

## Changes in fine-scale vertical distributions of ciliate microzooplankton related to anoxia in Chesapeake Bay waters<sup>1</sup>

J. R. DOLAN and D. W. COATS

*Smithsonian Environmental Research Center, P.O. Box 28 Edgewater, MD 21037, USA.*

### Abstract

Three locations in the Maryland (USA) portion of the Chesapeake Bay were sampled from April through September in 1986, throughout a complete cycle of the formation and subsequent erosion of water column oxyclines. The stations displayed similar ciliate distributions relative to gradients of dissolved oxygen (D.O.) despite differences in individual patterns of oxygen depletion and chlorophyll *a* distribution. In deep waters, marked decreases in ciliate densities and a shift in community composition corresponded with oxygen depletion. Conspicuous aggregations of bacterivorous ciliates were occasionally found at the water column anoxic/oxic interface, but the bulk of the ciliate community, dominated by oligotrichs and tintinnids, was largely restricted to waters containing at least 2 ml/l D.O.

*Key words:* Plankton, Ciliates, Anoxia, Chesapeake.

### Résumé

Variations des distributions verticales à fine échelle des ciliés microzooplanctoniques, reliées à l'anoxie, dans les eaux de la baie de Chesapeake

En trois points de la partie de la baie de Chesapeake qui se trouve dans le territoire du Maryland (USA), un échantillonnage a été réalisé d'avril à septembre 1986, pendant un cycle complet allant de la formation à la disparition des oxyclines dans la colonne d'eau. Les stations ont montré des distributions similaires des ciliés par rapport aux gradients d'oxygène dissous malgré des différences dans les types de répartition de la diminution en oxygène et de la teneur en chlorophylle *a*. Dans les eaux profondes, des diminutions

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marquées dans la densité des ciliés et un changement dans la composition de la communauté allaient de pair avec la réduction de l'oxygène. Des rassemblements notables de ciliés bactérivores ont été parfois trouvés dans la colonne d'eau à l'interface entre les eaux anoxiques et oxygénées, mais la masse de la communauté de ciliés, dominée par les oligotriches et les tintinnides, était grandement limitée aux eaux contenant au moins 2 ml/l d'oxygène dissous.

## Introduction

Changes in the vertical distributions of marine and mesohaline plankton have long been associated with changes in water column characteristics (Harder, 1968). However, relatively few studies have attempted to relate shifts in ciliate microzooplankton communities to changes in water column structure (Holligan *et al.*, 1984; Revelante and Gilmartin, 1983, 1987; Revelante *et al.*, 1985). Furthermore, none have considered the influence of seasonal changes in chemical gradients on planktonic ciliate distributions. This is surprising considering that investigations of benthic marine ciliates have shown the existence of distinct communities arranged along gradients of oxygen and sulfides (Fenchel, 1969) and many studies of freshwater lakes have shown that profound changes in the ciliate microzooplankton community coincide with the development of dissolved oxygen gradients (Bark, 1981, 1985; Bark and Goodfellow, 1985; Bark and Watts, 1984; Finlay, 1981, 1982; Pace, 1982; Finlay *et al.*, 1988; Pace and Orcutt, 1981; Psenner and Scholtt-Idl, 1985).

This study documents changes in the fine-scale vertical distribution of ciliates relative to the development of anoxic bottom water in the Chesapeake Bay, a large, temperate zone estuary located on the eastern coast of the USA.

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## Methods and materials

### *Study Site and Sampling*

The Chesapeake Bay is a partially mixed coastal plain estuary with salinity dominated density stratification present most of the year (Schubel and Pritchard, 1986). The study site was located in mesohaline waters (surface salinities = 5-20 ppt) which extend from approximately 39°N latitude to the mouth of the Potomac River (Fig. 1). This area of the Chesapeake Bay encompasses the zone of maximum phytoplankton productivity and biomass (Harding *et al.*, 1986) and supports an abundant metazoan zooplankton community (Brownlee and Jacobs, 1987) as well as high bacterial densities (Malone *et al.*, 1986; Tabor and Neihof, 1984).

The occurrence of anoxic bottom water has been well documented (Taft *et al.*, 1980; Officer *et al.*, 1984; Seliger *et al.*, 1985; Tuttle *et al.*, 1987). The magnitude, timing, and duration of the spring freshet determines the onset and strength of

early spring stratification which decreases advective transport of oxygen to bottom waters. Oxygen concentrations typically begin to decline by April at the northern extreme of the deep central channel (39°N Lat.), and anoxic bottom waters are usually present as far south as the mouth of the Patuxent River from June through August (see Fig. 1). Sulfide concentrations of 3-15  $\mu\text{M}$  are often detectable in deep central channel waters by midsummer. Brief periods of reoxygenation of bottom waters can occur during summer months as the result of summer storms. However, reoxygenation generally happens in the fall when mixis occurs as the result of the cooling of surface waters and wind-mixing events.

Station locations in the study site are given in Figure 1. Three stations were sampled: "858" (38°58'N Lat., 77°40'W Long.), "845" (38°45'N Lat., 77°32'W Long.), and "834" (38°34'N Lat., 77°31'W Long.). Station protocol consisted of first obtaining depth profiles of physical parameters with a Plessey-Grundy conductivity-temperature-depth-*in vivo* fluorescence-D.O. probe with a Niskin bottle rosette. Following assessment of physical parameters, 8 to 10 Niskin bottles were tripped at

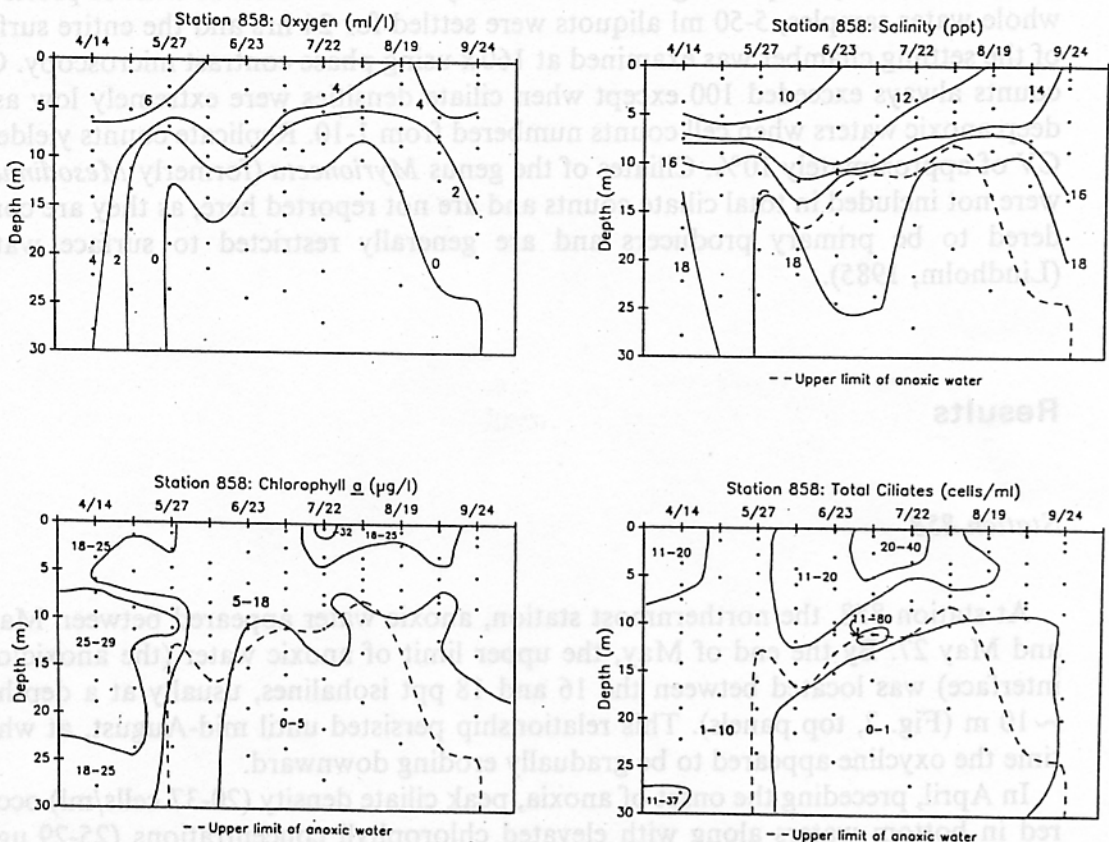


Fig. 2. Depth-time charts for station 858 of salinity, dissolved oxygen, chlorophyll *a*, and total ciliates: April through September 1986. Dashed lines represent the 0 ml/l dissolved oxygen isopleth. For chlorophyll *a* and total ciliates, lines enclose the areas of concentration indicated by the labels. Dots indicate measurement locations.

selected depths to give 2 to 3 samples in the surface layer, 3 to 4 samples through the oxygen or density transition zone, and 2 to 3 bottles in bottom waters.

Water for Winkler dissolved oxygen determination (Carpenter, 1965) was immediately drawn from each Niskin bottle using plastic tubing. Bottles were then emptied into buckets, and aliquots were taken for the determination of ciliate abundance (150 ml) and chlorophyll *a* concentration (100 ml). Samples for chlorophyll were filtered onto 25 mm A/E filters (Gelman Corp.), stored frozen, and processed using the acetone extraction method (Strickland and Parsons, 1972). Aliquots taken for ciliate counts were preserved by rapidly injecting a modified Bouin's solution (Coats and Heinbokel, 1982) to yield a final fixative concentration of 5%.

### Microscopic Methods

Ciliates were enumerated by the Utermöhl inverted microscope technique (Utermöhl, 1958). Depending on ciliate density and the detrital content of preserved whole-water samples, 5-50 ml aliquots were settled for 24 hrs and the entire surface of the settling chamber was examined at 160x using phase contrast microscopy. Cell counts always exceeded 100 except when ciliate densities were extremely low as in deep anoxic waters when cell counts numbered from 1-10. Replicate counts yielded a CV of approximately 10%. Ciliates of the genus *Myrionecta* (formerly *Mesodinium*) were not included in total ciliate counts and are not reported here, as they are considered to be primary producers and are generally restricted to surface waters (Lindholm, 1985).

## Results

### Station 858

At station 858, the northernmost station, anoxic water appeared between May 5 and May 27. By the end of May, the upper limit of anoxic water (the anoxic/oxic interface) was located between the 16 and 18 ppt isohalines, usually at a depth of ~10 m (Fig. 2, top panels). This relationship persisted until mid-August, at which time the oxycline appeared to be gradually eroding downward.

In April, preceding the onset of anoxia, peak ciliate density (20-37 cells/ml) occurred in bottom waters along with elevated chlorophyll concentrations (25-29  $\mu\text{g/l}$ ). The ciliate community in deep waters was dominated by *Cyclidium* sp., however small tintinnids (*Tintinopsis acuminata*, *T. rapa*, *T. levigata*) and oligotrichs (largely *Strombidium* sp.) were found throughout the water column. Following the onset of anoxia bottom waters coincided with chlorophyll minimum (0-5  $\mu\text{g/l}$ ) areas (Fig. 2, bottom left panel). Maximum concentrations of ciliates occurred in shallow depths

with oxygen levels of 2 ml/l or greater (Fig. 2, bottom right panel) and chlorophyll *a* concentrations ranging from 5-32  $\mu\text{g/l}$ . The surface layer community from June through September was generally dominated by small oligotrichs (*Strombidium* spp., 10-40  $\mu\text{m}$  diameter) and tintinnids (*Eutintinus pectinus*, *Tintinopsis subacuta*, *T. minuta*, *T. rapa*) but occasionally small (10-30  $\mu\text{m}$  diameter) *Balanion* sp. were abundant especially in June and July.

The bulk of anoxic bottom water contained few ciliates, ranging from 0 to 1 cell/ml but constituted a distinct assemblage commonly composed of large trachloercids, *Condylostoma magnum*, *Euplotes woodruffi* and *Pleuronema* sp. One notable exception to low cell densities was a distinct aggregation of ciliates (80 cells/ml), composed largely of the scuticociliate *Pleuronema*, observed at the anoxic/oxic interface in early July.

### Station 845

At station 845, anoxia did not occur until late June. From late June to late August, the upper limit of anoxic water was generally 11-14 m below the surface and 3-5 m

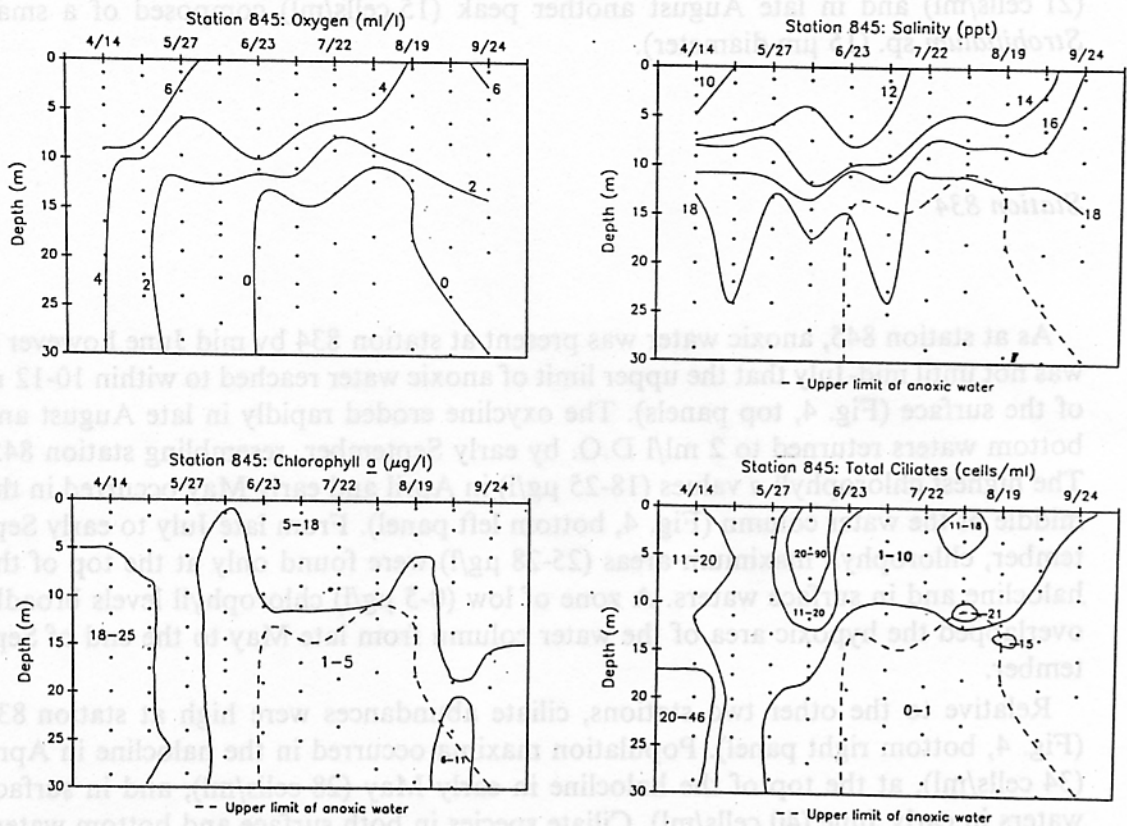


Fig. 3. Depth-time charts for station 845 of salinity, dissolved oxygen, chlorophyll *a*, and total ciliates: April through September 1986. Dashed lines represent the 0 ml/l dissolved oxygen isopleth. For chlorophyll *a* and total ciliates, lines enclose the areas of concentration indicated by the labels. Dots indicate measurement locations.

below the 16 ppt isohaline (Fig. 3, top panels). Re-oxygenation of bottom waters began in late August, and bottom water oxygen concentration had returned to 2 ml/l by the end of September. In contrast to station 858, chlorophyll *a* distributions at station 845 did not show a clear relationships with the development of anoxic water (Fig. 3, bottom left panel). High values (18-25  $\mu\text{g/l}$ ) were recorded throughout the water column from April to early May. From mid-June through September moderate (5-18  $\mu\text{g/l}$ ) levels of chlorophyll with no distinct maxima were present in the surface waters, and a zone of low (1-5  $\mu\text{g/l}$ ) chlorophyll concentration very broadly overlapped the hypoxic zone (< 2 ml/l D.O.) of the water column.

Similar to station 858, high concentrations of ciliates, primarily *Cyclidium*, occurred in bottom water (46 cells/ml) in April while in May and June depths above the halocline contained maximum abundances (90 cells/ml) of typical ciliate microzooplankters: oligotrichs and tintinnids (Fig. 3, bottom right panel). An anoxic ciliate community like that found at station 858 populated an area of low ciliate density which corresponded with the low oxygen water mass. Two anoxic/oxic interface peaks of ciliates were detected: in early August an aggregation of *Pleuronema* sp. (21 cells/ml) and in late August another peak (15 cells/ml) composed of a small *Strobilidium* sp. (15  $\mu\text{m}$  diameter).

#### Station 834

As at station 845, anoxic water was present at station 834 by mid June however it was not until mid-July that the upper limit of anoxic water reached to within 10-12 m of the surface (Fig. 4, top panels). The oxycline eroded rapidly in late August and bottom waters returned to 2 ml/l D.O. by early September, resembling station 845. The highest chlorophyll *a* values (18-25  $\mu\text{g/l}$ ) in April and early May occurred in the middle of the water column (Fig. 4, bottom left panel). From late July to early September, chlorophyll maximum areas (25-28  $\mu\text{g/l}$ ) were found only at the top of the halocline and in surface waters. A zone of low (0-5  $\mu\text{g/l}$ ) chlorophyll levels broadly overlapped the hypoxic area of the water column from late May to the end of September.

Relative to the other two stations, ciliate abundances were high at station 834 (Fig. 4, bottom right panel). Population maxima occurred in the halocline in April (34 cells/ml), at the top of the halocline in early May (28 cells/ml), and in surface waters in early June (40 cells/ml). Ciliate species in both surface and bottom waters were the same as those found at stations 858 and 845. Anoxic bottom water again contained low densities except for a short period in early July when deep waters contained moderate (1-7 cells/ml) numbers of a 30  $\mu\text{m}$  diameter *Strombidium* and in late July when *Pleuronema* (13 cells/ml) was found at the anoxic/oxic interface.

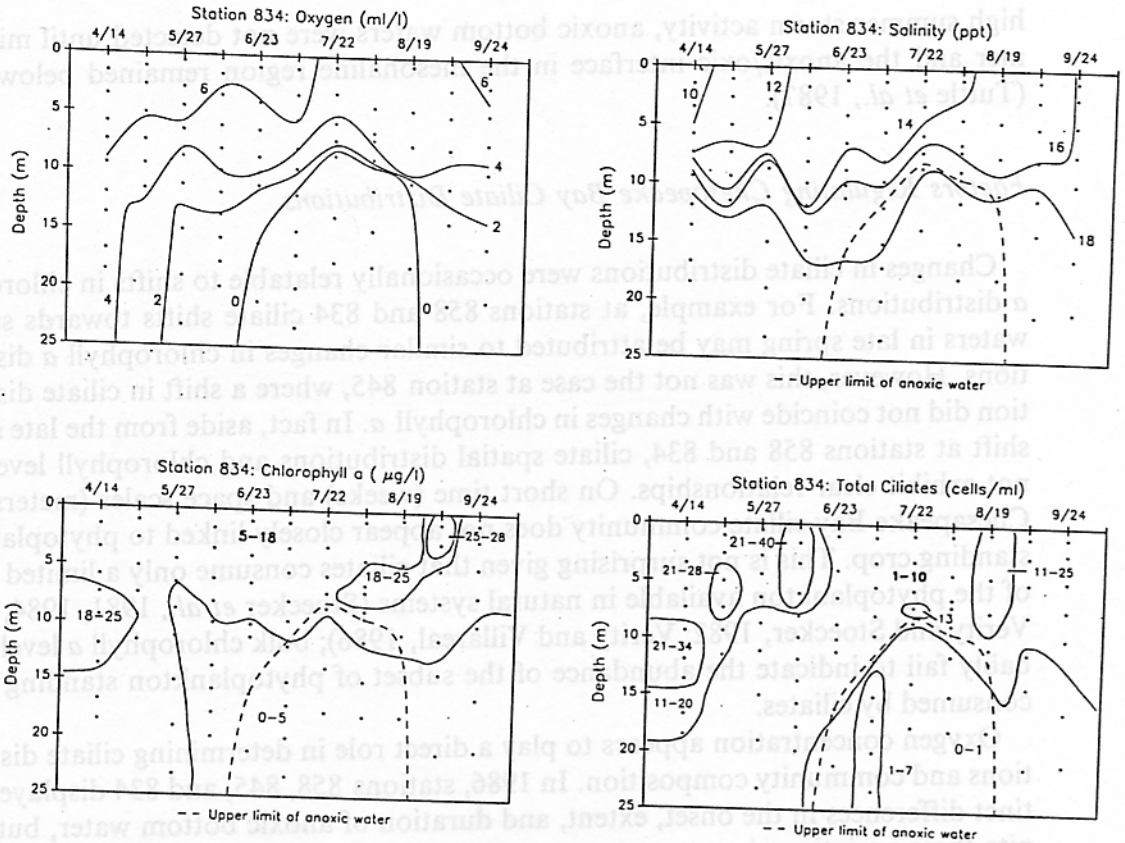


Fig. 4. Depth-time charts for station 834 of salinity, dissolved oxygen, chlorophyll *a*, and total ciliates: April through September 1986. Dashed lines represent the 0 ml/l dissolved oxygen isopleth. For chlorophyll *a* and total ciliates, lines enclose the areas of concentration indicated by the labels. Dots indicate measurement locations.

## Discussion

### *Chesapeake Bay Anoxia in 1986*

The temporal and spatial extent of bottom water anoxia during the study period was moderate for the mesohaline portion of the Chesapeake Bay. Both the timing of the onset of anoxia (late June) and the midsummer depth of the anoxic/oxic interface (11-14 m) at the central station, 845, were intermediate to extremes reported in recent years. For example, extensive ("catastrophic") anoxia occurred in the mesohaline Chesapeake Bay in 1984, a year characterized by an early onset of anoxia, beginning in April, and an anoxic/oxic interface that rose to within 8 m of the surface in August (Seliger *et al.*, 1985). In 1985, a year of low spring stream flow and

high summer storm activity, anoxic bottom waters were not detected until midsummer and the anoxic/oxic interface in the mesohaline region remained below 12 m (Tuttle *et al.*, 1987).

### *Factors Regulating Chesapeake Bay Ciliate Distributions*

Changes in ciliate distributions were occasionally relatable to shifts in chlorophyll *a* distributions. For example, at stations 858 and 834 ciliate shifts towards surface waters in late spring may be attributed to similar changes in chlorophyll *a* distributions. However, this was not the case at station 845, where a shift in ciliate distribution did not coincide with changes in chlorophyll *a*. In fact, aside from the late spring shift at stations 858 and 834, ciliate spatial distributions and chlorophyll levels did not exhibit clear relationships. On short time (weeks) and space scales (meters), the Chesapeake Bay ciliate community does not appear closely linked to phytoplankton standing crop. This is not surprising given that ciliates consume only a limited range of the phytoplankton available in natural systems (Stoecker *et al.*, 1981, 1984, 1986; Verity and Stoecker, 1982; Verity and Villareal, 1986); bulk chlorophyll *a* levels probably fail to indicate the abundance of the subset of phytoplankton standing stock consumed by ciliates.

Oxygen concentration appears to play a direct role in determining ciliate distributions and community composition. In 1986, stations 858, 845, and 834 displayed distinct differences in the onset, extent, and duration of anoxic bottom water, but, despite these variations in pattern, oxygen depletion clearly influenced ciliate distributions in a similar manner. All tintinnid ciliates and the majority of oligotrichous ciliates were restricted to oxygenated waters. The onset of anoxia in bottom waters corresponded to a shift in the distributions of these forms toward surface waters at stations 858 and 834 while at station 845 the shift corresponded to bottom water hypoxia (2 ml/l D.O.).

At all three stations a distinct community of ciliates developed in anoxic water during summer months. Interestingly, the community was composed, at least in part, of forms generally found in anoxic or hypoxic sediments *i. e.*, trachlocercid ciliates (Fenchel, 1969). It is possible that these forms behave like their freshwater counterparts and colonize the water column during periods of anoxic bottom water (Bark, 1981, 1985; Bark and Goodfellow, 1985; Bark and Watts, 1984; Finlay, 1981, 1982; Finlay *et al.*, 1988). Unfortunately the relatively low densities of ciliates in anoxic waters combined with the small volumes sampled did not allow reliable assessment of this possibility.

Exceptions to the general low abundance of ciliates in anoxic water were the occurrence of peaks associated with the anoxic/oxic interface at each station. At the northern station (858), the peak occurred in early July; at the middle station (845), peaks occurred in August; and in the southern station (834), a peak occurred in late July. Had these peaks appeared simultaneously or in sequence, either temporally or spatially (*i. e.* north-south), or had all been composed of the same species, they might have represented an isolated event. Yet the aggregations did not occur sequentially



north-south, nor simultaneously, nor were they all composed of the same species, and so appear to be independent events. Most of the aggregations were composed of *Pleuronema*, a member of the anoxic community, but on two occasions the interface region contained relatively dense populations of a small *Strombidium* sp.

In the Chesapeake Bay distinct communities of ciliates can be distinguished. Oxygenated waters are dominated by oligotrichs and tintinnids. Anoxic bottom waters are populated largely by ciliates resembling benthic forms. The anoxic/oxic interface is the site of intermittent accumulations of forms found both in oxygenated waters (small *Strombidium* sp.) and anoxic waters (*Pleuronema* sp.).

### *The Effects of Anoxia in the Chesapeake Bay Compared to Other Systems*

The effect of seasonal anoxia on ciliate distributions in the mesohaline Chesapeake is quite different from similar phenomena in freshwater lakes. In the mesohaline Chesapeake Bay, as in fresh water lakes, deep anoxic waters contain low densities of ciliates (0-1 cell/ml) and ciliate aggregations occur at the anoxic/oxic interface. However, the magnitude of the aggregations at the oxycline, both in absolute and relative terms, distinguishes the Chesapeake Bay phenomenon from similar events in small eutrophic lakes which develop anoxic hypolimnions.

In the Chesapeake Bay, aggregations of ciliates only occurred sporadically and maximum concentrations at the oxic/anoxic interface (12-80 cells/ml) were similar to the maxima found in shallow surface waters. Throughout the period of anoxic bottom water the ciliate community as a whole remained dominated by the surface-layer assemblage of oligotrichs and tintinnids.

In freshwater systems, ciliate densities of  $10^1$  to  $10^3$  cells/ml develop in the oxycline region and represent a distinct area of maximum concentration (Bark, 1981, 1985; Bark and Goodfellow, 1985; Bark and Watts, 1984; Finlay, 1981, 1982; Pace, 1982; Finlay *et al.*, 1988; Pace and Orcutt, 1981; Psenner and Scholtt-Idl, 1985). The ciliate communities are generally dominated by either large benthic ciliates which have migrated into the water column or small bacterivorous ciliates.

These communities are apparently fuelled by high levels of particulate organic carbon (Pendl and Stewart, 1986) and elevated rates of bacterial activity (McDonough *et al.*, 1986) which are associated with the oxycline regions of freshwater lakes. Similarly, in marine systems where deep water anoxia is a semi-permanent feature, such as deep ocean trenches and in the Black Sea, peak concentrations of labile dissolved organic carbon (Carlucci *et al.*, 1987), elevated bacterial growth rates (Karl *et al.*, 1977), and occasionally high ciliate concentrations (Sorokin, 1981, 1983; Vinogradov *et al.*, 1986) correspond with the oxycline region. Thus, in both freshwater and saltwater systems, anoxic/oxic interfaces are zones of increased heterotrophic activity. In the Chesapeake Bay the aggregations of ciliates at the interface layer were composed of bacterivorous forms which supports the notion that the interface layer is a zone of increased bacterial activity.

The generally low density of ciliates at the anoxic/oxic interface in the Chesapeake Bay could be ascribed to a variety of causes: low growth rates in low oxygen waters,

predation pressure, or dispersion due to the Chesapeake's two layer circulation pattern. Unfortunately, comparative data from other systems with complex circulation patterns are sparse. Only one study, which focused on trophic relationships, has been conducted in such a system, the Kiel Bight (Smetacek, 1981). No oxygen data were presented, and the only ciliate-oxygen relationship mentioned was that anoxic waters were characterized by very low ciliate abundances.

Further studies will be necessary to determine what factors regulate the abundance of ciliates at the anoxic/oxic interface in the Chesapeake Bay and determine the origin of the anoxic water ciliate community.

## References

- Bark A. W., 1981. The temporal and spatial distribution of plankton and benthic protozoan communities in a small productive lake. *Hydrobiologia*, 85, 239-255.
- Bark A. W., 1985. Studies on ciliated protozoa in eutrophic lakes: 1. seasonal distribution in relation to thermal stratification and hypolimnetic anoxia. *Hydrobiologia*, 124, 167-176.
- Bark A. W. and Goodfellow J. G., 1985. Studies on ciliated protozoa in eutrophic lakes: 2. field and laboratory studies on the effects of oxygen and other chemical gradients on ciliate distribution. *Hydrobiologia*, 124, 177-188.
- Bark A. W. and Watts J. M., 1984. A comparison of the growth characteristics and spatial distribution of hypolimnetic ciliates in a small lake and an artificial lake ecosystem. *J. Gen. Microbiol.*, 130, 113-122.
- Brownlee D. C. and Jacobs F., 1987. Mesozooplankton and microzooplankton in the Chesapeake Bay, 217-269. In: *Containment Problems and Management of Living Chesapeake Bay Resources*, Majumdar S. K., Hall L. W. jr. and Austin H. M. (eds.). Easton, PA, Penn. Acad. Sci.
- Carlucci A. F., Shimp S. L. and Craven D. B., 1987. Bacterial response to labile dissolved organic matter increases associated with marine discontinuities. *FEMS Microb. Ecol.*, 45, 211-220.
- Carpenter J. H., 1965. The Chesapeake Bay Institute technique for the Winkler dissolved oxygen method. *Limnol. Oceanogr.*, 10, 141-143.
- Coats D. W. and Heinbokel J. F., 1982. A study of reproduction and other life cycle phenomena in planktonic protists using an acridine orange fluorescence technique. *Mar. Biol.*, 67, 71-79.
- Fenchel T., 1969. The ecology of the marine microbenthos. IV. structure and function of the benthic ecosystem. *Ophelia*, 6, 1-182.
- Finlay B. J., 1981. Oxygen availability and seasonal migrations of ciliated protozoa in a freshwater lake. *J. Gen. Microbiol.*, 123, 173-178.
- Finlay B. J., 1982. Effects of seasonal anoxia on the community of benthic ciliated protozoa in a productive lake. *Arch. Protistenk.*, 125, 215-222.
- Finlay B. J., Clarke K. J., Cowling A. J., Hindler R. M., Rogerson A. and Beringer U.-G., 1988. On the abundance and distribution of protozoa and their food in a productive freshwater pond. *European Journal of Protistology*, 23, 205-217.
- Harder W., 1968. Reactions of plankton organisms to water stratification. *Limnol. Oceanogr.*, 13, 156-168.
- Harding L. W., Meeson B. W. and Fisher T. R., 1986. Phytoplankton production in two east coast estuaries: photosynthesis-light functions and patterns of carbon assimilation in Chesapeake and Delaware Bays. *Estuarine, Coast. Shelf Sci.*, 3, 773-806.

- Holligan P. M., Harus R. P., Newell R. C., Harbour D. S., Head R. N., Linley E. A. S., Lucas M. I., Tranter P. R. G. and Weekley C. M. W., 1984. Vertical distribution and partitioning of organic carbon in mixed, frontal, and stratified waters of the English Channel. *Mar. Ecol. Prog. Ser.*, **14**, 111-127.
- Karl D. M., LaRock P. A. and Schultz D. J., 1977. Adenosine triphosphate and organic carbon in the Cariaco Trench. *Deep-Sea Res.*, **25**, 105-113.
- Lindholm T., 1985. *Mesodinium rubrum* - a unique photosynthetic ciliate. *Adv. Aquat. Microbiol.*, **3**, 1-48.
- Malone T. C., Kemp W. M., Ducklow H. W., Boynton W. R., Tuttle J. W. and Jonas R. B., 1986. Lateral variation in the production and fate of phytoplankton in a partially stratified estuary. *Mar. Ecol. Prog. Ser.*, **32**, 149-160.
- McDonough R. J., Sanders R. W., Porter K. G. and Kirchman D. L., 1986. Depth distribution of bacterial production in a stratified lake with an anoxic hypolimnion. *Appl. Environ. Microbiol.*, **52**, 992-1000.
- Officer C. B., Biggs R. B., Taft J. L., Cronin L. E., Tyler M. A. and Boynton W. R., 1984. Chesapeake Bay anoxia: origin, development, and significance. *Science*, **223**, 22-27.
- Pace M. L., 1982. Planktonic ciliates: their distribution, abundance, and relationship to microbial resources in a monomictic lake. *Can. J. Fish. Aquat. Sci.*, **39**, 1106-1116.
- Pace M. L. and Orcutt J. D. Jr., 1981. The relative importance of protozoans, rotifers and crustaceans in a freshwater zooplankton community. *Limnol. Oceanogr.*, **26**, 822-830.
- Pendl M. R. and Stewart K. M., 1986. Variations in carbon fractions within a dimictic and a meromictic basin of the Junius Ponds, New York. *Freshwater Biol.*, **16**, 539-555.
- Psenner R. and Scholtt-Idl K., 1985. Trophic relationships between bacteria and protozoa in the hypolimnion of a meromictic mesotrophic lake. *Hydrobiologia*, **121**, 111-120.
- Revelante N. and Gilmartin M., 1983. Microzooplankton distribution in the Northern Adriatic Sea with emphasis on the relative abundance of ciliated protozoans. *Oceanol. Acta*, **6**, 407-415.
- Revelante N. and Gilmartin M., 1987. Seasonal cycle of the ciliated protozoan and micrometazoan biomass in a Gulf of Maine estuary. *Estuarine, Coast. Shelf Sci.*, **25**, 581-598.
- Revelante N., Gilmartin N. and Smolaka N., 1985. The effects of Po River induced eutrophication on the distribution and community structure of ciliated protozoa and micrometazoan populations in the northern Adriatic Sea. *J. Plankton Res.*, **7**, 461-471.
- Schubel J. R. and Pritchard D. W., 1986. Response of upper Chesapeake Bay to variations in discharge of the Susquehanna River. *Estuaries*, **9**, 236-249.
- Seliger H. H., Boggs J. A. and Biggley W. H., 1985. Catastrophic anoxia in the Chesapeake Bay in 1984. *Science*, **228**, 70-73.
- Smetacek V., 1981. The annual cycle of protozooplankton in the Kiel Bight. *Mar. Biol.*, **63**, 1-11.
- Sorokin Y. I., 1981. Marine microheterotrophs, 293-342. In: *Analysis of Marine Ecosystems*, Longhurst H. (ed.). London, Academic Press.
- Sorokin Y. I., 1983. The Black Sea, 253-292. In: *Estuaries and Enclosed Seas*, Ketchum B. (ed.). Amsterdam, Elsevier.
- Stoecker D. K., Cucci T. L., Hulbert E. M. and Yentsch C. M., 1986. Selective feeding by *Balanion* sp. (Ciliata: Balanionidae) on phytoplankton that best support its growth. *J. Exp. Mar. Biol. Ecol.*, **95**, 113-130.
- Stoecker D. K., Davis L. H. and Anderson D. M., 1984. Fine scale spatial correlation between planktonic ciliates and dinoflagellates. *J. Plankton Res.*, **6**, 829-842.
- Stoecker D. K., Guillard R. L. and Kavee R. M., 1981. Selective predation by *Favella ehrenbergii* (Tintinnina) on and among dinoflagellates. *Biol. Bull.*, **160**, 136-145.
- Strickland J. R. and Parsons T. R., 1972. A practical handbook of seawater analysis. *Bull. Fish. Res. Bd Can.*, **167**, 185-205.
- Tabor P. S. and Neihof R. A., 1984. Direct determination of activities for microorganisms of Chesapeake Bay populations. *Appl. Environ. Microbiol.*, **48**, 1012-1019.

- Taft J. L., Taylor W. R., Hartwig E. O. and Loftus R., 1980. Seasonal oxygen depletion in Chesapeake Bay. *Estuaries*, 3, 242-247.
- Tuttle J. H., Jonas R. J. and Malone T. C., 1987. Origin, development and significance of Chesapeake Bay anoxia, 442-472. In: *Containment Problems and Management of Living Chesapeake Bay Resources*, Majumdar S. K., Hall L. W. Jr. and Austin H. M. (eds.). Easton, PA, Penn. Acad. Sci.
- Utermöhl H., 1958. Zur Vervollkommnung der Quantitativen Phytoplankton-Methode. *Mitt. Int. Ver. Theor. Angew. Limnol.*, 9, 1-38.
- Verity P. G. and Stoecker D. R., 1982. Effects of *Olithodiscus luteus* on the growth and abundance of tintinnids. *Mar. Biol.*, 72, 79-87.
- Verity P. G. and Villareal T. A., 1986. The relative food value of diatoms, dinoflagellates, flagellates, and cyanobacteria for tintinnid ciliates. *Arch. Protistenk.*, 131, 71-84.
- Vinogradov M. YE., Shushkina E. A., Flint M. V. and Tutmantsev N. I., 1986. Plankton in the lower layers of the oxygen zone in the Black Sea. *Oceanology*, 26, 222-228.
- Wetzel, R. G., 1983. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 1985. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 1986. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 1987. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 1988. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 1989. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 1990. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 1991. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 1992. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 1993. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 1994. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 1995. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 1996. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 1997. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 1998. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 1999. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2000. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2001. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2002. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2003. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2004. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2005. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2006. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2007. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2008. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2009. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2010. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2011. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2012. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2013. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2014. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2015. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2016. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2017. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2018. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2019. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2020. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2021. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2022. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2023. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2024. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.
- Wetzel, R. G., 2025. *Limnology*. St. Louis, Missouri, C.V. Mosby Co., 550 pp.