

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/>



Journal of MARINE RESEARCH

Volume 39, Number 4

Tidal stirring and the distribution of phytoplankton in Long Island and Block Island Sounds

by Malcolm J. Bowman¹, Wayne E. Esaias^{1, 2} and Michele B. Schnitzer^{1, 3}

ABSTRACT

Phytoplankton distributions in Long Island and Block Island Sounds measured during a 1978 fall equinox cruise are interpreted in terms of tidal mixing variations and water column stratification. A stratification depth-scaled-by-light diagram is used to quantify the preferred physical environments of the two major morphological groups (diatoms and microflagellates). The success of the method in clearly distinguishing these physical regimes suggests its value as a useful biological growth index in estuarine systems.

Introduction

Plankton patchiness in the sea is a subject of fundamental importance in marine ecology. This patchiness arises from a variety of mechanisms such as mechanical aggregation by convergence, behavioral response to hydrographic, light, and nutrient distributions, exclusion of certain zooplankton by phytoplankton, predator-prey interactions and schooling and swarming behavior (Okubo, 1980).

The purpose of this paper is to present some measurements of phytoplankton abundance taken in a major, moderately stratified estuary, and to discuss horizontal variations or patchiness in two major morphological groups in relation to some bulk

1. Marine Sciences Research Center, State University of New York, Stony Brook, New York 11794, U.S.A.

2. Present address: Marine and Applications Technology Div./272, NASA Langley Research Center, Hampton, Virginia 23665, U.S.A.

3. Present address: Environmental Sciences and Engineering, 5406 Hoover Boulevard, Suite D, Tampa, Florida 33614, U.S.A.

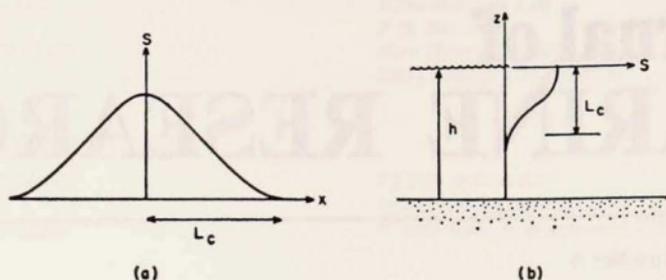


Figure 1. Coordinate system for discussion of horizontal and vertical plankton dynamics. The patch size is just critical.

parameterizations of the physical environment, *viz.*, submarine light levels and tidally driven turbulence. In particular, we assess the essential elements of Margalef *et al.*'s (1979) phytoplankton mandala and the application of Pingree's (1978) *s-kh* diagram as useful ways of characterizing and separating important factors in controlling the observed distributions.

Conceptual discussion

We consider the one dimensional equation for the exponential cell growth in a diffusing environment with some advective influence.

$$\frac{\partial s}{\partial t} = \frac{D \partial^2 s}{\partial x^2} - \frac{\partial(vs)}{\partial x} + \alpha s \quad (1)$$

where s = cell concentration	(cell l^{-1})
t = time	(sec)
D = (constant) diffusivity	($cm^2 \text{ sec}^{-1}$)
v = velocity	($cm \text{ sec}^{-1}$)
x = horizontal distance	(cm)
α = growth rate	(sec^{-1})

This equation can be applied in both the horizontal plane or in the vertical. The effective value of D will be many orders of magnitude greater in the horizontal case (typically 10^4 to $10^6 \text{ cm}^2 \text{ sec}^{-1}$; Okubo, 1976) than in the vertical. Also, vertical diffusivity will be a strong function of stratification and may be as low as $1 \text{ cm}^2 \text{ sec}^{-1}$ (Pritchard *et al.*, 1971; Kullenberg, 1978) or even $0.02 \text{ cm}^2 \text{ sec}^{-1}$ (Jacobsen, 1913; Kullenberg, 1968) within a strong pycnocline. For application of equation (1) in the vertical, z replaces x and is positive upwards. The origin is taken at the sea surface (Fig. 1).

In the horizontal, the velocity v is associated with a surface divergence as in coastal upwelling, or a surface frontal convergence. In the vertical, v can be con-

sidered a sinking velocity of negatively buoyant phytoplankton falling through the water column (Lannergren, 1979; Bienfang, 1980). The effective growth rate, α includes the effects of grazing and mortality (Platt, 1975; Platt and Denman, 1975).

i) $v = 0$. Two basic parameters emerge from the solution of (1): the Skellam (1951), Kierstead and Slobodkin (1953) critical length scale L_c , for the case of an absorbing boundary condition (i.e., $s \equiv 0$ for $x > L$, where L is the radius of the patch

$$L_c = \pi(D/\alpha)^{1/2} \quad (2)$$

and the "diffusion velocity" or population wave frontal velocity

$$v_f = 2(\alpha D)^{1/2} \quad (3)$$

This is the asymptotic expansion rate of a surface of constant concentration of an unbounded patch into the surrounding fluid (Okubo, 1980).

ii) $v \neq 0$. The critical length scale changes to (Okubo, 1972)

$$L_c = 2\lambda(D/\alpha)^{1/2}$$

where

$$\lambda = \pm \frac{\tan^{-1}(m^{-1} - 1)^{1/2}}{(1 - m)^{1/2}} > 0$$

and

$$m = v^2/4\alpha D$$

The positive sign refers to convergence and the negative sign to divergence.

Thus $0 < \lambda < \pi/2$, $m > 0$ for convergence, and $\pi/2 < \lambda < \infty$, $0 < m < 1$ for divergence.

A growing population can exist in the presence of divergence only if

$$|v| < 2(\alpha D)^{1/2},$$

(Riley *et al.*, 1949) for then the critical patch size becomes infinite. In the horizontal plane, for example, given reasonable values for α and D , a surface divergence of only a few cm sec^{-1} can disperse the strongest patch (Okubo, 1978). Conversely, a surface convergence allows the existence of a growing patch at a reduced horizontal critical length scale. In the vertical, $2(\alpha D)^{1/2}$ is the maximum sinking speed allowed to maintain a viable concentration of phytoplankton in the euphotic zone.

Margalef *et al.* (1979) conceptualized $(\alpha D)^{1/2}$ as representing "production potential" or a measure of the patch's tendency to expand into the surrounding environment. Alternatively, in the vertical, it describes its ability to survive attrition by diffusion and sinking. The $(\alpha/D)^{1/2}$ has the dimensions of a gradient, and hence represents the maximum wavenumber (corresponding to a minimum dimension) that can persist for a growing population in the presence of diffusion.

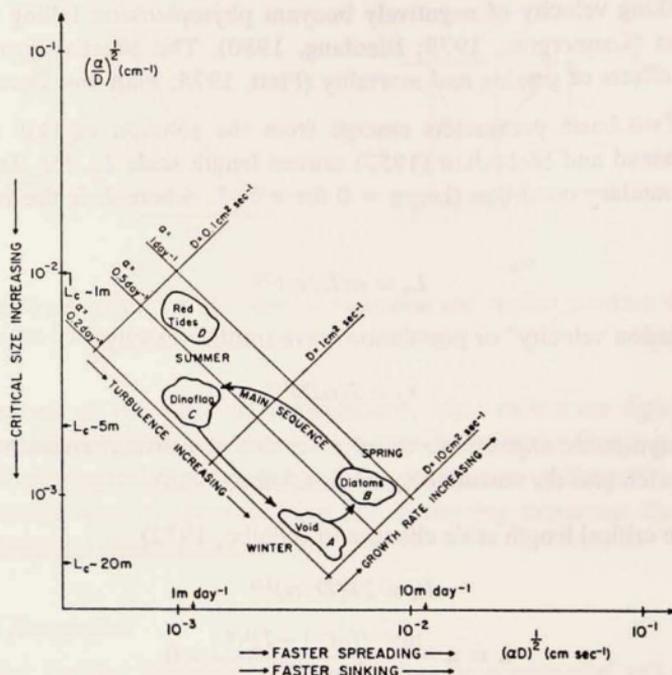


Figure 2. Margalef's phytoplankton mandala. The vertical axis is the inverse of the critical length scale, L_c . The horizontal axis is the "diffusion velocity", v_f . The intersections of lines of constant vertical diffusivity, D , and lines of constant growth rate, α , delineate the four basic growth regimes.

Margalef's mandala

These considerations lead to the "phytoplankton mandala" which is an ecological space defined by the population growth rate α (which implicitly is considered to be a function of light and nutrient availability) and the intensity of turbulent mixing which is parameterized through D . The α itself may be a function of D since nutrient availability to the photic zone will be a function of turbulent mixing for deep water cases.

Figure 2 is a schematic diagram of the mandala where the ordinate is $(\alpha/D)^{1/2}$, the abscissa is $(\alpha D)^{1/2}$, and the orthogonal intersecting straight lines (on a log-log scale) represent isopleths of α and D . (The numerical values are for discussion only and should not be taken too seriously but are of the order often quoted for coastal waters.) In subsequent discussion, D refers to vertical diffusivity.

Four distinct regions emerge:

Region A) Void (low α , high D), typical of deep, mixed water where nutrient values remain high, but average light levels are too low to allow significant produc-

tion, i.e., the depth is greater than Sverdrup's (1953) critical mixing depth. Any residual growth is too slow to allow sporadic cell accumulations to attain the large critical size demanded by the high diffusivity, and thus are rapidly mixed away.

Region B) (high α , high D), typical of shoal, mixed or marginally stratified, well illuminated water, and probably also with high nutrient concentrations. High sinking rates are allowed (~ 10 m day⁻¹). The intermediate critical length scale allows the accumulation of significant populations in spite of high diffusivity.

These are the conditions under which diatom populations would be expected to become dominant, for example during the spring bloom, or inshore of summer tidal frontal boundaries where stratification never becomes established.

Region C) (low α , low D), As offshore, deeper water columns stratify (and hence D decreases) under the influences of a surface heating flux and calm weather, nutrient limitation may reduce growth rates in the surface mixed layer, and non-motile cells will sink fatally through the thermocline. Dinoflagellates will become dominant.

Region D) (high α , low D), This unusual combination of conditions occurs only in transitory situations. Examples in the literature include the deep, fjord-like bays of northwest Spain (Margalef et al., 1956, 1978), in shallow sea frontal zones Holligan, 1979; Seliger et al., 1979) or from the tips of headlands and islands under certain conditions where the mixing and circulation tends to concentrate organisms (Yentsch and Mague, 1979).

Red tides sometimes form under these conditions characterized by high light and nutrient levels coupled with strong stratification during calm weather. In the case of tidal mixing or headland frontal zones, a strong surface convergence plays a key role in concentrating cells who have sufficient motility (usually dinoflagellates) to maintain themselves in the photic zone against sinking at the front. In the dimensions of the mandala, these red tide conditions are conceptualized in terms of small critical length scales coupled with low sinking rates. The presence of strong surface convergence at fronts also allows a reduced horizontal critical length scale, but at the same time requiring strong phototaxis for survival.

Pingree's *s-kh* diagram

While accurate growth rate estimates of α may be difficult (e.g., Falkowski, 1980), they are routinely made by biologists during primary productivity studies. There is no easy way to measure D . Diffusivity is estimated either through difficult tracer (e.g., dye or radio-isotope) experiments, or as an adjustable parameter in numerical models of ocean and estuarine circulation and mixing.

Pingree has avoided this problem, and at the same time, explicitly incorporated

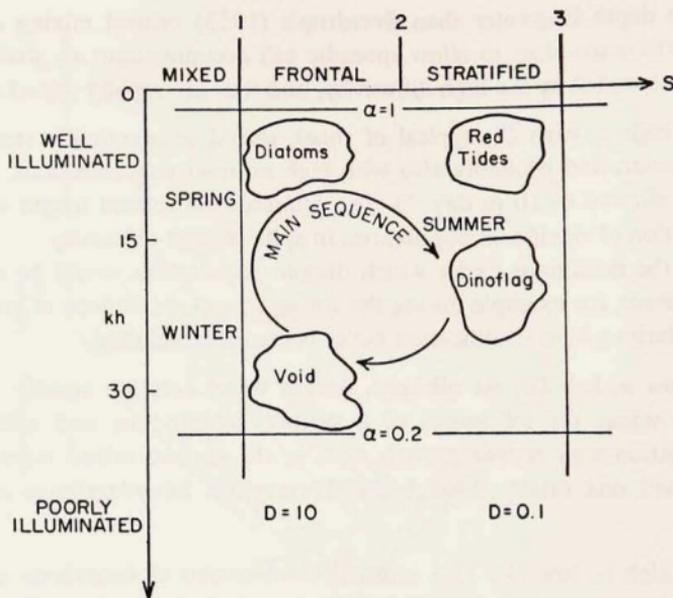


Figure 3. Schematic of Pingree's s - kh diagram illustrating the conceptual equivalence with Margalef's mandala.

the dependence of growth on light levels through his s - kh diagram. This stratification versus depth-scaled-by-light plot appears to be an effective ecological plane on which to summarize the spring, summer and autumn production in the Celtic Sea and English Channel (Pingree, 1978; Pingree *et al.*, 1978).

The s is defined as

$$s = \log_{10} \left(\frac{h}{C_D u^3} \right),$$

i.e., the Simpson-Hunter (1974) stratification index, where h is water column depth, C_D is a dimensionless frictional drag coefficient, and u^3 is the mean cubed semi-diurnal tidal current. The vertical scale is the number of optical depths kh in the water column where k is the diffuse extinction coefficient. Equivalently, $\exp(-kh)$ is the fraction of incident light found at the sea floor. Growth rate α is not presented explicitly.

Although he considered only chlorophyll a concentrations as a measure of production, Pingree's approach has the advantage that the axis parameters can be directly measured (in the absence of sufficient current measurements, h/u^3 can be conveniently derived from numerical tidal models; Pingree, 1978; Bowman *et al.*, 1980).

Figure 3 suggests how Margalef's mandala maps directly into the s - kh diagram.

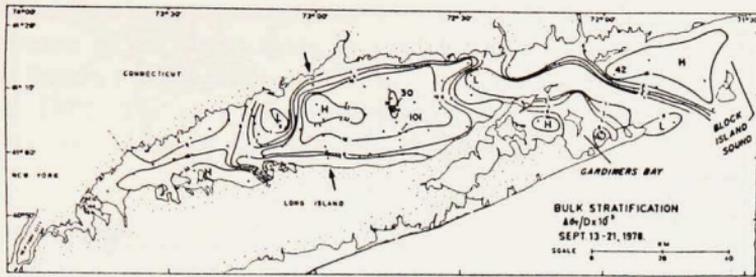


Figure 4. Station positions (dots) and observed bulk stratification in Long Island and Block Island Sounds, Sept. 13-21, 1978.

Values of $s < 1$ represent well mixed regions (high D) where nutrients are likely to be uniformly high, while $s > 2$ represents summer stratified regions (low D) where nutrients are likely to be depleted in the euphotic zone. Intermediate values ($1 < s < 2$) are associated with marginally stratified frontal waters where a favorable light regime coupled with a shallow thermocline may support high growth rates.

The four sequences of the mandala appear rotated and inverted by the transformation. Conditions favoring red tides (*Region D*) represent an anomaly since there high nutrients are found in the presence of high light levels and low turbulence.

An example from Long Island and Block Island Sounds

A two week sampling cruise was made in Long Island and Block Island Sounds near the fall equinox of 1978. This provided an initial opportunity to investigate the control of stratification by tidal mixing variations in a major "moderately stratified" estuary and, if possible, to relate these variations to the distributions of major phytoplankton taxonomic groups. The Sounds are favored estuarine environments for these studies since they possess a wide range of light, depth, nutrient and tidal streaming variations in a relatively small region. Hence we hope the data are near synoptic.

A comprehensive discussion of the physical, chemical, and biological oceanography of Long Island Sound is Riley *et al.* (1956). A further, more detailed, description of the physical oceanography is Riley (1956). Conover (1956) discussed the seasonal succession of major taxonomic groups. The population in both inshore and offshore stations was dominated by diatoms except in summer, when dinoflagellates and other smaller flagellates ("microflagellates") largely replaced the diatoms. There was a clear-cut species succession, but with changes in the relative importance of certain species from year to year.

Station positions and observed bulk stratification are shown in Figure 4. CTD profiles were taken at 109 stations with a modified Interocean 550 instrument. A

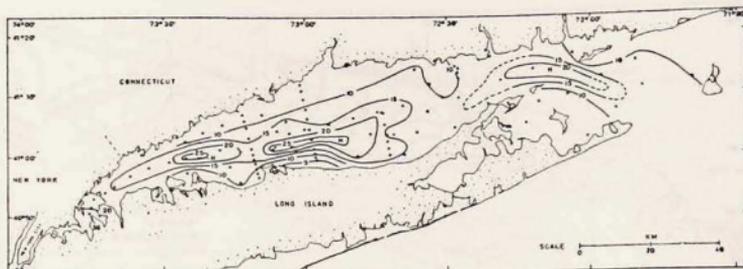


Figure 5. Distribution of kh (extinction coefficient times depth), Sept. 13-21, 1978.

correlation coefficient r^2 of 0.62 was established between observed bulk stratification ($\delta\sigma_T/h$) and h/u^3 which varied as $10^3 \delta\sigma_T/h = 3.8 + 0.10 h/u^3$ (σ_T units m^{-1}); values of u were determined from historical current measurements (Bowman and Esaias, 1981). Submarine light levels and the extinction coefficient k were measured with 2 Lambda Quantum sensors spaced vertically on a rigid pole 2 m apart suspended in the water column.

Phytoplankton samples were gathered at each station in Niskin bottles from within the euphotic zone, usually from the chlorophyll maximum. Organisms were identified to species when possible. A "microflagellate" category was created for the inclusion of those cells possessing flagella that were not members of the dinoflagellate (*div. Pyrrhophycophyta*) classes. Specimen preparation and counting methods are discussed in Schnitzer (1979). Vertical profiles of chlorophyll a were determined with an *in situ* profiling fluorometer calibrated, usually at three depths, against extracted chlorophyll a values. Inorganic nutrients ($NO_2 + NO_3$, PO_4) were measured with a Technicon Autoanalyzer.

Discussion of results

Physical properties and the description of the observed stratification are discussed in Bowman and Esaias (1981). Briefly, the "central basin" contained a large elliptical shaped body of stratified water surrounded by marginally stratified frontal zones. The shallow (~ 12 m mean depth) western reaches supported a moderate pycnocline since tidal streams diminish rapidly towards the head of the estuary. Strong currents ($\sim 2-3$ m sec^{-1}) through the narrow, deep, eastern passes ($\sim 50-80$ m depth) to the Atlantic Ocean maintained well mixed conditions. This main channel is flanked by the relatively highly stratified, embayments of Gardiners Bay and Block Island Sound. Other locally mixed areas were located near headlands, shallows and islands.

Distribution of optical depths kh

Contours of kh (Fig. 5) tended to follow depth variations modulated by a gradual

three fold increase in transparency from the eutrophic western Sound to the coastal oceanic waters of the eastern parts. A sharp increase in turbidity and depth occurred at Station 1 ($kh = 36$) near the entrance to the highly eutrophic East River (Bowman, 1977). The three enclosed maxima lay over corresponding depth depressions in the main channel axis of Long Island Sound.

Transverse sections

A section taken across the central basin provided some insight into the effects of tidal stirring on stratification, nutrient and chlorophyll *a* distribution (Fig. 6 a-f).

A local temperature maximum was found at the bottom of the estuary which was an indication of early stages of fall overturning during a prior cooling event. Static stability was maintained, however, by an increase of salinity with depth which compensated for the destabilizing effects of temperature. Temperature increased marginally again near the surface, due to the local heating during the fair weather that prevailed during most of the experiment.

Although the central region was moderately stratified, evidence of vertical mixing was found closer inshore, particularly intense near the Connecticut shore, where strong tidal streams wash over shoal waters. Temperature and salinity were essentially density compensated in these coastal boundary zones, and ensured both high nutrient concentrations and enhanced horizontal diffusion along isopycnal surfaces into the central stratified zone. Indeed, nutrients were bountiful over the entire section.

Nearshore, maximum chlorophyll *a* concentrations $\sim 14 \text{ mg m}^{-3}$ were located in the productive frontal zones, dropping to about 8 mg m^{-3} in the offshore chlorophyll maximum above the 1% light level.

Distribution of diatoms and flagellates

Contours of diatom abundance (Fig. 7) showed highest concentration ($\sim 2 \times 10^6$ cells l^{-1}) in a narrow band in the near shore frontal zone along the Connecticut coast. Local maxima with slightly lower values ($\sim 10^6$ cells l^{-1}) lay along the Long Island north shore in the central and eastern sections, and in western Long Island Sound. Minimum values were found at the confluence of Long Island and Block Island Sounds, especially in the northern region where a tongue of low concentration extended up the central axis of Long Island Sound. Microflagellate concentrations were highest in the deepest regions of the stratified central basin (Fig. 8). Relatively low values ($< 5 \times 10^5$ cells l^{-1}) were located in the deep but mixed eastern passes.

Distributions of the three most abundant taxonomic groups are presented in Schnitzer (1979). Microflagellates were by far the most widespread. The diatoms

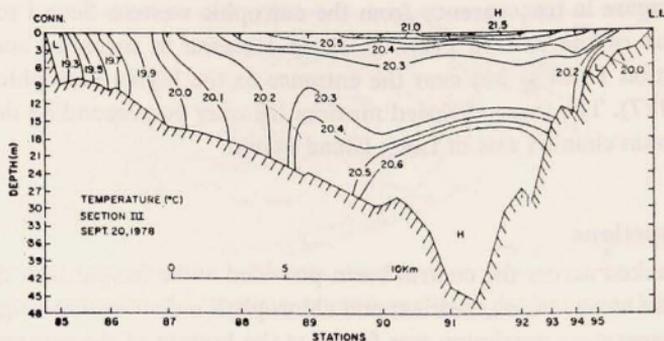
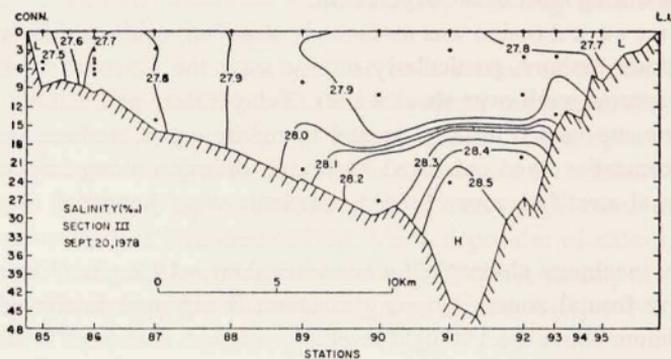
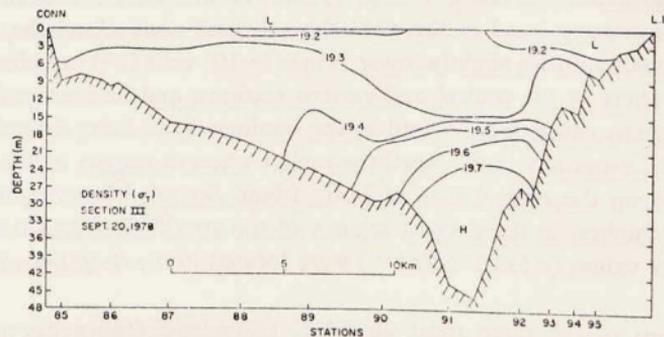


Figure 6. Vertical sections across central basin of Long Island Sound, Sept. 13-21, 1978. The section is delineated by the arrows in Figure 4.

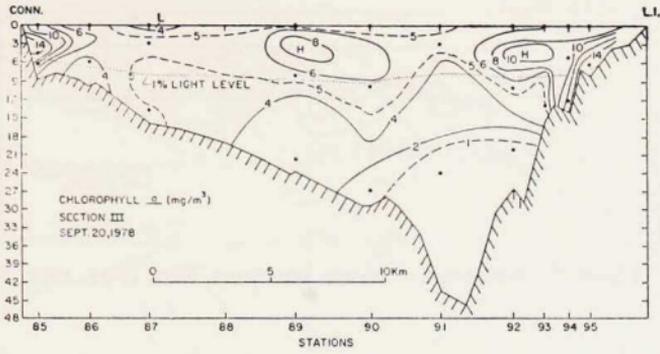
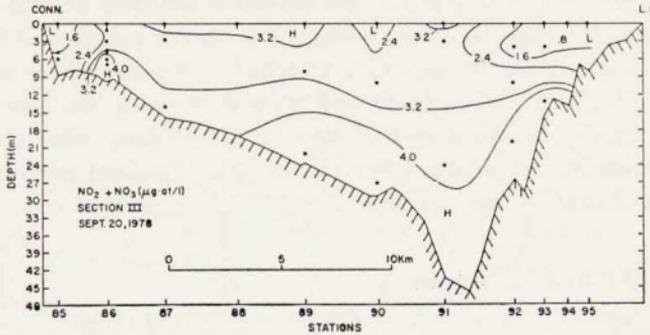
a) Temperature



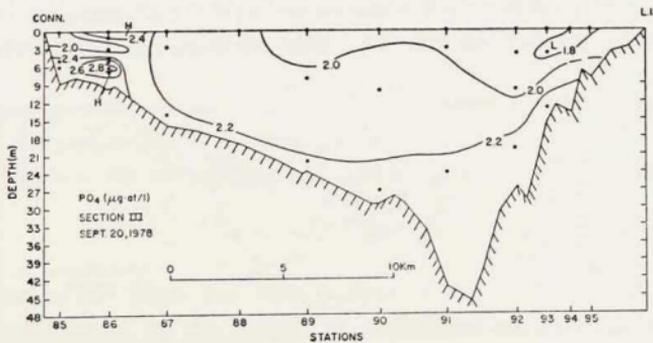
b) Salinity



c) Density (σ_T)

d) Chlorophyll a 

e) Nitrite + Nitrate



f) Phosphate

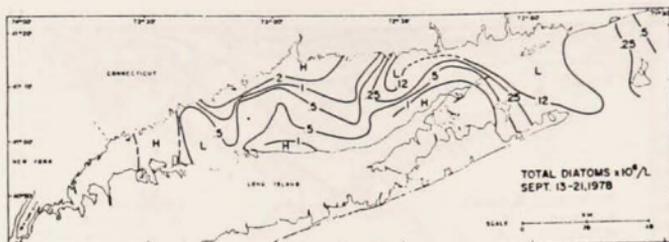


Figure 7. Distribution of diatom abundance, Sept. 13-21, 1978.

Rhizosolenia spp (*R. setigera*, *R. stolterfothii*, *R. delicatula*, *R. fragilissima*) were the most abundant only in far eastern Block Island Sound. *Skeletonema costatum* was most abundant in localized areas. Others in this group included *Nitzschia seriata* and *Thalassiosira* spp and small centrics (10-25 μm). Dinoflagellates had highest concentrations ($\sim 10^5$ cells l^{-1} ; not shown) in stratified western Long Island Sound waters with a sharp decrease towards the eastern mouth and Block Island Sound, where values stabilized at $\sim 1.2 \times 10^4$ cells l^{-1} . Dinoflagellates never formed more than 10% of any station count and often were much less than that. These results are generally consistent with Conover's (1956) data, when dinoflagellates started to decline in the fall when the deepening and gradual erosion of the pycnocline reduced stratification and began to bring nutrient rich water to the surface.

Application of the *s-kh* diagram

Two *s-kh* diagrams for diatoms and microflagellates are shown in Figure 9a and b. Either h/u^2 or $\delta\sigma_T/h$ serves as the horizontal scale. The horizontal dashed line represents a water column depth equal to the 1% light depth. Each dot derives from a station where counts were obtained, and represents the bulk stability and the optical depth of the water column, and not local values at the sample depth (usually surface or at chlorophyll *a* maximum depth). Cell concentration contours are drawn using a geometrical interval. These contours clearly demonstrate that a

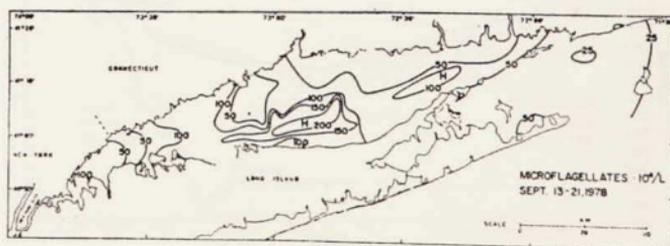


Figure 8. Distribution of microflagellate abundance, Sept. 13-21, 1978.

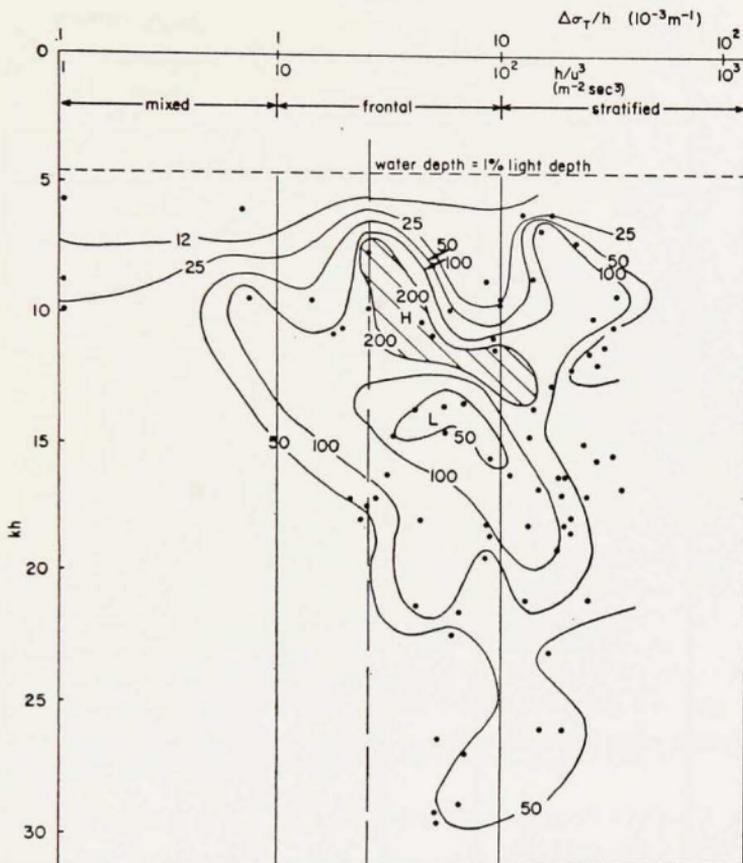
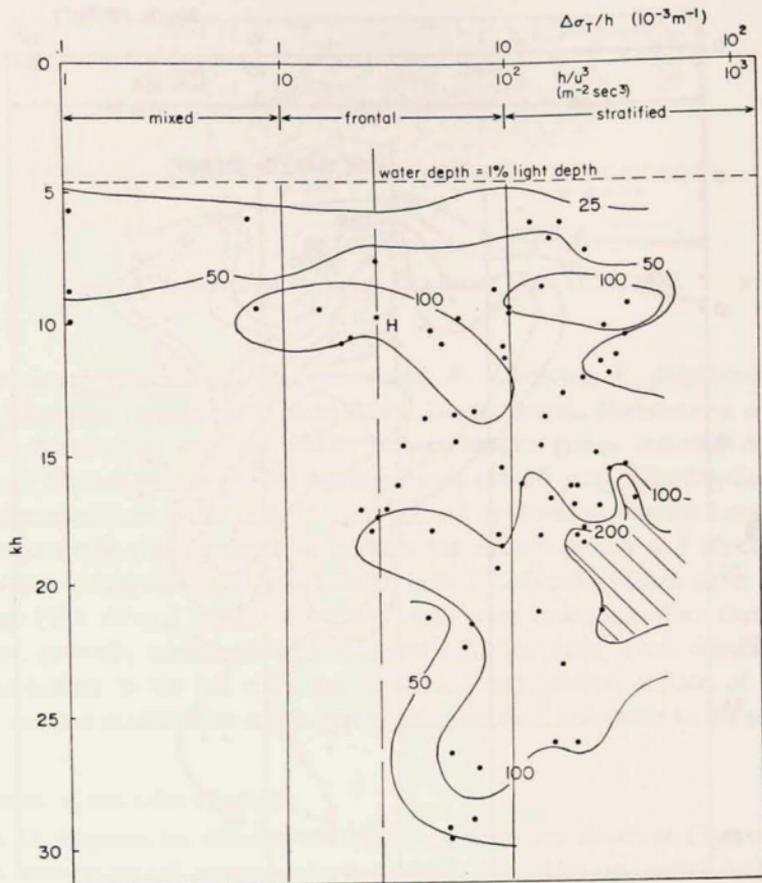


Figure 9. a) s - kh diagram illustrating contours of constant concentration (cells l^{-1}) of diatoms. The dashed vertical line represents a value of s traditionally associated with shallow sea tidal mixing fronts. The solid vertical lines separate mixed, frontal, and stratified water.

unimodal distribution exists in both cases. Thus a functional relationship emerges by mapping the data into the ecological space defined by the variables which affirms in a quantitative way the results already observed. Highest diatom concentrations are found in marginally stratified, well illuminated, shallow waters while microflagellates dominate in the surface layers of deeper, darker, stratified waters.

Discussion

Our intention in this paper has been to draw a common thread through some theoretical contributions on the control of phytoplankton distributions and productivity by physical mechanisms and to relate these ideas to some preliminary



b) s - kh diagram illustrating contours of constant concentration (cells l^{-1}) of microflagellates.

observations in a major estuary. We have emphasized the importance of understanding spatial variations in vertical mixing on horizontal structure.

Neither the use of bulk stratification nor the stability index s contains any information on the vertical structure of turbulence and hence, the depth and intensity of the pycnocline. Although the hypothetical density section shown in Figure 10a exhibits three distinct hydrographic regimes, the water column bulk stratification is the same. The resolution of the available data set shows that indeed there were many examples where marked differences in the vertical structure of chlorophyll a was associated with corresponding structure in the vertical density gradient (Fig. 10b). At this early stage of development of the s - kh diagram, our intent is to show that to a first order, light levels and horizontal variations in tidal mixing do correlate

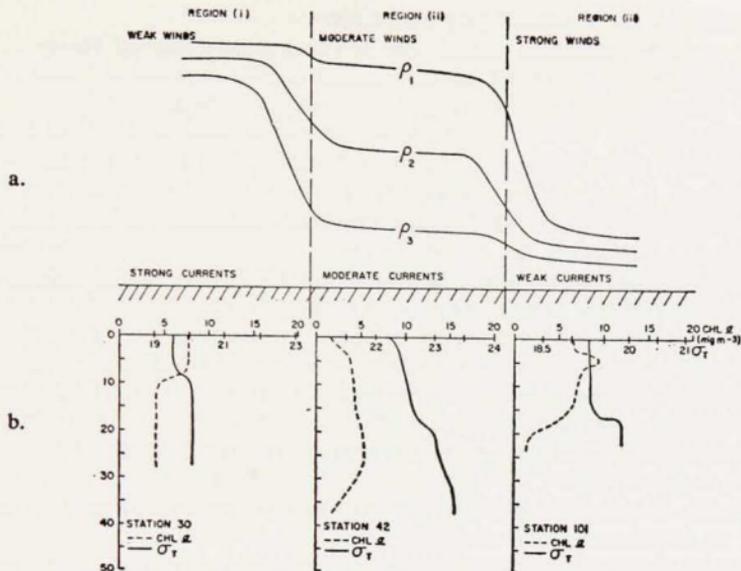


Figure 10. a) Hypothetical density section with 3 hydrographic regions:

- i) a shallow, intense pycnocline
- ii) a diffuse linear density gradient
- iii) a deep, intense pycnocline

b) Some examples of density and chlorophyll *a* profiles from the cruise corresponding to the three above regions. Depth in m.

with representative samples of major morphological classification (i.e., motility) during this one cruise. One next step, to investigate the vertical structure of turbulence and its control of the phytoplankton abundance and productivity with depth is much more difficult, although some progress has been made.

Further testing at different times during the growing season is necessary to test our hypothesis that broad taxonomic classes prefer some characteristic and separable combination of light and turbulence levels, where turbulence is parameterized by either a bulk stratification or the stratification index (or equivalently its inverse, the kinetic energy dissipation rate per unit mass ($C_D u^2/h$)). Hopefully others will be stimulated to test the generality of these ideas to other areas to determine whether or not the approach has wide applicability to estuaries and coastal regions where tidal mixing is an important physical process.

Acknowledgments. This study was supported by NSF grant #OCE 77-26970. Thanks are expressed to the Captain and crew of the R/V *Ridgely Warfield* and to the numerous individuals who participated in these cruises and subsequent analysis. Contribution 296 of the Marine Sciences Research Center (MSRC) of the State University of New York at Stony Brook.

REFERENCES

- Bienfang, P. K. 1980. Phytoplankton sinking rates in oligotrophic waters off Hawaii, U.S.A. *Mar. Biol.*, 61, 69-77.
- Bowman, M. J. 1977. Nutrient distributions and transport in Long Island Sound. *Est. & Coastal Mar. Sci.*, 5, 531-548.
- Bowman, M. J., A. C. Kibblewhite and D. E. Ash. 1980. M_2 tidal effects in greater Cook Strait, New Zealand. *J. Geophys. Res.*, 85, 2728-2742.
- Bowman, M. J. and W. E. Esaias. 1981. Fronts, stratification, and mixing in Long Island and Block Island Sounds. *J. Geophys. Res.*, 86, 4260-4264.
- Conover, R. J. 1956. Oceanography of Long Island Sound, 1952-54. IV. Phytoplankton. *Bull. Bingham Oceanogr. Coll.*, 15, 62-112.
- Falkowski, P. G. 1980. Ed. Primary Productivity in the Sea. Plenum Press, New York, 531 pp.
- Holligan, P. M. 1979. Dinoflagellate blooms associated with tidal fronts around the British Isles, in *Toxic Dinoflagellate Blooms*, D. L. Taylor and H. H. Seliger, eds., Elsevier/North Holland Inc. New York, 249-256.
- Jacobsen, J. P. 1913. Beitrag zur Hydrographie der dänischen Gewässer. *Komm. f. Havunders. Medd., Ser. Hydr.*, 2, 94 pp.
- Kierstead, H. and L. B. Slobodkin. 1953. The size of water masses containing plankton bloom. *J. Mar. Res.*, 12, 141-147.
- Kullenberg, G. E. B. 1968. Measurements of horizontal and vertical diffusion in coastal waters. Københavns Universitet, Institut for Fysisk Oceanografi. Tech. Report No. 3. Copenhagen.
- 1978. Vertical processes and the vertical-horizontal coupling, in *Spatial Pattern in Plankton Communities*, J. H. Steele, ed., Plenum Press, New York, 43-71.
- Lannergren, C. 1979. Buoyancy of natural populations of marine phytoplankton. *Mar. Biol.*, 54, 1-10.
- Margalef, R. 1956. Estructura y dinamica de la "purga de mar" la Ria de Vigo. *Inv. Pesq.*, 5, 113-134.
- 1978. Life forms of phytoplankton as survival alternatives in an unstable environment. *Oceanologica, Acta.*, 1, 493-509.
- Margalef, R., M. Estrada, and D. Blasco. 1979. Functional morphology of organisms involved in red tides, as adapted to decaying turbulence, in *Toxic Dinoflagellate Blooms*, D. L. Taylor and H. H. Seliger, eds., Elsevier/North Holland Inc. New York, 89-94.
- Okubo, A. 1972. A note on small organism diffusion around an attractive center: A mathematical model. *J. Oceanog. Soc. Japan*, 28, 1-7.
- 1976. Remarks on the use of "diffusion diagrams" in modeling scale-dependent diffusion. *Deep Sea Res.*, 23, 1213-1214.
- 1978. Advection-diffusion in the presence of surface convergence, in *Oceanic Fronts in Coastal Processes*, M. J. Bowman and W. E. Esaias, eds., Springer-Verlag, New York, 23-28.
- 1980. Diffusion and Ecological Problems: Mathematical Models, Springer-Verlag, New York, 254 pp.
- Pingree, R. D. 1978. Mixing and stabilization of phytoplankton distributions on the Northwest European continental shelf, in *Spatial Patterns in Plankton Communities*, J. H. Steele, ed., Plenum Press, 181-220.
- Pingree, R. D., P. M. Holligan, and G. T. Mardell. 1978. The effects of vertical stability on phytoplankton distributions in the summer on the Northwest European shelf. *Deep Sea Res.*, 25, 1011-1028.

- Platt, T. 1975. The physical environment and spatial structure of phytoplankton populations. Mem. Soc. Roy. de Sci. Liege, 6th series, 7, 9-17.
- Platt, T. and K. L. Denman. 1975. A general equation for the mesoscale distribution of phytoplankton in the sea. Mem. Soc. Roy. de Sci. Liege, 6th series, 8, 31-42.
- Pritchard, D. W., R. O. Reid, A. Okubo, and H. H. Carter. 1971. Physical processes of water movement and mixing, in *Radioactivity in the Marine Environment*, National Academy of Sciences, Washington, D.C., 90-136.
- Riley, G. A. 1956. Review of the oceanography of Long Island Sound. *Deep Sea Res., Suppl.* 3, 224-238.
- Riley, G. A., H. Stommel and D. F. Bumpus. 1949. Quantitative ecology of the plankton of the western North Atlantic. *Bull. Bingham Oceanog. Coll., Yale University*, 12, Article 3, 1-169.
- Schnitzer, M. B. 1979. Vertical stability and the distribution of phytoplankton in Long Island Sound. M.S. Thesis, Marine Sciences Research Center, Stony Brook, New York.
- Seliger, H. H., M. A. Tyler and K. R. McKinley, 1979. Phytoplankton distributions and red tides resulting from frontal circulation patterns, in *Toxic Dinoflagellate Blooms*, D. L. Taylor and H. H. Seliger, eds., Elsevier/North Holland Inc., New York, 239-248.
- Simpson, J. H. and J. R. Hunter. 1974. Fronts in the Irish Sea. *Nature*, 250, 404-406.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika*, 38, 196-218.
- Sverdrup, H. U. 1953. On conditions for the vernal blooming of phytoplankton. *J. Cons. Explor. Mer.*, 18, 287-295.
- Yentsch, C. M. and F. C. Mague. 1979. Motile cells and cysts: Two probable mechanisms of intoxication of shellfish in New England waters, in *Toxic Dinoflagellate Blooms*, D. L. Taylor and H. H. Seliger, eds., Elsevier/North Holland Inc., New York, 127-130.