Table II. It can be seen that the fraction of total extinction due to phytoplankton, k_p/k_i , increased as the phytoplankton increased

1958]

in the early spring and then remained about the same in April and May.

It appears from an examination of the relation between salinity and transparency that the turbidity of incoming river water must have decreased as extinction by the phytoplankton increased. On each cruise in February, March and April there were 18 simultaneous measurements of transparency and salinity in the upper 20 m at Sts. 1–5. If it is assumed that the nonphytoplankton extinction, $k_t \cdot k_p$, in a given water sample with salinity S_x is the result of simple dilution of turbid fresh water by clear ocean water, then one would expect to find a simple relation between the proportion of river water as represented by salinity and nonphytoplankton extinction. The empirical relation between extinction and salinity for these three months was found by least squares to be:

> February, $k_t \cdot k_p = 4.46 - 0.147 \ (S_x);$ March, $k_t \cdot k_p = 4.01 - 0.129 \ (S_x);$ April, $k_t \cdot k_p = 0.54 - 0.015 \ (S_x).$

It is obvious that no great reliance can be placed on these expressions, since transparency will certainly be affected by other processes, such as settling. However, they do give at least some indication of the magnitude of the seasonal change in the turbidity of river water, which is here estimated as having a k that is greater than 4.0 in February and March but is only 0.54 in April.

Seasonal changes in radiation and transparency, such as those outlined above, may be expected to result in marked changes in the depth of the euphotic zone. For present purposes the bottom of this zone has been set at the depth at which light is reduced to the compensation intensity observed by Jenkin (1937) in the English Channel, i. e., $3 g \operatorname{cal/cm^2/day}$. The approximate depths at which this intensity occurred were determined from radiation and transparency data (see Table II). Note that in the early part of the year the euphotic zone was extremely thin; in fact, somewhat different assumptions about the compensation intensity and about the vertical variation of transparency would certainly have resulted in defining a euphotic zone that was at times only a few centimeters in depth. Nonetheless there can be little question that there were increases in the depth of this zone between January and March and that the simultaneous increase in radiation and transparency in April must have resulted in a more pronounced deepening of the euphotic zone. The subsequent decrease in its depth in May is clearly the result of large increases in phytoplankton.

DISCUSSION

During this survey, changes in temperature and salinity seem too small to have had important physiological effects, and the phosphate distribution suggests that nutrient concentrations were probably too high to have been limiting. Although no attempts have been made to evaluate the standing crop of zooplankton, the general nature of seasonal changes in zooplankton abundance in similar regions elsewhere makes it improbable that the zooplankton could have been abundant enough in this period to have effected any noticeable changes in the phytoplankton populations. Thus at first glance it seems probable that the seasonal changes in abundance were a response to changes in the radiation available to the plant cells.

It has been pointed out that a brackish surface layer was always present. This layer was so dilute that there were always relatively great density differences between it and the underlying water; density differences between the surface and 20 m ranged from $d\sigma_t = 1$ to $d\sigma_t = 6$. Thus density gradients were such that there must have been little effective vertical turbulent transport of phytoplankton below the surface layer. This is borne out by the fact that chlorophyll concentrations in the deeper water remained relatively low at all times.

Within this surface layer there were great changes in the radiation available to plant cells because of the combined effects of changes in solar radiation and transparency. Riley (1957) has pointed out that the mean radiation in such a layer is given by

$$\bar{I}=\frac{I_0\left(1-e^{-\bar{k}z}\right)}{\bar{k}z},$$

in which I_0 is the surface radiation; z, the depth of the mixed layer; and k, the mean transparency in the mixed layer. Here the depth of the mixed layer was estimated from the vertical distribution of salinity while the mean transparency was determined from plots of transparency vs depth. As shown in Table III, there was little difference in mean radiation between March and April, the values scattering around a mean of about 50 g cal/cm²/day. Riley (1957) has found that in a number of temperate coastal regions a mean

		Depth of Mixed	Mean Radiation
Date	Station	Layer (m)	$(g \ cal/cm^2/day)$
January	1	10	4
o all and j	3	10	6
	5	10	5
Mean, Sts. 1–5		9	3
February	1	5	20
10000000	3	5	39
	5	15	24
Mean, Sts. 1–5		9	25
March	1	5	50
	3	5	64
	5	17	26
Mean, Sts. 1–5		8	52
April	1	7	53
	3	5	64
	5	7	48
Mean, Sts. 1–5		7	51
May	1	5	169
	3	5	130
	5	12	56*
Mean, Sts. 1–5		8	110

TABLE III. MEAN RADIATION IN MIXED LAYER OF HOOD CANAL, WASHINGTON. INDIVIDUAL VALUES GIVEN FOR STS. 1, 3 AND 5; MEANS INCLUDE ALL STS. 1-5 (SEE FIG. 1)

* Assuming transparency to be the same as at St. 3.

radiation in the mixed layer of about 43 g cal/cm²/day is necessary for the initiation of vernal augmentation. This evidently represents a critical value below which photosynthesis and growth do not proceed fast enough to permit rapid population growth in these regions. It is interesting to note that the mean radiation in March and April was close to Riley's critical value and that this was the period when the population exhibited remarkable changes in abundance.

This great change in mean radiation in the surface layer must have resulted in great changes in the rate of production of organic matter by the phytoplankton population. Because of differences in the vertical distribution of both phytoplankton and transparency, the quantitative nature of these changes is not immediately obvious. The effect of changes in radiation, transparency and phytoplankton distribution on rate of production was evaluated by using Ryther's (1956) investigation of the relation of photosynthesis by marine phytoplankton to light intensity.

Since neither phytoplankton nor transparency was uniform with depth, it was necessary to determine total production by estimating the production in successive meter-thick strata within the euphotic zone. It has been assumed that $50 \, ^{\circ}/_{0}$ of the surface radiation is effective in photosynthesis (Edmondson, 1956) and that 1 g cal/cm²/day = 15,500 lux (Ryther, 1956). Mean hourly relative photosynthesis in each meter was then determined from transparency and hourly radiation data by using Ryther's (1956) diagram showing relative photosynthesis as a function of light intensity in lux. The hourly means were then summed to give the total daily relative photosynthesis of the population at that depth. Rates of production of carbon were determined from the mean chlorophyll a in the stratum, using the assumption that each gram of chlorophyll produced 3.7 g C/day at light saturation (Ryther and Yentsch, 1957). Results of these computations are shown in Table IV.

Comparison of the production rates in Table IV with the mean radiation in the mixed layer shown in Table III shows that it was not until mean radiation exceeded 50 g cal/cm²/day in March and April that there were marked increases in production rates. This makes quite clear the strong effect that the great turbidity of the early spring must have had on the growth of the population, for the mean radiation in the shallow mixed layer in February would have exceeded 50 g cal/cm²/day if the water had been as transparent then as it became in April. Differences in turbidity also clearly affected the rates of production of the population at the several stations; for example, compare the production in February at St. 1 (k = 2.25) with that at St. 3 (k = 0.81), or of that in March at St. 1 (k = 1.50) with that at St. 5 (k = 0.93), etc.

As a result of these changes in solar radiation, transparency and standing crop, there was an increase of more than 200 times in the rate of production per unit area in the five months studied. Note, however, that in the same time there was barely a doubling of the rate per unit of chlorophyll. Despite large changes in radiation and transparency, it appears that when the population is always confined to a relatively shallow layer, remarkably effective utilization of available light is permitted.

Date	Station	Total	Per gram Chlorophyll
January	1	$13 imes 10^{-3}$	11 × 10 ⁻³
0 andar y	3	12	10
	5	10	9
Mean, Sts. 1–5		12	9
February	1	41	15
	3	93	17
	5	77	10
Mean, Sts. 1–5		73	15
March	1	310	15
	3	330	15
	5	830	18
Mean, Sts. 1–5		452	16
April	1	810	16
	3	480	22
	5	210	21
Mean Sts. 1-5		686	20
May	1	1,820	18
	3	2,440	19
	5	3,480*	21
Mean Sts. 1-5		2,646	19

TABLE IV. PRIMARY PRODUCTION IN HOOD CANAL, WASHINGTON. INDIVIDUAL Values given for Sts. 1, 3 and 5; Means Include all Sts., 1-5 (See Fig. 1). g C/m²/Day

* Assuming transparency to be the same as at St. 3.

The seasonal events considered offer no explanation for the population decrease between March and April; in fact, there seems little basis even for speculation about possible causes. All that can be suggested is that it may be in some way related to the great decrease in accumulated river water that took place between the March and April surveys. It is true that, despite this decrease, there was no increase in the flushing rate, but the fact that the least population change occurred where there was no decrease in accumulated river water, *i. e.*, at Sts. 1 and 2, lends some credence to this suggestion. It any event, this unexplained population change does serve to emphasize that, in such regions, the population growth is strongly influenced by opposing effects of river flow; on the one hand the flow creates a shallow and stable surface layer which acts to retain the population in the euphotic zone whereas on the other hand, at times of great runoff, it may cause such increases in the rate of seaward transport and in the turbidity of the surface layer that the population growth is reduced. Considering the complex nature of the effect of the runoff, one may expect some such population fluctuations.

ACKNOWLEDGMENTS

I am indebted to Dr. Clifford A. Barnes for advice and suggestions, to Dr. Bostwick H. Ketchum for helpful discussions, and to the officers and crew of the R. V. BROWN BEAR for patient and intelligent co-operation. I am also indebted to Dr. Thomas G. Thompson for pleasant and stimulating associations during my stay at the Department of Oceanography of the University of Washington.

EDMONDSON, W. T.

REFERENCES

1956. The relation of photosynthesis by phytoplankton to light in lakes. Ecology, 37 (1): 161-174.

JENKIN, PENELOPE M.

- 1937. Oxygen production by the diatom *Coscinodiscus excentricus* Ehr. in relation to submarine illumination in the English Channel. J. Mar. biol. Ass. U.K., 22: 301-342.
- KETCHUM, B. H., A. C. REDFIELD, AND J. C. AYERS
 - 1951. The oceanography of the New York Bight. Pap. phys. Oceanogr., 12 (1): 4-46.
- POOLE, H. H. AND W. R. G. ATKINS
 - 1929. Photo-electric measurements of submarine illumination throughout the year. J. Mar. biol. Ass. U.K., (N. S.) 16: 297-324.

RICHARDS, F. A. WITH T. G. THOMPSON

1952. The estimation and characterization of plankton populations by pigment analyses. II. A spectrophotometric method for the estimation of plankton pigments. J. Mar. Res., 11 (2): 156-172.

RILEY, G. A.

- 1956. Oceanography of Long Island Sound, 1952–1954. II. Physical Oceanography. Bull. Bingham oceanogr. Coll., 15: 15–46.
- 1957. Phytoplankton of the North Central Sargasso Sea, 1950-1952. Limnol. Oceanogr., 2 (3): 252-270.

ROBINSON, R. J. AND T. G. THOMPSON

1948. The determination of phosphates in sea water. J. Mar. Res., 7 (1): 33-41. Ryther, J. H.

1956. Photosynthesis in the ocean as a function of light intensity. Limnol. Oceanogr., 1 (1): 61-70.

RYTHER, J. H. AND C. S. YENTSCH

1957. The estimation of phytoplankton production in the ocean from chlorophyll and light data. Limnol. Oceanogr., 2 (3): 281-286.