Bacteria, Dissolved Organics and Oxygen Consumption in Salinity Stratified Chesapeake Bay, an Anoxia Paradigm

ROBERT B. JONAS
Department of Biology George Mason University, 4400 University Drive, Fairfax, Virginia, VA 22030

SYNOPSIS. Chesapeake Bay is a bacterially dominated ecosystem driven, at least under summer conditions, by high levels of labile dissolved organics. Bacterioplankton are exceptionally abundant (20 x 10^9 cells liter^-1) and productive (7 x 10^9 cells liter^-1 d^-1), and their biomass can equal or exceed 60% of phytoplankton biomass. In the salinity stratified Chesapeake Bay bacterioplankton account for 60–100% of planktonic oxygen consumption, potentially driving the Bay to anoxia in days to weeks. Sulfide, released from sediments by sulfate reducing bacteria, chemically consumes oxygen at rates up to 9 mg O_2 liter^-1 d^-1 maintaining the oxygen deficit. The organic matter driving this oxygen demand in the summer season is functionally dissolved. Dissolved organics, measured as biochemical oxygen demand, account for about 60% of microbially labile organics throughout the water column and 80% (sometimes 100%) in the subpycnoclinal water. Field studies suggest that reduced oyster stocks in Chesapeake Bay may be a major factor in the shift to this bacterially dominated trophic structure.

INTRODUCTION

Although the importance of bacterial communities in ecosystem function is not in dispute, bacterial distributions and metabolism of organic matter are rarely considered directly in zoological investigations. The reason for considering these topics here is that there is now a large body of evidence indicating that, in some aquatic ecosystems, bacterial processes have changed, and now control important aspects of the physicochemical environment in which the macrobiota live. Therefore, investigating the distributions and adaptations of the macrobiota must begin with an understanding of bacterial dynamics in these systems.

The goal of this paper is to present evidence that dissolved organic matter and bacterial metabolism of that organic matter are, quantitatively, major components of aquatic ecosystems, including salinity stratified Chesapeake Bay, the nation’s largest estuary. It is a mesotrophic ecosystem which suffers from seasonal hypoxia and anoxia, produced directly, and maintained directly and indirectly, by bacterial activity (Jonas and Tuttle, 1990; Jonas, 1992). Consideration of data from Chesapeake Bay indicate that a modified trophic paradigm is needed. Rather than the classical trophic pyramid, the high concentrations of dissolved organics and extreme abundance of metabolically active bacteria imply that a “teardrop” shape might better represent this portion of the trophic model or paradigm (Fig. 1). In grammar the term “paradigm” is an example of a conjugation giving ALL the inflections of a word. In the Chesapeake Bay and, perhaps other estuaries, the critical role of bacteria should be recognized as one important “inflection” of ecosystem structure and function.

Low oxygen conditions in Chesapeake Bay are not new. Sale and Skinner (1917) (Fig. 2A) found deep water oxygen concentrations in the lower Potomac River to be only 20% of saturation in the summer of 1912. Newcomb and Horne (1938) reported “true” anoxia in the Bay’s mainstem during 1936. Salinity stratification, high salt concentrations in the deep water, provides the physical environment which allows oxygen depletion in the Bay (Boicourt, 1992), but anoxia events were quite rare and transient
BACTERIA AND ANOXIA IN CHESAPEAKE BAY

Trophic Models

Grazer Detrital Microbial

PYRAMID TROPHIC TEARDROP

BACTERIA DOM

FIG. 1. Trophic models including the classic pyramid representing grazer/detrital food webs and the proposed teardrop shape representing a bacterially dominated aquatic ecosystem. The wider base of the latter indicates the quantitative importance of dissolved organic matter (DOM) and bacteria.

until the 1970s, even in years when the water column was highly stratified (EPA, 1982). During the past two decades summer-long anoxia has occurred almost yearly, affecting the mainstem, from north of Annapolis, Maryland to an area south of the Potomac River, and the lower reaches of the subestuaries. The damage which can be done by this situation is evident from the seiching event documented in 1984 (Fig. 3) (Malone et al., 1986). Anoxic water, containing toxic hydrogen sulfide (H₂S), "sloshed" to the western side of the Bay mainstem reaching depths as shallow as 2 meters and covering nearly all of the benthos.

It is generally understood that heterotrophic microbial processes led to the oxygen depletion. However, very little was known about the nature of the microbial community involved, its rate of metabolism or the organic matter fuelling the oxygen consumption. Therefore, extensive investigations were conducted to probe the relationships among nutrient enrichment, phytoplankton production and bacterioplankton distributions and metabolism (Tuttle et al., 1987a; Smith et al., 1992).

EXPERIMENTAL APPROACH

It is beyond the scope of this summary to describe these studies in detail. The basic approach was to conduct repeated seasonal cruises on the Chesapeake Bay occupying multiple stations along cross-bay transects located within the region affected by anoxia. At each station, vertical profiles of nutrient conditions, phytoplankton and bacterial distributions and activities, and organic carbon distributions were determined. In the case of the bacteria and organics, measurements were made of bacterial abundance, production, and metabolism of selected organic carbon compounds. Biochemical oxygen demand (BOD) (measured by oxygen concentration changes during 5-day incubations in dark bottles) and "dissolved" BOD (filterable organics passing Gelman Type A/E glass fiber filters under 5 in. Hg vacuum) were measured to estimate the amount of bacterially available organic matter. Concentrations of reducing sugars (reported as glucose) and amino acids were assayed chemically (Bell et al., 1988; Jonas et al., 1988a; Jonas and Tuttle, 1990; Jonas, 1992).

RESULTS AND DISCUSSION

Figure 2B is a typical vertical profile of water quality parameters under summer conditions in the mainstem of Chesapeake Bay and in the lower reaches of the rivers feeding the Bay. Although there is little change in temperature with depth, salinity increases dramatically in the mid-water, usually at depths of about 9 to 13 meters. The resulting rapid increase in density of the water (pycnocline) physically isolates and limits reaeration of the deep water. Biological and/or chemical oxygen demand drives oxygen concentrations from near saturation to zero (anoxia) over a vertical distance of only about 2 meters. Bacterially produced, H₂S diffuses upward from its source in the sediments (Tuttle et al., 1987a; Tuttle et al., 1987c; Divan and Tuttle, 1988). Although the H₂S concentrations shown in Figure 2B are some of the highest found in Chesapeake Bay water, in other locations H₂S concentrations routinely range around 10 μM or less.

Bacterial abundance and production

The simple fact that heterotrophic processes consume dissolved oxygen was known. However, the physical location of oxygen consumption could be either the sediments or the water column (or both) (Kemp et al., 1987), and the biological con-
Fig. 2. A. Dissolved oxygen concentrations in surface and bottom water of the Potomac River from Washington D.C. to the river mouth at the Chesapeake Bay in 1912. B. A typical vertical profile of salinity, temperature, dissolved oxygen, pH and hydrogen sulfide in the lower Potomac River near Piney Point in the 1980s.

Our investigations (Tuttle et al., 1987a; Tuttle et al., 1987b; Jonas, 1992; Smith et al., 1992) of bacterial distributions and activity revealed unprecedentedly high bacterial abundances (Fig. 4A) and secondary production (Fig. 4B). During summer, bacterial abundances, assessed by direct microscopic enumeration of acridine orange...
Fig. 3. Cross-Chesapeake Bay depth profile of water density (sigma-t) and dissolved oxygen on 20 August and 23 August, 1984. On 20 August wind blew strongly from the northwest pushing surface water to the east which caused tilting of the deep layers toward the west. During this period anoxic water covered both flanks of the Bay to depths as shallow as 2 meters (west).

Fig. 4. Seasonal distributions of depth integrated mean (A) bacterial abundance and (B) bacterial production in three depth zones along a cross-Chesapeake Bay transect located near the mouth of the Potomac River. Open triangles represent sampling cruises.
stained cells (Hobbie et al., 1977), routinely rise to 10–20 \( \times 10^9 \) cells liter\(^{-1} \) with occasional values as high as 50 \( \times 10^9 \) liter\(^{-1} \). These are the highest sustained bacterial abundances reported from any estuary. Usual values range from about 1–7 \( \times 10^9 \) cells liter\(^{-1} \).

There was also a repeating seasonal pattern of bacterial abundance changes (Ducklow et al., 1988; Jonas, 1992). Depth integrated abundance (Fig. 4A) along a cross-bay transect south of the Potomac River, in the Virginia portion of the mainstem which suffers from anoxia, are representative of the entire mesohaline Chesapeake. Typically, abundances throughout the water column are a few billion liter\(^{-1} \) in early spring, and rise through April and May, tracking, with a time lag of one to two weeks, the spring phytoplankton bloom (Allen et al., 1996). Subsequently, abundances decline following the phytoplankton population crash, only to rise to very high levels in July and August, in the absence of high phytoplankton populations.

Our multiyear studies show that the large majority of the bacteria in Chesapeake Bay are "free-living" and very small; more than 90% are less than 1 \( \mu \)m long. In other estuaries, more than half of the bacteria would be attached to detritus particles. It is generally believed that "particle association" helps bacteria efficiently "find" food. Therefore, the free-living habit of bacteria in Chesapeake Bay suggested that they easily find food without being attached to particles and that there may be high concentrations of microbially labile organics available to them.

Although the seasonal pattern of bacterial production (Fig. 4B), assayed by tritiated thymidine incorporation, does not correlate well with bacterial abundance, it too is repetitive on an interannual basis, and summer values are very high. Seasonal maximum of about \( 10^{10} \) cells produced liter\(^{-1} \) d\(^{-1} \) occur in late May and June. Bacterial production in the euphotic zone is often 30% of phytoplankton production and sometimes reaches value 100% or more of phytoplankton production (Ducklow et al., 1988). Assuming that bacterial abundance is constant on a day to day basis, these production values indicate that the bacterial community "turns over" completely once every 0.5 to 2 days.

### Oxygen consumption

There are two bacterially driven, water column oxygen consumption process which can account for oxygen depletion in the Bay:

1) direct aerobic respiration:

\[
\text{CH}_2 + \text{O}_2 \rightarrow \text{CO}_2 + \text{H}_2\text{O}
\]

2) oxidation of \( \text{H}_2\text{S} \) which is a by-product of anaerobic respiration

\[
2[\text{CH}_2\text{O}] + \text{SO}_2^- \rightarrow \text{S}^2^- + 2\text{CO}_2 + 2\text{H}_2\text{O}
\]

\[
\text{S}^2^- + 2\text{O}_2 \rightarrow \text{SO}_4^2-
\]

Directly measured oxygen consumption rates in Chesapeake Bay, estimated from short-term oxygen concentration changes in sealed, dark bottles, are about 1–1.5 mg O\(_2\) liter\(^{-1}\) d\(^{-1}\) (Tuttle et al., 1987a). Calculated O\(_2\) consumption rates based on measured bacterial abundances and biomass specific oxygen consumption rates are also about 1–1.5 mg O\(_2\) liter\(^{-1}\) d\(^{-1}\). Oxygen consumption correlates strongly \((r^2 = 0.90)\) with bacterial abundance over several years. Experimentally, oxygen consumption is accounted for primarily (70–100%) by organisms smaller than 3 \( \mu \)m (Sampou et al., 1988).

It is seems likely that water column oxygen consumption is primarily due to bacterial processes in the water column when free molecular oxygen is available. Thus, bacteria consume the oxygen, and, assuming oxygen saturation of about 7 mg liter\(^{-1}\) they can drive the dissolved oxygen to zero in about 5–7 days. Once anoxia occurs, \( \text{H}_2\text{S} \) can diffuse from the sediment (evidence indicates that little water column sulfide production occurs (Tuttle et al., 1987a, c) into the overlying water and act as a chemical oxygen demand and maintain anoxic conditions.

### Microbially available organic matter

There must be a major source of organic matter to support the bacterial community.
in Chesapeake Bay. Although the Bay is enriched in nutrients (mesotrophic), the phytoplankton biomass is usually not exceptional (Smith et al., 1992). This condition along with the high percentage of free-living bacteria suggested the possible importance of dissolved organic matter. On average in Chesapeake Bay microbially labile organic matter, measured as BOD, ranged seasonally from about 1-4 mg O$_2$ liter$^{-1}$ (Fig. 5A), with the highest springtime values occurring in the bottom water and highest summer values in the surface. During phytoplankton blooms, surface BODs often exceed 7 mg O$_2$ liter$^{-1}$. Dissolved BOD was surprisingly high, ranging from about 0.5 to 2 mg O$_2$ liter$^{-1}$ (Fig. 5B) with peaks in late spring and summer. Dissolved BOD averaged about 50% of total BOD through spring and summer, and in the deep water, beneath the pycnocline, averaged 60% or more of the total (Fig. 6). At some stations dissolved BOD made up 100% of the microbially labile organic matter.

In spring, bacterial abundance ($r = 0.56$) and production ($r = 0.77$) correlate significantly with particulate BOD, but in summer they do not ($r = 0.27$, $r = 0.16$ respectively). In summer, bacterial abundance ($r = 0.62$) and production ($r = 0.54$) correlate significantly with dissolved BOD, but they do not in spring ($r = 0.12$, $r = 0.37$ respectively). It appears that the “excessive” bacteria in Chesapeake Bay during summer rely on a large pool of dissolved organic matter which is likely produced in situ by the phytoplankton (Zieman and Macko, 1988; Jonas, 1992).

Data indicate that average phytoplankton extracellular release of dissolved organic matter in mesotrophic systems ranges from 21 to 38% with exceptional values of 60% (Chrost, 1983; Bell and Kuparinen, 1984; Kato and Stabel, 1984; Rai, 1984). This re-
lease may occur as a result of active excretion, leakage, sloppy feeding by herbivores, and cell lysis. On a percentage basis it appears that phytoplankton extracellular release is greatest in mesotrophic systems compared with oligotrophic and eutrophic (including hypertrophic) aquatic systems which average about 20% and 10% respectively (Münster and Chrost, 1990).

Free dissolved reducing sugars, expressed as glucose, and free dissolved amino acids were present in very high concentrations in Chesapeake Bay water (Jonas et al., 1988a, b). We found that during summer glucose averaged about 500–800 nM and often peaked in concentration (1200 nM) at the pycnocline. Free amino acids averaged about 200 nM with dramatic peaks exceeding 1000 nM at the pycnocline. Glucose and amino acid concentrations alone account for about 60–70% of the BOD near the pycnocline, although they represent only about 30% of total BOD in the surface waters.

The remaining dissolved organic matter has not been accounted for in Chesapeake Bay, but the work of Münster and Chrost (1990) suggests that glycolic acid may be the single most abundant dissolved compound derived from algal release. They reported glycolic acid concentrations as high as 4,000 nM. Our investigations did not include assessments of this compound. Beneath the pycnocline, in Chesapeake Bay, fermentation end-products may also be important. In our studies, although we did not measure the concentrations, acetate turnover was extremely high (more than 70% of the acetate pool utilized per hour) just below the pycnocline (Bell et al., 1988).

Glucose and amino acid turnover rates were generally high during spring and summer, ranging from about 10 to 50% per hour for glucose and 4 to 20% per hour for amino acids (Tuttle et al., 1987b; Bell et al., 1988; Jonas et al., 1988a; Jonas, 1992). Turnover rates increased with increasing concentrations of these two types of organics, indicating that there is an active microbial community poised to take advantage of available dissolved organics.

**SUMMARY**

The high levels of bacterial activity in Chesapeake Bay indicate that there may have been a major shift in the trophic structure of this ecosystem. The Bay appears to have shifted from a metazoan chain in which the primary production was grazed by herbivores such as zooplankton and benthic filter feeders, to a microbiologically dominated system in which large amounts of primary production is now consumed by bacteria. It has been speculated that reductions in the biomass of benthic filter feeders, especially oysters, is one of the causes of this trophic shift (Newell, 1988). Filter feeder abundance declined due to overharvesting,
poor water quality and/or disease. This decline could lead to increased phytoplankton abundance and increased concentrations of dissolved, microbially available organics, which subsequently support high levels of bacterial abundance. Aerobic bacteria consume large amounts of organic matter which leads to hypoxia and, ultimately, anoxia in the water column. While hypoxia itself can be devastating to the macrobiota, anoxia in the water column can initiate a sequence of events (e.g., anaerobic respiration) which results in overly toxic conditions (high H₂S concentrations) and perpetuates itself through chemical oxygen demand.

REFERENCES


Newell, R. I. E. 1988. Ecological changes in Chesapeake Bay: Are they the result of overharvesting the American oyster, Crassostrea virginica. In M. P. Lynch and E. C. Krome (eds.), Understanding the estuary: Advances in Chesapeake Bay re-


