

## MICROBIAL PRODUCTIVITY IN VARIABLE RESOURCE ENVIRONMENTS

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**Abstract.** The rate, timing, and quality of resource supply exert strong controls on a wide range of ecological processes. In particular, resource-mediated changes in microbial activity have the potential to alter ecosystem processes, including the production and respiration of organic matter. In this study, we used field experiments and simulation modeling to explore how aquatic heterotrophic bacteria respond to variation in resource quality (low vs. high) and resource schedule (pulse vs. press). Field experiments revealed that one-time pulse additions of resources in the form of dissolved organic carbon (DOC) caused short-lived ( $\leq 48$  h) peaks in bacterial productivity (BP), which translated into large differences across treatments: cumulative BP was twice as high in the pulse vs. press treatment under low resource quality, and five times as high under high resource quality. To gain a more mechanistic understanding of microbial productivity in variable resource environments, we constructed a mathematical model to explore the attributes of bacterial physiology and DOC supply that might explain the patterns observed in our field experiments. Model results suggest that the mobilization rate of refractory to labile carbon, an index of resource quality, was critical in determining cumulative differences in BP between pulse and press resource environments ( $BP_{Pu:Pr}$  ratios). Moreover,  $BP_{Pu:Pr}$  ratios were substantially larger when our model allowed for realistic changes in bacterial growth efficiency as a function of bacterial carbon consumption. Together, our field and modeling results imply that resource schedule is important in determining the flow of material and energy from microbes to higher trophic levels in aquatic food webs, and that the effects of resource quality are conditional upon resource schedule. An improved understanding of the effects of resource variability on microorganisms is therefore critical for predicting potential changes in ecosystem functioning in response to environmental change, such as altered DOC fluxes from terrestrial to aquatic ecosystems.

**Key words:** *bacteria; CO<sub>2</sub>; dissolved organic carbon; episodic; microbial physiology; subsidies; temporal variability; terrestrial–aquatic linkages.*

### INTRODUCTION

Resource variability is a “bottom-up” control that has strong effects on a wide range of ecological processes in a diversity of ecosystems. Variability in the rate, timing, and quality of resource supply has well-documented effects on the population dynamics (Ostfeld and Keesing 2000), competitive interactions (Gebauer et al. 2002), and food web dynamics (Durant et al. 2005) of plant and animal systems. Less is known about how microorganisms respond to resource variability, although it is often assumed that they can lead a “feast to famine” existence and respond rapidly to sudden changes in their environment (Eilers et al. 2000, Wang et al. 2006). Microorganisms generally attain higher population densities, are more diverse, and have faster reproductive rates than macroorganisms (Whitman et al. 1998, Bohannan 2000, Jessup et al. 2004). Furthermore, some

microorganisms have the capacity to evolve in response to resource variability on ecologically relevant time scales (Vasi et al. 1994, Finkel and Kolter 1999). Together, these fundamental characteristics may influence the response of microbial systems to resource variability (Botton et al. 2006, Prosser et al. 2007).

Resource-mediated changes in microbial activity have the potential to alter ecosystem processes, such as the production and respiration of organic material. For example, changes in the temporal variability and quality of resource supply influence enzyme activity, community composition, stoichiometry, and metabolic processes of heterotrophic bacterial communities in a variety of ecosystems (Foreman et al. 1998, Findlay et al. 2003, Makino and Cotner 2004, Carrero-Colón et al. 2006). Moreover, temporal variability in resource supply generates pulses, or “hot moments,” of ecosystem activity (McClain et al. 2003) that constitute major biogeochemical fluxes of energy and nutrients (Lodge et al. 1994, Xu and Baldocchi 2004). Therefore, understanding the effects of resource variability on microorganisms is critical for predicting potential changes in ecosystem functioning in response to environmental change.

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Pelagic heterotrophic bacteria are one group of microorganisms that commonly experience variable resource environments. These aquatic bacteria derive their carbon and energy from dissolved organic carbon (DOC). One source of DOC is labile, high quality organic matter produced by phytoplankton and macrophytes (Cole 1982, Baines and Pace 1991). The supply schedule for this autochthonous carbon is regulated by endogenous factors such as senescence, lysis, and excretion by photosynthetic organisms (Bertilsson and Jones 2003).

In lakes, inputs of terrestrial organic matter represent a second major source of DOC (Kritzberg et al. 2004). Although relatively recalcitrant, this allochthonous material varies in quality depending on its plant source, lignin content, age, and stoichiometric properties (Sun et al. 1997, Raymond and Bauer 2001, Lennon and Pfaff 2005, Judd et al. 2006). Importantly, unlike locally produced DOC, the source and supply schedule of terrestrial-derived DOC are donor-controlled, and thus governed by external processes such as temperature (Freeman et al. 2001), hydrology (Schindler et al. 1997), and land cover (Canham et al. 2004). Typically, DOC accumulates in soils during prolonged dry periods and is then flushed to nearby aquatic ecosystems following episodic hydrologic events (Boyer et al. 1997, Schindler 1997, Judd and Kling 2002). These pulsed events account for a majority of the DOC export from terrestrial to aquatic ecosystems (Hinton et al. 1997, Buffam et al. 2001), but also represent a potentially important resource subsidy for aquatic heterotrophic bacteria (Bergström and Jansson 2000, Crump et al. 2003, Lennon 2004).

The metabolic responses of pelagic heterotrophic bacteria to DOC variability have important implications for aquatic food webs and biogeochemistry. First, DOC is converted into bacterial biomass (i.e., bacterial productivity, BP), which represents an important link to higher trophic levels in lake food webs (Cole and Pace 1995). Second, DOC is used by bacteria in catabolic reactions to generate energy and thus represents a source of CO<sub>2</sub> (i.e., bacterial respiration, BR) to the lake and atmosphere (Cole et al. 2002). The allocation of consumed DOC to BP vs. BR is expressed as bacterial growth efficiency (BGE = BP divided by BR + BP), which is notoriously variable in aquatic ecosystems (del Giorgio and Cole 1998). Understanding the effects of DOC variability on BP and BR may help us to better understand controls on BGE, which in turn will allow us to better understand the roles of microorganisms as members of food webs and as catalysts of biogeochemical processes. In this study, we used field experiments and simulation modeling to examine the metabolic responses (BP, BR, BGE) of pelagic heterotrophic bacteria to changes in the supply schedule and quality of terrestrial-derived DOC and to assess whether these responses have the potential to influence lake ecosystem functioning.

## FIELD EXPERIMENTS

### *Experimental approach*

We deployed mesocosms in Norford Lake (Orange County, Vermont) in July 2002 to explore how variation in resource quality and resource schedule affect bacterial metabolism, which we define as BP, BR, and BGE. Norford Lake is a small (8 ha), oligo-mesotrophic water body (chlorophyll *a* = 2.8–5.1 µg/L) with low DOC concentrations (2.4–3.3 mg/L). Mesocosms consisted of 25-L polyethylene bags suspended from styrofoam rafts. We filled mesocosms with unfiltered water obtained from the upper 1.5 m of the lake and let them equilibrate for 3 d prior to initiating experiments.

We conducted a 2 × 2 factorial experiment that manipulated variation in resource quality and schedule. We replicated each experimental treatment, plus a control treatment with no resource addition, four times for a total of 20 mesocosms. We obtained two different resource qualities by leaching DOC from soils underneath near-monoculture stands of white pine (*Pinus strobes*) and American beech (*Fagus grandifolia*). We leached 100 g of soil in 0.1 mol/L NaOH; this solution was filtered (0.7 µm), dialyzed (500 Da) to remove inorganic nutrients, and then sterilized via gamma irradiation (25 kGy dose). Previous laboratory experiments revealed that carbon-specific productivity of aquatic bacteria from Norford Lake was three times higher on beech-derived DOC than on pine-derived DOC, primarily due to differences in the dissolved organic phosphorus content of the leachates (Lennon and Pfaff 2005). Therefore, we refer to the beech leachate as high quality DOC and the pine leachate as low quality DOC. Lennon and Pfaff (2005) provide more detail regarding the soil leaching process, DOC chemical profiling, and microbial responses to different DOC sources.

We manipulated the resource schedule using a contrast between press and pulse additions of DOC. In order to standardize the press and pulse treatments, we added 100 mg of either low or high quality DOC to all experimental mesocosms. In the press treatment, 10 mg of DOC was added to mesocosms once every 24 h for 10 d, and in the pulse treatment, 100 mg of DOC was added to mesocosms once at the beginning of the experiment. The duration of the mesocosm experiment was based upon the regional frequency of precipitation events that are involved with the delivery of terrestrial-derived DOC to lake ecosystems (Lennon 2004; data available online).<sup>2</sup> We use the terms press and pulse to differentiate the resource schedule treatments, but recognize that because bacteria may double several times per day, both treatments may represent resource pulses.

We measured DOC, BP, BR, and BGE every 24 h throughout the experiment. Samples for these measurements were taken prior to any resource additions

<sup>2</sup> (<http://lwf.ncdc.noaa.gov>)

scheduled for that day. DOC was measured on a Tekmar-Dohrmann TIC/TOC analyzer (Teledyne Instruments, Mason, Ohio, USA) after H<sub>2</sub>SO<sub>4</sub> digestion. BP was measured as the uptake and incorporation of <sup>3</sup>H-leucine (50 nmol/L final concentration) into bacterial protein during 1-h incubations (Kirchman 1993). BR was estimated via changes in dissolved oxygen concentrations on filtered (Whatman GF/D, 2.7 µm) mesocosm samples that were incubated in situ for 24 h (Roland et al. 1999). We calculated BGE as BP/(BP + BR). Summary data from these and other variables can be found in Appendix A.

We analyzed the resulting time series in two ways. First, we determined the effects of resource quality, resource schedule, and time on DOC and bacterial metabolism using repeated-measures ANOVA (SAS PROC MIXED with covariance structure selected using the Bayesian Information Criterion [BIC]; Wolfinger and Chang 1999). Second, we calculated cumulative BP and cumulative BR using trapezoidal integration. These measures provided estimates of the total amount of bacterial carbon that was produced (cumulative BP) and respired (cumulative BR) over the course of the experiment. They also provided a common response metric for mesocosms in treatments that received the same total amount of DOC but on different resource schedules. For example, the total amount of DOC added to the press and pulse mesocosms was different until the last day of the experiment. We standardized the cumulative measurements in experimental mesocosms by subtracting the mean cumulative estimate from the control mesocosms, and then analyzed the corrected values using two-way ANOVA to test for treatment effects and interactions (SAS PROC GLM in SAS version 8.2 (SAS Institute, Cary, North Carolina, USA). To compare the pulse and press resource treatments, we report the ratio of the cumulative metabolic processes: BP<sub>Pu:Pr</sub> and BR<sub>Pu:Pr</sub> ratios.

#### Experimental results

DOC concentrations were affected by both resource quality and resource schedule over the duration of the experiment (RM-ANOVA, time × quality × schedule,  $P = 0.024$ , see Appendix A for complete ANOVA tables). In the press treatment, DOC increased gradually over time, whereas in the pulse treatment, DOC increased to high concentrations immediately following the single resource addition, and then declined slightly with time (Fig. 1a).

BP was affected by both resource quality and resource schedule (RM-ANOVA, time × quality × schedule,  $P < 0.0001$ ). We observed large, short-lived peaks in BP following pulse resource additions, although the peak in the low quality pulse treatment was approximately one-half as large as the peak in the high quality pulse treatment (Fig. 1b). In contrast, BP remained low in both the low and high quality press treatments (Fig. 1b). The effects of resource manipulations were also appar-

ent when expressed as cumulative BP (Fig. 2a, two-way ANOVA, quality × schedule,  $P = 0.038$ ). Cumulative BP was higher in the pulse treatment than in the press treatment, but was approximately twice as high in systems that received a high quality pulse than a low quality pulse (Fig. 2a). In contrast, cumulative BP was low in the press systems regardless of resource quality (Fig. 2a). These cumulative responses resulted in BP<sub>Pu:Pr</sub> ratios of 2.0 and 5.0 for the low and high quality DOC treatments, respectively (Fig. 2).

BR also responded to resource schedule, though the responses were slightly less pronounced than for BP (Figs. 1c and 2b). For example, mean BR ranged from 0.46 to 20.9 µg C·L<sup>-1</sup>·d<sup>-1</sup> while mean BP ranged from 0.06 to 25.2 µg C·L<sup>-1</sup>·d<sup>-1</sup>. BR was significantly higher in the pulse treatment than the press treatment over the duration of the experiment (Fig. 1c; RM-ANOVA, time × schedule,  $P = 0.014$ ), but was not affected by resource quality (RM-ANOVA, time × quality,  $P = 0.530$ ). Similarly, cumulative BR was marginally affected by resource schedule (Fig. 2b, two-way ANOVA,  $P = 0.060$ ), but not resource quality (two-way ANOVA,  $P = 0.121$ ). These cumulative responses resulted in a BR<sub>Pu:Pr</sub> ratio of 1.5 for both the low quality and high quality DOC treatments (Fig. 2b).

Despite significant effects of our treatments on both BP and BR, BGE did not respond to manipulations of either resource quality or resource schedule. However, BGE did change significantly with time (Fig. 1d; RM-ANOVA, time,  $P < 0.0001$ ). Mean BGE ranged from 0.05 to 0.77.

#### Interpretation of experiments

Resource manipulations generally had strong effects on bacterial metabolism in our field experiments. However, the nature of the effects was dependent on the metabolic response variable and the resource treatment. For example, BP was particularly sensitive to resource schedule, which had a pronounced effect on the temporal dynamics and cumulative amount of bacterial biomass production (Figs. 1b and 2b); similar peaks in BP were reported for Toolik Lake, Alaska, in response to inputs of high quality terrestrial-derived DOC during spring ice-out (Crump et al. 2003). In our experiment, although the response of BP to the resource pulse was short-lived (≤48 h), it translated into large differences in cumulative BP across treatments: cumulative BP was 2–5× greater in pulse vs. press DOC treatments depending on resource quality. Importantly, the effects of resource quality were only apparent in the pulse treatment. BR was also influenced by resource manipulations, although responses were less dramatic than for BP. As in other studies (e.g., Roland and Cole 1999), BR was generally more conservative and exhibited a much smaller metabolic range (20×) than BP (400×). This pattern suggests that BR is relatively constrained and possibly decoupled from anabolic pathways involved in biomass production, at least in

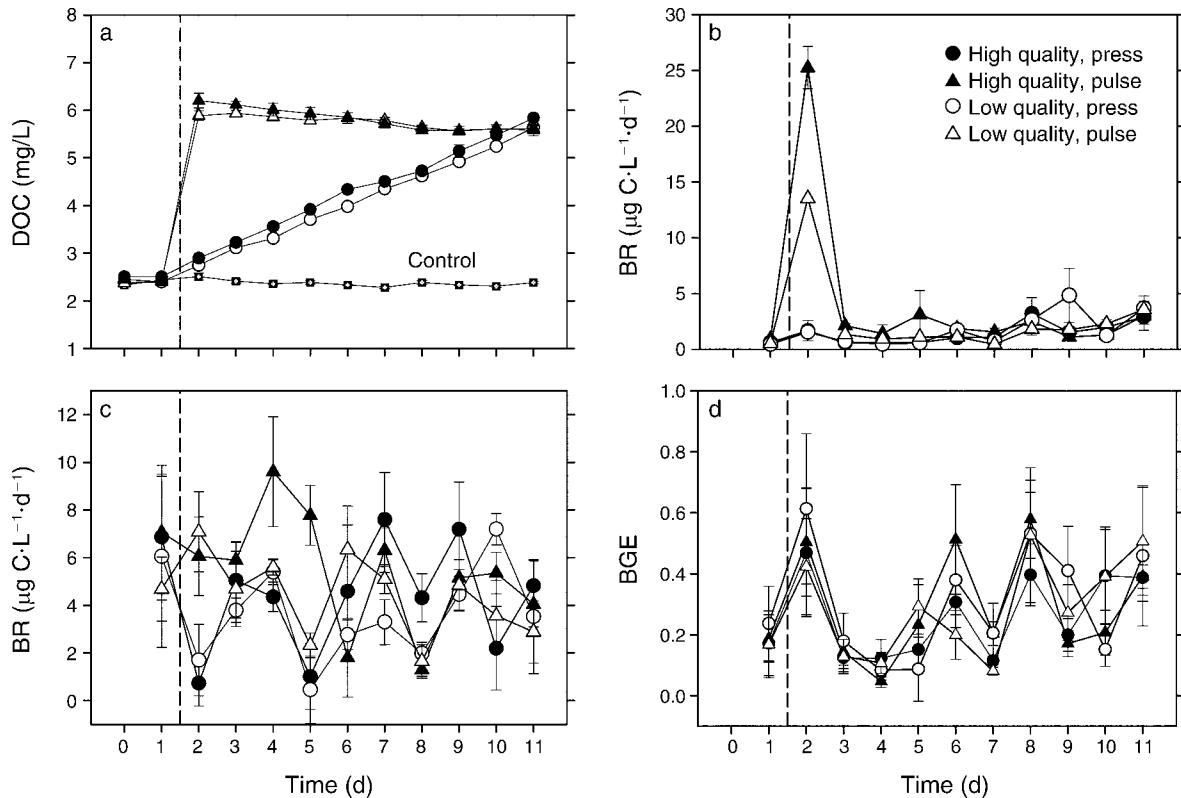


FIG. 1. Effects of variable resource schedule and resource quality on: (a) dissolved organic carbon (DOC), (b) bacterial productivity (BP), (c) bacterial respiration (BR), and (d) bacterial growth efficiency (BGE) in the field mesocosm experiment. Vertical dashed lines represent the time DOC treatments were initiated. Data are means  $\pm$  SE. For clarity, data are not shown for the controls in panels b–d.

some resource environments (Russell and Cook 1995). For example, although BR and BP were both higher in pulse than in press treatments, they did not share the same temporal trends. Moreover, BR was not affected by variation in resource quality, consistent with results from a laboratory microcosm experiment that used identical DOC sources and a microbial community from the same lake ecosystem as the current study (Lennon and Pfaff 2005).

Interestingly, BGE did not respond to either resource manipulation despite changes in BP and BR. This lack of effect may reflect the inherent variability associated with BR measurements and subsequent error propagation in BGE estimation (del Giorgio and Cole 1998, Roland and Cole 1999). For example, the coefficient of variation (CV) among replicate BR samples was 0.35, whereas the CV among replicate BP samples was only 0.03 (Lennon and Pfaff 2005). Thus, it is possible that the true effects of resource quality and resource schedule on BGE were masked by our BR measurements. However, BGE did change significantly through time, suggesting the importance of an external driver, such as temperature (Apple et al. 2006).

It is plausible that the significant effect of resource schedule on BP and BR may have been influenced by

our once-daily sampling resolution. For example, if there were concentration-dependent lags in microbial metabolism, we might have underestimated cumulative BP or cumulative BR. However, laboratory experiments indicate that both BP and BR increase linearly with DOC concentration (Lennon and Pfaff 2005). Furthermore, BP significantly increased in both the press and pulse treatment following the initial resource addition in proportion to the amount of DOC added (Fig. 1b). Together, these lines of evidence suggest that daily measurements adequately captured microbial responses to our resource treatments.

In sum, our field experiments indicate that resource schedule has a large effect on bacterial metabolism, especially BP. A one-time resource input was readily exploited by aquatic bacteria and presumably increased the amount of bacterial biomass that could be channeled to higher trophic levels. Interestingly, however, cumulative BP was lower when DOC was supplied daily, suggesting that the importance of resource quality is conditional upon resource schedule. In contrast, the effects of our resource manipulations on BR and BGE were less clear, although this may not accurately reflect the actual behavior of microbial communities due to underlying methodological issues associated with mea-

suring BR (del Giorgio and Cole 1998, Roland and Cole 1999).

#### SIMULATION MODEL

To gain a more mechanistic understanding of microbial metabolism in variable resource environments, we constructed a mathematical model to explore the attributes of bacteria physiology and DOC supply that might explain the differences observed in our field experiments. In building this model, our primary goal was not to “fit” the observed dynamics, but rather to explore the range of conditions that yielded similar results as our field experiments, especially the behavior of cumulative BP in pulse vs. press resource schedules. We also used this model to examine aspects of labile carbon utilization and potential feedbacks of bacteria to bulk DOC concentrations, both of which are difficult to assess under field conditions.

#### Model description

We constructed a deterministic, three-compartment simulation model to explore how heterotrophic bacteria respond to variation in resource quality and resource schedule (Fig. 3; Table 1). Some features of the model are analogous to soil organic matter models that distinguish among different carbon pools based on their relative lability (e.g., Parton et al. 1987, Moorhead and Sinsabaugh 2006). In contrast, very few studies have attempted to simulate interactions between microbial activity and carbon turnover for aquatic ecosystems (but see Anderson and Ducklow 2001, Polimene et al. 2006).

In our model (Fig. 3), bacteria ( $B$ ) are capable of taking up labile carbon ( $L$ ), but not refractory carbon ( $R$ ). Labile carbon is supplied to the system in two ways. First, a constant internally generated input of labile carbon is supplied to the system ( $I_i$ ), which simulates the release of DOC generated by primary producers. Second, an external input of carbon ( $I_e$ ) is supplied to the system to simulate additions of terrestrial-derived DOC. DOC quality was simulated in two ways. First, a fraction of  $I_e$  is refractory ( $r$ ) and goes to  $R$ ; the remainder ( $1 - r$ ) goes to  $L$  and is immediately available for bacterial consumption (BC). Second,  $R$  is converted to  $L$  based on a mobilization rate ( $m$ ). To evaluate how bacteria respond to variation in resource schedule,  $I_e$  enters the system either at a constant rate (press) or as a one-time addition (pulse).

The uptake of labile carbon, or bacterial consumption (BC), is determined by Michaelis-Menten dynamics, where  $M_C$  is the maximum carbon uptake rate and  $K_C$  is the half-saturation constant for carbon. The allocation of BC to bacterial production (BP) or bacterial respiration (BR) is determined by BGE. Bacterial death rate ( $d$ ) increases linearly with bacterial biomass ( $B$ ) and is attributed to viral lysis and grazing ( $l:g$ ). Carbon is lost from the system when all death is due to grazing (e.g.,  $l:g = 0$ ), is recycled to the labile carbon pool when due to viral lysis (e.g.,  $l:g = 1$ ), and is apportioned

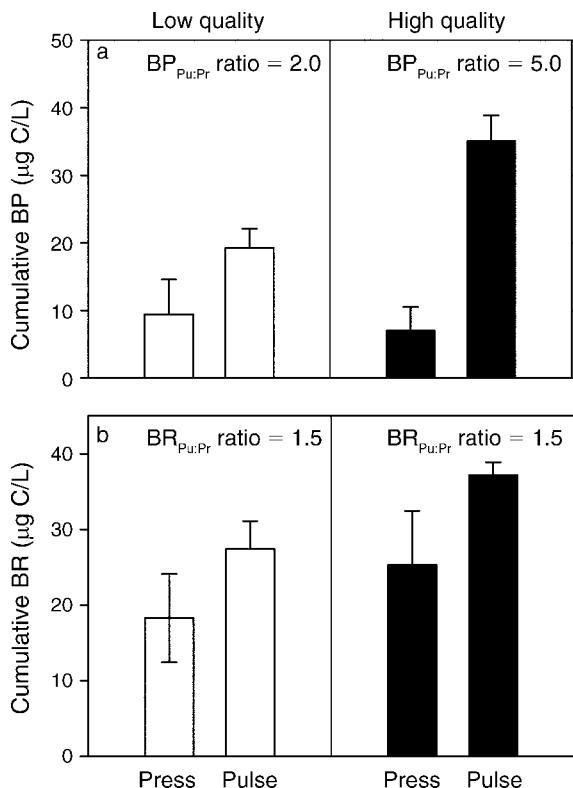


FIG. 2. (a) Cumulative bacterial productivity and (b) cumulative bacterial respiration in experimental mesocosms exposed to variable resource schedule (pulse vs. press) and variable resource quality (high vs. low). In the press treatment, 10 mg of DOC was added once every 24 h for 10 d; in the pulse treatment, 100 mg of DOC was added once at the beginning of the experiment. Cumulative BP and BR were calculated using trapezoidal integration over the time of the experiment.  $BP_{Pu:Pr}$  was calculated within a resource quality treatment as the ratio of cumulative BP in the pulse treatment relative to the press treatment. The same approach was used with BR data to calculate the  $BR_{Pu:Pr}$  ratio.

between losses and recycling for intermediate values of  $l:g$ .

The system of equations is written as:

$$\frac{dr}{dt} = I_e \times r - m \times R \quad (1)$$

$$\frac{dL}{dt} = I_i + (1 - r) \times I_e + m \times R + l : g(d \times B) - BC \times B \quad (2)$$

$$\frac{dB}{dt} = BGE \times BC \times B - d \times B \quad (3)$$

where

$$BC = M_C \left( \frac{L}{L + K_C} \right) \quad (4)$$

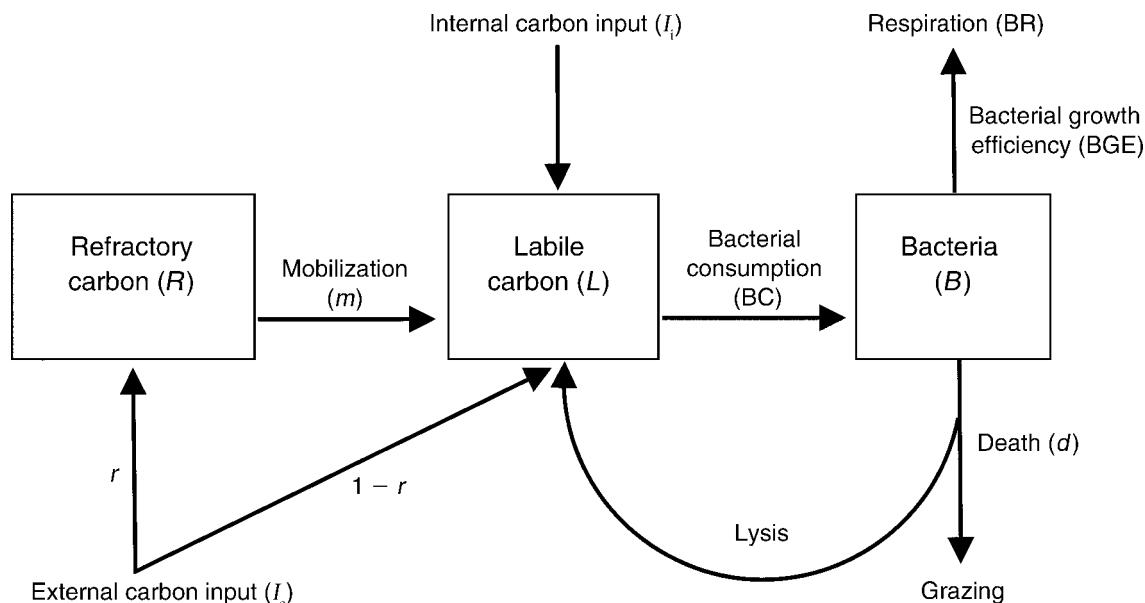


FIG. 3. The three-compartment simulation model used to explore bacterial responses to variability in DOC quality and supply rate. See *Simulation model: Model description* for more detailed explanation.

We also calculated per capita bacterial productivity (BP) as  $BGE \times BC$ .

One important aspect of our model is that BGE is a dynamic function. Comparative studies have shown that BGE increases hyperbolically with BP in aquatic ecosystems (del Giorgio and Cole 1998, Kritzberg et al. 2005). This means that the allocation of carbon to new biomass vs. respiration also changes as a nonlinear function of BC. We incorporated these realistic attributes of metabolic allocation into our model by modifying the equations described in del Giorgio and Cole (1998) and Kritzberg et al. (2005). First, we used the published BGE-BP equations to solve for BR, and then expressed BGE as a function of BC (i.e.,  $BP + BR$ ).

We then used curve fitting (Sigma Plot version 8.0, Richmond, California, USA) to estimate parameters of the BGE-BC function assuming Michaelis-Menten dynamics:

$$BGE = \frac{BC \times M_{BGE}}{BC + K_{BGE}} \quad (5)$$

where  $M_{BGE}$  is the maximum BGE and  $K_{BGE}$  is the rate of BC that is equivalent to one-half of the maximum BGE. Importantly, Eqs. 4 and 5 mean that BP, BR, and BGE are all coupled to BC, such that conclusions about responses to particular model parameters are qualitatively the same for all three metabolic responses. Therefore, we focus here on presenting results for BP

TABLE 1. Notation, description, units, and sources for the parameters that we used in our three-compartment simulation model.

Parameter	Description	Units	Nominal value	Range tested in one-at-a-time simulations	Values for factorial simulations	Source
$I_e$	external C input	$\mu\text{g C/simulation}$	3500	100–5000	500, 1500, 3500, 7000	1
$I_i$	internal C input	$\mu\text{g C}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$	1	0.1–100	1, 10, 50, 100	2
$r$	refractory portion of $I_e$	proportion	0.95	0.5–0.99	0.75, 0.85, 0.9, 0.95	3
$m$	mobilization rate (R→L)	proportion $\text{d}^{-1}$	0.001	0.0001–0.1	0.001, 0.01, 0.05, 0.1	4
$M_C$	maximum rate of BC	$\mu\text{g C}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$	15	0.5–1000	N/A	5
$K_C$	BC half-saturation constant	$\mu\text{g C}\cdot\text{L}^{-1}$	1	0.5–10000	N/A	6
$M_{BGE}$	maximum BGE	proportion of BC	0.83	0.1–0.83	0.1, 0.25, 0.46, 0.83	7
$K_{BGE}$	BGE half-saturation constant	$\mu\text{g C}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$	216	0–365.5	0, 66.5, 216	7
$d$	death rate	$\text{d}^{-1}$	0.25	0.1–0.5	N/A	8
$l:g$	Lysis : grazing ratio	proportion of $d$	0.5	0.0–1.0	N/A	9

Notes: For a given parameter, we have listed the nominal values, the range of values tested in one-at-a-time simulations, and the different levels used in the factorial simulations. Key to abbreviations: R, refractory carbon; L, labile carbon; BC, bacterial consumption rate; BGE, bacterial growth efficiency; N/A, parameter was not manipulated for the factorial simulations. Sources: (1) approximate carbon loading from the field experiment; (2) Baines and Pace (1991); (3) Sondergaard and Middelboe (1995), del Giorgio and Davis (2003); (4) Raymond and Bauer (2000), Wetzel (2001); (5) Robarts and Sephton (1988), Bianchi et al. (1998); (6) Overbeck (1994), Bianchi et al. (1998), Kirchman and Rich (1997), Kisand and Tammert (2000); (7) del Giorgio and Cole (1998), Kritzberg et al. (2005); (8) Thingstad et al. (1996), Fuhrman and Noble (1995); (9) Fuhrman and Noble (1995).

because it yielded the most interesting and reliable results in the field experiment. More detail on model assumptions, including BGE parameter derivation and the effects of initial conditions, can be found in Appendices B–D.

We implemented these equations in Matlab (MathWorks, Natick, Massachusetts, USA) using an adaptive step size Runge-Kutta algorithm (Jackson et al. 2000), which addresses some of the logistical limitations of the field experiments. We ran all simulations for the same duration as the field experiments. As in the field, total  $I_e$  was equal for pulse and press simulations. In pulse simulations, all of  $I_e$  was added on day 2 of the simulation, whereas  $I_e$  was added continuously throughout press simulations for 10 d beginning on day 2 (as compared to once daily in the field experiments). At the end of each run, the predicted values of  $R$ ,  $L$ , and  $B$  were interpolated at 0.5-d intervals to create a uniform time series for comparison across simulations.

#### Simulation approach

We conducted two simulation studies to determine which parameters had the strongest influence on the behavior of DOC ( $L + R$ ) and BP following press or pulse additions of external carbon ( $I_e$ ). First, we manipulated one parameter at a time over the entire range of feasible values (Table 1, Figs. 4 and 5) to explore the temporal trajectories of DOC and BP and to evaluate qualitatively how variation in each parameter might have contributed to the patterns observed in the field experiments. Using these same simulations, we then explored why there might have been differences in cumulative BP between press and pulse treatments in the field experiments, especially in response to high quality DOC (Fig. 1b). As in the field experiments, we calculated the ratio of the cumulative BP following the pulse addition to the cumulative BP following the press addition ( $BP_{Pu:Pr}$  ratio) from each simulation. Second, we conducted a factorial simulation experiment ( $n = 9216$ ) manipulating the parameters and initial conditions that appeared to be particularly influential in our single-factor manipulations (Table 1). We then  $\log_{10}$ -transformed the  $BP_{Pu:Pr}$  ratio to normalize the distribution and used PROC MIXED in SAS (version 8.2) to determine the extent to which variance in log-transformed ratios was due to individual parameters vs. two- and three-way interactions among parameters.

#### Simulation results

Our simulations captured the general behavior of DOC observed in the field experiments (compare Fig. 1 to Figs. 4 and 5). DOC increased steadily in response to continuous inputs of external carbon ( $I_e$ ) in the press treatment, and increased rapidly following the one-time inputs of external carbon in the pulse treatment (Fig. 4). In both supply schedules, DOC increased with  $r$  and declined with increasing  $m$  (Fig. 4), but was relatively insensitive to variation in  $I_i$  and all parameters relating

to the bacterial compartment ( $l:g$ ,  $d$ ,  $M_C$ ,  $K_C$ ,  $M_{BGE}$ ,  $K_{BGE}$ ; Appendix C).

Similarly, our simulations captured the general behavior of BP observed in the field experiments. For nearly all parameter values tested, BP increased slightly at the onset of DOC addition in the press treatment and then stayed at that approximate level through the rest of the simulation (Fig. 5). In contrast, BP showed large but short-lived peaks in the pulse treatment, with maximum values  $\sim 10$ – $100\times$  higher than in the press treatment (compare the  $y$ -axis scales for the left and right panels in Fig. 5). In both the press and pulse treatments, BP was sensitive to parameters relating to DOC and bacterial physiology, increasing with  $I_e$ ,  $I_i$ ,  $m$ , and  $M_{BGE}$  and decreasing with  $r$  and  $K_{BGE}$  (Fig. 5).

We then determined the effects of each model parameter on the  $BP_{Pu:Pr}$  ratio. If resource schedule had no effect on cumulative bacterial biomass production, the  $BP_{Pu:Pr}$  ratio would be 1.0. Consistent with our field observations, cumulative BP was almost always greater in pulse vs. press treatments in the simulations; only one of the 9216 combinations of parameters in the factorial simulation experiment produced a  $BP_{Pu:Pr}$  ratio  $< 1.0$ . The frequency distribution of  $BP_{Pu:Pr}$  from the factorial simulations was highly right-skewed with a median value of 6.75 (range, 0.95–63.52), which was significantly  $> 1.0$  (one-sample median test,  $P = 0.0001$ ).

The factorial simulation experiment allowed us to systematically explore variation in  $BP_{Pu:Pr}$  ratios and evaluate the potential for interactions among parameters. The rate of DOC mobilization ( $m$ ) contributed most strongly to variation in the  $\log_{10}$ -transformed  $BP_{Pu:Pr}$  ratio across simulations, while the denominator of the BGE-BC function ( $K_{BGE}$ ) also accounted for some variability (Fig. 6; Appendices E and F).  $BP_{Pu:Pr}$  ratios were relatively low when refractory DOC was mobilized rapidly ( $m = 0.1$ , Fig. 6). However, when refractory DOC mobilization rates were slower ( $m = 0.001$  or  $m = 0.01$ ),  $BP_{Pu:Pr}$  ratios increased, especially when we allowed for “dynamic” BGE in response to BC ( $K_{BGE} > 0$ ). For example, with slow rates of refractory DOC mobilization ( $m = 0.001$ ) and “static” BGE (i.e.,  $K_{BGE} = 0$ ),  $BP_{Pu:Pr}$  ratios were constrained to a low and narrow range (1.3–12.7). In contrast, when BGE was dynamic (i.e.,  $K_{BGE} > 0$ ),  $BP_{Pu:Pr}$  ratios were higher and had a much broader range (1–63.5; Fig. 6).

#### Interpretation of simulations

The behavior of DOC in the model matched the field experiments remarkably well. This consistency allowed us to make some inferences about the general properties of the DOC used in our field experiments. First, the similarity in the temporal dynamics of field-measured BP following daily DOC additions (Fig. 1b) to model estimates of BP following continuous DOC additions (Fig. 5) suggest that our field results are not an artifact of the once-daily sampling resolution. Second, it is reasonable to assume that a large fraction ( $> 95\%$ ) of the

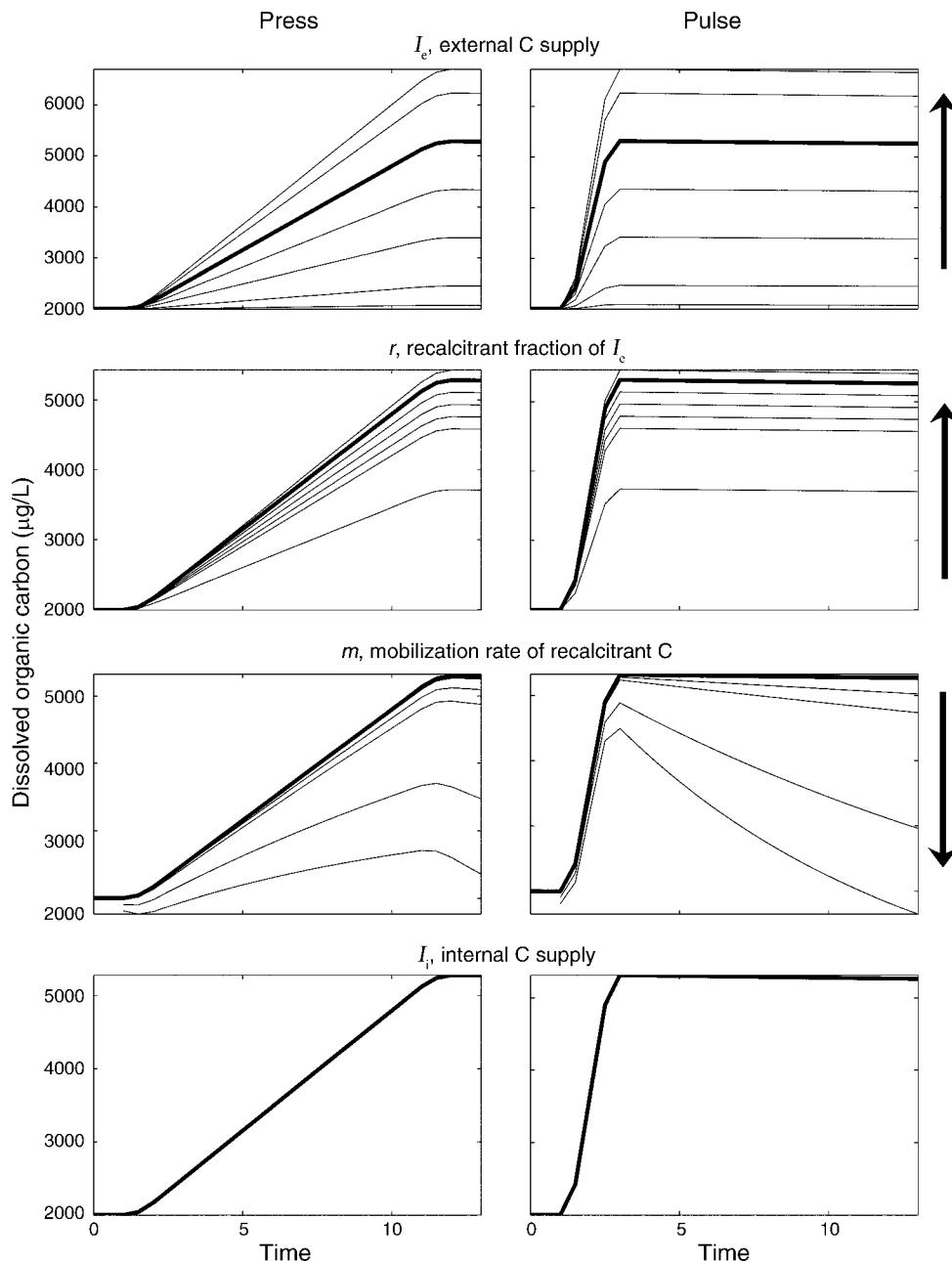


FIG. 4. Temporal dynamics of DOC expressed as the sum of labile ( $L$ ) and refractory ( $R$ ) carbon pools in the model simulations. Columns represent pulse (left) and press (right) inputs of carbon resources. Rows represent responses for parameter values that were sensitive to the manipulation of single parameters. The arrows at right indicate the direction of increasing parameter value.

DOC added to our mesocosms was refractory and mobilized to labile carbon at a rate of  $\leq 0.01 \text{ d}^{-1}$  (compare Fig. 1 and Fig. 4). In our simulations, total DOC concentrations ( $L + R$ ) were relatively unaffected by microbial activity across broad ranges of bacterial parameters because total DOC was dominated by the refractory carbon compartment ( $R$ ). In contrast, simulated concentrations of labile carbon ( $L$ ) fluctuated

through time and were strongly influenced by parameters controlling bacterial physiology (Appendix E). Third, in our field experiments, the effect of DOC quality was manifested in the height of the BP peak following the pulse resource addition (Fig. 1b). Our simulations demonstrated that the height of the BP peak following pulse resource additions was controlled primarily by the refractory fraction of the external

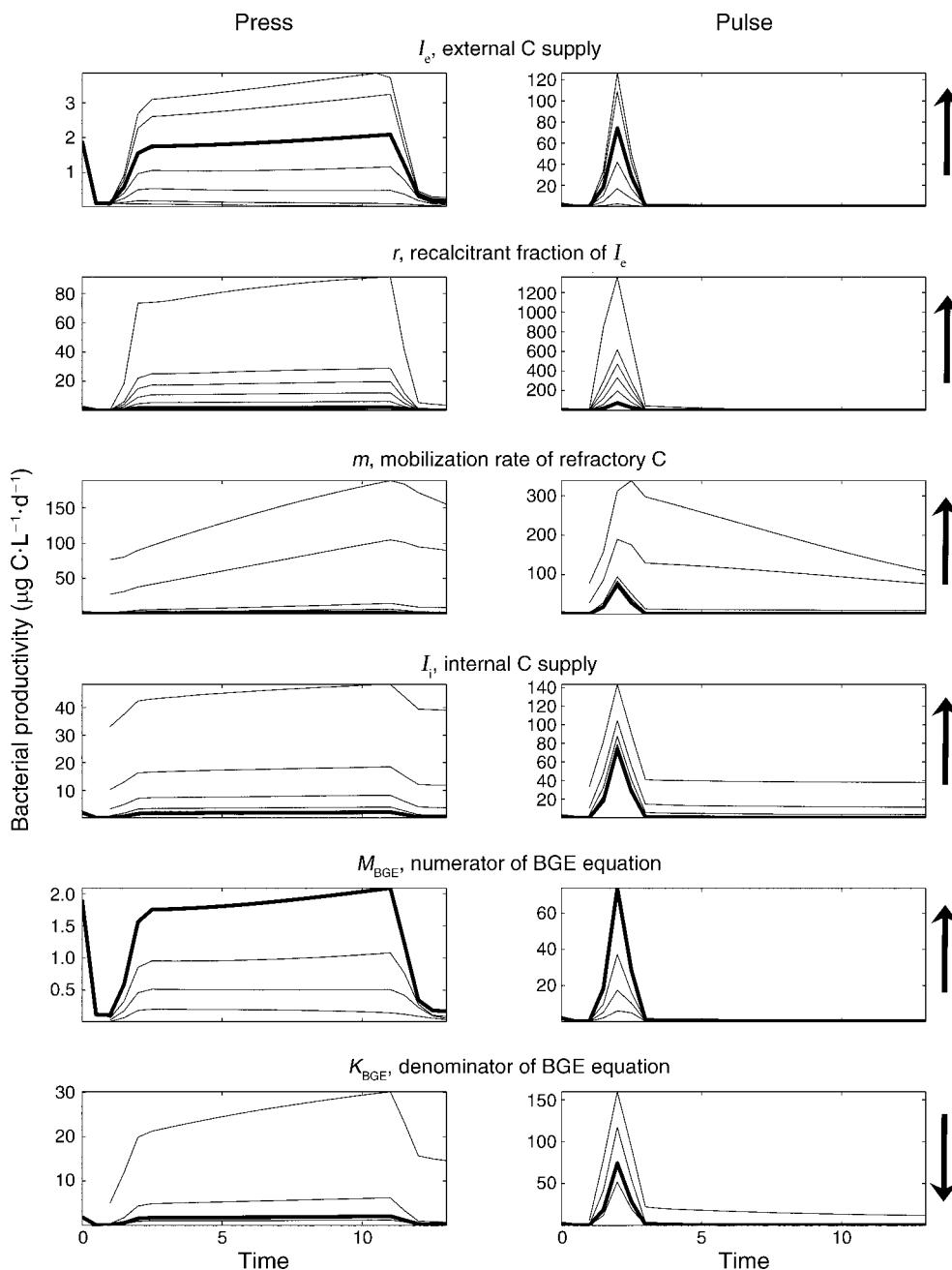


FIG. 5. Temporal dynamics of bacterial productivity (BP) in the model simulations. Columns represent pulse (left) and press (right) inputs of carbon resources. Rows represent responses for parameters values that were sensitive to the manipulation of single parameters. The arrows at right indicate the direction of increasing parameter value.

carbon input, ( $r$ ), but was also influenced by the parameters that determined BGE ( $M_{BGE}$  and  $K_{BGE}$ ; Fig. 5).

The temporal dynamics of BP in our simulations were driven by variation in both DOC quality ( $r$  and  $m$ ) and labile carbon concentration (via manipulations of  $I_i$  or dynamic changes in  $L$ ), suggesting that heterotrophic bacteria were often carbon-limited in both our experimental and model systems. In addition, BP in the

simulations was sensitive to variation in resource schedule. For example, the model consistently produced results where  $BP_{Pu:Pr} > 1$ ; this pattern was consistent for simulations that were run for up to 200 days suggesting that the results from our field study were not an artifact of the experimental time scale (Appendix G). Moreover, the interquartile range of  $BP_{Pu:Pr}$  ratios generated from the simulations (4.4–9.2) overlapped with the ratios observed in our field experiments (2.0–5.0). Thus, the

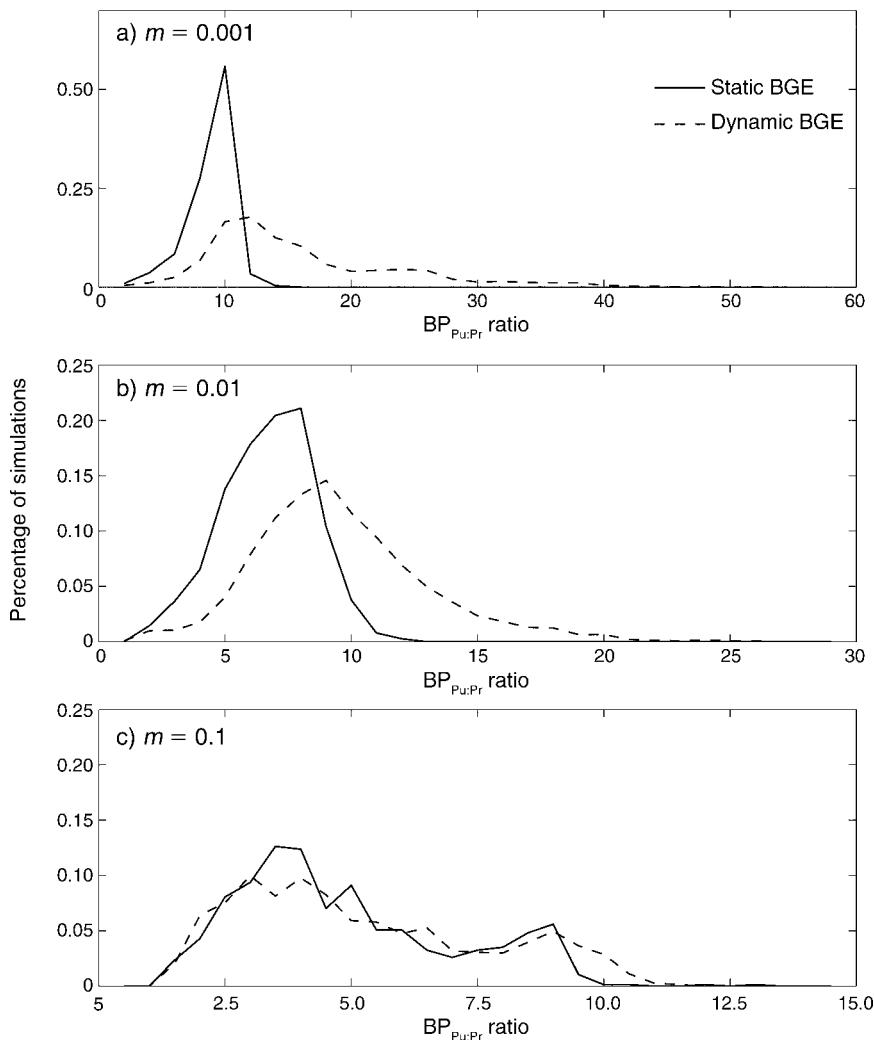


FIG. 6. Distributions of the ratio of cumulative bacterial production in pulse vs. press resource schedules ( $BP_{Pu:Pr}$  ratios) generated from the factorial manipulations of six model parameters. Solid lines represent simulations with static BGE (i.e.,  $K_{BGE} = 0$ ); dashed lines represent simulations with dynamic BGE (i.e.,  $K_{BGE} = 66.5$  or  $216$ ). From top to bottom, the three panels represent a gradient of slow ( $m = 0.001$ ), intermediate ( $m = 0.01$ ), and fast ( $m = 0.1$ ) conversion rates of refractory to labile carbon. Note differences in the range of the  $x$ -axis.

simulation results are consistent with the outcome of our field experiment: resource schedule can be quite important in determining the flow of material and energy through the bacterial compartment of plankton food webs. However, our study only contrasted a one time resource addition (pulse) with daily resource additions (press). Further studies are needed to explore how the timing and frequency of resource pulses affect microbial metabolism, potentially in conjunction with communities composed of taxa with different competitive abilities and growth rates.

The agreement between our field experiments and simulations also allowed us to identify parameters that may help explain the differential response of microorganisms to pulse and press resource schedules. In particular, the mobilization rate ( $m$ ) of refractory to

labile carbon, which serves as an index of resource quality, was critical in determining the magnitude of  $BP_{Pu:Pr}$  ratios. High  $BP_{Pu:Pr}$  ratios were less common in systems with rapid mobilization of refractory to labile DOC (Fig. 6), presumably because high concentrations of labile C dampened the bacterial response to external resource inputs ( $I_e$ ). In nature, mobilization of refractory DOC may be influenced by UV absorption (Reche et al. 1998), microbial production of extracellular enzymes (Arnosti 2004), or the DOC source itself.

In addition,  $BP_{Pu:Pr}$  ratios were affected by the nature of the BGE function.  $BP_{Pu:Pr}$  ratios were considerably lower when the model was programmed with a static BGE (i.e.,  $K_{BGE} = 0$ ; Fig. 6), which is often assumed by researchers despite the fact that we know BGE is extremely variable in space and time (del Giorgio and

Cole 1998, Kritzberg et al. 2005). When we allowed for realistic changes in BGE in response to BC (i.e.,  $K_{\text{BGE}} > 0$ ), we observed fairly dramatic changes in the behavior of BP ratios due to the nonlinearity of the Michaelis-Menten function (Eq. 5). Specifically, when the half-saturation constant  $K_{\text{BGE}}$  is relatively small, bacteria reach their maximum growth efficiency ( $M_{\text{BGE}}$ ) at lower BC and thus operate at a higher BGE for a broad range of BC rates. In contrast, when  $K_{\text{BGE}}$  is relatively large, bacteria must reach higher rates of BC before they achieve  $M_{\text{BGE}}$  and thus tend to have a lower BGE. As a result, cumulative BP is most different between resource schedules when pulse inputs exceed  $K_{\text{BGE}}$  but press inputs do not (see also Appendix F).

In sum, our relatively simple model captured the metabolic responses of heterotrophic bacteria to variable resource environments over relatively short time scales. Importantly, it did this without having to introduce many of the complexities that are inherent to microbial systems. Bacteria may respond to resource schedule or resource quality through a variety of mechanisms, including life history trade-offs (Klappenbach et al. 2000), extracellular enzyme activity (Arnosti 2004), shifts in cell dormancy (Cole 1999), and storage of carbon reserves (Kadouri et al. 2005). Furthermore, the ability to understand microbial responses to resource variability in lakes could be hampered by the indirect effects that terrestrial-derived DOC have in aquatic ecosystems (Lennon 2004). Such complexities might become more important when investigating the effects of resource variability over longer temporal and spatial scales; in these cases a more advanced model would likely be needed.

#### SYNTHESIS

Our field experiments and simulation models reveal a striking pattern regarding resource schedule: when supplied with the same quantity of DOC, cumulative bacterial productivity was much higher in pulse vs. press resource treatments over 1–2 week time scales. In general, pulse effects were less apparent when there were high concentrations of labile DOC, which in our simulations could be attributed to a combination of DOC properties and bacterial traits. Thus, our results support the general prediction from subsidy theory that external resource inputs are less important in systems with high local productivity (Polis et al. 1997, Huxel and McCann 1998). Also, our results suggest that changes in the timing or quality of DOC export from terrestrial systems could have important and nonadditive implications for both food web dynamics and the biogeochemistry of aquatic ecosystems. Such findings are particularly important given the observed changes in DOC flux from terrestrial to aquatic ecosystems, which may be due to a combination of increasing temperature, altered hydrologic regimes, and atmospheric nutrient deposition (Roulet and Moore 2006).

Resource schedule seems to be an important ecological feature of both microbial and macrobial systems. For example, it is well documented that soil bacteria are responsible for pulses of ecosystem activity following rewetting events, due in part to the mineralization of growth limiting substrates (Fierer and Schimel 2003), while carcasses from periodic cicada outbreaks increase microbial biomass, nitrogen concentrations, and seed mass in forest ecosystems (Yang 2004) and increase nutrient availability and plankton biomass in pond ecosystems (Nowlin et al. 2007). Moreover, many studies have documented the importance of precipitation variability in terrestrial ecosystems on plant physiology, competitive interactions, maintenance of species diversity, and primary productivity (BrassiriRad et al. 1999, Gebauer et al. 2002, Fay et al. 2003, Suttle et al. 2007). Thus, strong biological responses to variable resource schedules appear to be a common feature of ecological systems and are worthy of further study under current scenarios of environmental change.

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#### APPENDIX A

Summary of measurements taken from the mesocosms in the field experiment for each treatment, summary tables for the repeated-measures analysis of variance (RM-ANOVA) for each response variable in the field experiment, and summary tables for the two-way analysis of variance (ANOVA) for cumulative bacterial productivity (BP) and cumulative bacterial respiration (BR) in the field experiment (*Ecological Archives* E089-060-A1).

#### APPENDIX B

Derivation of the bacterial growth efficiency (BGE) function and parameters (*Ecological Archives* E089-060-A2).

#### APPENDIX C

Detailed figures for single parameter sensitivity analysis (*Ecological Archives* E089-060-A3).

**APPENDIX D**

Effects of initial conditions (*Ecological Archives* E089-060-A4).

**APPENDIX E**

Output from PROC MIXED for the factorial manipulations of six parameters plus initial bacterial carbon concentrations (*Ecological Archives* E089-060-A5).

**APPENDIX F**

Labile carbon concentrations are the key to understanding the effects of variable BGE on pulse/press differences (*Ecological Archives* E089-060-A6).

**APPENDIX G**

The effect of simulation duration on cumulative BP and  $BP_{Pu-Pr}$  ratios for nominal parameter values (*Ecological Archives* E089-060-A7).