Seasonal depletion of oxygen from bottom waters of Chesapeake Bay: roles of benthic and planktonic respiration and physical exchange processes

W. M. Kemp[1], P. A. Sampou[1], J. Garber[2, 3], J. Tuttle[2], W. R. Boynton[2]

[1] University of Maryland, Center for Environmental and Estuarine Studies, Horn Point Environmental Laboratories, Cambridge, Maryland 21613, USA

[2] University of Maryland, Center for Environmental and Estuarine Studies, Chesapeake Biological Laboratory, Solomons, Maryland 20688, USA

[3] U. S. Environmental Protection Agency, Narragansett Marine Laboratory, Narragansett, Rhode Island 02882, USA

ABSTRACT: Seasonal O_2 budgets were developed for the mesohaline region of Chesapeake Bay (USA), which experiences bottom water O_2 depletion in summer. Rates of O_2 production and consumption by the planktonic community and O_2 consumption by the benthos were measured at 1 to 4 wk intervals from March to October at 2 stations. Under summer anoxic conditions, rates of sulfide diffusion from sediments were also measured directly with in situ chambers. Weekly observations of water column temperature, salinity and O_2, combined with wind data and regression models, allowed calculation of air-sea gas exchange. Using these rates in mass-balance analyses for the upper and lower water column layers, we were able to compute net physical O_2 transport across the pycnocline and longitudinally through the bottom layer. Mean monthly estimates of these net physical O_2 transports were highly correlated to their respective O_2 gradients. Slopes of these correlations provided estimates of the average spring-summer vertical dispersion coefficient (0.2 cm^2 s^{-1}) and net gravitational water velocity (5 cm s^{-1}), both of which correspond to previous reports. Vertically integrated planktonic respiration rates in the lower water column layer were compared to benthic O_2 consumption from April to August. In general, planktonic processes dominated O_2 consumption, comprising almost two-thirds of the total. Oxygen consumption associated with benthic processes, however, exceeded planktonic rates in early spring prior to vernal warming and in late August when large S^{2-} fluxes resulted from release of accumulated pore water pools. By combining our respiration data with values from other coastal environments and plotting rates versus water-column depth, we find a general relation in which planktonic respiration exceeds benthic respiration for systems deeper than 5 m. Hence, for stratified estuaries with bottom layers thicker than 5 m, seasonal O_2 depletion is driven primarily by planktonic respiration rather than benthic consumption of accumulated organic pools. A comparison of mean monthly rates for bottom respiration (plankton plus benthos) and net physical O_2 replenishment here revealed that the 2 processes were highly correlated between March and October; both rates increased through July and declined thereafter. This strong correlation underscores a fundamental interdependence of biological O_2 consumption and net physical transport, which is based on the O_2 gradient by which the 2 processes are coupled. Consequently, relatively large reductions in respiratory O_2 consumption (e.g. with decreased organic inputs) would lead to substantially smaller decreases in the extent of bottom water O_2 depletion because of an inherent adjustment between the coupled biological and physical processes.

INTRODUCTION

A common feature of many estuarine and coastal systems is the summer depletion of dissolved oxygen (O_2) from deep waters. Seasonally anoxic or hypoxic ($O_2 < 2$ mg l^{-1}) bottom waters have been reported for a variety of estuarine ecosystems (May 1973, Jørgensen 1980, van Es & Ruardij 1982, Caumette et al. 1983, Jøsefson & Widbom 1988). Episodic anoxic events have been observed also in shallow continental shelf

regions (Falkowski et al. 1980, Leming & Stuntz 1984, Faganeli et al. 1985). In most partially-stratified temperate coastal systems, O_2 depletion events are limited to the warm summer months when stratification strengthens following the spring freshet of river flow (Turner et al. 1987, Seliger & Boggs 1988). The reduced vertical exchange of water and solutes associated with stratified conditions limits the rate at which O_2 can be replenished to bottom waters. Organic matter derived from spring and summer phytoplankton production provides substrate for planktonic and benthic respiratory processes (Malone et al. 1988), which tend to increase with warming waters. Thus, it is the combined effects of vernal increases in both biological (respiration) and physical (stratification) processes which lead to summer depletion of bottom water O_2.

Chesapeake Bay (USA) is a large temperate estuary which has experienced summertime occurrences of anoxia/hypoxia in its bottom waters since at least the mid-1930's (Newcombe & Horne 1938). The temporal and spatial dimensions of O_2 depletion, however, appear to have increased in recent decades for the main bay (Officer et al. 1984), as well as for certain tributaries (Heinle et al. 1980). Within this decade-scale trend, major meteorological and climatic events and attendant variations in runoff and wind conditions may have contributed to fluctuations in anoxia for a given year (Seliger et al. 1985). Furthermore, in response to local and far-field winds, the depth to the O_2 depleted layer at any position in the Bay may vary greatly between days due to oscillations in the cross-Bay orientation of the pycnocline (Malone et al. 1986). This can result in hypoxic water welling up into shallow (< 3 m) regions of the estuary (Breitburg 1990).

For many coastal regions, documented historical increases in the frequency and magnitude of anoxic events have been attributed to anthropogenic inputs of nutrients (Jørgensen 1980, Rosenberg 1985, Andersen & Rydberg 1988). It has similarly been suggested that the recent increase in volume of Chesapeake Bay's hypoxic waters has resulted from a general eutrophication trend (Officer et al. 1984). Indeed, the mounting evidence for a widespread pattern of coastal eutrophication throughout the world (Walsh et al. 1981, Nixon et al. 1986) suggests such anoxic events in marine waters may occur with increasing frequency in the future.

Nutrients entering coastal marine systems such as Chesapeake Bay are delivered chiefly in terrestrial runoff (Nixon 1987). It appears that phytoplankton growth and biomass accumulation are directly related to these riverborne nutrient inputs (Boynton et al. 1982, Malone et al. 1988). Thus, years with higher riverflow are marked by greater algal biomass which, in turn, can support elevated respiration and more rapid depletion of bottom water O_2. This relationship is confounded, however, by the fact that interannual variations in salinity stratification are also directly related to riverflow (Seliger & Boggs 1988), so that distinguishing between effects of physical and biological process on interannual variations in anoxia becomes problematic.

Respiratory processes consuming O_2 from coastal waters can be functionally separated into the metabolism of planktonic and benthic communities. This is a useful distinction in the analysis of O_2 depletion events because of the inherently different time-scales associated with processes occurring in the water column compared to the sediments. Strong positive correlations between planktonic respiration and primary production on scales of hours to days (Jensen et al. 1990) suggest a close coupling between the 2 processes. Benthic metabolism in some estuaries may respond rapidly (days to weeks) to variations in particulate organic inputs (e.g. Graf et al. 1987). The absence of correlations between primary production and benthic O_2 consumption in Chesapeake Bay (Kemp & Boynton 1981), however, suggests that the 2 processes were weakly coupled on these time-scales. The quantitative contributions of planktonic and benthic respiration to O_2 consumption varies with season (Hopkinson 1985) and total water column depth (Hargrave 1973) in coastal environments. Two previous reports considering respiration effects on O_2 depletion in the mesohaline region of Chesapeake Bay attributed most of the total O_2 consumption either to planktonic respiration (Taft et al. 1980) or to benthic processes (Officer et al. 1984).

We describe herein direct measurements of benthic and planktonic O_2 consumption and planktonic O_2 production at selected mesohaline Chesapeake Bay sites that experience seasonal hypoxia. We compare these measurements, which focus on the spring-summer period, to observed rates of change in oxygen pools in upper and lower layers of the estuarine water column at time-scales of weeks to months. Using these data, we have developed O_2 budgets to compare: planktonic O_2 consumption; benthic O_2 consumption; and physical transport (advective plus diffusive) of O_2.

METHODOLOGY

Oxygen concentrations, temperature, salinity and rates of oxygen production and consumption were measured at 2 stations (Stns 2 & 3) located in the mesohaline region of Chesapeake Bay along an east-west transect (38° 33.5' N) at 9 m and 18 m (MLW) depth, respectively. Stations were visited at 1 to 2 wk intervals during March to May and again in August 1986 and 1987 and once in the months of June, July and October 1987. These sites are part of a transect which was

established in 1984 (Kemp et al. 1990). In addition, vertical profiles of temperature, salinity and dissolved O_2 concentration were measured routinely at 1 to 2 wk intervals throughout the period March to October during both years as a part of a schedule for deployment and retrieval of sediment-trap arrays (Boynton et al. 1990).

Rates of sediment oxygen consumption (SOC) were measured using intact cores incubated in darkness at ambient temperature on shipboard (Boynton et al. 1990). Triplicate cores were obtained with a modified Bouma box corer in clear acrylic liners which were removed from the corer to serve as incubation chambers. Cores were visually inspected, and only those exhibiting no signs of disturbance were used for incubations. Each core was adjusted to obtain a water-column height of 12 to 15 cm (Boynton et al. 1981). Water-tight plates were attached to the top and bottom of the cores, which were placed in a darkened water bath to maintain near-ambient water temperatures ($\pm$ 2 °C). Temperature and O_2 concentration in the overlying water were measured at 10 to 20 min intervals throughout the incubation with polarographic O_2 electrodes and thermistors (Orbisphere Laboratories, Geneva), whereas water samples (20 ml) were obtained and filtered (GF/C) every 30 to 45 min for ammonium and sulfide (S^{2-}) analysis where appropriate. Overlying water was mixed continuously with stirrers built into the electrode system (Hopkinson 1985). Velocity profiles and mixing rates in cores appear to have approximated *in situ* conditions reasonably well (Boynton et al. 1981).

On 2 occasions, *in situ* measurements of SOC and sulfide flux across the sediment-water interface were also made using opaque acrylic or aluminum chambers, cylindrical in shape with a circular area of 0.30 m², a height of 18 cm (12 cm above sediment surface) and an enclosed volume of 38 l. Details of this method have been provided elsewhere (Boynton et al. 1981, Boynton & Kemp 1985) and are described briefly below. The chambers were mounted on a square flange (87 cm wide), which provided a base to rest on the benthic surface and allowed 6 cm of the chambers' edge to penetrate the sediments, insuring proper seal. Temperature and O_2 were monitored in the enclosed water using electrodes and thermistors (YSI 5739) mounted in the top of each chamber. A submersible pump with a diffuser outlet was regulated by a pre-calibrated rheostat to provide reasonably uniform, near-ambient water circulation under the chambers (Boynton et al. 1981). Oxygen electrodes and pumps were connected to shipboard via cables. Triplicate chambers were placed on the bottom within an area of about 20 m diameter. Water samples were collected hourly by pumping water from each chamber into air-tight flasks; a 2-way valve mounted in the chamber

allowed replacement of water removed during sampling with external water. Changes in O_2, S^{2-} and NH_4^+ concentrations were also monitored in bottom water samples incubated in triplicate opaque bottles (300 ml), which served as controls to account for water-column processes.

Planktonic respiration rates were also measured at Stn 3 by monitoring temporal changes in O_2 concentration of unfiltered water incubated in opaque glass bottles (300 ml). Water samples were collected simultaneously with CTD profiling to ensure proper representation for specific depth strata. Five replicate opaque bottles were filled with surface water collected from a depth of 2 m below the air-water interface and with subsurface water from 2 m above the sediment surface in spring and fall or from the steepest region of the oxycline when bottom water was anoxic. Initial and final oxygen concentrations were measured with polarographic electrodes (Orbisphere Laboratories, Geneva). Oxygen was also determined by Winkler titrations (Strickland & Parsons 1972) for 3 additional initial bottles from each depth and for approximately 30 % of all bottles at the end of the incubation. Dark bottles were incubated at ambient temperature ($\pm$ 2 °C) for periods of 6 to 24 h (e.g. Jensen et al. 1990). On 3 occasions O_2 concentrations were measured in triplicate samples sacrificed from a pool of replicate bottles at 4 to 6 h intervals over 24 h. In agreement with previous studies (e.g. Hopkinson 1985), rates of O_2 depletion were linear over the entire incubation period in all cases (Sampou et al. unpubl.).

Rates of photosynthetic O_2 production were also measured during each cruise in 1986. Replicate clear glass bottles (300 ml) were filled with water obtained during the morning (08:00–10:00 h) with Niskin bottles (10 l) from a depth of 2 m. Triplicate bottles were placed in a series of shrouds made from neutral density screen to provide ambient irradiance levels of 100, 26, 13, 7, 3 and 1 % and incubated at ambient temperature under natural light in shipboard water baths for 7 to 8 h. Initial and final O_2 concentrations were measured with polarographic electrodes. Vertical attenuation of diffuse downwelling irradiance (400 to 700 nm) was measured on each date with a Licor (Model LI-1925A) cosine-corrected opal irradiance sensor. Vertically integrated rates of photosynthetic O_2 production were estimated from photosynthesis-irradiance relations and profiles of chlorophyll a (Malone et al. 1986). 'Apparent' O_2 production of the plankton community was calculated as the rates measured during incubations extrapolated over the full daylight period. Diel and nighttime respiration values were estimated by extrapolating measured dark-bottle incubation rates to the respective time periods.

During each cruise and at each station, water-column profiles were routinely described at 1 to 2 m intervals from surface to bottom during the morning period from 09:30 to 10:30 h. At each depth, temperature (T), salinity (S), and O_2 were measured using a CTD/O_2 system (Hydrolab Model Surveyor II or 4000). All salinity data are presented in 'practical salinity units' (psu; e.g. Sanford et al. 1990), which are essentially the same as ppt but are dimensionless values referenced to a standard. Subsamples of water collected at the same depths were analyzed for dissolved sulfide, chlorophyll a and phaeopigments (Strickland & Parsons 1972). Surface water O_2 values measured as mg l^{-1} were also expressed as percent of saturation, estimated using ambient T and S data and the empirical relation developed by Green & Carritt (1967). Water samples for sulfide analysis were immediately analyzed on ship or fixed with 10 % (w/v) zinc acetate and refrigerated for subsequent laboratory analysis (within 24 h) using a methylene blue colorimetric technique (Trüper & Schlegel 1964).

RESULTS AND DISCUSSION

Oxygen distributions and water column structure

From mid March to late July 1986, surface waters (2 m depth) in this region of Chesapeake Bay underwent a continual vernal warming from 8 to 27 °C at a rate of about 5 °C mo^{-1} (Fig. 1a). Surface salinity, although more variable than temperature, also exhibited a steady increase from 7 psu (mid April) to 14 psu (mid August). The April depression of salinity probably represents effects of the late February peak in river-flow, which would indicate an average transit time of 1.5 to 2 mo for fresh water from the Susquehanna River to our study site (Malone et al. 1988).

Surface O_2 concentrations (Fig. 1b) decreased from seasonally maximal values exceeding 12 mg l^{-1} in March to low values near 6 mg l^{-1} in late June and August. Mid-morning surface O_2 concentrations exceeded 100 % of saturation concentrations for most of the spring and summer period. As suggested previously, for shallow coastal seas (Hoppema 1991), surface O_2 percent saturation values appeared to be directly related to net planktonic production. Low values in late May to early June and late August corresponded to the end of the spring phytoplankton bloom and the late summer decline in plankton production, respectively (Malone et al. 1988).

As indicated by the difference between surface and bottom salinities from late March through late August (Fig. 1c), there was no significant trend in the strength of vertical salinity stratification. Typically, the period of
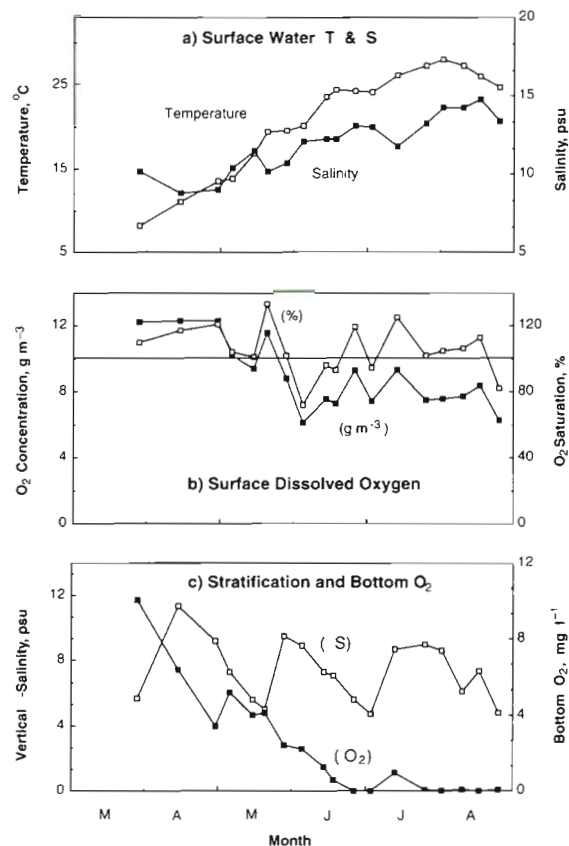

Fig. 1. Seasonal variations in surface (2 m depth) and bottom (16 m) water temperature (T), salinity (S) and dissolved oxygen (O_2) at Stn 3 during Mar to Aug 1986: (a) surface T, S; (b) surface O_2 and % O_2 saturation; and (c) bottom O_2 and vertical S difference (2 m to 16 m). Data are from Boynton et al. (1990)

rapidly increasing stratification in this region of Chesapeake Bay occurs in late winter rather than spring (Taft et al. 1980). In general, vertical salinity differences contribute to the majority (> 90 %) of the density stratification in this region of the Bay (e.g. Goodrich et al. 1987). Once vertical stratification is established and vernal warming begins, bottom water O_2 concentrations declined steadily through the spring. The mean rate of decline in O_2 from April through June was about 0.1 mg O_2 l^{-1} d^{-1}, similar to rates found for this region of the estuary in previous years (Taft et al. 1980, Officer et al. 1984).

The potential influence of advective transport on spring-summer patterns of O_2 distribution with depth can be qualitatively inferred from time-space isopleths of salinity and O_2 at Stn 3 (Fig. 2). In general, the seasonal decrease in O_2 from April through August corresponded to an increase in salinity in bottom waters at this site. Hypoxic events in late June and July to August appear to be have been associated with preceding intrusions of high salinity water from downbay
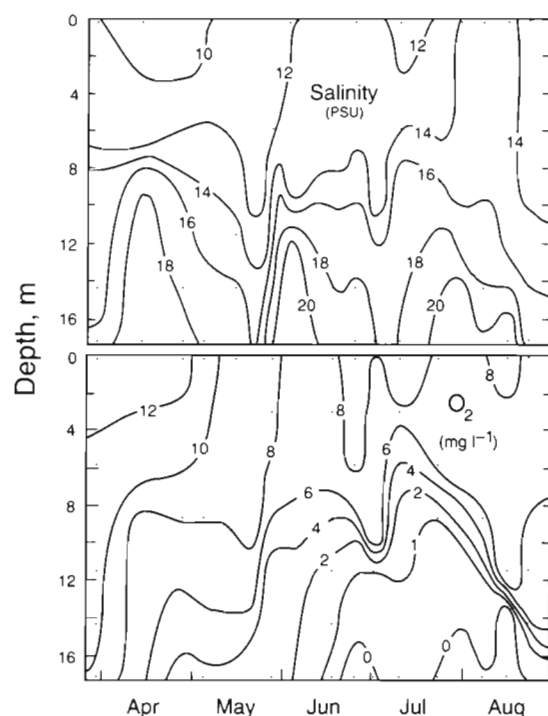
Fig. 2. Isopleths describing vertical and seasonal distributions of salinity and dissolved oxygen (O_2) for Stn 3 from Mar to Aug 1986. Data are from Boynton et al. (1990)

Table 1. Phytoplankton production measurements at Stn 3 as O_2 evolution in this study and as ^{14}C incorporation from contemporaneous studies in spring to summer 1986

Time period	Apparent O_2 production $(g\ O_2\ m^{-2}\ d^{-1})$[a]	[14]C production (Malone et al.) $(g\ C\ m^{-2}\ d^{-1})$[b]	[14]C production (Sellner et al.) $(g\ C\ m^{-2}\ d^{-1})$[c]
Mar 10–27	1.9	0.3	0.3
Apr 4–10	4.5	1.1	1.3
Apr 18–25	3.8	1.1	1.2
May 5–14	3.8	–	1.2
May 17–27	–	–	1.4
Jun 10–24	–	1.8	1.7
Jul 10–15	–	2.0	1.3
Jul 20–30	–	1.9	1.3
Aug 5–14	7.0	1.7	–
Aug 14–22	5.4	1.8	1.8

[a] Apparent (net daytime) production data from this study based on 6 to 8 incubations
[b] Data from Malone et al. (1988) based on 24 h incubations
[c] Data from Sellner et al. (unpubl.) based on 2 h incubations

sites. Time-series data from a nearby Chesapeake Bay tributary site (Sanford et al. 1990) revealed that variations in bottom water O_2 at tidal and event scales correspond to variations in salinity, implying advection as an important mechanism for O_2 transport. In the mainstem Bay, however, it is unlikely that O_2-depleted water would be transported from downbay into the mesohaline region because O_2 concentrations tend to be higher seaward of this area (e.g. Officer et al. 1984). A more probable explanation is that bottom respiration (planktonic plus benthic) in this region is periodically stimulated by transport of organic matter which was concentrated in seaward bottom waters (e.g. Jonas & Tuttle 1990).

Oxygen metabolism by planktonic and benthic communities

Rates of apparent O_2 production (daytime net) by the planktonic community $P(O_2)$ ranged from 1.9 g $O_2\ m^{-2}\ d^{-1}$ in March to 7.0 g $O_2\ m^{-2}\ d^{-1}$ in August (Table 1). Contemporaneous measurements of photosynthetic ^{14}C incorporation (Malone et al. 1988, Sellner unpubl.), made at approximately fortnightly intervals at the same site (Table 1), correlated significantly $[P(O_2) = 0.81 + 2.95\ P(^{14}C),\ r^2 = 0.84]$ with O_2 production rates within the same time periods (the mean of

both ^{14}C values was used when available). For all measurements, the mean molar $P(O_2):P(^{14}C)$ ratio (cf. photosynthetic quotient) was approximately 1.10 (Williams et al. 1983). In developing O_2 budgets, we used this regression to estimate $P(O_2)$ from the $P(^{14}C)$ data during periods when direct O_2 measurements were unavailable.

Oxygen consumption rates (diel respiration) by planktonic communities at Stn 3 were similar in upper and lower water column layers in the spring, but were consistently higher in the upper layer in summer months (Fig. 3a). Despite variability in these data, a significant ($p < 0.05$) seasonal trend was evident for the upper layer, where respiration rates were twice as high in July to August as in April to May. Similar rates of planktonic community respiration have been reported previously for this region of Chesapeake Bay (Kemp & Boynton 1980, Taft et al. 1980, Kemp & Boynton 1981, Tuttle et al. 1987). Rates here are at the upper end of the range of values reported for temperate coastal plankton communities (Williams 1984). Our data (Fig. 3a) suggest that planktonic respiration reaches its annual maximum in July prior to the time of peak annual temperatures, a pattern observed earlier by Tuttle et al. (1987) for the mesohaline Chesapeake. This contrasts with Georgia coastal waters, where respiration follows the annual temperature cycle (Hopkinson 1985).

SOC rates at Stn 2 ranged from about 0.5 g O_2 $m^{-2}\ d^{-1}$ in March to April to 1.8 g $O_2\ m^{-2}\ d^{-1}$ in August (Fig. 3b), similar to the seasonal range reported for many temperate coastal benthic systems in water column depths less than 20 m (e.g. Nixon 1981, Boynton & Kemp 1985). Rates determined from *in situ*
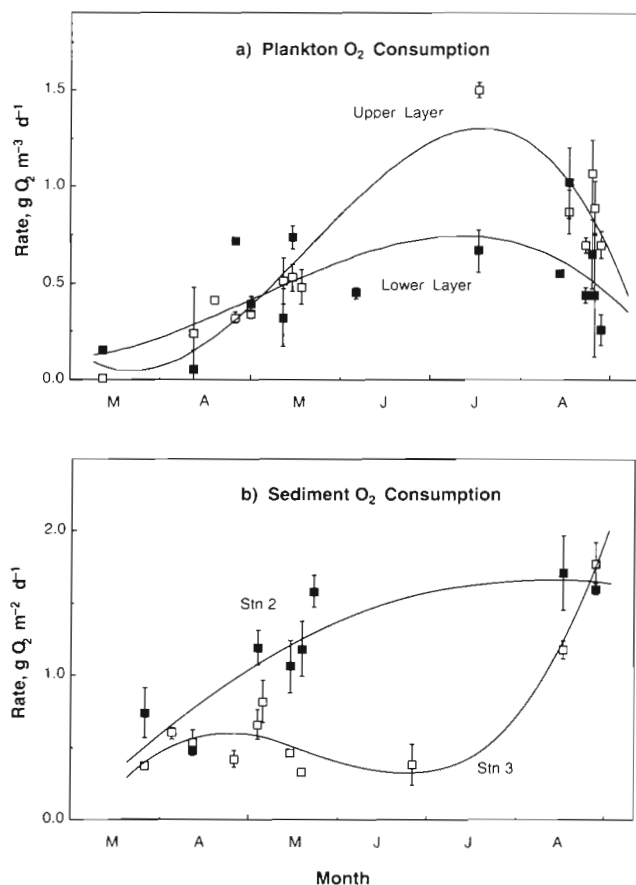
Fig. 3. Seasonal patterns of dissolved oxygen (O_2) consumption by (a) plankton in (□) upper layer (2 m) and (■) lower layer (16 m in Mar to May, 8 m in Jun to Aug) of water column and (b) sediments at (■) Stn 2 (western flank, 9 m depth) and (□) Stn 3 (main channel, 18 m depth). Data are given as means ± SD, and curves are drawn by polynomial regression ($r^2 > 0.90$). Data for Stn 3 in Aug are based on stoichiometric equivalent O_2 consumption associated with sulfide efflux ($S = 2\ O_2$; Jørgensen 1977) from sediments

chamber measurements were not significantly different (p < 0.05) from contemporaneous rates obtained using intact cores in May and August for both SOC and NH_4^+ fluxes (Table 2). Few SOC measurements were made at this station in June to July 1986, but peak annual SOC rates in an earlier study occurred in July prior to the August temperature maximum (Kemp & Boynton 1981). Although most of the annual deposition of particulate organic matter to these sediments occurs in spring, SOC peaks in mid-summer, and supplies of labile organic matter appear to be virtually exhausted by late summer (Boynton et al. 1990).

At Stn 3, SOC rates decreased in late May (Fig. 3b) as O_2 in the bottom waters fell below 3 mg l^{-1} (Fig. 1); by late June when anoxic conditions had been established, SOC rates were zero. Under anoxic conditions in August, however, we measured rates of sulfide

efflux from sediments to overlying water with *in situ* chambers at Stn 3. Rates of S^{2-} accumulation in these chambers were highly linear over a 4 h incubation period. To compare these rates with SOC values, the stoichiometric equivalent O_2 consumption in S^{2-} oxidation was estimated assuming a molar O_2:S ratio of 2:1 (e.g. Jørgensen 1977). These observations of sulfide effluxes are among the first ambient rates reported in the literature. Their comparison with other rates of sediment sulfur cycling at this site are detailed elsewhere (Roden & Tuttle 1992). Previous *in situ* measurements have been made in long-term incubations in which O_2 in the water overlying sediments was allowed to be depleted, after which sulfide fluxes were observed (Anderson et al. 1986, Koop et al. 1990). In most of these experiments, the sulfide fluxes (starting 2 to 8 wk after initiating the experiments) were substantially lower than expected from initial SOC rates and stoichiometric considerations, suggesting steady-state conditions were not achieved and/or organic substrates fueling sulfide production had become depleted over the experimental period (e.g. Koop et al. 1990). In contrast, our short-term sulfide flux measurements probably approximate ambient steady-state fluxes (Roden & Tuttle 1992). Summertime sulfide fluxes at Stn 3 were similar to contemporaneous measurements of sulfate reduction to free sulfide, indicating that rates of sulfide storage in sediments were minor at this time of year (Roden & Tuttle 1992).

Vertical water-column profiles of O_2 and S^{2-} exhibited steep concentration gradients across the oxycline in August 1986, with S^{2-} gradients ranging from 5 to 10 mmol m^{-4} (Fig. 4). Similar vertical S^{2-} profiles were

Table 2. Comparison of sediment-water flux measurements of O_2 and NH_4^+ using cores incubated on shipboard versus chambers incubated *in situ* [a]

Date	Stn	Oxygen flux [b] (g O_2 m^{-2} d^{-1})		Ammonium flux (μmol N m^{-2} h^{-1})	
		Cores	Chambers	Cores	Chambers
May 22	Stn 2	1.18 ± 0.34	1.32 ± 0.06	163 ± 29	238 ± 34
Aug 14	Stn 3	0	0	641 ± 57	585 [c]
Aug 15	Stn 2	1.52 ± 0.25	1.64 ± 0.27	331 ± 56	340 ± 35
Aug 25	Stn 3	0	0	721 [c]	734 ± 68

[a] Given are means of 3 replicates ± SD
[b] Oxygen was absent from bottom waters of Stn 3 in Aug
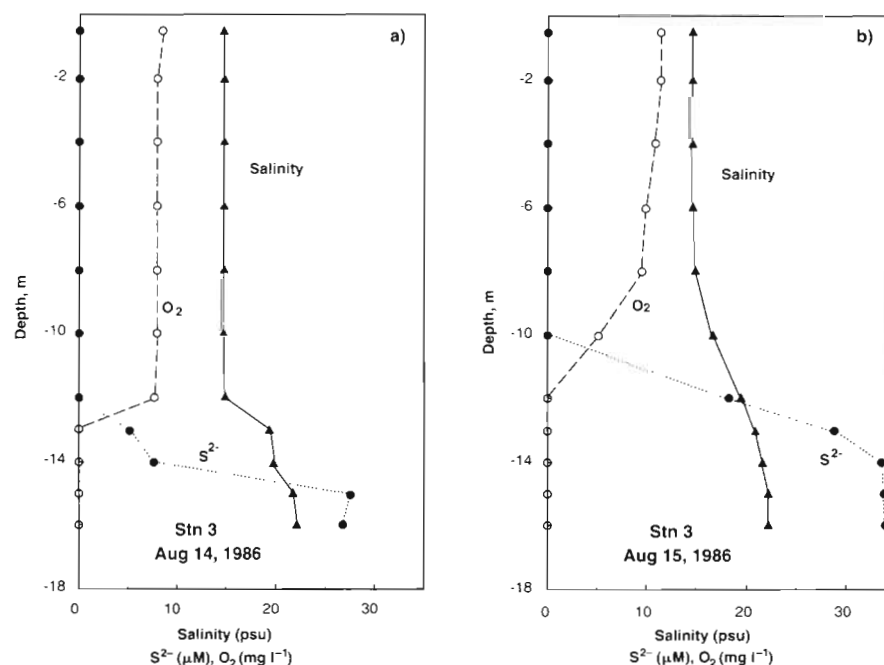[c] Only one measurement available

Fig. 4. Vertical water column profiles of salinity and concentrations of O_2 and S^{2-} measured in late morning at Stn 3 on (a) Aug 14, 1986 and (b) Aug 15, 1986

reported previously for late July 1984 in this same region of the Bay (Tuttle et al. 1987). We estimated rates of vertical S^{2-} flux in the water column using these gradients and an assumed a vertical diffusivity (2.0 m^2 d^{-1}, Officer 1976). Oxygen budget analyses developed later in this paper allowed us to independently compute vertical diffusion coefficients for this site (see 'Oxygen budget computations' below). Sulfide fluxes across the oxycline were thus on the order of 0.5 to 1.0 mmol m^{-2} h^{-1} (Table 3). These fluxes would result in O_2 consumption rates of 0.8 to 1.6 g O_2 m^{-2} d^{-1}, assuming sulfide was oxidized completely to sulfate. The similarity between sulfide fluxes estimated across the oxycline and those measured across the sediment-water interface (Table 3) suggests that anaerobic

sulfide oxidation in the water column (e.g. Luther et al. 1988, Millero 1991) was quantitively unimportant here.

We used correlative analysis to facilitate interpolation of rates for planktonic respiration and SOC during periods of the study when measurements were not available and to evaluate ecological factors regulating these processes. Planktonic community respiration was significantly correlated with water temperature (Table 4) in the upper layer ($r^2 = 0.69$), but weakly related to temperature for the lower layer community ($r^2 = 0.23$). In a contemporaneous study, temperature manipulation experiments in May and August revealed relations of surface planktonic respiration with temperature which were similar to those given in Table 4 (Sampou et al. unpubl.). The absence of a strong relation between

Table 3. Comparison of vertical sulfide fluxes at Stn 3 across the sediment-water interface ($\bar{x} \pm$ SE), measured with shipboard incubated cores and *in situ* chambers, and across the water column oxycline, estimated from sulfide concentration profiles and assumed diffusion coefficients

| Date (1986) | Sediment-water fluxes (mmol m^{-2} h^{-1}) | | Cross-oxycline fluxes | |
	Cores	Chambers	S^{2-} Gradient[a] (mmol m^{-4})	Calculated flux[b] (mmol m^{-2} h^{-1})
Aug 14	0.77 ± 0.05	0.54 ± 0.09	6.0	0.50
Aug 15	nd[c]	nd[c]	9.8	0.82
Aug 25	nd[c]	1.15 ± 0.13	nd[c]	nd[c]

[a] Depths of initial measurable sulfide (and anoxia) were at 12 m and 13 m, respectively on Aug 14 and 15, 1986 (see Fig. 4)
[b] Fluxes computed using simple 1-dimensional diffusion model with estimated vertical diffusivity of 2.0 m^2 d^{-1} (Officer 1976)
[c] Data not available

Table 4. Linear regression analysis of plankton community respiration for upper (R_{pu}) and lower (R_{pl}) layers at Stn 3 and for benthic community respiration at Stn 2 (R_{b2}) and Stn 3 (R_{b3}, or R_{b3s} including sulfide fluxes) versus water temperature (T), bottom water oxygen (O_2) and apparent plankton productivity (P) between Mar and Aug in 1986 and 1987

Respiration (Y variable)	Linear equation	r^2	n	F
Upper plankton	$R_{pu} = 0.04\ T - 0.16$	0.69	14	27.0 ***
Lower plankton	$R_{pl} = 0.02\ T + 0.16$	0.23	14	3.6
Benthos, Stn 2	$R_{b2} = 0.06\ T + 0.22$	0.81	8	25.0 **
Benthos, Stn 3	$R_{b3} = -0.03\ T + 0.86$	0.63	11	15.1 **
R_{b3} (incl. S^{2-} flux)	$R_{b3s} = 0.05\ T - 0.03$	0.53	11	10.2 *
Upper plankton	$R_{pu} = 0.48\ P - 0.15$	0.76	6	13.0 *
Lower plankton	$R_{pl} = 0.41\ P - 0.03$	0.49	5	2.8
Benthos, Stn 2	$R_{b2} = -0.17\ O_2 + 2.44$	0.29	8	2.5
Benthos, Stn 3	$R_{b3} = 0.04\ O_2 + 0.24$	0.31	6	4.0

* Statistical significance (ANCOVA) at: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

respiration and temperature for the lower layer suggests that variations in other factors (e.g. organic substrates) may have been more important in regulating planktonic metabolism in the bottom waters. Indeed, some of the highest respiration rates measured in the lower layer water occurred in spring when bottom water planktonic chlorophyll concentrations were also maximal (Malone et al. 1988). Previous attempts to correlate planktonic respiration with ambient temperature have indicated several patterns. For example, Hopkinson (1985) found a strong relation ($r^2 = 0.73$) between the 2 variables for the organic rich waters of the Georgia Bight, while no relation between respiration and temperature ($r^2 = 0.02$) was observed for stations along a eutrophication gradient in a Danish fjord (Jensen et al. 1990).

SOC was positively correlated with temperature at Stn 2 and at Stn 3 when Aug SOC rates were calculated from measured sulfide fluxes (Table 4). Q_{10} values for SOC at both stations were approximately 1.7 in the temperature range between 10 and 25 °C. Similar relations between SOC and temperature (and Q_{10} values) have been reported previously for other coastal ecosystems (Nixon 1981, Hopkinson 1985). A higher Q_{10} value (2.7) was evident for SOC at Stn 2 between 8 and 18 °C. This is comparable to Q_{10} estimates reported for colder Danish waters of the Øresund (Kanneworff & Christensen 1986).

Several lines of evidence suggest that availability of organic substrates played an important role in controlling planktonic respiration. We observed a strong correlation ($p < 0.05$, $r^2 = 0.76$) between dark respiration in the upper layer of the water column and apparent plankton production (Table 4), but only a weak, non-significant relation was evident for bottom water respiration. Previous studies have observed correlations between plankton production and respiration for a Danish fjord (Jensen et al. 1990) and for a region

of Chesapeake Bay near the present study site (Kemp & Boynton 1980). A similar seasonal coherence between the 2 community processes was found for Georgia coastal waters (Hopkinson 1985). On shorter time-scales, strong diel patterns have been reported for growth and metabolism of planktonic heterotrophs, with daytime rates significantly higher than those at night (Fuhrman et al. 1985, Wheeler et al 1989). These patterns suggest that much of the organic matter that fuels respiratory processes is composed of labile dissolved compounds released in algal excretion or zooplankton grazing, and that much of the respiration is associated with bacteria and protozoa (Williams 1984). Significant correlations between plankton respiration and bacterial abundance (Tuttle et al. 1987) indicate that total plankton community respiration at this site was dominated by bacterial metabolism. In contrast with previous reports from deeper coastal waters (Wassmann 1984, Kanneworff & Christensen 1986), we found little evidence from temporal patterns of SOC that sediment metabolism was related to seasonal trends in deposition of organic matter, which peaks in April (Boynton et al. 1990).

Seasonal balance of O_2 in mesohaline region of estuary

Conceptual framework for oxygen budgets

To compare the relative contributions of physical and biological processes to observed week-to-week variations in dissolved oxygen, we developed O_2 budgets for an average square meter of water column/sediments in the mesohaline region of Chesapeake Bay. Our model defines 2 vertical water column layers separated by a pycnocline, which tends to be well developed from March through November (Taft et al. 1980). Our

measured rates of biological O_2 production and consumption were combined with empirical estimates of air-water exchange and compared to observed rates of change for O_2 pools in the water. From these O_2 balances, we obtained first-order estimates of the net physical transport of O_2 for each layer. On the basis of spatial distributions of O_2, we rationalized assumptions as to which physical processes were most important in contributing to this net transport term.

The specific O_2 budget model used in this analysis can be described as follows:

Upper layer: $(dC_u/dt) Z_u = P_p - R_{pu} + F_{aw} - F_{vp} + F_{hu}$ (1)

Lower layer: $(dC_l/dt) Z_l = F_{vp} + F_{hl} - R_{pl} - R_b$ (2)

where C_u and C_l are mean O_2 concentrations in upper and lower layers, respectively; P_p is net daytime (apparent) photosynthetic production of O_2; R_{pu} and R_{pl} are planktonic consumption of O_2 in upper and lower layers (because P_p includes daytime respiration, R_{pu} is for nighttime only, while R_{pl} is a diel rate); F_{aw} is air-water exchange; F_{vp} is vertical exchange across the pycnocline; F_{hu} and F_{hl} are horizontal (longitudinal) dispersion in upper and lower layers; and R_b is benthic respiration. All of these terms have units of g O_2 m^{-2} d^{-1}. The terms Z_u and Z_l represent mean heights (m) of the upper and lower layers, respectively.

Surveys of O_2 distributions in the upper layer along a transect from about 10 km north of our stations to 10 km south of our site revealed only small, variable longitudinal O_2 gradients during our study period (Malone et al. unpubl.). Because net transport through a section of the water column tends to require a more substantial O_2 gradient (e.g. Kemp & Boynton 1980), we dropped the F_{hu} term, thus reducing the right hand side of Eq. (1) to 4 terms. In contrast, strong longitudinal O_2 gradients in the bottom layer in this region of the Bay indicated that this horizontal transport could not be ignored in Eq. (2) (e.g. Kuo et al. 1991). The correspondence between seasonal patterns of salinity and O_2 in bottom waters discussed above (Fig. 2b; Sanford et al. 1990) are consistent with this interpretation. We estimated air-water O_2 exchange from O_2 percent saturation data (Fig. 1b) and the following expression (Kemp & Boynton 1980):

$$F_{aw} = k_{aw} (C_{us} - C_s)$$ (3)

where k_{aw} is the air-water exchange coefficient (termed 'piston velocity' and having units of m d^{-1}); C_s is the saturation concentration of O_2 at ambient values of temperature and salinity; and C_{us} is the O_2 concentration in surface waters (0.5 to 1.0 m depth). Monthly means for k_{aw} were estimated using a relationship between wind speed, which was established previously for lake and

oceanic waters (Broecker et al. 1980) and modified for estuaries (Hartman & Hammond 1985). These estimates of k_{aw} were consistent with values reported previously for the mesohaline Bay (Kemp & Boynton 1980).

Thus, direct measurements or empirically determined values (F_{aw}) were available for all terms in Eqs. (1) & (2), except the transport terms, F_{vp} and F_{hl}. Because only one of these transport terms (F_{vp}) occurs in Eq. (1) for the upper layer, we were able to estimate it by difference; similarly, we calculated F_{hl} as the difference in the sum of all other terms in Eq. (2). This conceptual scheme differs from those in other O_2 budget analyses (e.g. Falkowski et al. 1980, Kemp & Boynton 1980, Kuo & Nielson 1987) in that it allows the major physical processes of O_2 transport to be estimated indirectly from O_2 distributions and biological rate data.

For this analysis, the height of the upper layer (Z_u) was taken to be 8 m for the entire study period. Although the actual depth of the pycnocline separating the 2 vertical layers at Stn 3 varied from 6 to 10 m (Fig. 2), at least some of this variation was likely attributable to lateral tilting associated with Ekman circulation driven by wind stress (Malone et al. 1986). In our budget, however, temporal variations in pycnocline depth appear as observed changes in mean O_2 pools for each layer and are accounted for in the net vertical exchange (F_{vp}). The mean height of the lower layer (Z_l) was more difficult to estimate because the shape of the cross-sectional area below the pycnocline is highly irregular. We were, however, able to estimate the mean thickness of the lower layer from hypsographic data for average width and cross-sectional areas for each depth at this Bay transect (Fig. 5a, b; Cronin & Pritchard 1975). We calculated cross-sectional areas of the bottom layer contained below various depths from 25 m to the water surface as the sum of cross-sectional areas given by Cronin & Pritchard (1975) for each 1 m depth interval (Fig. 5b). The mean height of the bottom layer at a given depth was then calculated by dividing these bottom layer cross-sectional areas by the average width of each depth interval (Fig. 5c). Thus, at the mean pycnocline depth (which we have taken to be 8 m), the mean height of the bottom layer (Z_l) is approximately 6 m. This dimension becomes very important when comparing rates of planktonic respiration (Fig. 3a), measured in volumetric units, with rates of benthic O_2 consumption (Fig. 3b), measured in areal units (e.g. Dyrssen 1986).

Oxygen budget computations

Several patterns for the upper layer of the water column are evident in the monthly mean mass-balance calculations provided in Table 5. While monthly mean rates of apparent O_2 production (P_p) varied directly
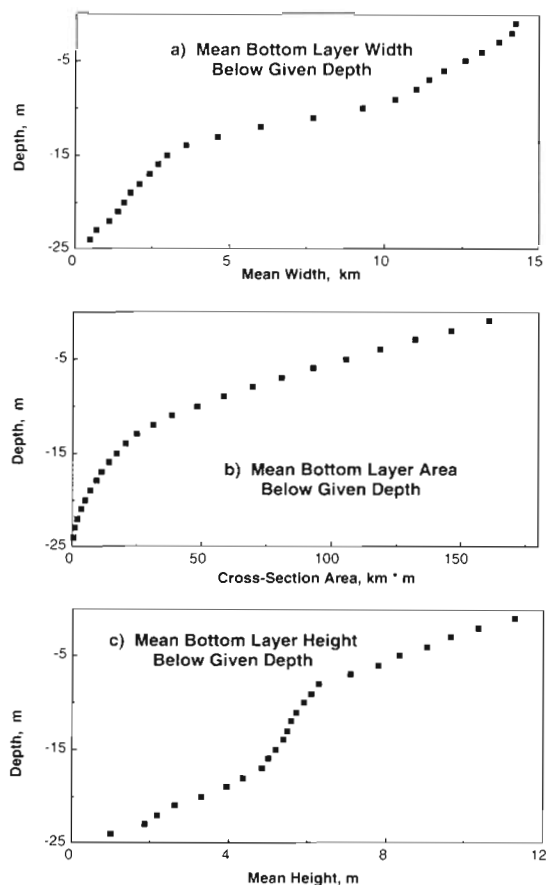
Fig. 5. Hypsographic relations for the cross-section of Chesapeake Bay at Stns 2 and 3 (38° 33.5' N) adapted from Pritchard & Cronin (1975). Relations indicate characteristics of bottom layer below given depth for: (a) mean width of bottom layer; (b) mean cross-sectional area of bottom layer; (c) mean height of bottom layer

with water temperature (cf. Fig. 1), plankton respiration rates (R_{pu} and R_{pl}) peaked in June and July. Mean rates of air-water O_2 exchange (F_{aw}) were generally directed to the atmosphere and accounted for 10 to 30 % of P_p. Although these calculations do not take into consideration the effects of bubble injection on air-water O_2 exchange (e.g. Broecker et al. 1980), we would expect this process to be relatively small in relation to the mean monthly fluxes in our budget (Stigebrandt 1991). These ratios of $F_{aw} : R_{pu}$ are similar to those estimated earlier based on diel O_2 budgets in this region of Chesapeake Bay (Kemp & Boynton 1980) and slightly lower than previously reported for shallower coastal systems (Peterson 1979, van Es & Ruardij 1982). Fluxes were calculated on the basis of O_2 concentrations (% saturation) measured during late morning in the upper 0.5 to 1.0 m of the water column. Previous diel observations of surface O_2 concentrations suggest that late morning observations were reasonably representative of the 24 h mean O_2 concentrations (Kemp &

Boynton 1980). Air-water exchanges were directed out of the water for most of this study because near-surface O_2 concentrations usually remained supersaturated, even when mean O_2 levels for the entire upper layer were undersaturated.

Calculated rates of vertical O_2 exchange between upper and lower layers (F_{vp}) ranged between 40 and 60 % of diel plankton respiration rates. This vertical exchange is a critical rate which has been suggested to control O_2 replenishment to the bottom layer over the entire estuarine region (e.g. Officer et al. 1984). Considering F_{vp} as a physical dispersion process (e.g. Pritchard 1969) implies that the calculated monthly mean rates would be directly proportional to the respective mean vertical O_2 gradients. By comparing estimates of F_{vp} with observed vertical O_2 gradients, we obtain an independent check on these rates which were calculated from Eq. (1) as described above. In fact, a significant ($p < 0.05$) correlation was obtained between the calculated rates and measured gradients (Fig. 6a). The slope of this relation estimates the mean 'effective' vertical dispersion coefficient (e.g. Officer 1976). By 'effective' dispersion coefficient, we imply that the mechanism of O_2 transport may involve both diffusive and net advective transport processes, both of which are a function of the O_2 concentration gradient (Pritchard 1969). The calculated dispersion coefficient, K_z', equal to $F_{vp} (dC/dz)^{-1}$, where dC/dz is the vertical O_2 gradient, had a mean value of 0.2 cm^2 s^{-1}, which is similar to summer values reported previously for partially stratified estuaries (e.g. Pritchard 1967, Officer 1976; see also rate calculations in Table 3). Although K_z' did not vary greatly over the period of our analysis, values computed for each month from this budget (ratio of calculated vertical flux and the measured O_2 gradient) were inversely related to the dimensionless mean vertical salinity gradient (dS/S). That this relation (not shown) was significant ($p < 0.05$, $r^2 = 0.56$) further supports the robustness of O_2 fluxes calculated from Eq. (1).

Mass balance calculations for O_2 in the lower layer of the water column for April, May and August (Table 5) also reveal interesting patterns. In the spring months, respiration rates exceeded physical O_2 exchanges (vertical plus longitudinal), leading to a substantial rate of concentration decline. Both benthic and planktonic respiration were important, with the latter ranging from 0.5 to 2.5 times larger than the former. Net longitudinal exchange of O_2 (F_{hl}) was negligible in early spring when bottom O_2 concentrations were closest to saturation and longitudinal O_2 gradients were relatively small; its importance increased in May and thereafter as bottom O_2 concentrations plummeted. Monthly mean values for F_{hl} (Mar to Oct) were variable, ranging from –0.1 in April to +3.5 g O_2 m^{-2} d^{-1} in July (Table 5). Although others (e.g.

Table 5. Summary of monthly mean oxygen fluxes (g O_2 m^{-2} d^{-1}) for upper and lower layers of water column in mesohaline Chesapeake Bay during Mar to Oct

Water column layer: oxygen fluxes	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
Upper layer:								
Plankton production[a]	+1.3	+3.9	+4.6	+4.4	+5.0	+6.3	+5.3	+3.1
Plankton respiration[b]	−0.5	−1.5	−2.1	−3.0	−2.9	−2.2	−2.4	−1.4
Air–water exchange[c]	−0.6	−1.4	−1.1	+0.5	−0.6	−1.2	0	−0.7
Change in O_2 pool	+0.2	+0.2	0	+0.4	+0.2	+0.3	0	−0.4
X-pycnocl. exchange[d]	−0.4	−1.2	−1.4	−2.3	−1.7	−3.2	−2.9	−0.6
Lower layer:								
X-pycnocl. exchange[d]	+0.4	+1.2	+1.4	+2.3	+1.7	+3.2	+2.9	+0.6
Plankton respiration[b]	−0.6	−1.3	−2.2	−3.0	−4.2	−2.4	−2.4	−1.8
Benthic respiration[e]	−0.4	−0.6	−0.9	−0.8	−1.0	−1.6	−1.2	−1.0
Change in O_2 pool	−0.4	−0.8	−0.6	−0.9	0	0	+0.6	+0.6
Net longit. exchange[f]	+0.2	−0.1	+1.1	+0.6	+3.5	+0.8	+1.3	+2.8

[a] Net daytime (apparent) O_2 production estimated from bottle incubations (6 to 8 h) adjusted for mean day length; rates for Sep and Oct were estimated from Malone et al. (1988) and relation given in Table 1
[b] Night time respiration rates (adjusted for mean length of night) for upper layer and diel respiration rates for lower layer; rates assume upper layer height of 8 m and mean height of lower layer equal to 6 m (Fig. 5); in Jul to Aug when bottom waters were anoxic, the oxygenated part of the lower layer was taken to be 3 m thick (Fig. 2); rates for Sep and Oct were estimated from regressions on temperature (Table 4)
[c] Assumes air-water exchange coefficients ranging from 0.8 to 1.4 m d^{-1} based on monthly mean wind speeds between 3 and 5 m s^{-1} (Hartman & Hammond 1985); monthly diel mean % O_2 saturation estimated from detailed surveys (see Fig. 1)
[d] Net O_2 exchange across pycnocline estimated as residual term in upper layer O_2 balance
[e] Benthic O_2 consumption estimated as mean of values measured at Stns 2 & 3 including sulfide efflux during Aug (see Fig. 3)
[f] Net longitudinal O_2 exchange estimated as residual term in lower layer O_2 balance

Kuo & Nielson 1987, Sanford et al. 1990) have emphasized the importance of horizontal transport in estuarine O_2 budgets, monthly mean values calculated here for longitudinal exchange (F_{hl}) were less than those for vertical exchange (F_{vp}) for 6 out of 8 months (Table 5). In all but 1 mo (April), F_{hl} was positive, implying longitudinal transport as a net source of O_2 inputs to (rather than outputs from) the study region. Because the net physical circulation of the lower layer is directed landward (Pritchard 1967), this is consistent with observed prevailing O_2 gradients, in which higher concentrations occur seaward of the study region (e.g. Malone et al. 1988).

Even though the primary mechanism of longitudinal transport is advective, under steady-state conditions, F_{hl} would be proportional to the longitudinal gradients of O_2 concentration (Pritchard 1969). This is because F_{hl} is a measure of net transport (inflow minus outflow), where inflow is a function of upstream O_2 concentrations and outflow is proportional to O_2 at the study site. As was the case for vertical O_2 transport, monthly mean estimates of F_{hl} were indeed significantly correlated (Fig. 6b) with their respective O_2 gradients between the upstream (seaward) source and the study area (Stn 3). The unusually large F_{hl} flux calculated for July was an outlier compared to the other months. The

slope of this correlation provides a measure of the mean net longitudinal velocity (v_{hl}) over this time interval. In this case, $v_{hl} = (F_{hl})^{-1} (Z_l)^{-1} (dC/dy)^{-1}$, where dC/dy is the longitudinal O_2 gradient, and F_{hl} is divided by Z_l to obtain an equivalent volumetric flux. Since $[(F_{hl}) (dC/dy)^{-1}]$ is the slope of the regression (Fig. 6b), $v_{hl} = (1.17$ m d^{-1}) $(10^4$ m) $(6$ m)$^{-1}$ $(8.6 \times 10^{-4}$ s d$^{-1})^{-1}$ $(100$ cm m$^{-1}) \approx 5$ cm s^{-1}, a value typical of those reported for coastal plain estuaries (Pritchard 1967, Kuo & Nielson 1987). We are encouraged by the fact that our mass-balance calculations for physical transport processes, F_{vp} and F_{hl} were well correlated with respective O_2 gradients and by the realistic magnitude of computed values for both vertical dispersion coefficients and net longitudinal velocities.

Relative contributions of benthic and planktonic O_2 consumption

Most of the temporal variations in total bottom respiration were associated with changes in planktonic respiration rather than SOC (Fig. 7a). While planktonic respiration exhibited 3 periods of substantial temporal variations (Apr 1 to 24, May 5 to Jun 24, Aug 15 to 24),
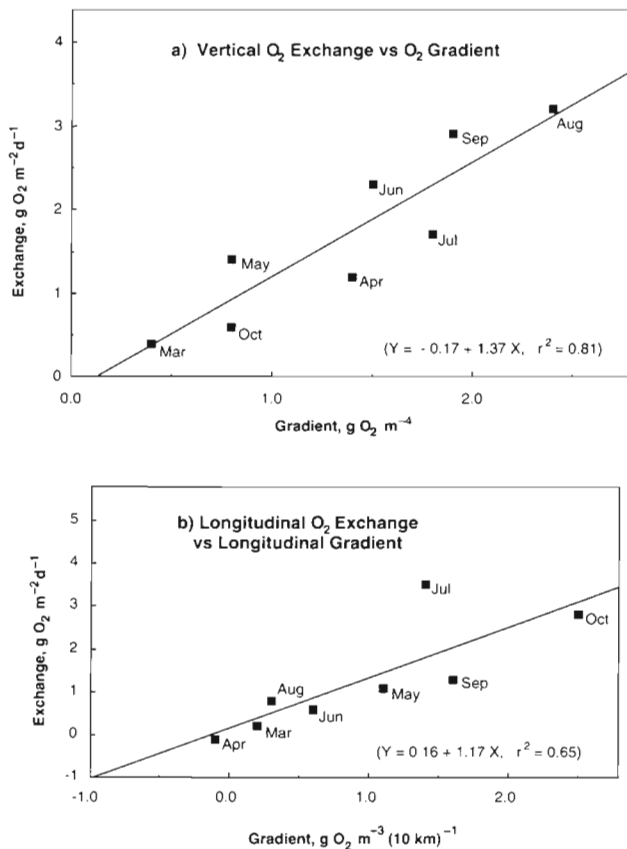
Fig. 6. Correlations between calculated physical O_2 transport and respective O_2 concentration gradients along axis of transport: (a) vertical exchange versus gradient; (b) longitudinal exchange versus gradient in bottom layer. Each point represents a monthly (Mar to Oct) mean O_2 flux calculated from a mass balance (Table 4)

Fig. 7 Seasonal (1986) sequences of: (a) planktonic versus benthic contributions to total O_2 consumption in bottom layer for 8 dates between Apr and Aug; and (b) calculated monthly mean values of total bottom layer respiration versus net physical (vertical plus longitudinal) O_2 exchange

there was virtually no change in SOC within these intervals (Fig. 7a). Planktonic rates dominated O_2 consumption for most of the period from late spring to late summer, comprising two-thirds of the total from late April to mid August (Fig. 7a). Benthic O_2 consumption, however, slightly exceeded plankton respiration in early April when water temperatures were still below 10 °C (Fig. 1) and again in late August when sulfide fluxes were high and plankton metabolism was starting its seasonal decline (Fig. 3).

The annual variation in SOC rates between warm and cold seasons was substantially less than that for planktonic respiration (Fig. 3); this pattern has been reported for numerous coastal ecosystems (Kemp & Boynton 1992). It is attributable, in part, to the fact that organic matter pools tend to turn over more rapidly in the water column than in the sediments, such that organic inputs to the benthos at a given time can support metabolism in subsequent seasons (Kemp & Boynton 1981, Rudnick & Oviatt 1986). Much of the O_2 consumption associated with sediment processes in sum-
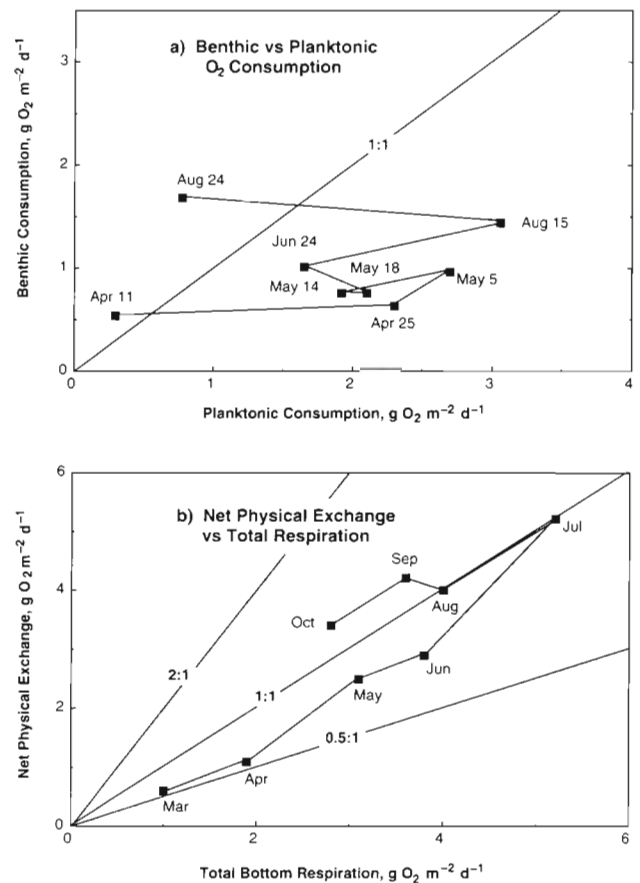
mer (and perhaps in autumn) results, however, from reoxidation of reduced sulfur compounds which accumulated from sulfate reduction earlier in the year (Jørgensen 1977, Sampou & Oviatt 1991). Hence, temporary storages of both organic substrates and reduced metabolites contribute to the damped seasonality of SOC in most coastal marine ecosystems. The extent to which such storage in sediments can contribute to significant retention of O_2 demand from one year to the next is less clear. The existence of significant correlations between mean annual rates of plankton production and SOC between sites (Wassman 1984) and years (Boynton et al. 1991), however, implies that interannual storage would be relatively insignificant in most coastal environments.

Averaged over annual time-scales, the relative importance of benthic and planktonic O_2 consumption should depend largely on mean depth of the water column (Hargrave 1973). Indeed, previous studies have shown that SOC is inversely proportional to water column depth across large (10 m to 10 km) depth

gradients (Harrison 1980, Suess 1981). We find a similar pattern (Fig. 8a) for estuaries and coastal shelf systems, which range over a much smaller depth gradient (1 to 60 m). This implies that the amount of euphotic zone organic matter which sinks to the sediment surface to support SOC decreases as longer water columns increase the transit time (and attendant opportunity for consumption by plankton) for sinking substrates. We have considered only sites for which contemporaneous summer and/or spring measurements of benthic and planktonic respiration rates were
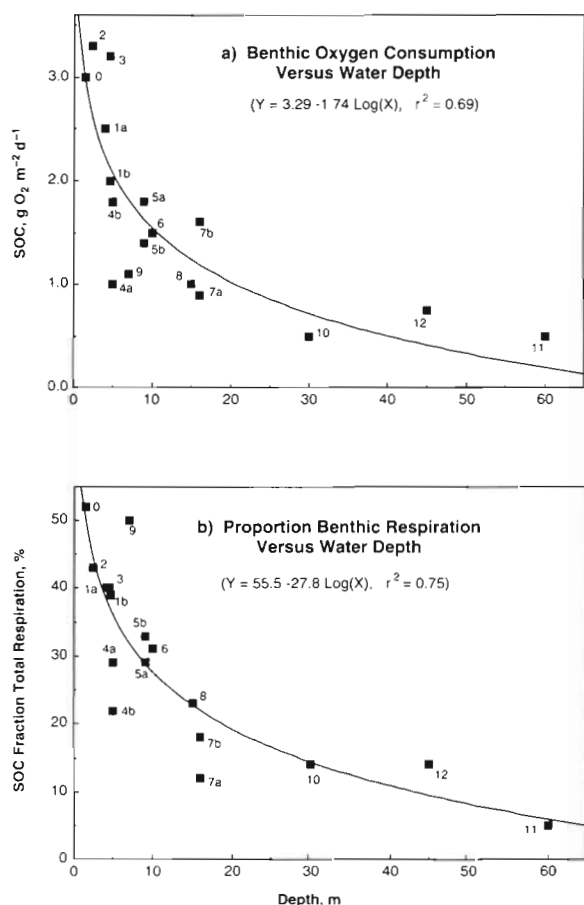

Fig. 8. Summary of mean spring and summer measurements of (a) sediment O_2 consumption (SOC) and (b) SOC as a percent of total respiration plotted against total water column depth. Numbers beside points refer to data sources: (0) Norman Creek Estuary (Connell et al. 1982); (1a, b) inner and outer Roskilde Fjord (Sand-Jensen et al. 1990); (2) Ems Estuary (van Es & Ruardij 1982); (3) Georgia Bight (Hopkinson 1985); (4a, b) MERL control and 8× mesocosms (Oviatt et al. 1986); (5a, b) mid Chesapeake Bay stations for spring and summer (Kemp & Boynton 1980); (6) lower Chesapeake Bay stations for spring and summer (Boynton & Kemp 1985); (7a, b) this study; (8) Gulf of Trieste (Herndl et al. 1989); (9) San Francisco Bay (Peterson 1979); (10) North Sea coast (Westernhagen et al. 1986); (11) New York Bight (Falkowski et al. 1980); (12) Mississippi Delta Bight (Turner & Allen 1982, Twilley unpubl.)

available. The strength of this relation is surprising given the fact that seasonal (rather than annual) mean rates are compared, and it suggests that the pattern is robust. A similar exponentially declining relation with depth is found when SOC is presented as a fraction of total community respiration (Fig. 8b). Here, plankton respiration is integrated over the entire water column rather than just the lower layer so as to include both stratified and unstratified systems in the comparison. Thus, for example, data from our study (points 7a, b in Fig. 8b) suggest that SOC represents a smaller fraction (10 to 20 %) of total respiration rather than the range (20 to 40 %) found for bottom layer respiration only (Fig. 7a). From this relation, we would expect SOC to dominate community respiration only in water columns (or bottom layers) of 5 m height or less.

Relative importance of biological and physical processes

To examine the relative significance of biological compared to physical processes on the bottom water O_2 budget in the study region, we have compared monthly mean estimates for measured total respiration $(R_{pl} + R_b)$ with the sum of vertical and horizontal O_2 exchanges $(F_{vp} + F_{hl})$ calculated from the budget (Table 5, Fig. 7b). Here, we find that mean monthly O_2 rates for physical exchange (Y) and biological respiration (X) were significantly correlated $(Y = 0.56 + 1.12X, r^2 = 0.87)$. The slope of this relation (1.12) indicates that most of the month-to-month shifts in this relation occurred along rather than across the plane of the 1:1 line of equal rates. Although summertime hypoxia results from biological consumption exceeding physical replenishment of O_2, this correlation (Fig. 7b) emphasizes the extent to which the 2 processes are poised in near balance over the entire spring-autumn period. Both rates increased through July and declined thereafter. A simple explanation for this balance lies in the nature of the diffusion-reaction interaction for any substrate (or product) in relation to physical transport and biochemical reaction (e.g. Rashevsky 1961). Because O_2 consumption in the bottom layer is coupled to O_2 transport by vertical dispersion and net longitudinal advection, the physical and biological processes will tend to compensate for one another. Because both vertical dispersion and net longitudinal advection of O_2 are driven by their respective O_2 concentration gradients, they are inversely related to O_2 concentration in the study site's bottom waters. As biological processes (respirations) increase, they reduce O_2 concentration in those waters, which tends to increase O_2 gradients, thereby increasing physical transport to the site. Conversely, as biological processes decrease, physical

transport must decrease. This coupled physical-biological process, by its nature, tends to operate at or near the point of balance. In that sense, the question of whether physical or biological O_2 fluxes dominate the O_2 budget in a given time or place is moot. The 2 processes depend on each other, and neither will exist (in a net sense) without the other.

Biological consumption and physical replenishment of O_2 in bottom waters are also both influenced by variations in freshwater loading to the Bay. Inputs of freshwater (riverflow, direct precipitation and groundwater seepage) represent the primary sources of nutrients to the estuary (Nixon 1987); they also contribute the buoyancy which controls both vertical stratification (Schroeder et al. 1990) and longitudinal transport (Pritchard 1967). Therefore, drought years marked by low freshwater inputs will tend to be characterized by reduced hypoxia, because of associated reductions both in physical O_2 replenishment and in nutrient-generated increases in algal biomass which fuel bottom water respiration. This double-edged effect of freshwater inputs to the estuary severely limits the ability to ascribe interannual variations in hypoxia to changes independently in either biological or physical processes (cf. Officer et al. 1984, Seliger & Boggs 1988).

Results of this O_2 budget analysis lead to 2 important implications regarding the efficacy of managing nutrient waste loading (and associated organic matter inputs to bottom waters) to improve Bay bottom water O_2 concentrations. On one hand, the fact that most of the O_2 consumption from bottom waters is associated with planktonic rather than benthic processes (Fig. 7a) suggests that O_2 consumption would respond rapidly to reductions in nutrient inputs. On the other hand, the apparent close correspondence between physical renewal and biological consumption of O_2 (Fig. 7b) indicates that the magnitude of O_2 response to changing nutrient inputs would tend to be buffered by the interaction of the coupled physical and biological processes. Thus, we expect that any reduction in nutrient loading to Chesapeake Bay (e.g. 40 %; Fisher & Oppenheimer 1991) would yield rapid but proportionally smaller increases in O_2 concentrations.

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