Limnol. Oceanogr., 46(6), 2001, 1298–1308
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Coulometric carbon-based respiration rates and estimates of bacterioplankton growth efficiencies in Massachusetts Bay

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Abstract

Heterotrophic bacterioplankton production rates have been measured in many aquatic ecosystems over the last two decades, whereas measurements of bacterioplankton respiration rates have been scarce. This paper reports and discusses measurements of carbon-based plankton respiration rates made in a coastal ecosystem over an annual cycle. The coulometric technique was used to measure total inorganic carbon (TCO_2) production rates in 0.8-μm filtered and unfiltered Massachusetts Bay surface seawater. Bacterioplankton respiration rates, defined as respiration in 0.8-μm filtered seawater, varied from 0.01 to 0.15 μmol C kg^{-1} h^{-1} (0.07 $\pm$ 0.01 μmol C kg^{-1} h^{-1}) (mean $\pm$ 1 SE) and accounted for a high proportion (median 70%) of respiration in unfiltered seawater. Microplankton (unfiltered seawater) respiration rates varied from 0.04 to 0.24 μmol C kg^{-1} h^{-1} (0.12 $\pm$ 0.02 μmol C kg^{-1} h^{-1}). Bacterioplankton growth efficiencies (BGEs), estimated with concurrent measurements of bacterial production and respiration rates, varied from 0 to 69% (median 22%) and were well correlated with specific production rates (r^2 = 0.67). To assess carbon flow in aquatic ecosystems, BGEs should be measured when possible because of their high variability. Compared with bacterioplankton specific production rates, bacterioplankton specific respiration rates were relatively constant (0.05 $\pm$ 0.01 fmol CO_2 $cell^{-1}$ h^{-1}). Given the apparent uncertainty in the values of respiratory quotients (Toolan 1996; Robinson and Williams 1999), carbon-based comparisons of microbial respiration and primary production rates will improve evaluations of the role of the coastal ocean in the global carbon cycle.

Relative to the plentiful literature on microbial productivity (growth rates of autotrophs and heterotrophs), respiratory activity in marine ecosystems has been understudied (Williams 1984; Biddanda et al. 1994; Jahnke and Craven 1995). Measurement of respiration rates in seawater has challenged oceanographers for decades because of the high precision required to measure small changes of 0.01–1 μmol kg^{-1} h^{-1} in O_2 or total inorganic carbon (TCO_2) relative to the naturally high background concentrations of O_2 (~200 μmol O_2 kg^{-1}) and TCO_2 (~2,000 μmol C kg^{-1}). Advances in endpoint detection and automation have increased the precision of the Winkler titration and made O_2 utilization rates in seawater measurable (Pomeroy et al. 1994 and references therein). It is now possible to estimate carbon-based respiration rates with the highly precise coulometric technique, wherein a seawater sample is acidified, and evolved CO_2 reacts with ethanolamine to form hydroxyethylcarbamic acid; the number of moles of OH^- that are generated to titrate the acid is related by the Faraday constant to the product of current and time and the number of moles of CO_2 in the seawater sample (Johnson et al. 1993). The precision ($\pm$1 μmol C kg^{-1}) of the coulometric technique makes measurement of respiratory CO_2 production in seawater possible, even at north temperate latitudes in winter when respiration rates are low.

Bacterioplankton growth efficiencies (BGEs) represent the efficiencies with which heterotrophic planktonic bacteria convert organic carbon into bacterial cellular carbon. Heterotrophic microorganisms, of which bacteria make up the greatest component, are the only biological populations capable of significantly depleting the large pool of dissolved nonliving organic matter in aquatic ecosystems. An examination of 54 studies (30 marine and 24 freshwater) of primary and bacterial production in the photic zone showed bacterial production averaging 20% of primary production (Cole et al. 1988). However, uncertainties in BGEs have confounded attempts to determine the amount of carbon necessary to support such high levels of bacterial production. In order to quantify carbon flow through bacterioplankton, understand water column oxygen budgets, and estimate yield at higher trophic levels, a clear understanding of the degree of variability in BGEs is crucial.

BGEs ranging from <5% to 69% have been reported for marine ecosystems using a variety of methodological approaches (del Giorgio and Cole 1998 and references therein). To calculate BGEs, rates of two out of three processes are needed: production (P), respiration (R), and/or dissolved organic carbon depletion (Dd), where BGE = P/(P + R), = P/Dd, or = 1 − (R/Dd). To convert O_2 utilization rates into units of carbon for bacterioplankton growth efficiency calculation, respiratory quotients (RQ = CO_2 produced/O_2 utilized) from 0.85 to 1 have been applied, but lower respiratory quotients have been measured (Toolan 1996). Measurements of dissolved organic carbon (DOC) depletion have been problematic given the many sources and sinks for

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Acknowledgments

I thank Jim McCarthy, Ralph Mitchell, and Catherine Goyet for critical comments on the work. Financial support was granted by the NASA Global Change Fellowship Program and MIT Sea Grant. Mike Connor, Mike Mickelson, the MWRA, and Battelle Ocean Sciences provided ship time, access to the data set of the Massachusetts Bay baseline monitoring program, and deckboard assistance. Catherine Goyet and DOE provided the SOMMA systems used in the TCO_2 analyses. I thank Tim Ford for use of his epifluorescence microscope, Eugene Tan for lab assistance, and Stephen Anderson for support in all areas of the work. I thank John Wehr, Associate Editor Jonathan Cole and two reviewers, Hugh Ducklow and André C. P. Cimbleris, for their valuable comments.

DOC and the controversy that has surrounded the measurement of DOC concentrations in seawater (reviewed in Williams 1992). Is the range in reported BGEs real or is it partially spurious, resulting from methodological issues (e.g., acidification of the sample to lower TCO_2 and make TCO_2 production more easily measurable, particulate organic carbon (POC)–DOC flux masking DOC depletion, or uncertainty in RQ values)?

In their review of BGEs in aquatic ecosystems, del Giorgio and Cole (1998) found very similar average values for BGEs based on long-term experiments (28%) and short-term metabolic measurements (26%). Carlson et al. (1999) estimated that BGEs varied more than fourfold, 9 to 38%, in a study in the Ross Sea, Antarctica, using coulometric respiration rate measurements, DOC depletion rates, and bacterial carbon production. Based on these investigations, it appears that the variability in BGEs is real and not based on methodological differences. Further concurrent rate measurements that include the carbon-based respiration rate will help narrow uncertainties in BGE values.

In the present study, BGEs were estimated in Massachusetts Bay by measuring bacterioplankton respiration and production rates with 0.8-μm filtered seawater incubated in the dark. The coulometric respiration measurement is carbon based and deemed preferable to oxygen-based respiration measurements because organic carbon is the energy source for heterotrophic aerobes. In addition, carbon-based respiration rates would be more useful in aquatic environments where anaerobic heterotrophs play a role. Carbon-based respiration rates can be compared with inorganic carbon fixation rates by primary producers without applying a respiratory quotient. RQs, often assumed to be 1, have been estimated as <0.5 (Toolan 1996) and $\sim$0.4 to 5 (mean = 0.60) with concurrent measurements of TCO_2 production and O_2 utilization (Robinson and Williams 1999) and merit further research. The present study investigates the variability in BGEs by using the same methodology (coulometric respiration measurement and production rate measurement) over an annual cycle for a northern, temperate, coastal ecosystem.

The contribution of the coastal ocean to the global carbon cycle and the extent to which it is a net source or sink of CO_2 depends on many terms and on the time scale examined. In terms of primary production and respiration, Smith and Hollibaugh (1993) considered estimating differences between rates of primary production and respiration and the change of that difference over time to be the most appropriate measure of the role of oceanic metabolism in the global carbon budget. Smith and Hollibaugh (1993) have argued that, on average, the coastal ocean is net heterotrophic, with planktonic plus benthic respiration exceeding production, and that the coastal ocean is a source of atmospheric CO_2. The coulometric technique for measuring respiration rates will allow carbon-based comparisons of respiration and net primary production and will lead to better estimates of the role of the coastal ocean in the global carbon cycle.

Materials and methods

Study site and design—The study was conducted in Massachusetts Bay in conjunction with the Massachusetts Water Resources Authority (MWRA) baseline monitoring program, which quantified baseline water column and sediment conditions in Massachusetts and Cape Cod Bays prior to the diversion of sewage effluent discharge from Boston Harbor to Massachusetts Bay (Giblin et al. 1995; Libby et al. 2000). The baseline monitoring included continuous vertical profiles from surface to bottom of hydrographic measurements (salinity, temperature, dissolved oxygen, fluorescence) at 21 stations throughout the Bay. Discrete water samples were simultaneously collected with Go-Flo® bottles for measurement of many parameters, including dissolved oxygen, dissolved inorganic nitrogen, dissolved inorganic phosphorus, total suspended solids, and chlorophyll *a* (Chl *a*) concentrations. Planktonic primary productivity measurements were made at several stations on a subset of the surveys.

Massachusetts Bay, a north temperate bay in the southwestern region of the Gulf of Maine, is bounded on the west by Boston Harbor, a shallow embayment with small freshwater input of 41 $m^3 s^{-1}$ (Signell and Butman 1992). The mean depth of Massachusetts Bay is 32 m (Kelly and Doering 1995). Surface seawater temperatures vary from $\sim$2 to 20°C, and salinity usually varies from $\sim$30.5 to 32.5, measured on the practical salinity scale (Kelly and Turner 1995).

Surface seawater was collected at stations N07 (42°21.38′N, 70°42.37′W) and N16P (42°23.64′N, 70°45.20′W), with depths of $\sim$52 and $\sim$40 m, respectively (Albro et al. 1993), the exact depth depending on sampling time (average tidal range was 2.7 m, Signell and Butman 1992). Station N07 was sampled on 9 Sep, 15 Oct, and 1 Dec 93 and on 17 Feb, 27 Apr, 22 May, 27 Jul, 8 Sep, and 1 Dec 94. Station N16 was sampled on 21 Jun, 23 Aug, and 11 Oct 94. Surface seawater was collected with Go-Flo bottles on every date except December 1993, when bucket samples were collected. Seawater was dispensed from Go-Flo bottles to 20-L polypropylene carboys via silicone tubing; the carboys and tubing had been washed in 10% HCl, rinsed with distilled water, and autoclaved.

To estimate microplankton respiration (R_{mic}), respiration in unfiltered seawater was quantified, and to estimate bacterioplankton respiration (R_{bac}) and BGEs, respiration and bacterioplankton production were measured in 0.8-μm filtered seawater. Unfiltered or 0.8-μm filtered seawater ($\sim$10 L) were incubated in acid-washed and distilled water–rinsed collapsible bags made of an opaque laminate gas-impermeable material with a low-density polyethylene inner layer (Scholle Corporation); the bags were found to have no toxic effect on microbial activity (Toolan 1996). There were two replicate bags per treatment, except for the October 1993 unfiltered seawater treatment, which had three. Setting up the experiments took approximately 5 h, and the first time point was typically 10 h later. The initial time point was not used to calculate the respiration rates for either treatment in October 1993 because it was 2 h, rather than the typical 10 h, after the bags were set up. Collected seawater was vacuum filtered with 0.8-μm Nuclepore filters except in October 1993, when a peristaltic pump was used and in September and October 1993, when seawater was filtered with GF/C filters on top of 0.8-μm Nuclepore filters to minimize filtration time.

Over the course of the study, surface seawater tempera-

tures ranged from 2 to 20°C. Most experiments were conducted at temperatures that were elevated and increasing slightly during the course of the incubation, reaching a temperature of 2.9°C, on average, above in situ conditions, probably as a result of heat transfer from the magnetic stirrers' electric motors. In examining the effect of temperature on respiration rate, to compensate for enhancement due to temperature elevation, actual measured rates were adjusted downward with the assumption of $Q_{10} = 2$ (Toolan 1996).

Respiration rate—To measure CO_2 produced via respiration, total dissolved inorganic carbon (TCO_2) was measured because CO_2^* is in equilibrium with HCO_3^- and CO_3^{-2}. TCO_2 (μmol kg^{-1}) is defined as the sum of the carbonate species in seawater: $TCO_2 = [CO_2^*] + [HCO_3^-] + [CO_3^{-2}]$ (Goyet and Brewer 1993). Replicate TCO_2 samples were collected from each bag at time points throughout the incubation. TCO_2 in seawater was measured with the coulometric technique (Johnson et al. 1993). The density of seawater was calculated using temperature and salinity according to the International one-atmosphere equation of state of seawater (Millero and Poisson 1981). For the experiments discussed here and in Toolan (1996), the precision for the TCO_2 analysis was ± 0.8 μmol C kg^{-1}. Details regarding sample collection and the coulometric measurements can be found in Toolan (1996).

Bacterioplankton abundances and production rates—Abundances at the initial time points used in the rate calculations were determined in both unfiltered and 0.8-μm filtered samples; the mean bacterioplankton abundance (± 1 SD) was $1.1 \times 10^9 \pm 0.5 \times 10^9$ cells kg^{-1} in the unfiltered treatment compared with $1.2 \times 10^9 \pm 0.6 \times 10^9$ cells kg^{-1} in the 0.8-μm filtered treatment. There was no significant difference between the two treatments (paired *t*-test; $P = 0.26$). The comparison of respiration in unfiltered and filtered samples should not be affected by differences in bacterioplankton abundances between the two treatments.

Bacterioplankton production was estimated by measuring changes in bacterial abundance over time in 0.8-μm filtered seawater. These bacterial production rates may be conservative estimates because removal of bacterial cells can occur by filtration itself, by viral lysis, and by grazers that manage to get through the filters. For production rates (the slope of cells kg^{-1} versus time), the cells were enumerated by the acridine orange direct count (AODC) method (Hobbie et al. 1977). Replicate samples for AODC were collected and preserved with formaldehyde at a minimum of three time points, except in August which had two time points. Sample volumes were adjusted to obtain 30 to 50 cells per field, and at least 10 fields per filter were counted or a minimum of 300 cells. The standard deviation was calculated for replicate samples collected from each bag at each time point (130 samples), and the precision of $\pm 1.4 \times 10^8$ cells kg^{-1} was the mean of the standard deviations. The mean coefficient of variation was 6%. To calculate BGE, production (as cells kg^{-1} h^{-1}) was converted (to μmol C kg^{-1} h^{-1}) using a factor of 15 fg C cell^{-1} (Ducklow and Carlson 1992).

Other variables—In situ temperatures, in situ Chl *a* concentrations, and ^{14}C primary production rates were determined as part of the MWRA baseline monitoring program (Albro et al. 1993, MWRA Environmental Monitoring and Mapping System, Boston, Massachusetts [MWRA EM&MS]). Measurements of in situ fluorescence were converted to concentrations of Chl *a* by calibration with Chl *a* determinations on discrete water samples collected with Go-Flo bottles (Albro et al. 1993). No photoinhibition for the surface seawater incubations was demonstrated, so primary production estimates were based on photosynthesis versus irradiance curves, where $P_B = P_{max}[1 - e^{(-\alpha I/P_{max})}]$. P_B is primary production normalized to chlorophyll concentration, P_{max} is the light-saturated maximal productivity, and α is the initial slope for the curve where productivity is proportional to light intensity (I). P_B values were multiplied by mean surface seawater Chl *a* concentrations to obtain primary production (PP) estimates (Kelly and Doering 1995). Kelly and Doering (1995) reported depth-integrated primary production values. The values in the Results section were calculated from P_{max} and α values (MWRA EM&MS) for surface seawater only. To calculate P_B for surface water, surface water irradiance values were obtained from the MWRA database (MWRA EM&MS).

Data analysis—Respiration and production rates were calculated using linear regression and pooled data from replicate bags. For respiration rate calculations, the mean of the TCO_2 concentrations measured for the initial time point was subtracted from the TCO_2 values at each time point. Production rates were based on the same time points used in the respiration rate calculations. The last time point was usually eliminated because longer incubations tended to change the rates, perhaps because of grazers, which can sometimes pass through filters, nutrient limitation, or changes in the community from the bacterioplankton community collected (Pomeroy et al. 1994). Three time points were used in the regression analyses for respiration with the following exceptions: For both R_{mic} and R_{bac}, four time points were used for June 1994 and two time points were used for August 1994. For R_{mic} in September 1993, two time points were used. The respiration rate for the 0.8-μm filtered treatment for May was included in the calculations of medians in Table 1, but it was excluded from the mean and standard error calculations and from the discussion of variability in respiration and in derived variables because it far exceeded the respiration rate in unfiltered seawater, unlike the results for the other 10 months.

Bacterioplankton abundances at the midpoints of the incubation times (B_m) were calculated as $B_m = B_i + P(T_f - T_i)/2$, where B_i is bacterioplankton abundance at the initial time point, P is the production rate, and T_f and T_i are the final and initial time points used in the rate calculations. BGEs in 0.8-μm filtered seawater were calculated by BGE $= P/(P + R)$, where P is production rate and R is respiration rate (both μmol C kg^{-1} h^{-1}). The standard error (SE) in the growth efficiency was calculated as $SE_{BGE} = (P + R)^{-2}\sqrt{(R^2 \cdot SE_P^2 + P^2 \cdot SE_R^2)}$, where SE_P and SE_R are the standard errors of the production and respiration rates, respectively. In the correlation analyses that examined concurrently

Table 1. Microplankton and bacterioplankton respiration rates (μmol C kg^{-1} h^{-1}). Rates significantly different from 0 ($P < 0.01$), except for Oct 93 bacterioplankton rate. R_{bac} and R_{mic} refer to bacterioplankton and microplankton respiration, SE is the standard error of the slope, and no data is denoted by nd.

Sampling time	Final time point (h)	Microplankton respiration rate			Bacterioplankton respiration rate			R_{bac}/R_{mic} (%)
		Slope	SE	r^2	Slope	SE	r^2	
Sep 93	16.8	0.24	0.02	0.96	0.15	0.02	0.82	63
Oct 93	23.7	0.09	0.03	0.40	0.01	0.04	0.01	11
Dec 93	90.8	0.13	0.02	0.76	nd	nd	nd	nd
Feb 94	178.3	0.04	0.003	0.95	0.03	0.003	0.90	75
Apr 94	39.0	0.10	0.01	0.86	0.07	0.01	0.82	70
May 94	31.5	0.14	0.01	0.98	1.26	0.10	0.94	900
Jun 94	25.1	0.11	0.01	0.88	0.07	0.02	0.54	64
Jul 94	13.4	0.19	0.02	0.90	0.11	0.02	0.76	58
Aug 94	23.5	0.12	0.02	0.90	0.08	0.01	0.88	67
Sep 94	16.5	0.10	0.02	0.66	0.07	0.01	0.75	70
Oct 94	22.2	0.14	0.01	0.94	0.11	0.01	0.94	79
Dec 94	30.0	0.05	0.01	0.68	0.04	0.01	0.60	80
Median	24.4	0.12	0.02	0.89	0.07	0.01	0.82	70

measured variables, Kendall's test of rank correlation, a nonparametric statistic, was used because sample sizes were not sufficient to determine whether the distributions of variables were normal (Data Description). Geometric mean Model II linear regression was used to analyze the relationships between BGE and both bacterioplankton specific production rate and bacterioplankton production rate (Ricker 1973).

Results

Respiration rates—The data from a representative experiment show that TCO_2 increased linearly with time in both unfiltered and 0.8-μm filtered seawater (Fig. 1). In April 1994, the microplankton respiration rate ($\pm$1 SE) was 0.10 $\pm$ 0.01 μmol C kg^{-1} h^{-1} compared with a bacterioplankton respiration rate of 0.07 $\pm$ 0.01 μmol C kg^{-1} h^{-1} (Fig. 1; Table 1).

Microplankton respiration rates, R_{mic}, in unfiltered Massachusetts Bay seawater varied sixfold, from 0.04 to 0.24 μmol C kg^{-1} h^{-1}, with both a median and mean of 0.12 $\pm$ 0.02 μmol C kg^{-1} h^{-1} (n = 12; Table 1). Rates were highest in September 1993 (0.24 μmol C kg^{-1} h^{-1}) and lowest in February 1994 (0.04 μmol C kg^{-1} h^{-1}). All R_{mic} values were significantly different from 0 ($P < 0.01$; Table 1) and were based on the same time points used to calculate bacterioplankton respiration and production rates.

Bacterial respiration rates, R_{bac}, varied 15-fold, from 0.01 to 0.15 μmol C kg^{-1} h^{-1} (Table 1) with a mean of 0.07 $\pm$ 0.01 μmol C kg^{-1} h^{-1} (n = 10; excludes May, which is discussed below). The median bacterial respiration rate was the same as the mean, 0.07 μmol C kg^{-1} h^{-1} (n = 11; Table 1). The lowest bacterioplankton respiration rates (0.01–0.04 μmol C kg^{-1} h^{-1}) were measured in October 1993 and February and December 1994 (Table 1). R_{bac} was significantly different from 0 in 10 of 11 cases (Table 1).

R_{bac} for May 1994 far exceeded the respiration rates measured in all other months in unfiltered or 0.8-μm filtered seawater (Table 1). The respiration rate (based on 0 through 31.5 h) was 1.26 $\pm$ 0.10 μmol C kg^{-1} h^{-1}, 18 times the mean rate for the other 10 months (0.07 μmol C kg^{-1} h^{-1}) and nine times the rate in unfiltered seawater for May (0.14 $\pm$ 0.01 μmol C kg^{-1} h^{-1}). The results for May were the opposite of the findings for all other months for which respiration rates in 0.8-μm filtered seawater were approximately two-thirds the respiration rates in unfiltered seawater. For this reason, the May respiration rate for 0.8-μm filtered seawater was excluded from the discussion of variability in respiration and in derived variables (see Methods).

Bacterioplankton respiration, defined here as respiration in the $<$0.8-μm size fraction, accounted for more than two-thirds (median = 70%; Table 1) of the respiration in unfiltered surface seawater in the study period. R_{bac}/R_{mic} varied from 11% in October 1993 to 80% in December 1994, with 90% of R_{bac}/R_{mic} in the 58–80% interval. Respiration rates were approximately equal in filtered and unfiltered seawater in February and December 1994 because the rates were uniformly low, 0.03 and 0.05 μmol C kg^{-1} h^{-1}.

Bacterioplankton production rates—Bacterioplankton abundances increased linearly with time and the increase was significantly different from 0 in 8 of 11 experiments (Table 2). Figure 1 shows the results from the April 1994 experiment, when the bacterioplankton production rate was 5.0 $\times$ 10^7 $\pm$ 0.4 $\times$ 10^7 cells kg^{-1} h^{-1} (Table 2). Bacterioplankton production rates varied from 0 to 5 $\times$ 10^7 cells kg^{-1} h^{-1} (Fig. 2), with a median of 2.3 $\times$ 10^7 cells kg^{-1} h^{-1} (Table 2). In August, September, and December 1994, bacterioplankton production rates were not significantly different from 0 (Table 2). In September and December, the production rate increased after the third time point, and in August, there were only two time points.

Specific respiration rates, specific production rates, and bacterioplankton growth efficiencies—Specific respiration rate, the respiration rate per unit cell (R/B), and specific production rate, bacterioplankton production per unit cell (P/B), were calculated using bacterioplankton abundances at initial, middle, and final time points of the incubations. Bac-

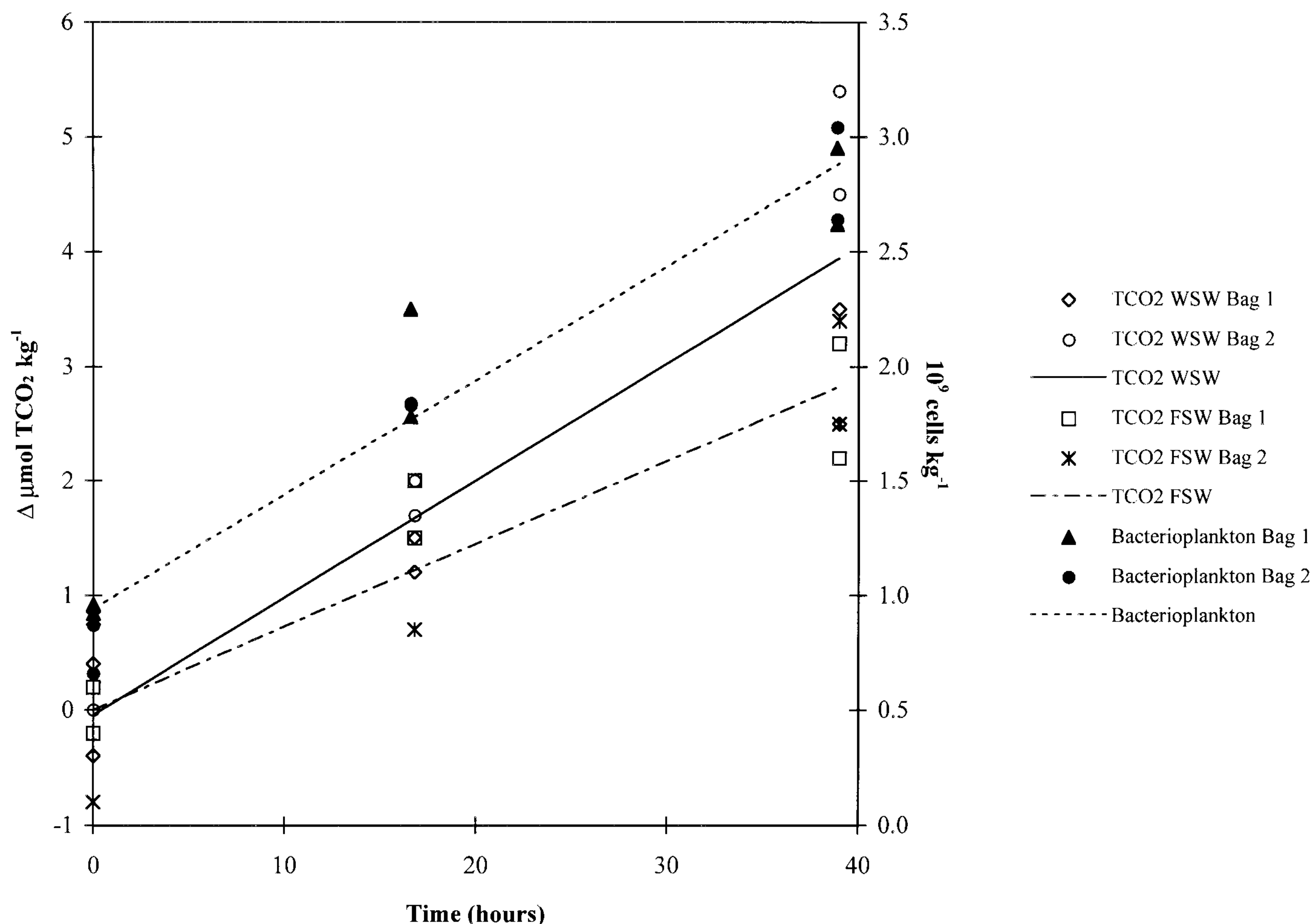

Fig. 1. TCO_2 versus time in unfiltered and 0.8-μm filtered seawater (primary axis); bacterioplankton abundance versus time in 0.8-μm filtered seawater (secondary axis). WSW denotes whole unfiltered seawater and FSW, 0.8-μm filtered seawater. Datapoints represent two replicate samples per replicate bag at each time point. Replicate values were equal for TCO_2 WSW Bag 2 at 0 h and TCO_2 FSW Bag 2 at 16.8 h and were almost equivalent (1.84×10^9 and 1.83×10^9 cells kg^{-1}) at 16.6 h for bacterioplankton Bag 2. One replicate value (0.8 Δ μmol C kg^{-1}) for TCO_2 FSW Bag 2 is obscured by other data points. Regression lines show respiration rates and bacterioplankton production rate.

Table 2. Bacterioplankton production rates (10^7 cells kg^{-1} h^{-1}). Rates significantly different from 0 ($P < 0.01$), except for Jul and Oct 94 ($P < 0.05$) and Aug, Sep, Dec 94 (not significant); SE is the standard error of the slope.

Sampling time	Final time point (h)	Production rate (10^7 cells kg^{-1} h^{-1})		
		Slope	SE	r^2
Sep 93	16.8	3.2	0.58	0.75
Oct 93	23.5	1.8	0.27	0.81
Feb 94	178.6	0.3	0.04	0.85
Apr 94	38.9	5.0	0.40	0.94
May 94	31.1	2.3	0.58	0.62
June 94	24.6	3.4	0.52	0.75
Jul 94	13.1	2.9	1.12	0.42
Aug 94	23.5	0.4	0.90	0.03
Sep 94	15.4	0.02	0.41	0.00
Oct 94	22.4	2.4	1.02	0.35
Dec 94	29.9	0.0	0.24	0.00
Median	23.5	2.3	0.52	0.62

terioplankton abundances at the middle time points of the incubations, B_m, varied from 0.6×10^9 to 2.3×10^9 cells kg^{-1}, with a median of 1.4×10^9 cells kg^{-1}. In five of 11 experiments, specific respiration rates were equal within the experiment whether calculated with B_i, B_m, or B_f (Toolan 1996). Specific respiration rates were less variable than specific production rates within experiments and over the annual cycle (Fig. 3).

Specific respiration rates (R/B_m) varied 10-fold, from 0.01 to 0.10 fmol C cell^{-1} h^{-1}, with a median of 0.05 fmol C cell^{-1} h^{-1} (Fig. 3), and specific production rates (P/B_m) varied by more than an order of magnitude, from 0 to 0.027 h^{-1}, with a median of 0.013 h^{-1} (Fig. 3). Turnover times (B_m/P) varied from 36 to >500 h (Table 3). The incubation time used in the respiration and production rate calculations was much shorter than bacterioplankton turnover times in nine of 11 experiments and was similar to bacterioplankton turnover times in two experiments: in April the final time point was 39 h and the turnover time was 36 h; in February,

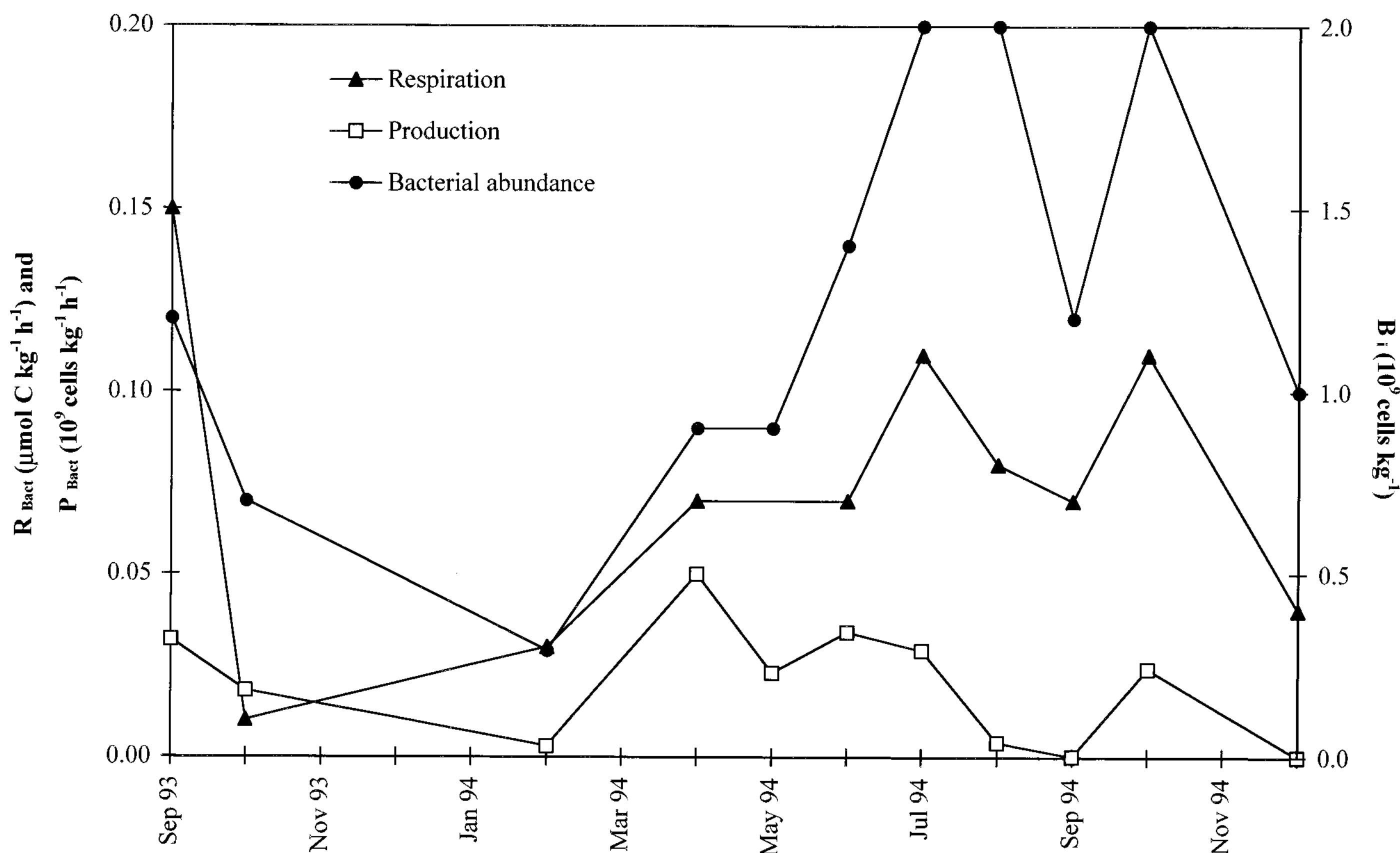

Fig. 2. Bacterioplankton abundances, respiration, and production rates.

the final time point was 179 h and the turnover time was 198 h. The incubations were designed to be shorter than the turnover times for the bacterioplankton community, minimizing both container effects and changes in species composition.

Bacterioplankton growth efficiencies in Massachusetts Bay varied from 0% in September and December 1994 to 69% in October 1993 (Table 3). Nearly all the BGEs were in the 0 to 50% interval, more than two-thirds were ≤25%, and the median BGE was 22%. If months with nonsignificant production or respiration rates are excluded, the median BGE is similar—24%. The magnitude of BGE is affected by the bacterial carbon conversion factor (CCF) employed (15 fg C $cell^{-1}$) (Ducklow and Carlson 1992); use of a higher CCF would have resulted in higher BGEs.

Correlation analyses—Higher respiration rates coincided with higher bacterial abundances in both unfiltered and 0.8-μm filtered seawater, and the correlation was significant in 0.8-μm filtered seawater ($P < 0.05$; Kendall's rank correlation coefficient $\tau = 0.634$; $n = 10$). The correlation between microplankton respiration in unfiltered seawater and bacterioplankton abundance was not significant ($\tau = 0.205$; $n = 12$), likely as a result of organisms other than bacterioplankton contributing to the respiratory signal. The correlation of the adjusted respiration rate (see Methods) and in situ temperature was significant for both microplankton and bacterioplankton respiration ($P < 0.05$; $\tau = 0.492$ for R_{mic} and $=0.614$ for R_{bac}). Respiration rates in both unfiltered seawater and 0.8-μm filtered seawater were not significantly correlated with in situ Chl *a* concentrations (0.6–5.7 μg kg^{-1}). BGEs increased with increasing specific production rates (P/B_m) (Fig. 4A), and BGE and specific production rate were well correlated ($r^2 = 0.67$; Fig. 4A). For turnover times of 36 to 95 h, BGEs were highly variable with values from 21 to 69% (Table 3; Fig. 4A). When the October 1993 data were excluded from the regression, bacterioplankton production and BGE were well correlated ($r^2 = 0.87$; Fig. 4B).

Bacterioplankton respiration rates were 11, 16, and 6% of net primary production rates in June, August, and October 1994. The primary production rate estimate for October (1.84 μmol C kg^{-1} h^{-1}) was three times higher than the primary production rates estimated in June and August (0.65 and 0.51 μmol C kg^{-1} h^{-1}), but the R_{bac} values were relatively stable (0.11, 0.12, and 0.14 μmol C kg^{-1} h^{-1} for June, August, and October, respectively).

Discussion

Comparison between TCO_2 production rates and literature values for O_2 utilization rates—If a respiratory quotient of 1 is used to compare CO_2 production estimates to O_2 utilization rates, the range in Massachusetts Bay microplankton respiration rates (0.04–0.24 μmol C kg^{-1} h^{-1}) is at the low end of the range in literature values for microplankton O_2 utilization rates measured in other coastal ecosystems

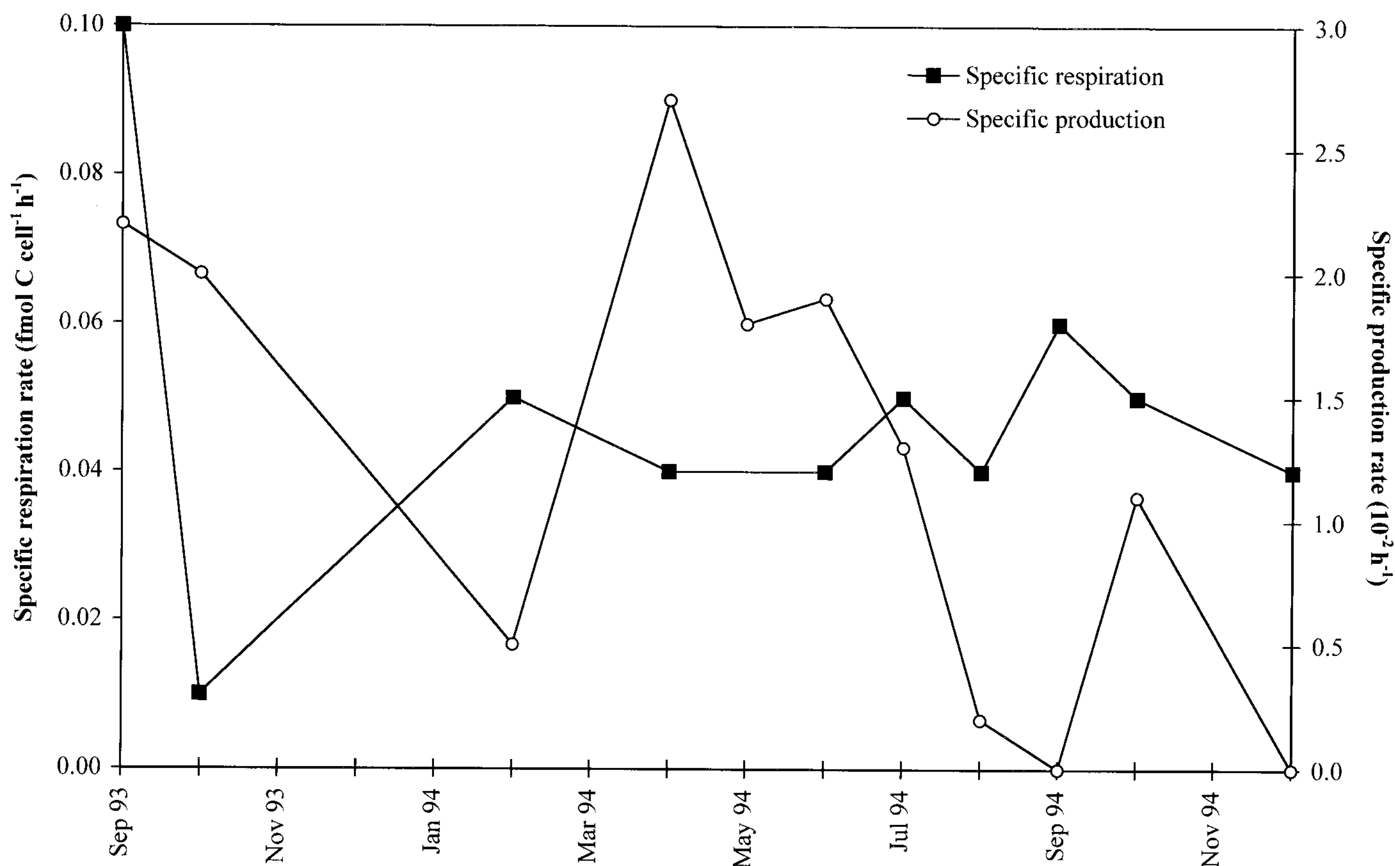

Fig. 3. Bacterioplankton specific respiration and specific production rates.

with unfiltered seawater and high-precision Winkler titrations. The mean respiration rate for Massachusetts Bay (0.12 μmol C kg^{-1} h^{-1}) was less than the mean respiration rates estimated in other coastal and shelf studies (0.19–0.42 μmol O_2 L^{-1} h^{-1}; Williams 1984 [Loch Ewe and Saanich Inlet treated separately]; Smith et al. 1986; Iriarte et al. 1991; Pomeroy et al. 1994; Pomeroy et al. 1995). The median CO_2 production rate for Massachusetts Bay (0.12 μmol C kg^{-1} h^{-1}) was closer to the medians calculated for the coastal and shelf studies cited above, which were in the range of 0.13–0.26 μmol O_2 L^{-1} h^{-1}. Despite the high mean and median literature values, 70% of the coastal and shelf rates were in the <0.03–0.31 μmol O_2 L^{-1} h^{-1} interval, which is similar to the range in Massachusetts Bay.

Table 3. Bacterioplankton growth efficiencies.

Sampling time	Turnover time* (h)	BGE (%)	SE (%)
Sep 93	45	21	4
Oct 93	49	69	81
Feb 94	198	14	2
Apr 94	36	46	4
Jun 94	52	38	7
Jul 94	76	25	8
Aug 94	>500	6	13
Sep 94	>500	0	7
Oct 94	95	22	7
Dec 94	>500	0	8
Median	86	22	7

* For turnover times >500 h, production rates were not significantly different from 0.

The Massachusetts Bay respiration rates may have been at the low end of the ranges in reported coastal O_2 utilization rates because the respiratory quotient (CO_2 produced/O_2 utilized) may have been less than 1 (Toolan 1996), because metabolic activity was lower in Massachusetts Bay, or both. The mean and median Massachusetts Bay respiration rates were lower than those reported by Iriarte et al. (1991) (0.25 and 0.16 μmol O_2 L^{-1} h^{-1}, respectively), and the temperature range was similar for both studies; however, the Chl *a* concentrations were much higher in the North Sea and English Channel (0.5–23.5 μg L^{-1}). High O_2 utilization rates were measured by Pomeroy et al. (1995) on the Florida continental shelf and in the Mississippi River plume where temperatures were much higher (9 out of 10 of the incubations with coastal seawater were at temperatures >21.3°C) than in Massachusetts Bay. Further concurrent measurements of CO_2 production and O_2 utilization rates will determine whether differences in respiration rates between ecosystems are real or result from departures from unity in RQ values (Toolan 1996).

Bacterioplankton and microplankton respiration rates—Microorganisms in the <0.8-μm size fraction accounted for

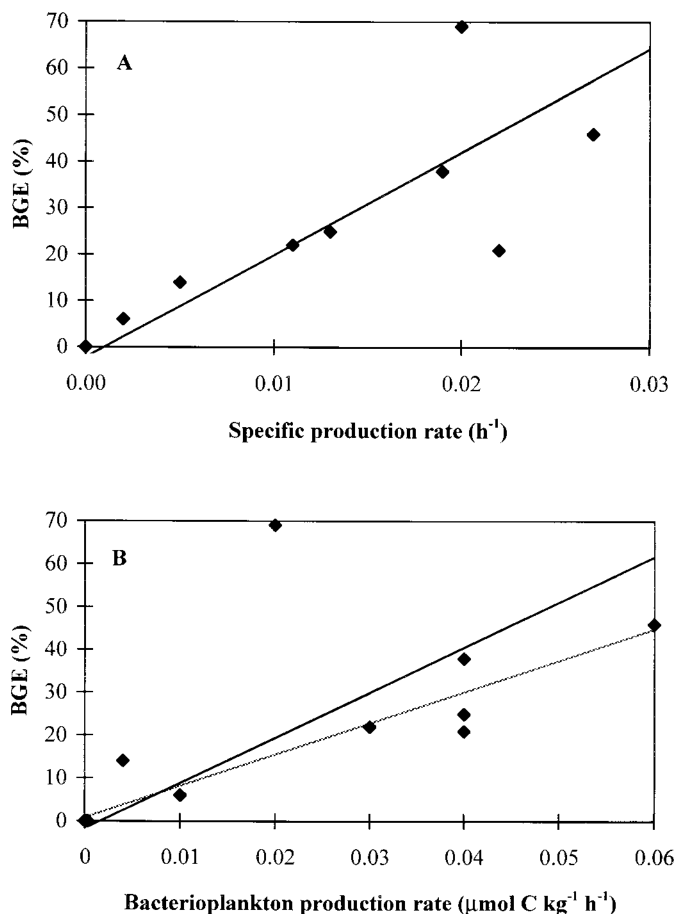

Fig. 4. (A) Bacterioplankton growth efficiencies and specific production rates P/B_m. The line represents the slope of the geometric mean Model II linear regression. The equation for the regression is $BGE = 2213.1(P/B_m) - 2.2$ ($r^2 = 0.67$). (B) Bacterioplankton growth efficiencies and production rates (P). The lines represent the slopes of the geometric mean Model II linear regressions. The equations for the regressions are $BGE = 1056.5(P) - 1.7$ (solid line; $r^2 = 0.35$) and $BGE = 732.9(P) - 0.85$ (stippled line; $r^2 = 0.87$; excludes Oct 93 data when bacterioplankton respiration rate was not significantly different from 0).

most (median = 70%) of the respiration measured in Massachusetts Bay surface seawater in this study. When size-fractionated respiration has been measured in other marine ecosystems, the smallest size fractions have contributed significantly to the respiratory signal. For example, in unfiltered coastal seawater, the <1-µm size fraction accounted for 60 and 26% (Williams 1984) and 49% (Biddanda et al. 1994) of respiration rates in unfiltered seawater. For offshore coastal stations, respiration by the <1-µm size fraction accounted for approximately 42–100% of respiration in the <200-µm size fraction (Smith et al. 1986). Respiration in the <3-µm size fraction was 70–100% (Iriarte et al. 1991) and 56% (Sampou and Kemp 1994) of respiration in unfiltered coastal and estuarine water, respectively. Iriarte et al. (1991) found that at low Chl *a* concentrations, heterotrophs in the <3-µm size fraction accounted for most of the respiration. Respiration measurements in different size fractions on the Grand Banks showed that relative to the <200-µm size fraction, 5-µm screening did not remove a substantial portion of the respiration in the <200-µm size fraction (Smith et al. 1986). Consistent with other studies, these results show that microorganisms in the smallest size fractions account for a sizable fraction of the respiration measured in seawater.

Bacterioplankton specific respiration and production rates—Specific respiration rates (R/B_m) were much more stable than specific production rates (P/B_m) in this study (Fig. 3). The mean specific production rate (± 1 SD) was 0.013 ± 0.010 h^{-1}, and the mean specific respiration rate was 0.05 ± 0.02 fmol CO_2 $cell^{-1}$ h^{-1}. Cimbleris and Kalff (1998) measured bacterioplankton respiration rates in units of carbon and oxygen and found a strong negative correlation between bacterial specific oxygen consumption rates and bacterial abundances in a study of 14 Canadian lakes during summer. This trend was confirmed with a larger data set that included bacterial abundances in the 10^6 to 10^7 cells ml^{-1} range to represent bacterial densities prevalent above 15°C (Cimbleris and Kalff 1998). For this study, there are few (five) data points for specific respiration rates at temperatures >15°C, and over the annual cycle, bacterioplankton specific respiration rates were fairly constant, with 8 of 10 values in the range of 0.04–0.06 fmol CO_2 $cell^{-1}$ h^{-1} (Fig. 3).

There have been several estimates of specific respiration made with O_2 utilization rates in coastal studies. Biddanda et al. (1994) found that the ratio of respiration rate to bacterial abundance was 0.04 fmol O_2 $cell^{-1}$ h^{-1} in concentrated seawater as compared with 0.10–0.36 fmol O_2 $cell^{-1}$ h^{-1} in 1-µm filtered seawater at a shelf station near Louisiana. If a respiratory quotient for bacterioplankton of 0.23 (Toolan 1996) is used to convert the specific respiration rates measured by Biddanda et al. (1994) into units of carbon, the rates are 0.02–0.08 fmol TCO_2 $cell^{-1}$ h^{-1} in 1-µm filtered seawater, similar to the range in specific respiration rates measured for Massachusetts Bay (0.01–0.10 fmol TCO_2 $cell^{-1}$ h^{-1}). Much higher specific respiration rates were measured in coastal seawater and coastal 5,000-L mesocosms in Denmark with a mean of 140 fmol O_2 $cell^{-1}$ (Daneri et al. 1994).

Bacterioplankton production rates and specific bacterioplankton production rates were relatively low compared with literature values. The median bacterial production rate, 2.3 × 10^7 cells kg^{-1} h^{-1}, is at the low end of the range of literature values for bacterial production estimates for coastal ecosystems (2.5–7 × 10^7 cells kg^{-1} h^{-1}) (Ducklow and Carlson 1992). Specific bacterioplankton production rates varied from 0 h^{-1} in September and December 1994 to 0.027 h^{-1} in April 1994 (Fig. 3); bacterioplankton turnover times, 36 to >500 h (Table 3), were at the high end of the range of literature values 14–133 h for coastal waters (Biddanda et al. 1994). Bacterioplankton turnover times of 22–648 h have been estimated for open ocean areas (Ducklow and Carlson 1992). Consistent with the respiration rates, the production and specific production rates also appear to be at the low end of the observed range.

Bacterioplankton growth efficiencies—The data show that BGEs were highly variable. For turnover times of 36 to 95 h, BGEs varied from 21% in September 1993 to 69% in

October 1993 (Table 3), with a median BGE of 22%. BGEs in April and June 1994 were 46 and 38%, or approximately double the estimates for September 1993 and July and October 1994 (21, 25, and 22%, respectively).

BGEs and turnover times: In this study, BGE and turnover time (B_m/P) were negatively correlated (Table 3). A negative correlation between BGE and turnover time also was found in a continuous flow culture study in Roskilde Fjord, Denmark, and off the New Zealand Coast: at turnover times longer than 66 h, the mean growth efficiency was 25%, and at turnover times less than 53 h, the mean efficiency was 36% (Middelboe et al. 1992). In a comprehensive review of BGE, del Giorgio and Cole (1998) found all possible relationships (none, positive, and negative) between bacterial growth rates and BGE and concluded that the relationship may vary with growth conditions. In Massachusetts Bay, there was a strong positive relationship between BGE and specific production rate (r^2 = 0.67; Fig. 4A). Finding lower growth efficiencies at longer turnover times is consistent with the theory that at longer turnover times, the proportion of substrate used for cellular maintenance increases (Middelboe et al. 1992).

BGEs and production rates: BGEs were positively correlated with bacterioplankton production rates (Fig. 4B). The October 1993 BGE of 69% appears to be an outlier in Fig. 4B, and the bacterioplankton respiration rate was not significantly different from 0 that month. With October 1993 excluded, the correlation between BGEs and production rate is strong (r^2 = 0.87; Fig. 4B). Using a much larger data set, del Giorgio and Cole (1998) also found a pattern of increasing BGE with increasing bacterioplankton production. In the present study, the maximum bacterioplankton production rate was much less than 5 μg C L^{-1} h^{-1}, the region where del Giorgio and Cole (1998) found BGEs reaching maximal values near 50%. If the October 1993 BGE of 69% is excluded, BGEs in Massachusetts Bay also were less than 50% and according to the model of del Giorgio and Cole (1998), the mean predicted BGE was 10% compared with 24 $\pm$ 14%, the mean and mean standard error for observed BGEs. The model of del Giorgio and Cole (1998) covers bacterioplankton production rates that are much higher than those measured in Massachusetts Bay, yet the predicted and observed BGEs agree to within one standard error.

There were not enough data to assess whether BGEs in Massachusetts Bay followed the trend of increasing BGE with increasing primary productivity discussed in del Giorgio and Cole (1998). For the data available, no trend is apparent: in June, August, and October 1994, BGEs were 38, 6, and 22%, respectively, whereas primary production rates were 0.65, 0.51, and 1.84 μmol C kg^{-1} h^{-1}, respectively.

Effect of time scale: BGEs can be highly variable, even within the time scale of a single incubation period. For example, in February 1994 when the lowest bacterial abundances in this study were observed, the BGE calculated using the first 28 h of the incubation period was 0%, compared with 14% for the first 178 h. In September 1994, bacterial abundances did not increase through 15 h, and the BGE calculated was 0%. After 15 h, bacterial abundances increased and BGE calculated using these data would be higher because the respiration rate remained relatively constant. Similarly, for a Weddell Sea study, there was no apparent change in POC for the first 4 d of a 13-d incubation, and the efficiency for this time period would be 0%, but for the full 13-d incubation, the growth efficiency was 40% (Bjornsen and Kuparinen 1991). The time scale over which BGEs are calculated can greatly affect the values computed, and ideally the incubation time should be less than the turnover time.

Respiration, production, BGEs, and other measured variables—Respiration rates and bacterioplankton production and abundances: Bacterial abundances, respiration rates, and production rates showed similar seasonal variation, with coincident trends through the annual cycle (Fig. 2). All three variables were at minima in February 1994, and bacterioplankton respiration rates and abundances were at maxima in September 1993 and July and October 1994. In Massachusetts Bay, the water column is vertically stratified from approximately April through October (Kelly and Turner 1995). Based on chlorophyll data from 1992 through 1998, Libby et al. (2000) concluded that the spring bloom in Massachusetts Bay is not as common as once thought, with large spring blooms only occurring in 1992, 1994, and 1996, whereas the fall bloom regularly develops as stratification deteriorates.

The 1993 fall bloom was the largest for the period 1992–1998 (Libby et al. 2000). The combination of plentiful phytoplankton carbon and the second highest temperature of the study, 17.2°C, likely explain why the highest respiration rates for both bacterioplankton and microplankton (Table 1) and the second highest bacterioplankton production rate (Table 2) were measured in September 1993. The large 1993 fall bloom culminated in October and was dominated by the diatom *Asterionellopsis glacialis* (Kelly and Turner 1995). Interestingly, the bacterioplankton respiration rate was only 0.01 μmol C kg^{-1} h^{-1} and the microplankton respiration rate was 0.09 μmol C kg^{-1} h^{-1} in October 1993. The lower respiration rates may be partially attributed to a much lower temperature: 11.1°C. Respiration rates had local maxima in July 1994 when the temperature was the highest of this study, 19.7°C, and in October, when the 1994 fall bloom peaked (Kelly and Turner 1995) and the temperature was 13.7°C compared with only 11.1°C in October 1993 (Fig. 2). Temperature was likely the more important factor because it was significantly correlated with both bacterioplankton and microplankton respiration, whereas Chl *a* concentrations were not.

Although the correlation between respiration rate and bacterioplankton abundance was significant in 0.8-μm filtered Massachusetts Bay seawater (Fig. 2), the literature has not shown consistent trends for coastal ecosystems in general because concurrent measurements of these two variables have been rare. del Giorgio et al. (1997) found a strong positive relationship between bacterial abundance and bacterial respiration in their analysis of a data set combining both freshwater and marine ecosystems. Cimbleris and Kalff (1998) found a positive correlation between bacterial carbon respiration rates and bacterial abundances in lakes. At a site in the Chesapeake Bay, the highest respiration rate measured over several years of study coincided with the highest bac-

terioplankton levels (Sampou and Kemp 1994). By contrast, Biddanda et al. (1994) observed similar respiration rates and very dissimilar bacterial abundances at two stations, one on the Louisiana shelf and the other on the slope. Jensen et al. (1990) found no significant correlation between bacterial biomass and respiration with a depth-integrated data set, but the depth integration might have masked some of the variability in bacterial biomass. Further studies will shed light on the relationship between bacterioplankton respiration and abundances, but in general, a positive correlation would be expected and was found in the present study.

Bacterioplankton production rates and bacterial abundances (Fig. 2) were not significantly correlated in this study ($\tau = 0.153$; $n = 11$). Ducklow and Carlson (1992) also found no significant correlation between bacterial production rate and biomass for data collected when temperatures were between 10 and 20°C for the mesohaline Chesapeake Bay; for extreme temperatures, <10°C and >20°C, the correlation was significant (Ducklow and Carlson 1992).

A weak positive correlation (0.426; $n = 11$) was found between bacterial production rate and microplankton respiration rate ($P < 0.10$), and other investigators also have found weak correlations between respiration in unfiltered seawater and bacterial production (Jensen et al. 1990; Chin-Leo and Benner 1992; Biddanda et al. 1994). There was no significant correlation (0.303; $n = 10$) between bacterioplankton production and respiration rates. Bacterioplankton respiration rates were predicted using production rates and the model II regression equation in del Giorgio and Cole (1998); the mean respiration rate obtained with the model was 0.12 μmol C kg^{-1} h^{-1} compared with the observed mean of 0.07 μmol C kg^{-1} h^{-1}. If RQ values differ from 1 (Toolan 1996), then the relationship between production and respiration will be different depending on whether respiration rates are carbon or oxygen based.

Temperature: The correlation between the adjusted microplankton respiration rate (see Methods) and in situ temperature was significant. Iriarte et al. (1991), Pomeroy et al. (1991), and Sampou and Kemp (1994) also found that temperature has a significant effect on respiration rate. Jensen et al. (1990) found no significant correlation between temperature and respiration rate for a depth-integrated data set.

There was no significant correlation between bacterioplankton growth efficiency and in situ temperature in this study ($\tau = -0.045$; $n = 10$). Other studies have found that the effect of temperature is weak or that there is no significant relationship between BGE and temperature (del Giorgio and Cole 1998 and references therein).

Chlorophyll *a* concentration: No significant correlation was observed between respiration rate in unfiltered or 0.8-μm filtered Massachusetts Bay seawater and in situ Chl *a* concentrations. Correlations between respiration rates in unfiltered seawater and Chl *a* concentrations have been found in ecosystems with Chl *a* concentrations greater than those found in Massachusetts Bay surface seawater (Jensen et al. 1990; Iriarte et al. 1991). For a study in the North Sea and English Channel, at Chl *a* concentrations from 0.46 to 5 μg L^{-1}, there was no significant correlation between respiration rate and Chl *a* concentration; at Chl *a* concentrations >5 μg L^{-1}, the correlation with respiration rate was significant (Iriarte et al. 1991). In a shallow eutrophic estuary with mean Chl *a* concentrations of at least 7 μg L^{-1}, Jensen et al. (1990) found a significant correlation between Chl *a* concentration and respiration rate. The relatively low Chl *a* concentrations found during the course of this study might explain the lack of a significant correlation between micro- and bacterioplankton respiration rates and Chl *a* concentrations.

Primary production and bacterioplankton metabolic rates: Both bacterioplankton respiration and bacterioplankton production represented a small fraction of net primary production. In Massachusetts Bay, net primary production rates were relatively high (>70–120 μg C L^{-1} d^{-1} [del Giorgio et al. 1997]), and respiration rates were much lower than net primary production rates. Similarly, bacterioplankton production rates, converted into units of μmol C kg^{-1} h^{-1}, were 1–7% of net primary production rates, which is at the low end of the reported range in BP/PP (2 to 80% for coastal waters [Ducklow and Carlson 1992]). The calculated BP/PP for Massachusetts Bay falls in the lower half of the 54 data sets analyzed by Cole et al. (1988), in which the median BP/PP was 16.5%. Results for Massachusetts Bay were similar to those reported for the Celtic Sea, where bacterial production was only 0.2–6% of primary production (Joint and Pomroy 1983, 1987).

Although microplankton and benthic respiration rates were not measured concurrently with net primary production rates, comparisons may be made. Microplankton respiration rates averaged 16% of net primary production (17, 24, and 8% in June, August, and October 1994, respectively). Benthic respiration also was a small percentage of net primary production in Massachusetts Bay, averaging 11–28% for July, August, and October 1994 (or 5–12% if the low percentage of depositional environments is taken into account) (Giblin et al. 1995). The 1994 data were based on measurements at three to seven Massachusetts Bay stations depending on the sample date, benthic respiration also was a low percentage of net primary production in 1993 (Giblin et al. 1995). These comparisons between production and respiration are made over the summer and fall and it is possible that the system may be net heterotrophic at other times of the year.

Further study will reveal whether Massachusetts Bay is more similar to the net autotrophic outlier discussed by Smith and Hollibaugh (1993), Narragansett Bay, or to what Smith and Hollibaugh (1993) described as the more typical situation: the coastal ocean as a source of atmospheric CO_2 (i.e., as net heterotrophic with planktonic plus benthic respiration exceeding production). It has been argued that respiration rate measurements will further our understanding of pelagic cycling of carbon to a greater extent than measurements of bacterial production because respiration rate measurements are made in terms more comparable to measurements of primary production (Jahnke and Craven 1995). This will be true if both primary production and bacterial respiration rates are made in the same units: carbon or oxygen. The coulometric technique makes measurement of respiratory TCO_2 production in seawater possible, even in a north temperate ecosystem in winter.

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Received: 13 July 2000
Accepted: 21 March 2001
Amended: 30 April 2001