Interactions Between Physics and Biology in the Estuarine Turbidity Maximum (ETM) of Chesapeake Bay, USA

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ABSTRACT

Three seasonal research cruises in the upper Chesapeake Bay during 1996 were planned to describe the Estuarine Turbidity Maximum (ETM) and to study processes in and near it that lead to enhanced biological activity. We hypothesized that the ETM was a region of particle entrapment, increased biomass, and production potential of plankton and fish. The highly turbid ETM was mapped (CTD and Transmissometry) and its water currents monitored (ADCP). A wide array of biological measures and collections was made using traditional and new technologies. The ETM proved to be a dynamic and consistently present feature. Its position is strongly associated, but not coincident, with the estuarine salt front. Position varies in response to freshwater input, winds and the quarter-wave seiche. Levels of total suspended solids, zooplankton, and young-of-the-year fish were high in the ETM. In contrast, primary production was low and community metabolism was net heterotrophic. Abundance of the copepod *Eurytemora affinis* was greatly elevated in and near the ETM as were abundances of most YOY anadromous fishes and, surprisingly, juvenile blue crabs. Stable isotope (N and C) analyses suggested that microzooplankton served as an important intermediary for higher trophic-level production in the upper Bay. Recruitment potential of fish and crabs may be enhanced in the ETM as a consequence of physics-induced entrapment of particles, aggregation of foods, and behavior of organisms that promote retention and favor elevated growth.
INTRODUCTION

Background

During the past several decades much has been learned about some aspects of estuarine and coastal ecosystems. The fact that they are characterized by strong physical, chemical and biological gradients and that these gradients develop and dissipate on a variety of temporal scales is not the least of these achievements. More specifically, understanding of inputs, transformations and fates of nutrients and organic matter (Nixon et al. 1996; Boynton et al. 1995) at the land-sea margin has improved as has understanding of the factors regulating primary production (Howarth 1988). At the other end of estuarine food webs estimates of fish abundance and distribution have been improving with the use of bioacoustic technologies (Brandt 1992), larger-scale experimental studies (Houde et al. 1993) and analytical models (Brandt et al. 1992).

However, a great deal remains uncertain in these very productive, gradient-rich and fluctuating ecosystems. For example, Nixon (1988) synthesized primary production and fishery yield data collected from many marine, coastal and estuarine ecosystems and found a significant positive relationship which was somewhat surprising given the diversity of systems considered and the complexities of food web processes. In this same synthesis, a production-fisheries yield relationship reported earlier for lakes (Oglesby 1977) indicated that fisheries yield per unit primary production in lakes was much lower than in marine, coastal or estuarine systems. We added information from Chesapeake Bay and found both high primary production and fisheries yields and, most interestingly, higher conversion efficiency between primary and secondary production than for other marine systems. The mechanisms responsible for this remain unclear. Are tidal energies and other transient physical structures (i.e., fronts) the central feature? Are high conversion efficiencies a general feature of these systems or are these restricted in time and space, yet of sufficient magnitude to influence fisheries yields at the full ecosystem scale? Are these features influenced by the degree of nutrient enrichment? How will currently eutrophic coastal and estuarine food webs respond to management-induced nutrient load reductions?

Chesapeake Bay LMER-TIES Program and Study Objectives

Land-Margin Ecosystem Research (LMER) programs (supported by the US National Science Foundation) have been conducted at several sites in the USA, including Chesapeake Bay, during the last decade. The primary focus of these medium-duration (6-year) studies is to investigate the influences of land, ocean and atmosphere on estuarine systems. In the case of Chesapeake Bay, freshwater, organic matter and nutrient input effects on circulation, transport, primary production and nutrient cycling were examined in one LMER program. The current LMER program examines relationships between primary and secondary production and the physical processes which may influence this coupling. Spatial gradients play a central role in these studies.

The central hypothesis being tested in this program states that in large land-margin ecosystems, regional and interannual variations in primary and secondary production are strongly influenced by the pulsing nature of inputs from the adjacent watershed, atmosphere and coastal ocean and by the associated temporal variabilities in circulation and fine-scale (1-10,000 m) physical structures which act as sites of intense ecological activity. In this paper we report on measurements collected at a fine-scale physical structure called the Estuarine Turbidity Maximum, or ETM. The ETM is a zone of increased suspended particle concentration, which in Chesapeake Bay is located at the northern end of the Bay. Its location is closely associated with the limit of salt intrusion but does not necessarily coincide with it.

There are few, if any, studies in the Chesapeake Bay ETM region with sufficient sampling density and interdisciplinary breadth to address the range of ecosystem effects that may be associated with, or attributable to, the ETM feature. It is especially unknown how this may vary
seasonally or interannually. This paper presents a descriptive overview of a study designed to
dress physical and biological effects associated with the ETM. We hypothesized that secondary
production in the ETM would be higher than predicted from primary production rates because of
substantial and seasonally-pulsed additions of terrestrial organic matter. We suggest that an
important fuel for secondary production is of terrestrial origin while additional nutritional needs are
satisfied from phytoplankton production, which is dominated by diatoms in this region. The
physical retention characteristic of the ETM would further promote secondary production. Our
specific objectives were to delineate the hydrography, sediment characteristics and spatial
variability of the ETM, measure plankton and fish distribution and abundance relative to the ETM,
study recruitment mechanisms and clarify the possible role of the ETM as an entrapment zone for
biological communities as well as for sediments.

SITE, APPROACH AND METHODS

Chesapeake Bay Study Area

The Chesapeake Bay (Figure 1) is the largest estuary in the United States, having an area of
6,500 km², a length of 315 km and mean depth of 8.4 m. It is closely embraced by the land and
has a drainage basin surface area to water surface area ratio of 28:1. European habitation of the
Chesapeake region began more than 350 years ago and has altered the Bay's landscape, its water
quality and its living resources (US EPA 1983). The Bay and its watershed lie in the coastal
corridor of dense human population between New York and Virginia. The current population in
the watershed is 13.6 million and is projected to grow to 16.2 million by 2020 (Year 2020 Panel
1988). Chesapeake Bay and its resources are intensively used by diverse commercial and
recreational interests. Fisheries for historically important species have declined significantly, a
consequence of overfishing, habitat alterations, and degradation of water quality (Richkus et al.
1992). New threats from introduced species, and the unknown consequences of global climate
change and rising sea level are factors which will continue to alter the quality and character of the
Bay in coming decades.

Because Chesapeake Bay is a large system, entire populations of many animals are
contained within it and its production supports the large part of their productivity (Baird and
Ulanowicz 1989). A strong salinity gradient from the head of the Bay to its mouth (0 to 28 psu)
acts to control the distribution of organisms.

High seasonal and interannual variability in freshwater inputs are a distinctive characteristic
of Chesapeake Bay. Since 1968, annual average flows have varied by slightly more than a factor
of two (Figure 2a) and peak flows within a year do not always occur during the same month or
even season (Figure 2b). Studies at the ETM were conducted during 1996, a particularly wet year
with an unusual annual flow pattern.

Approach

Our approach was to combine rapid mapping techniques (towed sensor system) along axial
transects of the upper Bay with repeated CTD casts, underway ADCP measurements of current
structure, and net collections along transects inside the ETM and outside the ETM (Gibson Island
transect; Figure 1). Physical structure was characterized simultaneously with process rate
measurements (e.g. primary production rates, zooplankton and egg production) on shipboard or
derived later from samples brought to the laboratory (e.g. fish feeding and growth). These
measurements were coordinated with aerial remote sensing for larger scale spatial coverage.
Studies of 5-7 days duration were conducted in 1996 during spring, summer and fall seasons to
establish ranges of both short-term (e.g. tidal stage, day versus night) and seasonal-scale
variability.
Methods

**High Intensity Physical and Biological Measurements:** Continuous measurements of temperature, salinity, chlorophyll-a, optical backscatterance and zooplankton abundances were made along axial transects with an undulating towed body (GMI Scanfish) augmented by a near-surface pumped sampling system. The Scanfish is an automatic undulating device providing rapid vertical undulations from near-surface to near-bottom in depths as shallow as 5 m. The device is towed at 4-5 knots from an outrigger to minimize the effect of ship wake. For most variables this provides vertical resolution of <1 m and horizontal resolution of 50-100 m, depending on water depth.

Water property distributions along repeated axial and lateral transects were measured with a Seabird Sealogger CTD with auxiliary turbidity, fluorescence, and irradiance sensors. An acoustic zooplankton sensor (TAPS) and a high volume pump were attached to the CTD cage as well. The pump was used to obtain in situ water samples for calibration of the turbidity, fluorescence, and zooplankton measurements. Selected samples of resuspended sediments were collected for settling velocity analysis using a modified Owen settling tube (manufactured by Valeport, Ltd.).

Detailed 24 hr. time series of near-bottom conditions were collected inside and outside the ETM with a bottom tripod containing a WHISSL current meter/wave gauge and turbidity sensors distributed within 1.5 m from the bottom. Underway current profiling using an RD Instruments Broad Band Acoustic Doppler Current Profiler (ADCP; Geyer and Signell 1990; Geyer 1993; Thevenot and Krause 1993) was used to measure spatially and temporally variable current patterns (0.5 m vertical resolution and approximately 150 m horizontal resolution) along repeated lateral transects at 1.5 hr. intervals for 24 hrs. at a time.

**Airborne Remote Sensing:** Remote sensing measurements of ocean color were made with a simple, airborne radiometer, the Ocean Data Acquisition System (ODAS) that has been deployed regularly on Bay-wide flights since 1989. ODAS consists of three nadir-viewing radiometers of 15 nm bandwidth at wavelengths of 460, 490, and 520 nm, Loran-C navigation, and a data acquisition and transmittal package. The instrument is flown at an altitude of 500 feet and an airspeed of 100 knots (~50 m s⁻¹), giving a spatial resolution of 5.2 m at the 10 Hz sampling rate. This gives approximately 5 x 50 m resolution when data are averaged over 1 second. Data (12 bit) from these sensors are stored together with time, frame number and gain values on a PC aboard the aircraft. A typical data file includes a record of 2 to 15 minutes duration corresponding to an individual flight line.

The radiometric data from ODAS are processed to estimate surface chlorophyll concentrations by combining matching airborne and shipboard data, as described previously (cf. Harding et al. 1992, 1994). Recovery of chlorophyll from ODAS data uses a spectral curvature algorithm applied to the three radiances. Estimates of total algal biomass are determined from relationships of surface chlorophyll (mg m⁻³) and integrated, water-column chlorophyll (mg m⁻²) made in the EPA Chesapeake Bay Program’s monitoring cruises and applied to remotely-sensed surface measurements.

**Algal Biomass and ¹⁴C Production Measurements:** Phytoplankton biomass as chlorophyll-a was measured on a Turner Designs model 10 fluorometer calibrated against spectrophotometric determinations on standards, using standard methods (Strickland and Parsons, 1972). Phytoplankton production was measured using ¹⁴C bicarbonate assimilation in simulated in situ sunlight incubations (cf. Harding et al. 1986; Malone et al. 1988).

During the studies described here, samples were collected at stations inside and outside the ETM using the shipboard rosette. Phytoplankton production was measured for surface water incubated for either 4-6 hours or for 24 hours in 350 ml bottles at 7 irradiance
levels (from 4 to 100% ambient light) using neutral density screening of individual bottles. All incubations were carried out under natural light in shipboard incubators supplied with flowing surface water to provide temperature control. Incident irradiance was measured continuously with a Li-Cor quantum probe and recorded on a data logger. At the end of incubations, samples were collected by gentle (< 150 mm Hg) vacuum filtration onto Whatman GF/F filters, rinsed, acidified and placed in LSC cocktail for counting on a shipboard LSC (Packard) to determine activity.

Community Oxygen Production and Respiration Rates. Plankton community $O_2$ production and respiration rates were estimated using standard light/dark bottle techniques, measured as in vitro changes in dissolved oxygen in multiple-replicate BOD incubation bottles (Smith and Kemp 1995). Oxygen concentrations were determined by high-precision Winkler titration of whole samples with computer-controlled photometric end-point detection (Sensoren Instrumente Systeme; Kiel, Germany). This automated titration system has a minimum precision of 0.01%.

Plankton production was measured in bottles containing surface water and incubated for 4-6 hours at 7 irradiance levels (from 3-100% ambient light) using neutral density screening of individual bottles. All incubations were carried out under natural light in incubators supplied with flow-through surface water providing temperature control. Gross $O_2$ production at each light level was determined as light bottle production plus dark bottle consumption minus initial concentration. Gross production (P) versus irradiance (I) relationships were then modeled as a hyperbolic tangent function (Jassby and Platt 1976) and integrated over the depth of the euphotic zone (to 1% surface irradiance) based on vertical attenuation of light. Daily integrated rates of gross community production ($g O_2 m^{-2} d^{-1}$) were then calculated as hourly production rates multiplied by the fraction of total daily PAR occurring during the course of the incubation. Daily integral rates of total community respiration were calculated as hourly rates multiplied by 24 and integrated over the depth of the water-column. The difference between the calculated gross production and community respiration rates is the net metabolism of the plankton community (NPM, $g O_2 m^{-2} d^{-1}$), and is taken as a measure of the integrated production or consumption of organic matter within the plankton community as a whole.

Zooplankton: Measurements of zooplankton abundance in the surface and bottom mixed layers were obtained with oblique tows of a 1 m$^2$ Tucker trawl with a 280 $\mu$m mesh and with 10 liter Niskin bottles deployed at the bottom, pycnocline and surface and drained through a 35 $\mu$m mesh. Tucker trawl samples were preserved in ethanol, while Niskin bottle samples were preserved in formalin. Zooplankton sampling was conducted primarily during the daytime. Other approaches to measuring zooplankton in the ETM are described by Roman et al (this conference).

Egg production rates were estimated using two techniques. For Eurytemora affinis, which carries its eggs, the eggs per female were counted. Estimated egg development time from the published relationships of Heinle and Flemer (1975) were used. Egg production rates for the copepod Acartia tonsa, which is a broadcast spawner, were estimated by incubating females in 64 $\mu$m - filtered water for 24 h, then counting the eggs produced. Egg production estimates are the mean of at least 7 replicates.

Fish: Fisheries acoustic data were collected along transect in northern Chesapeake Bay with a Simrad EY-500 Split-Bean Echosounder operating at 120 kHz (beamwidth 7.1°). The downward looking transducer was towed near the bow of R/V Cape Henlopen on a deadweight towbody at approximately 2.5 m s$^{-1}$. Data were collected continuously (ping rate: 3 s$^{-1}$) on transects oriented along the north-south axis of the Bay in the main shipping channel. These data were collected at night to maximize numbers of fish acoustically recognized as individuals in the water column. "Raw" acoustic data (Simrad designation: sample power and sample angle telegrams) and simultaneous GPS navigation data were stored for later processing and analysis. Calibration of the echosounder was done during each cruise using the in situ standard target method by lowering a tungsten carbide sphere (target strength = -40.4 dB) directly beneath the
transducers. Received signals were compared to the known target strength (Foote 1983, Brandt 1997).

Fisheries acoustic data were processed using DEVIS (Jech and Luo 1997). DEVIS is a fisheries acoustic data processing and visualization system developed to process digital acoustic data for use in fisheries ecology and management. Data were corrected for sound absorption, calibrations and spreading losses \((40 \log_{10} R \text{ TVG} \text{ for individual targets and } 20 \log_{10} R \text{ TVG} \text{ for volume scattering})\). Individual targets were discriminated and their spatial location and acoustic backscattering cross-section were stored for merging with volume scattering data. Volume scattering \((i.e. \text{Integrated Echo})\) was integrated over 120 pings (horizontal resolution of 100 m, at a ship speed of 2.5 m sec\(^{-1}\)) and 0.5 m (vertical) to obtain spatially-explicit arrays of relative density (Brandt et. al., 1992). Individual target information was then meshed with the corresponding relative density array. Numeric density \(\# \text{ m}^{-3}\) in each cell was calculated using the average \(<\sigma_b>\) for fish in each cell. Biomass density \(\text{g m}^{-3}\) was calculated using a \(<\sigma_b>\) to fish length relationship (Love, 1971), a length - weight relationship representative of the fish community (E. Houde, personal communication), and then multiplying numeric density by biomass in each cell.

Juvenile and adult fish abundances were also assessed from catches in towed nets. Depth-discrete samples of zooplankton and ichthyoplankton were collected using Tucker trawls as described above for zooplankton. A mid water trawl with a nominal mouth area of 8 m\(^2\) and a cod end mesh size of 6 mm was towed obliquely for 20 minutes, primarily at night, to capture juvenile and some species of adult fish. Length-frequency distribution of all fish species and blue crabs and mean weights for fish species were recorded from measurement made immediately after each mid water trawl tow. Sub-samples of fish collected in the mid water trawls were frozen or preserved in ethanol for stomach analysis and age and growth determinations.

**Stable Isotope Collection and Analysis:** Samples of several organic matter pools, including seston, zooplankton and bay anchovy (Anchoa mitchilli, a zooplankton predator) were collected on or near the ETM transect, on or near the Gibson Island transect and in the middle and southern regions of Chesapeake Bay (Figure 1). Seston was collected by filtering water collected in a 10-liter Niskin bottle from bottom, pycnocline, and surface layers until a precombusted Whatman GF/F filter was clogged. Zooplankton were collected from Tucker trawls as described above, except that a single oblique tow spanned the entire water column. Bay anchovy were collected from mid water trawls. Heads, fins and guts were removed prior to further processing. All samples were immediately frozen until they were dried at 60°C for 24 hours and ground to a fine powder. Analyses for stable isotope ratios (carbon and nitrogen) were conducted by the stable isotope laboratory at The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA.

**RESULTS AND DISCUSSION**

**Physics and Movement of the ETM**

The defining physical feature of the upper Chesapeake Bay is the limit of salt intrusion, which occurs variably between latitude 39.2° N and 39.4° N (Figure 1). On average, the ETM tended to be centered on the intersection of the 1 psu isohaline with the bottom of the channel (Figs. 3 and 4). However, the ETM center frequently varied by as much as 10 km from the 1 psu isohaline, independent of the phase of the tide (Figure 5). It is likely that this variation represented a lag of the resuspendable sediment pool behind the motion of the salt front (Figure 6). The salinity structure in upper Chesapeake Bay responds quickly to freshwater inflow fluctuations and wind forcing, but a resuspension phase lag such as that discussed by Dyer (1988) prevents the sediment particles from moving as quickly. This lag may explain the large extent of the Chesapeake ETM (> 20 km) relative to a tidal excursion in the upper Bay (< 10 km), as the particle pool is dispersed over a broader extent than one tidal excursion (Figure 4).

Tidal variations in current profiles, salinity stratification, and suspended sediment concentration are consistent with a major role for tidal asymmetries in the Chesapeake ETM. Thus,
the flood tide currents exhibit less vertical shear than the ebb tide currents in Figure 6. Near the bottom, the tide tends to turn to flood sooner and flood tends to last longer. Increases in suspended sediment concentration high in the water column during the first part of ebb are consistent with the particle trapping scenario proposed by Geyer (1993).

The efficiency of particle trapping by the Chesapeake Bay ETM appeared to vary seasonally, primarily in response to changes in particle settling velocity. Early in 1996, following an immense discharge peak during winter (Figure 2), suspended sediment concentrations were highest in the fresh surface layer and appeared to be flushed from the upper Bay (at least over the channel). Late in the year, following another large discharge peak in late October, the sediments appeared to be trapped almost immediately into a well-defined ETM. Settling velocities estimated using a modified Owen tube indicated at least an order of magnitude increase in settling velocity between February and October (not shown). This behavior also is consistent with the particle trapping scenario proposed by Geyer (1993). The reasons for the increase in settling velocity are not clear, but they may include higher organic content and greater zooplankton fecal pellet production later in the year (e.g., Schubel and Kana 1972).

Primary Production: Algal Biomass and Community Metabolism

During 1996 algal biomass accumulation, and presumably primary productivity rates, were highly elevated in many sectors of the bay in response to very large freshwater flows (and associated nutrients) entering from the Susquehanna River. Much of the nutrient load penetrated the lower bay before being exhausted by primary producers in the upper bay which is the more usual case. Record algal biomass levels were recorded in 1996 in the lower bay contrasting sharply with 1995 which was a dry year with the largest concentrations of algal biomass in the upper half of the bay.

In the context of bay-wide conditions in 1996, there were also some reasonably sharp gradients in algal production and biomass between the ETM and adjacent downstream areas. Chlorophyll-a concentrations were generally higher downstream of the ETM as were rates of primary production (1.5 to 4.5 times higher) and assimilation numbers (1.4 to 1.8 times higher). While there may be many factors regulating primary production rates and algal biomass levels in the ETM, light availability in these turbid waters is probably a primary determinant (Table 1).

Net metabolism within the microplankton community of the ETM was heterotrophic, with total respiration exceeding gross production, during all sampling cruises (Table 2). This community was thus a net sink, rather than net source, for available organic matter, as has been observed previously in this region of the Bay (Smith and Kemp 1995). Although rates of net plankton metabolism (NPM) were most negative within the ETM during the spring sampling period, this was not the case during summer or fall, and in general there were no consistent spatial gradients in rates of NPM within the ETM relative to stations above or below this feature. At all stations there was a clear seasonal trend of greatest net heterotrophy during the summer period, when individual rates of both gross production and respiration were maximal. This effect was due to a seasonal trend in respiration that was more pronounced than that of production.

Respiration rates are an integrated measure of heterotrophic activity that can be directly related to the oxidation of organic matter (Williams 1981) and, as such, are an unambiguous index of energy use by consumer organisms (Pomeroy and Wiebe 1993, Jahnke and Craven 1995). In light of this, it is perhaps provocative that volumetric rates of planktonic respiration measured within the ETM were the same as, or significantly lower than, respiration rates measured at the surrounding stations (Figure 7), in spite of the higher concentrations of particulate organic matter within the ETM. Furthermore, respiratory rates in the bottom waters of the ETM, where organic concentrations were maximal, were in fact also lower than those in the overlying euphotic zone. This suggests that the higher amounts of organic matter within the ETM went largely unconsumed by the microbial assemblages within this feature. Although this area is indeed a net sink of organic matter, the nature of the allochthonous production entrained within the ETM apparently is resistant to the heterotrophic activity of the microbial and microplankton community.
Zooplankton Distribution. Abundance and Egg Production

A partial analysis of net zooplankton collections has been completed. Zooplankton data collected in the vicinity of the ETM using optical plankton counters and acoustic techniques are being processed are discussed by Roman et al (S:18). The zooplankton data reported in this paper were based upon Tucker trawl and Niskin bottle collections. Overall abundances of the signature copepod species (E. affinis and A. tonsa) were high in the ETM and in the immediate region downstream of the ETM. There was a dramatic decrease in abundance upstream of the ETM (Figure 8a) probably related to low salinity conditions. With the exception of one summer observation, copepod abundance was higher, and at times much higher, in bottom than in mid and surface waters (Figure 8b). Because of the dynamic nature of the physical circulation in this region, this suggests a behavioral mechanism by which these organisms could maintain position in the estuary. In the ETM regions of the Patuxent River Estuary (Herman et al. 1968; Heinle and Flemer 1975) and the St. Lawrence Estuary (Bousfield et al. 1975), E. affinis densities reached greater than 1000 nauplii l$^{-1}$ and greater than 100 adults l$^{-1}$. These previous studies integrated the high and low abundances in the water column by taking oblique tows. Thus, the high numbers of E. affinis collected by the Niskin bottles, though high relative to other parts of Chesapeake Bay and other marine systems (White and Roman 1992), are not unreasonable. In this study, the highest E. affinis abundances were observed near the bottom during both night and day, suggesting that these copepods do not vertically migrate in response to light. The copepods were distributed much like suspended sediments: near the foot of the salt wedge, where convergent flow traps particles. Increases in upper water column zooplankton abundance (not shown) occurred only during the late ebb, out of phase with the suspended sediment peak and independent of the time of day. We found maximum concentrations of adults and nauplii in bottom waters where low or no light may provide a refuge from visual predators. In addition, the bottom waters usually have the highest concentration of phytoplankton and detritus, thus providing a relatively rich food environment.

The observed egg production rates spanned the range of published values. The median published egg production rates are in the range of 10 eggs female$^{-1}$ day$^{-1}$ (Table 3). Thus, the value of 3 observed downstream of the ETM in October is relatively low and the values 22 and 30 are relatively high. These measurements were made at only one station in the ETM transect and a single station on the GI transect. There may be considerable variability associated with tide at any fixed station in this region, since both the salt wedge and ETM migrate. Higher variability in repeated samples might be expected.

Fish and Blue Crabs

Spatial patterns of numeric and biomass density and average fish length measured with hydroacoustics changed with season and location relative to the ETM. July biomass and numeric density were higher than May and October. October distributions of numeric and biomass density were more layered than in May and July. In October, numeric densities were higher near the surface while biomass densities were highest near the bottom. Spatial patterns of mean fish length showed differences among seasons and locations relative to the ETM. Fish lengths were less variable in July and October relative to May. Mean fish lengths ranged from 20 mm to almost 300 mm, whereas July and October lengths ranged from 20 mm to 100 mm (July) and 20 to 200 mm (October). Mean fish lengths tended to be more variable in or near the ETM, especially in July and October. May lengths were more variable downbay of and in the ETM, and less variable upbay of the ETM.

Biomass of fishes and numbers of blue crabs (Callinectes sapidus) in midwater trawl collections were highest in the upper Bay regions and lower in the middle and south Bay regions during 1996 (Figure 9). Catches routinely exceeded 10 kg tow$^{-1}$ near and within the ETM, but were lower in other Bay regions. Young-of-the-year(YOY) anadromous fishes were the dominant species during summer 1996, indicating the probable
importance of the ETM in the recruitment process of these species. Catches of hundreds or thousands of YOY river herrings (Alosa aestivalis and A. pseudoharengus) and white perch (Morone americana) were typical in the upper Bay. Catches of striped bass (M. saxatilis), while lower, were the highest observed in any Bay region. The fish biomass in the upper Bay and ETM region was dominated by white perch of several ages. Fish biomass and numbers in other regions of the Bay were dominated by bay anchovy (Anchoa mitchilli).

YOY fish distributions overlapped broadly with the highest abundances of zooplankton, especially the copepod *E. affinis*. It is unclear at present whether YOY fish are aggregated in the ETM and surrounding areas because of feeding opportunities or salinity preferences, or perhaps a combination of these factors. Relatively high numbers of age 0+ blue crabs and recruiting bay anchovy also occurred near the head of the salt front and ETM region, suggesting that up-Bay transport processes or active migrations attracted these species to a zone of relatively good feeding opportunities. The numbers of YOY fish and crabs observed in 1996 was higher than that observed in 1995, possibly because of the high volume of freshwater runoff in 1996 and an enhancement or expansion of the nursery zone adjacent to the ETM region (Secor et al. 1996).

Anadromous species spawn in tidal freshwater parts of the Chesapeake tributary and the upper Bay is an important spawning area. In early May 1996, larvae of river herrings, white perch, and striped bass were very abundant within the ETM and immediately below it. The smallest river herring larvae also were abundant above the ETM, creating a bimodal distribution pattern (Figure 10). While the smallest size classes of white perch and river herring larvae were found upbas of the ETM, larger larvae occurred in or below the ETM and appeared to be trapped there since no larvae occurred at any appreciable distance below it. Striped bass larvae of all size classes were most common in the ETM or immediately below it. Depth distributions of larvae indicated that both striped bass and white perch larvae were more abundant in the lower half of the water column, but the alosid larvae were more common near surface. Mechanisms of transport, dispersal, or entrapment are not known yet, but are being studied in conjunction with feeding analyses and estimates of larval production.

Diets and feeding of fishes are being determined. Foods of YOY alosids, white perch, and striped bass were broadly similar in and below the ETM. In an analysis of YOY white perch diets during July 1996, the mysid Neomysis americana was an important food in the ETM and just below it (Figure 11A). Gammarid amphipods occurred in YOY white perch stomachs throughout the upper Bay. During July, copepods (E. affinis and *A. tonsa*) were dominant items in diets of white perch YOY only above the ETM. However, in October 1996 (data not shown), *E. affinis* constituted a major part of the diet in fish collected within and below the ETM. Diets of YOY white perch in and below the ETM overlapped substantially (Schoener index = 0.58), but were less similar (Schoener index = 0.41 to 0.48) above the ETM (Figure 11A). Amounts of food in stomachs of YOY white perch were higher below and in the ETM than upbas from it (Figure 11B). Stomach contents constituted >1.0% of body weight of YOY white perch in the ETM and below it, but were only 0.5% of body weight upbas from it, suggesting that feeding was less successful upbas.

Analysis of fish feeding, bioenergetics and growth are far from complete. Hydroacoustics surveys of the Bay have indicated high fish biomasses in the upper Bay and the ETM. Eventually, a spatially-explicit bioenergetics model of trophic relationships in the upper Bay will be a product of our LMER research. Age and growth analyses of dominant fish species also are underway, from which a regional, age-specific, trophic evaluation of the Bay is evolving.

**Preliminary Analyses of Trophic Relationships**
Stable isotope analyses were applied to determine if there were detectable differences in trophic structures and organic matter sources between the ETM and immediately adjacent areas outside the feature, as well as in other regions of the Bay. The pelagic food web was the focus of this effort and included suspended organic matter (phytoplankton and other sources), herbivorous grazers (mostly the copepods *E. affinis* and *A. tonsa*), and the planktovorous bay anchovy (*Anchoa mitchilli*). Carbon and nitrogen stable isotope ratios for seston, zooplankton and anchovy are summarized in Table 4. Additional samples remain to be processed, therefore, the analyses are necessarily incomplete.

Carbon stable isotope ratios ($\delta^{13}C$) increased markedly from north to south, suggesting a decrease in the contribution of terrigenous carbon from north to south. In contrast, $\delta^{15}N$ did not vary systematically along the axis of the Bay. There was little difference between $\delta^{13}C$ at the ETM transect and the down-Bay Gibson Island (GI) transect, indicating that, despite detectable differences Bay-wide, no difference in organic matter sources attributable to the ETM feature could be detected. A single observation of $\delta^{13}C$ = -30.6 near the mouth of the Susquehanna River during fall 1995 suggests that the ETM mesozooplankton diet might contain more allochthonous (terrigenous or freshwater aquatic) carbon than is present in ETM seston as a whole. Similarly, $\delta^{13}C$ for ETM mesozooplankton during spring 1996 was lower than for ETM seston, also suggesting a contribution from allochthonous carbon sources greater than that present in ETM seston. Unfortunately, seston was not collected directly from the Susquehanna River during spring 1996.

There were clear fractionation effects associated with trophic transfers of nitrogen from seston to zooplankton. Given the expected fractionation effect on $\delta^{13}C$ and $\delta^{15}N$ for each trophic step ($\Delta\delta^{15}N = 3.4 \pm 1.1$ ppt; Montoya et al. 1990; $\Delta\delta^{13}C = 1.5$ ppt, Peterson et al. 1985) the data are not consistent with the simple trophic structure depicted in Figure 13. Of eight contemporaneous observations of seston and zooplankton $\delta^{15}N$ values, only two (spring 1996 in mid-bay, Fall 1995 in south-bay) were consistent with a single trophic interval from seston to zooplankton. The remaining instances had $\Delta\delta^{15}N$ values between 5.1 and 6.6, suggesting that 50% to 94% of the trophic transfer passed through a single intermediate trophic step, thereby suggesting an alternative trophic structure (Figure 12). Microzooplankton, a plankton group that includes copepod nauplii and rotifers is a likely candidate for the intermediate position (Lacouture et al. 1993). The highest $\Delta\delta^{15}N$ between seston and zooplankton was observed during summer 1996 in the ETM region. Greater numbers of intermediate steps are also a possibility, but are likely to be quantitatively less important due to the inefficiency of trophic transfer. Zooplankton may also have fed selectively on a component of the seston with a higher $\delta^{15}N$ than that of seston as a whole (e.g. freshwater algae from the reservoirs of the Susquehanna River). There were also clear nitrogen fractionation effects observed with the zooplankton to bay anchovy trophic link. For the GI transect, the mid-Bay and the south-Bay, the fractionation was consistent with the expected single trophic link. However, in the ETM region, the $\Delta\delta^{15}N$ suggested two full trophic steps from zooplankton to bay anchovy. Since analysis of stomach contents for bay anchovy indicates that zooplankton are indeed the primary food source (Klebasco 1991), the diet must have included zooplankton eaten outside the ETM region. This suggests that these fish had recently migrated into the ETM zone of the estuary; they were of sufficient size (30 to 100 mm) and age to have moved from the central bay region into the ETM. The $\delta^{13}C$ data are also inconsistent with the simplest model because the observed values are much higher than expected if ETM zooplankton were the major component of the diet.

**SUMMARY**

The ETM cruises during 1996 revealed intriguing new aspects of the ETM region of the Chesapeake Bay, and pointed to the importance of trapping mechanisms associated with the limit of salt intrusion for the recruitment success of several species of anadromous fish and blue crabs. However, 1996 was an exceptionally high freshwater runoff year for the Chesapeake Bay (Figure 2). The salinity structure of the upper Bay, estuarine circulation patterns, sediment input rates, and
fishery habitats all were affected. Data from a lower freshwater flow years will be needed to more fully evaluate the role of the ETM in the larger context of production along estuarine gradients.

Despite the early stage of most analyses, several features of the ETM have become apparent. These are:

1. The salt front and the turbidity maximum together serve to define the ETM region of the bay. The location of the ETM shifts on seasonal and shorter time-scales in response to freshwater inflow and wind forcing. The ETM is a dynamic zone of tidal mixing and periodic resuspension of sediments.

2. Primary production is relatively low in the upper bay and was lower in the ETM than in adjacent downstream areas which had less turbid waters. Metabolism of the plankton community was net heterotrophic in the upper bay and was similar in the ETM and surrounding areas.

3. Copepod abundances, especially E. affinis, were high in the ETM and immediately downstream of it. Abundances were especially high in the bottom mixed layer. Egg production by E. affinis in the ETM and downstream of the ETM were similar.

4. Fish and blue crab biomasses were generally maximal in or near the ETM. Larval and young-of-the-year anadromous fishes were generally most abundant in or immediately below the ETM. Distributions (axial and vertical) and size structure populations of anadromous fish larvae indicate potential retention of larvae of the ETM or selection of the ETM as a nursery habitat by larvae.

5. Feeding success by young-of-the-year white perch was higher within and immediately downstream of the ETM than upbay of the ETM. Stable isotope analyses (C and N) indicate an increase in the importance of allochthonous carbon sources toward the north-Bay, but few differences in stable isotope ratios or implied food webs between the ETM and adjacent areas outside the ETM. Differences in trophic pathways along the whole axis of Chesapeake Bay were suggested. In the upper Bay (including the ETM) microzooplankton may be an important trophic step between seston and mesozooplankton. In addition, there is evidence based on δ¹³C and δ¹⁵N that anchovies move from the mid-bay region to the ETM zone as summer progresses.
LITERATURE CITED


Table 1. Light attenuation coefficients ($K_{par}$, m$^{-1}$), primary productivity (PP, g C m$^2$ d$^{-1}$), surface chlorophyll (Chl, mg m$^{-3}$), and PP/Chl (g C g Chl$^{-1}$ d$^{-1}$) in the upper Chesapeake Bay. Locations: GI - Gibson Island transect; ETM - estuarine turbidity maximum. See Figure 1 transect locations.

<table>
<thead>
<tr>
<th>Property</th>
<th>Location</th>
<th>Spring</th>
<th>Summer</th>
<th>Fall</th>
</tr>
</thead>
<tbody>
<tr>
<td>$K_{par}$</td>
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<td>1.2</td>
<td>1.5</td>
</tr>
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<td></td>
<td>ETM</td>
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<td>2.7</td>
<td>3.5</td>
</tr>
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<td>GI</td>
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Table 2. Integrated rates of net plankton community metabolism (NPM = gross production minus total community respiration) within the ETM and at stations above and below this feature during 1996.

<table>
<thead>
<tr>
<th>Month</th>
<th>Upbay NPM (g O$_2$ m$^{-2}$ d$^{-1}$)</th>
<th>ETM NPM (g O$_2$ m$^{-2}$ d$^{-1}$)</th>
<th>Downbay NPM (g O$_2$ m$^{-2}$ d$^{-1}$)</th>
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</thead>
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<tr>
<td>May</td>
<td>+ 0.4</td>
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<tr>
<td>July</td>
<td>- 10.0</td>
<td>- 4.7</td>
<td>- 5.5</td>
</tr>
<tr>
<td>October</td>
<td>- 6.6</td>
<td>- 4.4</td>
<td>- 2.1</td>
</tr>
</tbody>
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Table 3. Estimates of copepod egg production based upon measurements made during three cruises in 1996. For the locations of the ETM transects and the Gibson Island transect, see figure 1.

<table>
<thead>
<tr>
<th>Date</th>
<th>Species</th>
<th>Egg Production (# female$^{-1}$ d$^{-1}$)</th>
<th>Weight-Specific Egg Production (d$^{-1}$)</th>
<th>Gibson Island Transect Egg Production (# female$^{-1}$ d$^{-1}$)</th>
<th>Weight-Specific Egg Production (d$^{-1}$)</th>
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</thead>
<tbody>
<tr>
<td>April</td>
<td>$E. affinis$</td>
<td>8</td>
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<tr>
<td>July</td>
<td>A. tonsa</td>
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<td>27</td>
<td>0.27</td>
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<tr>
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<td>A. tonsa</td>
<td>-</td>
<td>-</td>
<td>3</td>
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<td>0.77</td>
<td>22</td>
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Table 4. Stable isotope ratios for nitrogen (upper panel) and carbon (lower panel) and differences across trophic levels for seston, zooplankton and bay anchovy (*Anchoa mitchilli*) in four regions of Chesapeake Bay on four cruises from fall 1995 through fall 1996. Missing values indicate that either samples were not taken or that the data are not yet available. The numbers in parenthese are the estimated number of trophic levels assuming 3.4 and 1.5 ppt/trophic level for N and C, respectively.

<table>
<thead>
<tr>
<th>Location/Cruise</th>
<th>Seston</th>
<th>$\Delta^15N$</th>
<th>Mesozooplankton</th>
<th>$\Delta^13C$</th>
<th>Bay Anchovy</th>
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<td>6.8</td>
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<tr>
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<td>Fall 95</td>
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Figure 1. Hierarchy of location maps showing Chesapeake Bay and watershed, the bay and tributary river and the upper portion of the bay where the ETM is located. The center of the ETM is indicated for each sampling period as is the location of the Gibson Island transect. The mid-Bay and South-Bay regions noted in the Chesapeake Bay map are the general regions other than the ETM and GI transects within which samples were collected for stable isotope analysis.
Figure 2. a. Bar graphs of water year (October - September) average annual river flow for the Susquehanna River for the period 1968 through 1996; b. Bar graphs of average monthly river flow from the Susquehanna River for 1993 -1996. All flows were measured at Conowingo, MD Station # 01578310. (James et al., 1995; Monthly summaries of cumulative streamflow in Maryland, Pennsylvania and Virginia, USGS Pamphlet).
Figure 3. Salinity (upper panel) and relative backscatterance (lower panel) measured by the Scanfish along an axial transect from 39.4 N to 39.15 N on July 16, 1997. A distance of 13 km corresponds to 39.3° N. The Scanfish made more than 200 vertical passes through the water column along the transect. The maximum backscatterance is coincident with the 2 psu isohaline, well downstream of the head of salt, but approximately coincident with the transition to vertically homogeneous salinity structure.
Figure 4. The distribution of salinity and total suspended solids along an axial transect of Chesapeake Bay through the ETM region during May 1996. See figure 1 for the location of Havre de Grace.
Figure 5. This distance of the tip of the salt wedge and the center of the ETM from Havre de Grace, a town at the north end of Chesapeake Bay (see figure 1), as determined from axial CTD surveys on a series of cruises to the upper Chesapeake Bay during 1996. The tidal stage is indicated for each date, where SF = slack before flood, SE = slack before ebb, E = ebb, and F = flood.
Figure 6. A one-day time series of salinity and total suspended solids (CTD Survey) and along-channel current speeds (ADCP) at the ETM on October 24 and 25, 1996. The postings shown on panel C indicate the locations within the current profiles of the CTD casts that were made to determine salinity and TSS shown in panels A and B.
Figure 7. Volumetric rates of plankton community respiration within surface (solid bars) and bottom (hatched bars) waters of the ETM region compared to stations directly up-bay and down-bay for the three sampling cruises. Values are replicate means. Error bars represent the standard error of the replicate means. ND = No Data.
Figure 8. Bar graphs summarizing some aspects of zooplankton densities in the upper bay during ETM studies: (A) surface and bottom water densities of *copepods* at the ETM and at a series of stations downstream of the ETM. Zooplankton were collected using a Tucker trawl (280 μm mesh) during a cruise in October, 1996; (B) surface, mid-water and bottom densities of *E. affinis* (adults) collected from Niskin bottle casts at stations in the ETM and downstream of the ETM during spring, summer and fall, 1996 cruises.
Figure 9. Fish wet-weight biomass per 20-minute tow in July 1996. Tows were conducted at night with an 8 m² mid water trawl. Postings indicate the locations of the tows.
Figure 10. The abundance of larval river herrings (*Alosa* spp.), white perch (*Morone americana*), and striped bass (*Morone saxatilis*) in the upper Chesapeake Bay during early May 1996. Catches were made in a 1-m$^2$ Tucker trawl with 280-μm meshes.
Figure 11. (A) the diet composition (proportion by weight) of young-of-the-year white perch (approximate length 40-70 mm; Morone americana) collected above the ETM, within the ETM and below the ETM during July 1996. The values between the pie charts indicate Shoener’s (1970) index of similarity for the diets. (B) The ratio of prey weight in stomachs to body weight for young-of-the-year white perch in each region during July 1996.
Figure 12. An idealized food chain (A) depicting the trophic transfer from phytoplankton through zooplankton to bay anchovy. The nitrogen stable isotope ratios increase by 3.4‰ per trophic step. In the ETM during fall 1994 (B), $\delta^{15}N$ for mesozooplankton was 5.1‰ greater than seston. Assuming a fractionation of 3.4‰ per trophic step, 50% of the transfer must have occurred via an intermediate such as microzooplankton. The $\delta^{15}N$ for bay anchovy was 6.8‰ greater than for ETM mesozooplankton in fall 1995. Since copepods are the main component of the anchovy diet, this suggests feeding on mesozooplankton at other times and places where $\delta^{15}N$ was greater than 11.4‰. Given the age and probable migrations of the anchovies, this is not unexpected.