Factors regulating plankton community respiration in Chesapeake Bay

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ABSTRACT: Rates of plankton community respiration were measured in surface and bottom waters during spring, summer and autumn in the mesohaline region of Chesapeake Bay, USA. Seasonal patterns of plankton respiration generally followed the annual temperature cycle, with peak rates in July and August of 40 to 70 µg O_2 l^{-1} h^{-1}, which are among the highest values reported in the literature. In addition, strong diel variations in surface water community respiration, with mid-day maxima, were coherent with cycles of irradiance and photosynthesis, suggesting the dependence of community respiration on recently produced organic matter. The range of diel variations in respiration during summer was almost half the annual range in mean rates. Size-fractionated incubations demonstrated the importance of picoplankton (< 3 µm) respiration compared to total rates. On average, picoplankton accounted for most of community respiration in surface waters (56 %) and dominated total rates in the summer pycnocline (89 %). This size fraction was less important in the bottom waters during spring (23 %). Temperature per se as a control on plankton respiration was investigated by comparing rates at *in situ* temperatures against those measured in temperature-manipulated experiments in spring and summer. Strong relations between respiration and temperature were observed in all cases; least-squares regressions (exponential and linear) for experimental data were not significantly different between seasons, nor between the experiments and the seasonal rates measured at *in situ* temperatures. These results suggest the absence of significant physiological adaptation and/or selection for temperature optima over the annual cycle. Respiration by bacterioplankton (< 1 µm) exhibited no oxygen dependence down to concentrations of 0.16 mg O_2 l^{-1}; however, rates for whole water (unfiltered) declined with decreasing oxygen below 0.8 mg O_2 l^{-1}. Evidently, diffusion limited oxygen consumption by proto- and metazoans as well as bacteria associated with detrital particles and organic flocs.

KEY WORDS: Community respiration · Seasonal cycles · Chesapeake Bay

INTRODUCTION

Studies over the last decade have demonstrated the importance of plankton community respiration in estuarine carbon and oxygen budgets, even for relatively shallow coastal ecosystems (Garside & Malone 1978, Kemp & Boynton 1980, Van Es 1982, Hopkinson 1985, Kemp et al. 1992). Furthermore, recent focus on planktonic processes associated with bacteria and protozoa (e.g. Azam et al. 1983) clearly indicates the degree to which microbial metabolism can dominate plankton carbon dynamics (e.g. Williams 1984, Smith et al. 1986, Hopkinson et al. 1989, Griffith et al. 1990, Sand-Jensen et al. 1990).

Strong seasonal cycles of plankton respiration are often evident in temperate coastal waters with peak rates coinciding with the annual maxima of temperature and primary productivity (Hagström & Larsson 1984, Hopkinson 1985). Water temperature can be a good predictor of seasonal variations in planktonic community respiration and/or microbial activity for many of these ecosystems (Iriberri et al. 1985, Unanue et al. 1992, Shia & Ducklow 1994). Furthermore, planktonic respiration and microbial activity have been linked to diel patterns of phytoplankton production and release of exudates (Fuhrman et al. 1985, Wheeler et al. 1989, Jensen et al. 1990, Malone et al. 1991). Recent evidence suggests that temperature may

affect bacterioplankton respiration differently than it does metabolism of larger plankton and that substrate availability modulates simple temperature relations (Pomeroy & Deibel 1986, Scavia & Laird 1987, Pomeroy et al. 1991, Shia 1993, Wiebe et al. 1993). There are, however, few studies examining the influence of temperature per se on plankton community respiration.

Studies of dissolved oxygen dynamics and plankton respiration rates have a long history in Chesapeake Bay, USA (Kemp & Boynton 1980, Taft et al. 1980, Kemp et al. 1992). There is growing concern that the duration and spatial extent of bottom water oxygen depletion has increased in Chesapeake Bay as a consequence of cultural eutrophication (Officer et al. 1984). The timing of the spring oxygen depletion event is associated with 3 factors: (1) deposition of the spring diatom bloom; (2) vernal warming; and (3) enhanced stability of the water column (Kemp et al. 1992). During most of this spring period of oxygen decline, planktonic respiration is the dominant sink for oxygen in the bottom layer (Kemp et al. 1992). However, little information is available on how oxygen concentration might influence observed rates in any coastal waters.

In the present study, we combine 2 years of field measurements of plankton community respiration with laboratory manipulation of temperature and dissolved oxygen. This research is focused in a well-described portion of the mesohaline region of Chesapeake Bay, which experiences seasonal oxygen depletion in bottom waters (see Malone et al. 1986, Kemp et al. 1992). Plankton community respiration rates are presented for whole water and for pre-incubation filtrates (< 1 and < 3 µm), to evaluate the relative contribution of picoplankton respiration and variations in this component with seasons and depth.

MATERIALS AND METHODS

Plankton community respiration rates were measured for surface and bottom water samples, collected from the mesohaline region of Chesapeake Bay (Stn 3, 38° 28.0' N; Malone et al. 1986, Kemp et al. 1990) at approximately 2 to 3 wk intervals during spring (March through early June) and summer (August) in 1986 and 1987. Additional samples were collected in July and November 1987 and again in May 1988. This station (MLW depth 20 m) was typified by a strong pycnocline, with hypoxic ($O_2 < 2.0$ mg l^{-1}) to anoxic conditions occurring in bottom waters from early June through August (Kemp et al. 1992). Vertical profiles of temperature, salinity and dissolved oxygen were measured at 2 m intervals (finer scale across the pycnocline) using a Hydrolab monitoring system equipped with thermistor, induction salinometer and

polarographic electrode. Surface (2 to 3 m below air-sea interface) and bottom (2 m above sediment-water interface) waters were retrieved with a Niskin bottle. During summer, aphotic waters were sampled from within the pycnocline (generally 10 to 12 m deep), rather than from the anoxic bottom layer.

Water used for respiration incubations was always collected between 08:00 and 10:00 h. Incubations were conducted in opaque bottles (300 ml with ground glass stoppers) in a water bath at in situ temperatures (± 1 °C). Water samples were either incubated immediately on shipboard (in 1986) or placed on ice in the dark and transported back to the laboratory (in 1987), where incubations were initiated within 4 to 12 h after water collection. Incubation times were adjusted seasonally, varying from 6 to 24 h, so that changes in dissolved oxygen concentration during experiments were generally in the range of 0.2 mg l^{-1}.

Studies of diel periodicity in plankton respiration were conducted in May and August 1987. Water samples were collected from an anchored vessel at approximately 6 h intervals over a 36 h period, and incubations were initiated immediately on shipboard at in situ temperatures. Incubation periods were generally 6 to 8 h during these experiments. At each sampling time, vertical hydrocasts of temperature, salinity and dissolved oxygen were conducted to observe variations in water column structure over the course of the experiment.

On most occasions, plankton respiration was measured both for the total community (unfiltered water) and for picoplankton-size (< 3 µm) organisms and particles. Picoplankton respiration was estimated using a gentle reverse filtration prior to incubations (Williams 1981). Water samples were size-fractionated through 142 mm Nuclepore filters (1 or 3 µm) using an 18" (ca 46 cm) gravity head and distributed into 6 to 9 replicate 300 ml incubation bottles. Initial oxygen concentrations were measured non-destructively in each bottle with a polarographic electrode (precision of 0.02 mg l^{-1}; Orbisphere Laboratories, Geneva). One-third of the initial bottles (including those with maximum and minimum values measured by electrode) were immediately fixed for Winkler titration (Lambert & Oviatt 1986). The range of initial oxygen concentrations among these replicates was less than 0.10 mg l^{-1}. Final dissolved oxygen was measured for all replicate incubations using the electrode, with half of these fixed for Winkler titration. Rigorous standardization of the polarographic electrode was necessary since the meter could experience a slight drift over a 24 h period.

Linearity of respiration rates over time was examined on 3 different dates for whole water and once for the < 3 µm size fraction. Dissolved oxygen concentrations were measured as described above. Standard

errors for replicate samples during the time-course experiments were generally less than 0.01 mg l^{-1}. Temperatures ranged from 5 to 25 °C over the 4 dates. Rates of oxygen consumption were linear for the duration of all experiments (Fig. 1). Bacterial abundance was also measured by the acridine orange direct count method (Hobbie et al. 1977) during one of these to evaluate potential changes in bacterial populations during incubations. In general, bacterial abundance remained constant (< 10 % change) in all replicates (E. R. Peele unpubl. data).

Effects of temperature per se on surface plankton respiration rates were examined on 2 separate dates in 1987. Whole water collected on May 13 (in situ temperature 18 °C) and August 25 (25 °C) was distributed into replicate bottles and placed into 1 of 4 or 5 temperature-controlled incubation chambers. Replicate (6 to 8) samples were allowed to equilibrate to the experimental temperature for 4 to 6 h, followed by incubations of 20 to 40 h. Dissolved oxygen concentrations were measured as described above. In the May experiments, temperatures were maintained at 5, 10, 15, 20, 25 °C; in August, replicates were incubated at 5, 15, 20, 30 °C (± 1.0 °C).

Effects of hypoxic conditions (< 2.0 mg l^{-1}) on plankton respiration rates were also studied under controlled laboratory conditions for both whole water and the < 1 µm size fraction. Two experiments were conducted when in situ oxygen concentrations were approximately 1 mg l^{-1}: one using bottom water collected in early June, the other with pycnocline water in August. Water was collected at mid-morning and transported back to the laboratory for experimentation.
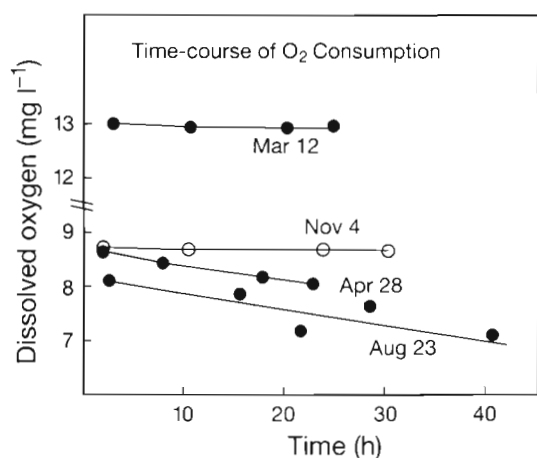
Initial dissolved oxygen levels were adjusted to experimental levels (0.2 to 2.0 mg l^{-1}) by bubbling with air or with N_2 gas. Experimental oxygen concentrations declined by 0.03 to 0.4 mg l^{-1} over the course of an incubation. Four dissolved oxygen treatments (3 or 4 replicates each) were used in June and 3 in August. Respiration rates were graphed against the average oxygen concentration over an incubation. Oxygen concentrations were measured using a combination of Winkler and polarographic methods, as described above.

RESULTS AND DISCUSSION

Temporal respiration patterns

Plankton community (whole water) respiration in the well-mixed surface layer exhibited a steady increase in rates throughout the vernal warming period, with the largest increase (10-fold) occurring between mid March and late May (Fig. 2a). The maximum summer rates (40 to 70 µg O_2 l^{-1} h^{-1}) are among the highest values reported in the literature (e.g. Williams 1984, Hopkinson 1985, Sand-Jensen et al. 1990). Previous studies have indicated that phytoplankton production in this region generally follows a similar seasonal pattern, with springtime increase to annual maxima in July or August (e.g. Boynton et al. 1982, Malone et al.
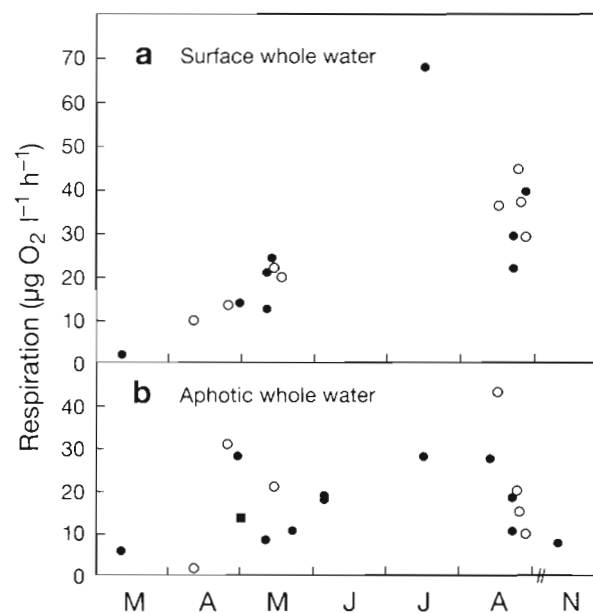

Fig. 1. Time course of incubations, showing linear depletion of oxygen over time. Whole water respiration rates (± 1 SE) were: for March at 5 °C, 5.06 ± 0.60 µg O_2 l^{-1} h^{-1}; for April at 13 °C, 28.0 ± 0.57 µg O_2 l^{-1} h^{-1}; and for August at 25 °C, 39.4 ± 3.7 µg O_2 l^{-1} h^{-1}. Size-fractionated (< 3 µm) rates in November at 14 °C were 1.90 ± 0.24 µg O_2 l^{-1} h^{-1}

Fig. 2. Seasonal patterns of whole water respiration in surface waters and aphotic waters. (O) 1986; (●) 1987; (■) 1988. Aphotic samples included bottom water for March to June (and November 1987), and pycnocline waters for July to August

1988). In contrast, annual peaks in phytoplankton bio-mass in the euphotic zone tend to occur in April with considerably lower values in summer (Malone et al. 1988). The exceptionally high plankton respiration rate measured in July coincided with the highest bacterio-plankton abundance levels observed at this site during the years of the present study (Malone et al. 1991). Rates of both phytoplankton exudation and bacterio-plankton uptake of DOC (dissolved organic carbon) were also particularly high on this date (Malone et al. 1991).

Bottom water respiration did not follow the same monotonic increase in rates through the spring (Fig. 2b). Respiration was low when temperatures were below 10°C but quickly rose to peak values in late April, the only time when bottom water rates exceeded those in the euphotic zone. During spring 1987, for which 5 dates were sampled, peak bottom water respiration rates were coincident with maximum algal biomass levels (28 μg O_2 l^{-1} h^{-1} and 48 μg chlorophyll a l^{-1}, respectively). High rates of respiration would be expected from the sedimenting phytoplankton and associated bacterial community. In bottom waters of the mesohaline Chesapeake Bay region, annual max-ima for both phytoplankton biomass and dissolved oxygen depletion tend to occur in late April through May (Malone et al. 1988, Kemp et al. 1992). The period of relatively low plankton respiration rates measured in May (Fig. 2) coincided with rapidly declining chloro-phyll a concentrations in bottom water (Malone et al. 1988). Sinking and accumulation of spring diatom blooms has been reported to coincide with maximal respiration rates below the euphotic zone in other coastal environments (Kuparinen 1987). Plankton res-piration rates in pycnocline waters were high in July and early August but decreased sharply in both years through the end of August (Fig. 2), following a pattern similar to that reported for phytoplankton production at this site (Malone et al. 1988, 1991). Thus, it appears that seasonal variations in plankton respiration rates in aphotic waters tend to follow variations in algal bio-mass in spring and rates of production in summer, suggesting the importance of organic substrate avail-ability.

On a shorter time scale, diel periodicity of plankton respiration in surface waters exhibited a characteristic pattern in both May and August with peak rates after mid-day, decreasing to a nighttime minimum (Fig. 3). Although the diel cycle is pronounced for August, plankton respiration did not significantly decrease over the course of the night in May, suggesting the absence of substrate limitation in spring compared to summer This tight coupling of plankton respiration to the daily pattern of primary production (especially in August) is consistent with diel cycles of plankton
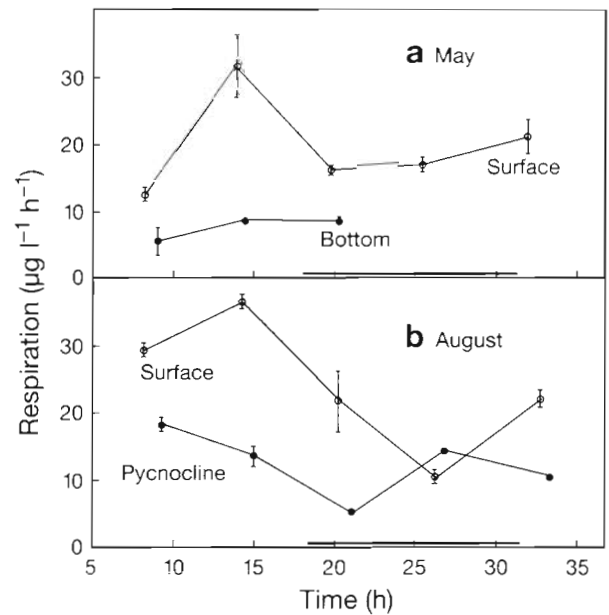

Fig. 3. Diel patterns of whole water respiration on (a) May 11 and (b) August 20, 1987. Error bars are ± 1 SE. Nighttime indicated by dark horizontal bar

processes observed for a variety of aquatic systems, where mid-day peaks and nighttime minima have been reported for algal DOC release and bacterial activity (Hagström & Larsson 1984, Fuhrman et al. 1985, Herndl & Malačič 1987, Wheeler et al. 1989) and for plankton respiration (Kamp-Nielsen 1981, Mark-ager & Sand-Jensen 1989, Szyper et al. 1992).

Diel cycles in plankton respiration were not appar-ent for either bottom or pycnocline waters (Fig. 3). Res-piration of an aphotic plankton community, physically separated from the euphotic zone by a strong pycno-cline, would not be expected to exhibit 24 h periodicity associated with photosynthesis. While tidal variations associated with advective transport of plankton com-munities in relation to our anchored vessel may have obscured actual diel cycles, other investigators have also noted the absence of patterns in plankton processes for sub-pycnocline layers underlying surface waters with strong diel cycles (Herndl & Malačič 1987). Respiration rates for an aphotic plankton community (at or below the pycnocline) would be dependent largely on sinking of particulate organic matter pro-duced in the overlying surface waters. In Chesapeake Bay, the summertime plankton community is domi-nated by smaller algal cells with slow sinking rates (Sellner 1987). In principle, respiration of a plankton community situated below the euphotic zone would exhibit a temporal dependence on organic production in overlying waters, with a time-lag between the 2 processes. If particle sinking rates are slow enough, however, much of the production would be consumed

in the euphotic zone prior to transit into the pycnocline layer, greatly reducing the apparent diel cycle.

The range of respiration rates over a diel cycle was large compared to that observed seasonally. The diel range (20 µg l^{-1} h^{-1}), observed for upper layer respiration in August, was roughly equivalent to the seasonal change in rates observed between March and May or between May and August. These large diel swings in respiration illustrated the importance of consistently sampling at the same time of day to elucidate seasonal trends; rates from mid-morning incubations (08:00 to 10:00 h, our routine protocol) were representative of diel means (Fig. 3). Peak afternoon rates were very similar for the 2 dates even though temperature and phytoplankton biomass were different (18 and 25 °C, 11 and 5 µg chlorophyll a l^{-1}, for May and August respectively). Evidently, the relatively high respiration observed in mid afternoon (Fig. 3) corresponds to peak DOC release by phytoplankton exudation (Malone et al. 1991).

Size fractionation

The relative contribution of respiration rates associated with picoplankton compared to total respiration was examined by segregating rates into 4 distinct groups: surface water, spring; surface water, summer; bottom water, spring; pycnocline water, summer. In these partitioned data, the <3 µm size-fractionated rates were significantly related to whole water rates (Fig. 4). Regressions were forced through the origin, so that slopes represent the fraction of total respiration attributable to picoplankton. No statistical differences were observed between the slopes of the spring and summer surface water relations; therefore the data sets were combined. Picoplankton accounted for virtually all of the oxygen consumption during July and August in the pycnocline (average = 89%). The <3 µm size fraction accounted for only 23% of the total respiration rate in the bottom waters of spring and autumn, in marked contrast to their dominance of summer respiration rates. Overall, picoplankton contributed 56% of the total respiration rate in surface waters.

Size fractionation in this study distinguishes between the respiration of free-living picoplankton (e.g. bacteria, protozoa, small phytoplankters) and that of larger organisms plus particle-attached bacteria. Under most circumstances, free-living cells dominate total bacterial production in the mesohaline Bay (Ducklow 1982). The relative contributions of free versus attached bacteria to plankton community respiration, however, will depend in part on the concentration of suspended particles, with attached organisms being more important in particle-rich environments (Goulder
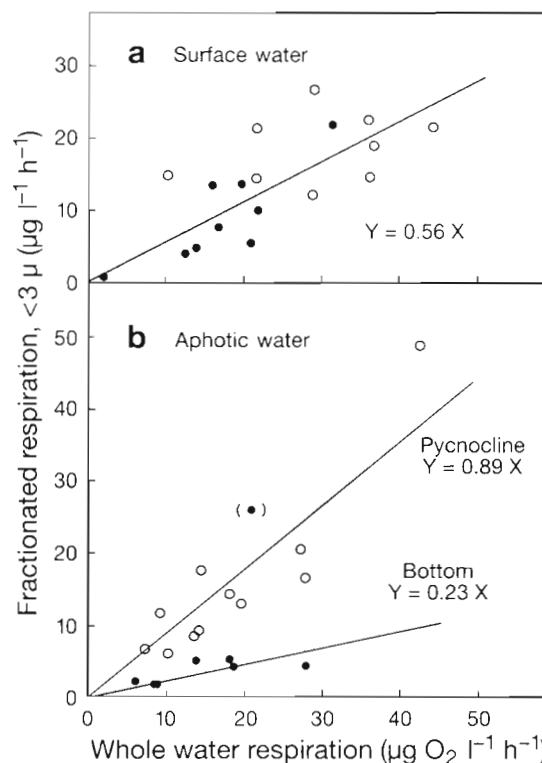

Fig. 4. Size-fractionated (<3 µm) respiration rates plotted against concurrent measurements of whole water rates for (a) surface water and (b) aphotic waters (bottom and pycnocline) (spring and fall data, ●; summer data, ○). Regressions were forced through zero, so that the slope represents the percentage of respiration accounted for by the <3 µm size fraction. Data point in parentheses was left out of the spring bottom water regression

1977, Hanson & Wiebe 1977, Harvey & Young 1980, all cited from Wangersky 1984; Kirchman & Mitchell 1982, Palumbo et al. 1984, Griffith et al. 1990). Because pre-incubation filtration techniques can result in removal of protozoan grazers from bacterioplankton assemblages, respiration can exceed those in unfiltered whole-water samples (Hopkinson et al. 1989). In the present study, 3 µm filtered rates were rarely significantly greater than those of whole water (Fig. 4).

One would predict changes in the relative importance of these 2 functional groups in an environment which experiences gross seasonal changes in the particle field. Chesapeake Bay is a relatively shallow turbid estuary, with phytoplankton communities characterized by large diatom cells in spring followed by nano- and picoplankton dominance during summer (Malone et al. 1986, 1988, 1991). The relative dominance of plankton respiration by large particles in bottom waters during spring (Fig. 4) could be associated with the formation and settling of organic aggregates (Alldredge & Gotschalk 1989, Simon et al. 1990). Rapid sinking (and presumably flocculation) of particulate

material is evident in late April and is coincident with the incipient decline of the spring diatom bloom (Malone et al. 1988, Kemp & Boynton 1992). Metabolic activity would likely be focused on large cells, chains and aggregates of senescent diatoms. Indeed, the ratio of filtered (< 1.2 µm) to total labile organic material tends to be especially low in springtime subpycnocline waters (Jonas & Tuttle 1990). This is also consistent with the observation that both biomass and productivity of autotrophic picoplankton are minimal in winter and spring and maximal in summer in the mesohaline region of Chesapeake Bay (Malone et al. 1991).

Temperature effects

Temperature should have a pronounced effect on rates of metabolism in a temperate estuarine ecosystem. Variations in plankton community respiration for several coastal ecosystems have been largely explained by variations in water temperature (de Souza Lima & Williams 1978, Turner 1978, Hopkinson 1985). Although there was considerable variability in summer rates for surface layer plankton communities, significant exponential and linear relations were found between respiration rates and *in situ* water temperatures (Fig. 5). We attempted to examine the importance of temperature per se as a control on plankton community respiration by conducting temperature-manipulation experiments in spring and summer. Relations (both linear and exponential) between respiration of surface layer communities and temperature in these 2 laboratory experiments were not significantly different from each other, nor were they different from that obtained for *in situ* measurements (Fig. 5). The relationship between plankton respiration and temperature was not significant for the bottom waters, indicating greater importance of other environmental variables.

Temperature regulation of ecological processes might be expected to occur either via physiological adaptation for eurythermal organisms or through ecological selection among stenothermal organisms for changing temperature optima over the annual cycle. At the physiological level, adaptation to a predictable annual temperature cycle could be manifested by: (1) long-term selection for maximum metabolic processes at peak annual temperatures; (2) seasonal acclimatization based on changing biochemistry within the organism; or (3) temperature-independent metabolism for organisms experiencing large diel temperature cycles (e.g. Somero & Hochachka 1971) Alternatively, at the ecosystem level of organization, a seasonal succession of temperature-adapted species may occur for organisms with life-cycles substantially shorter than 1 yr, for instance coastal marine bacteria
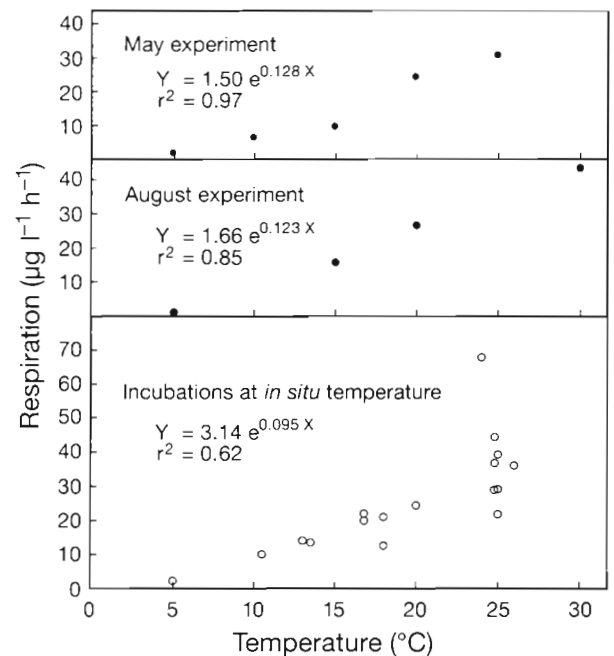

Fig. 5. Whole water surface respiration rates as a function of water temperature for temperature manipulation experiments conducted on May 13 and August 25, 1987, and seasonally varying rates at *in situ* temperatures. Exponential equations are graphed, linear regressions are as follows: May 13, $Y = 1.50X - 7.7$ ($r^2 = 0.93$); Aug 25, $Y = 1.72X - 8.3$ ($r^2 = 0.99$); and at *in situ* temperatures (excluding the July maximum rate), $Y = 1.64X - 7.6$ ($r^2 = 0.60$)

(Sieburth 1967). Several previous papers have reported evidence for seasonal temperature-selection of bacterial populations from estuarine assemblages associated with water columns (Sieburth 1967), intertidal sediments (Nedwell & Floodgate 1971) and salt marsh peat (Kaplan et al. 1977).

In contrast to these studies, our results for plankton communities in Chesapeake Bay indicate the absence of seasonal adaptation or selection by temperature. These data do, however, illustrate the strong effects of temperature in regulating plankton community respiration. Other studies have similarly reported significant temperature effects in explaining seasonal variations in rates of estuarine bacterioplankton activity, although no consideration was given to the question of adaptation or selection processes (Hagström & Larsson 1984, Malone et al. 1991, Pomeroy et al. 1991). Consistent with our findings, a recent study using seasonal temperature-manipulation experiments has, however, revealed both strong temperature effects on bacterioplankton production and the absence of significant selection for temperature optima over the course of an annual cycle in Chesapeake Bay (Shia 1993, Shia & Ducklow 1994). In that study, substrate limitation was found to override temperature effects only at high

summer temperatures (> 20°C). At minimum annual temperatures, bacterioplankton have been found to grow and respire at very low rates (Pomeroy & Deibel 1986), although large substrate amendments can greatly enhance bacterial activity at these low temperatures (Wiebe et al. 1993).

How organisms and communities adapt to changing temperatures has important ecological implications. Although algal growth rates decline in colder months, relatively active growth tends to occur in natural assemblages even at annual minimum temperature (Karentz & Smayda 1984). In this study, seasonal variations in water temperature were shown to regulate rates of plankton community respiration. As a result of this greater retardation of respiration compared to photosynthesis at lower temperatures, rates of net planktonic community production (P – R) would be higher in late winter and early spring than in summer. Indeed, in temperate estuaries, net plankton community production tends to be highest during the winter/spring period (Smith 1992, Oviatt et al. 1993). During this period a higher percentage of primary production could be finding its way into metazoan consumers, thus enhancing the biomass yield of larger organisms (Pomeroy & Deibel 1986, Wiebe et al. 1993).

The strong response of planktonic community respiration to seasonal variations in water temperature combined with the apparent absence of temperature-selection/adaptation observed for this Chesapeake Bay community suggests that simple models would be effective for simulating this important ecological process. Various investigators have included exponential temperature control functions for simulating respiration of planktonic organisms in numerical models of estuarine ecosystems (e.g. Kremer & Nixon 1978, Bartleson & Kemp 1991). Although other investigators have suggested the importance of seasonal temperature selection for microbial metabolic processes (Sieburth 1967), complex models for representing these processes may not be warranted for eutrophic temperate estuaries such as Chesapeake Bay. Results of this study should be useful for developing and calibrating simple numerical models to describe and analyze seasonal and diel cycles of plankton community respiration in Chesapeake Bay.

Dissolved oxygen

The mesohaline region of Chesapeake Bay experiences anoxic and hypoxic conditions in waters below the pycnocline each year between late May and early September (Taft et al. 1980, Officer et al. 1984, Kemp et al. 1992). Seasonal oxygen budgets for this region have shown plankton community respiration

to be the largest sink regulating oxygen dynamics in bottom waters during this period (Kemp et al. 1992). No previous study has, however, considered possible direct or indirect effects of oxygen concentration on plankton respiration. Laboratory oxygen manipulation experiments (Fig. 6) revealed that respiration rates of bacterioplankton (< 1 μm filtrate) were unaffected by dissolved oxygen concentrations down to 0.16 mg l^{-1} in June and August, remaining virtually constant over the range of 0.2 to 2.0 mg l^{-1}. In contrast, respiration rates for unfiltered water exhibited significant oxygen dependency at concentrations below 0.8 mg l^{-1} in both experiments (Fig. 6). In the June experiment, respiration rates for larger organisms and particles (whole minus filtered rates) fell from 13 μg l^{-1} h^{-1} to 3.5 μg l^{-1} h^{-1} as oxygen concentration declined to 0.2 mg l^{-1}. Whole water rates were equal to filtered rates at 0.5 mg l^{-1} in August. The observation that whole water respiration was only 80% of the filtered rate at 0.2 mg l^{-1} is enigmatic. While there is surprisingly little information dealing with oxygen effects on respiration for natural plankton communities, our results are similar to those reported in a much earlier paper (Zobell & Stadler 1940). In that study, no oxygen effects on respiration by lake bacteria were found at concentrations as low as 0.3 mg l^{-1}; however, oxygen concentrations below 1 to 2 mg l^{-1} did limit rates in water samples enriched with particulate matter.
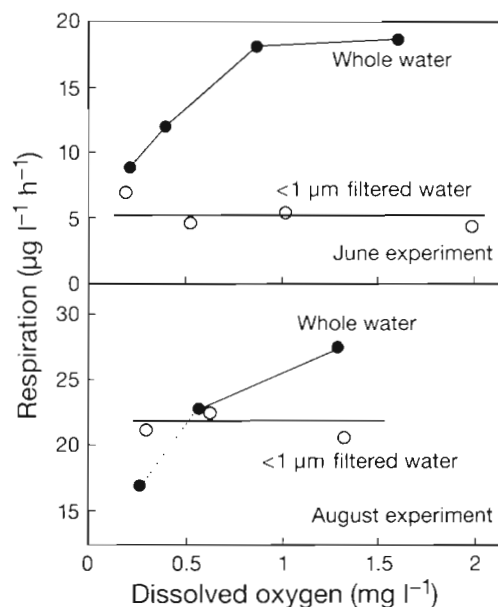

Fig. 6. Plankton respiration rates versus dissolved oxygen concentrations for (a) bottom water collected in June and (b) pycnocline water collected in August (b). Water collected on both dates had a dissolved oxygen concentration of approximately 1 mg l^{-1}

The absence of oxygen dependency for respiration of free-living bacteria even at low oxygen concentrations indicates no diffusion limitation for these organisms. Previous studies have shown that when bulk water substrate concentrations are above kinetic half-saturation values, molecular diffusion is sufficient to mitigate any local substrate limitation for small, micron-sized cells in water (Pasciak & Gavis 1974, Williams 1978, Morris 1984). Although 0.2 mg l^{-1} was the lowest concentration that we could control dependably in these studies, this is only slightly higher than biochemical half-saturation coefficients for mitochondrial oxygen consumption which have been reported in the literature. Hence, we would expect no oxygen limitations for respiration of bacterioplankton during the late spring period of incipient hypoxia in the mesohaline region of the Bay.

The significant decreases in whole water respiration rates below oxygen concentrations of 0.8 mg l^{-1} in both June and August (Fig. 6) is likely due to oxygen consumption by modest- to large-sized (3 to 30 μm) organic aggregates composed of senescent algal cells and decomposing fecal material. Such organic aggregates might be characterized by internal regions of low oxygen concentrations, maintained by metabolism of attached bacteria, and by relatively long pathways of molecular diffusion from the bulk external water to the low-oxygen micro-sites (e.g. Paerl 1984, Shanks & Reeder 1993). Organic aggregates composed of diatom cells have been shown to be highly active sites of bacterial metabolism (Simon et al. 1990), and such diatom flocs might be expected to be abundant in late June following the decline in the spring bloom at our site (Malone et al. 1988). As dissolved oxygen concentrations approach zero in the bottom waters of mesohaline Chesapeake Bay in early June, the diffusive flux of oxygen into metabolically active particles would decrease. This would increase the volume within aggregates which are anoxic. Bacteria within these anoxic microhabitats would be forced to rely on fermentation or alternate terminal electron acceptors to meet their catabolic needs and could result in high rates of denitrification using the nitrate still available in bottom water (Paerl 1984, Kemp et al. 1992). Particle active metabolism (which dominates spring bottom-water oxygen consumption) would be inhibited as the system approaches anoxia. This negative feedback mechanism would impede the absolute rate of plankton metabolism. The relative importance of bacterioplankton respiration pushing the system to anoxia would increase.

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