Vol. 38: 103–111, 2005 | AQUATIC MICROBIAL ECOLOGY
Aquat Microb Ecol | Published February 9

Does autochthonous primary production drive variability in bacterial metabolism and growth efficiency in lakes dominated by terrestrial C inputs?

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ABSTRACT: During the past 20 yr, aquatic microbiologists have reported 2 strong patterns which initially appear contradictory. In pelagic systems, bacterial growth and biomass is well correlated with the growth and biomass of primary producers. However, bacterial respiration often exceeds net primary production, which suggests that bacteria are subsidized by external inputs of organic matter. We hypothesize that bacterial growth efficiency (BGE) varies systematically between autochthonous and allochthonous carbon (C) sources and that this variation resolves the above conundrum. To test these ideas, we examined the ecological regulation of bacterial secondary production (BP), bacterial respiration (BR) and BGE in a series of lakes dominated by terrestrial (allochthonous) C inputs. BP was correlated with autochthonous C sources (chlorophyll *a*) even though the lakes were net heterotrophic (i.e. heterotrophic respiration consistently exceeded primary production). The results were simulated by a simple steady-state model of bacterial utilization of autochthonous and allochthonous dissolved organic C. A higher preference and greater growth efficiency of bacteria on autochthonous C may explain why BP is coupled to autochthonous production also in net heterotrophic ecosystems where the use of allochthonous C by bacteria is high. These results suggest that little of the allochthonous C assimilated by bacteria is likely to reach higher consumers.

KEY WORDS: Bacterial growth efficiency · DOC · Allochthonous · Autochthonous · Bacterial production · Models

INTRODUCTION

Bacteria are the most numerous planktonic organisms in aquatic systems and the major remineralizers of organic carbon (C) and nutrients. Production of bacterial biomass provides a link between dissolved organic carbon (DOC) and higher organisms. Indeed, consumption of DOC by heterotrophic bacteria is one of the largest fluxes of C in most aquatic ecosystems (Cole 1999). This DOC can be either transformed to bacterial biomass (bacterial secondary production, BP) or respired to inorganic carbon (bacterial respiration, BR). The relative magnitudes of BP and BR are controlled by bacterial growth efficiency (BGE = BP/[BP + BR]), which is the fraction of assimilated organic C that supports growth. While the importance of DOC to lake metabolism is widely recognized (Williamson et al. 1999), there is no consensus on the regulation of BGE, which is key to understanding the bacterial influence on C dynamics and food webs.

The source of DOC and its chemical composition could be a key regulator of BGE. In lakes, DOC originates either from primary production within the lake (autochthonous) or in the terrestrial watershed (allochthonous). Because DOC is a complex mixture of compounds, the origin of the fraction used by bacteria is poorly known (Tranvik 1998). Traditionally, phytoplankton-derived C has been considered to be the main source for bacterial as well as other secondary production. Bacteria rapidly use organic C of

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algal origin (Chen & Wangersky 1996) and bacterial abundance and productivity are consistently related to algal abundance and primary productivity in cross-system comparisons (Bird & Kalff 1984, Cole et al. 1988). Terrigenous DOC, on the other hand, was long considered relatively recalcitrant to microbial degradation (Wetzel et al. 1972, Hobbie 1988), although it was recognized early on that allochthonous organic matter might support aquatic food chains (Naumann 1918). Recent research has shown that allochthonous DOC can be metabolized by bacteria (Tranvik 1988, Moran & Hodson 1990). Even if only a small fraction of the allochthonous DOC pool is readily available for bacterial utilization (Tranvik 1988, Moran & Hodson 1990), the large pool size of DOC implies that it may contribute significantly to bacterial C consumption and energy mobilization. In lakes which are both humic-rich and oligotrophic, a common lake type in north temperate and boreal regions, allochthonous C may largely replace phytoplankton photosynthesis as a basis for secondary production (Jones 1992, Tranvik 1992, Jansson et al. 1999). Multiple lines of evidence suggest that many aquatic systems are net heterotrophic, i.e. total respiration exceeds gross primary production (Cole et al. 1994, del Giorgio & Peters 1994). This net heterotrophy can occur only if external subsidies of organic C support some portion of lake metabolism. It has been debated whether bacteria effectively link this detrital DOC to the phagotrophic food web (Pomeroy 1974, Pace et al. 1984) or represent the terminal group in a detrital food chain, and thus act as a respiratory sink rather than a source of C for higher organisms (Ducklow et al. 1986).

The extent to which bacteria link detrital DOC to the rest of the food web depends in part on BGE. BGE increases with system primary productivity (del Giorgio & Cole 1998, Biddanda et al. 2001) and the low BGE values characteristic of oligotrophic areas are suggested to be related to high maintenance costs in environments with low concentrations of DOC and nutrients (del Giorgio & Cole 1998). However, it may be the quality of the DOC, rather than quantity, that accounts for the higher BGE in more eutrophic systems (Eiler et al. 2003). If autochthonous DOC is qualitatively superior, so that it can support a higher yield than allochthonous C, terrestrial C may be primarily respired and never reach the higher levels of the food chain even in net heterotrophic systems where bacterial utilization of terrestrial C is high.

In this study, we made experimental measurements of BGE in 10 lakes that covered a broad range of chlorophyll and DOC concentrations, representing various degrees of allochthonous and autochthonous loading of organic C. Combining these measurements with the results from whole-lake ^{13}C additions which traced the flow of allochthonous and autochthonous C through bacteria (see Kritzberg et al. 2004) we created a model that relates the regulation of BGE with DOC of both allochthonous and autochthonous origin.

MATERIALS AND METHODS

Lake survey. Ten lakes at the University of Notre Dame Environmental Research Center near Land O'Lakes, Wisconsin, USA (89° 32′ W, 46° 13′ N), were sampled 1 to 3 times from June through August 2001. The lakes, which vary in area from 0.8 to 45 ha (Pace & Cole 2002), are all in a similar hydrogeographic setting, and are surrounded by wetlands and upland forests without human habitation or agriculture (Carpenter & Kitchell 1993). Some key characteristics of the sampled lakes are shown in Table 1. From each lake, 10 l of water was collected from 0.5 m depth and transported to the laboratory for subsequent analysis of pH, DOC, color, total dissolved phosphorus (TDP), total dissolved nitrogen (TDN), chlorophyll *a* (chl *a*) and bacterial abundance (BA). Methods followed procedures in many other studies on these lakes and details are published elsewhere (Pace & Cole 1996, 2002). Briefly, pH was measured with an Orion digital meter with 2-point calibration and electrodes with automatic temperature compensation. Samples for DOC were filtered through ashed Whatman GF/F filters (nominal pore size 0.7 µm), acidified with H_2SO_4 to pH ≈ 2 and stored in

Table 1. Selected physical, chemical and biological characteristics of the 10 survey lakes at the University of Notre Dame Research Center, Wisconsin, USA. All values are means of 4 measurements during the summer season of 2001. H-bird: Hummingbird Lake; TP: total phosphorus; DOC: dissolved organic carbon; Chl *a*: chlorophyll *a*

Lake	Area (ha)	pH	TP (mg m^{-3})	DOC (g m^{-3})	Chl *a* (mg m^{-3})
Roach	45.1	5.4	9.9	2.1	1.9
Crampton	25.8	6.1	8.1	3.9	3.7
Peter	2.5	6.9	6.7	4.7	3.1
Paul	1.7	6.4	9.7	3.7	5.4
Ward	2.7	7.7	28.1	6.5	7.3
Brown	32.9	9.1	30.0	7.7	23.2
Tuesday	0.9	6.2	10.0	7.6	6.1
East Long	2.3	5.5	23.2	10.1	19.2
Morris	5.9	7.6	19.9	12.9	9.8
H-bird	0.8	4.9	28.4	20.7	46.4

the dark for later analysis. The concentration of DOC was measured with a Schimadzu 5050 high-temperature organic carbon analyzer. Water color was quantified on the GF/F filtrate as absorbance (m^{-1}) at 440 nm. Samples for TDP and TDN were GF/F filtered, frozen and later analyzed with a TRAACS 800 autoanalyser.

Chl *a* was determined using a Turner 450 fluorometer. Duplicate subsamples (200 ml) were filtered through GF/F filters that were stored frozen and subsequently extracted with methanol for 24 h. Fluorescence of extracts was determined before and after acidification to correct for pheopigments (Carpenter et al. 1996). Bacterial abundance was established by direct counts with an epifluorescence microscope. Preserved water samples (2% final concentration buffered formalin) were stained with acridine orange and filtered through 0.2 µm pore size Nuclepore filters (Hobbie et al. 1977). At least 10 grids with a minimum of 30 bacteria were counted for every sample.

Each lake (except for Brown Lake) was sampled once for dissolved inorganic C (DIC), which was determined using the method of Stainton (1973), where headspace from acidified samples was injected into a gas chromatograph (Schimadzu GC-8AIT with thermal conductivity detector). DIC and pH were used to calculate the partial pressure of CO_2 (pCO_2) (Stumm & Morgan 1996).

BGE was calculated from BP and BR which were measured from water that had been filtered through Whatman GF/D filters (nominal pore size 2.7 µm) to remove phytoplankton and bacterial grazers. The GF/D filter retained essentially all phytoplankton and bacterial grazers while bacterial numbers were only slightly reduced (94 ± 6% of planktonic bacteria were recovered in the filtrate). The filtered water was siphoned into 300 ml BOD (biological oxygen demand) bottles. Three bottles were used to measure BP at time zero and after 24 h. Another 10 identical bottles were used to estimate respiration. All bottles were kept in darkness at *in situ* temperature.

BP was estimated by measuring incorporation of ^{3}H-leucine following the method developed by Smith & Azam (1992). Water samples (1.5 ml, 4 replicates and 1 killed control) were incubated with 35 nM final concentration of ^{3}H-leucine (42.5 Ci $mmol^{-1}$) at *in situ* temperature for 45 min. The incubation was terminated with 30 µl of 50% TCA (immediately after addition of leucine in the controls). The samples were then centrifuged at 17 000 × *g* for 10 min and the supernatant discarded. Subsequently, 1.5 ml of 5% TCA was added and followed by centrifugation. After the supernatant was discarded, 0.5 ml of scintillation cocktail (Scintiverse BD) was added and ^{3}H-activity measured with a Beckman LS 6500 scintillation counter. BP was calculated according to Smith & Azam (1992). To calculate the accumulated BP over 24 h, values of BP at time zero and 24 h were integrated following Roland & Cole (1999).

BR was estimated from the consumption of dissolved oxygen in BOD bottles (GF/D filtrate), assuming a respiratory quotient of 1. Five control samples were immediately fixed with Winkler reagents. Another 5 bottles were kept at the *in situ* temperature in darkness for 24 h before fixation. Dissolved oxygen concentration (DO) was determined by the spectrophotometric modification of the Winkler method (Roland & Cole 1999) that provides accurate measurements of DO changes of 0.05 mg l^{-1}.

Relationships among variables were investigated with simple correlation analysis using SPSS statistical software. Data did not need transformation to meet the assumptions of normality and equal variances.

Steady-state model. We created a simple box-flow model to simulate bacterial utilization of autochthonous and allochthonous DOC separately. The model, which assumes steady-state to simplify the computations, has 6 flows: (1) IN_{allo}, the input of allochthonous C to the DOC pool; (2) IN_{auto}, the input of autochthonous C to the DOC pool; (3) BR_{allo} and (4) BP_{allo}, the utilization of allochthonous DOC by bacterial respiration and bacterial production, respectively; and (5) BR_{auto} and (6) BP_{auto}, the utilization of autochthonous DOC by bacterial respiration and bacterial production, respectively. At a daily time step (d), autochthonous and allochthonous C enter the DOC pool; the only losses from the DOC pool considered by the model are BP and BR. The fraction of the DOC pool that is of autochthonous origin (DOC_{auto}) is calculated as $DOC_{auto(d-1)} + IN_{auto(d)} - BP_{auto(d)} - BR_{auto(d)}$.

The model is constrained by data and several assumptions. Since steady-state is imposed, the DOC pool remains constant. IN_{allo} is set to balance the excess of total system respiration (R) above gross primary production (GPP). IN_{auto} is derived by assuming that 10% of GPP is reoxidized by autotrophic respiration and that 13% of the resulting production per day is lost to the DOC pool according to the literature-based model estimate by Baines & Pace (1991). The input data used for the model (GPP, R and BP) were seasonal averages from field sampling of Peter Lake in 2001. This is a moderately unproductive (7 mg epilimnetic phosphorus m^{-3} and 3 mg chl *a* m^{-3}), slightly acidic (pH 6.9), small lake (2.5 ha). Further, it was strongly net heterotrophic as indicated by supersaturation in CO_2 (mean pCO_2 for the 2001 field season 673 µatm) and undersaturation in O_2 (mean saturation 94%). GPP and R were estimated from continuous measurements of water column dissolved oxygen using probes as described in Cole et al. (2000). A BGE value for the model (BGE_{tot}) was achieved by applying the seasonal average of BP in Peter Lake to Eq. (1) (see

'Results'), which was derived from the relationship between BP and BGE in the lake survey. Total BP (e.g. $BP_{auto} + BP_{allo}$) and total BR were related by BGE_{tot} and set to equal the inputs to the DOC pool ($IN_{auto} + IN_{allo}$) at steady-state. We varied 2 parameters, P_{assim} (the selectivity coefficient for DOC_{auto}; $1 - P_{assim}$ is the selectivity coefficient for DOC_{allo}), and the growth efficiency on allochthonous DOC (BGE_{allo}). The selectivity coefficient was defined as P_{assim} = (autofrac$_{bacteria}$/allofrac$_{bacteria}$)/(autofrac$_{DOC}$/allofrac$_{DOC}$), where autofrac is the fraction of bacterial carbon assimilation (BP + BR) and standing stock DOC that is autochthonous and allofrac the fraction that is allochthonous. BGE_{allo} and BGE_{auto} were restricted by BGE_{tot}. The model produces different responses of BP_{auto}, BR_{auto}, BP_{allo}, BR_{allo}, DOC_{auto} and DOC_{allo}, as they are constrained by the model equations.

RESULTS

Lake survey

The 10 lakes sampled covered a broad range in terms of DOC and chl *a* concentration (Table 2). Measured BGE values ranged from 0.01 to 0.34 (Table 2), with a majority (80%) of the measurements between 0.01 and 0.17. BGE was not significantly correlated to any of the environmental state variables we measured (pH, DOC, color, chl *a*, TDP or TDN), nor was it correlated to BR. BGE could, however, be predicted from BP and BA. BP explained 74% of the variation in BGE (Table 3, Fig. 1A) according to the hyperbolic equation:

$$BGE = 0.015 + 0.41 \times BP/(0.48 + BP) \quad (1)$$

BR was weakly correlated with BA (Table 3), but not with BP or any of the other measured variables. Because BGE is calculated from BP and BR, the form of the relationship between BGE and BP is a result of the equation itself (BGE = BP/[BP + BR]). However, the good correlation between BGE and BP is driven by the small range in BR over a wide range in BP, and the lack of correlation between BP and BR. Further, the 3 constants in Eq. (1) are a result of the way in which BP and BR (and therefore BGE) are related.

BP showed a positive relation with chl *a* and TDP (Table 3). TDP proved not to be significantly related to the residuals of the BP–chl *a* relationship ($r = 0.06$, $p = 0.79$). Thus, for a given concentration of chlorophyll, TDP did not explain any of the variation in BP. Similarly, the observed correlation between chl *a* and DOC was likely due to a strong relationship between DOC and TDP (Table 3), as there was no significant correlation between the residuals of the chl *a*–TDP relationship and DOC ($r = 0.09$, $p = 0.73$). BP was not correlated to DOC.

All the lakes, except for Brown Lake which was not sampled for DIC, were found to be supersaturated with CO_2. There was a strong positive relationship between pCO_2 and DOC in the lakes (Table 3). Based on previous measurements of DIC and pH, Brown Lake can be considered undersaturated in CO_2 (Reche et al. 1999).

Table 2. Parameters measured in the 10 survey lakes. DOC: dissolved organic carbon; Chl *a*: chlorophyll *a*; BA: bacterial abundance; BP: bacterial production; BGE: bacterial growth efficiency; pCO_2: partial pressure of carbon dioxide; H-bird: Hummingbird Lake

Lake	Day of year	DOC (g m^{-3})	Chl *a* (mg m^{-3})	BA (10^9 cells l^{-1})	BP (mg C m^{-3} d^{-1})	BGE	pCO_2 (µatm)
Roach	236	2.08	1.9	1.6	2.5	0.07	558
Crampton	174	3.64	3.3	1.2	1.2	0.02	725
	234	4.14	4.1	1.0	6.0	0.17	
Paul	191	3.65	4.3	2.3	9.9	0.05	1373
	212	3.76	6.5	2.2	7.9	0.13	
Peter	178	4.54	2.2	1.2	4.1	0.01	1129
	228	4.77	3.9	2.1	1.6	0.03	
Ward	230	6.5	8.3	3.2	5.8	0.10	2239
	240	6.47	6.3	2.9	6.5	0.12	
Brown	208	7.64	18.6	4.0	24.2	0.26	
	237	7.79	27.8	3.6	10.4	0.12	
Tuesday	238	7.57	6.1	2.2	6.4	0.15	1294
East Long	167	10.3	33.2	5.2	10.1	0.34	784
	231	9.87	5.2	2.7	4.1	0.20	
Morris	181	13	5.8	3.5	3.5	0.05	1782
	235	12.7	13.7	4.0	10.8	0.30	
H-bird	187	21	55.6	3.1	13.3	0.05	3354
	214	19.9	52.2	2.9	18.1	0.24	
	228	21.3	31.4	1.9	4.5	0.11	

Table 3. Significant correlations in the lake survey data. Correlations were performed on untransformed data (n = 20 except for pCO_2 with DOC, where n = 9). Significance: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. TDP: total dissolved phosphorus; BR: bacterial respiration. See Table 2 for other abbreviations

Correlation	r
BP and chl *a*	0.60**
BP and TDP	0.47*
Chl *a* and TDP	0.87***
Chl *a* and DOC	0.82***
TDP and DOC	0.91***
BGE and BP[a]	0.86***
BGE and BA	0.66**
BR and BA	0.54*
pCO_2 and DOC	0.79**

[a]All correlations are positive and linear except for BGE = $0.015 + 0.41 \times BP/(BP + 0.48)$

Steady-state model

Under the assumptions that bacteria utilize DOC unselectively ($P_{assim} = 1$) and that the growth efficiency is similar on autochthonous and allochthonous DOC, the model produces a scenario where both BP and total bacterial carbon consumption (BCC) is derived largely from allochthonous C (Fig. 2A). The same result is achieved if we assume equal growth efficiency but selective utilization of autochthonous C (Fig. 2B). However, the selective consumption results in a depletion of autochthonous C in the DOC pool. If bacteria utilize autochthonous DOC more efficiently than allochthonous DOC, BP is heavily dependent on autochthonous C, while total bacterial C consumption is mainly supported by allochthonous C (Fig. 2C). The bacterial dependence on the respective C sources is the same under the assumption that bacteria utilize autochthonous C both preferentially and more efficiently. The difference is a depletion of standing stock autochthonous C (Fig. 2D).

DISCUSSION

In the lake survey we found that BP explained most of the variation in BGE and that BP was correlated to chl *a*. In addition, the same lakes were net heterotrophic. The steady-state model suggests that higher BGE on autochthonous than on allochthonous DOC can explain how BP is controlled by primary production in systems where allochthonous C provides major support to lake metabolism.

The hyperbolic relationship between BGE and BP agrees with previous findings (del Giorgio & Cole 1998, Roland & Cole 1999). This relationship is in fact driven by an inherent autocorrelation in that BP is part of the BGE calculation and should not be looked at as a statistical number. The hyperbolic shape is a consequence of a lack of strong correlation of BP and BR in combination with a smaller dynamic range of BR compared to BP. Nevertheless this relationship is useful, since it implies that one can predict BGE for a given value of BP alone. For example, had BP and BR been well correlated and of the same dynamic range, the correlation between BP and BGE would be much weaker. Further, the 3 constants in Eq. (1) are the result of the way in which BP, BR, and therefore BGE are related, and are a statistical result. Data from this study provide a good fit to the models derived by Roland & Cole (1999) ($r = 0.83$, $p < 0.001$) and del Giorgio & Cole (1998) ($r = 0.84$, $p < 0.001$). However,

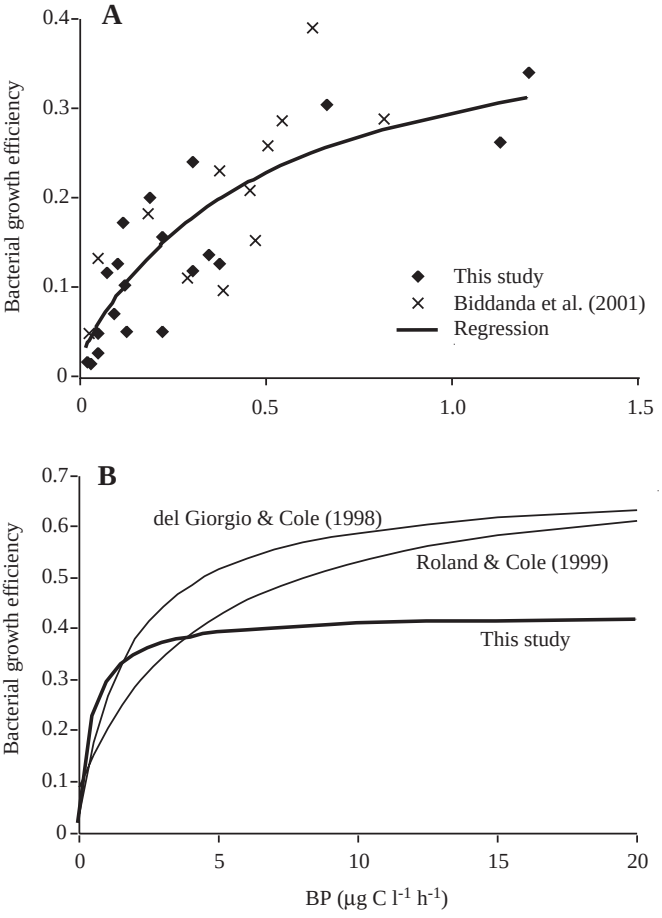

Fig. 1. Relationship between bacterial growth efficiency and bacterial production (BP). (A) ◆: data from our lake survey and the regression line is based on these points (BGE = $0.015 + 0.41 \times BP/[BP + 0.48]$; $r = 0.86$, $p < 0.001$). ×: data from a lake survey by Biddanda et al. (2001). (B) Regression lines from this study and studies by del Giorgio & Cole (1998) and Roland & Cole (1999)

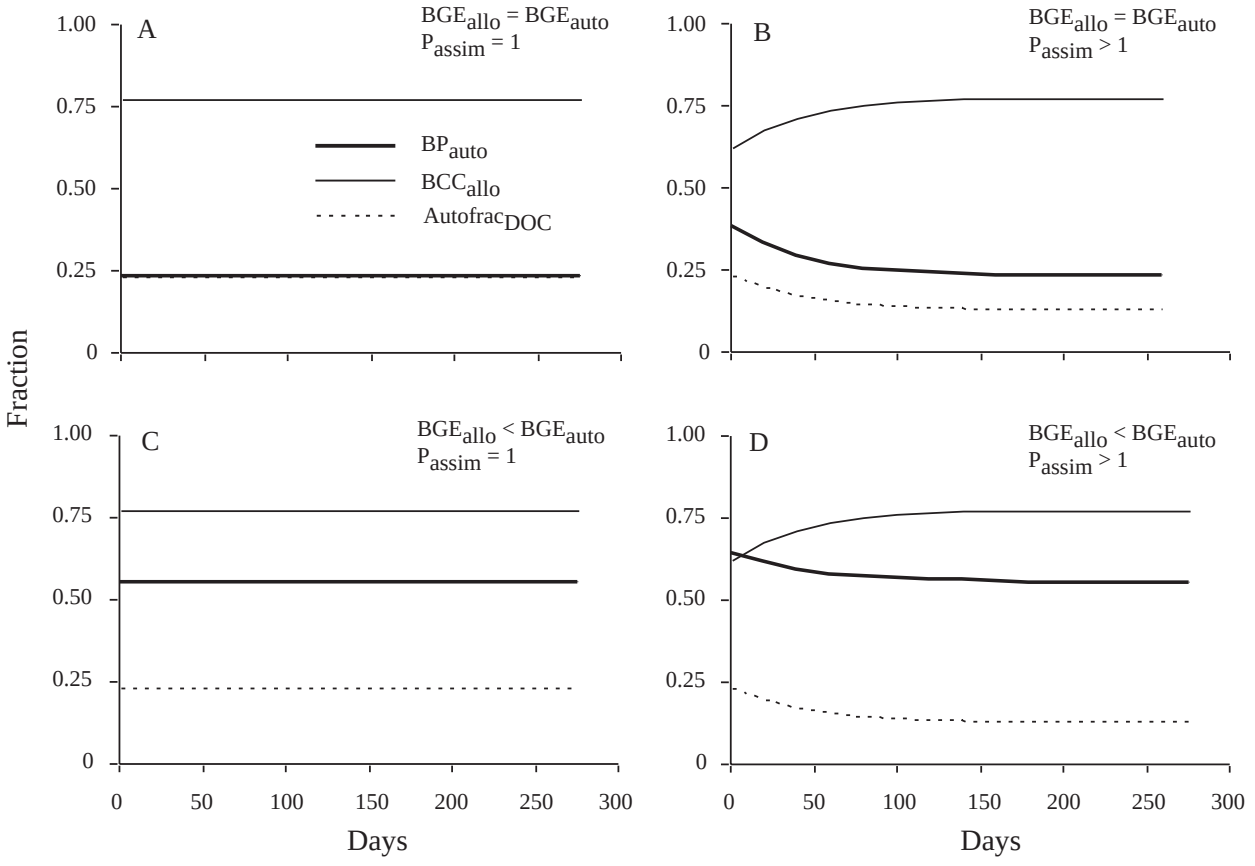

Fig. 2. Predictions from steady-state model simulations. BP_{auto}: fraction of BP that derives from autochthonous DOC; BCC_{allo}: fraction of total bacterial carbon consumption that derives from allochthonous DOC; $autofrac_{DOC}$: fraction of the DOC pool that is of autochthonous origin; BGE_{allo} and BGE_{auto}: bacterial growth efficiencies on allochthonous and autochthonous DOC, respectively; P_{assim}: relative availability; $P_{assim} > 1$: autochthonous DOC is more available to bacteria than allochthonous DOC; $P_{assim} = 1$: no difference in availability. In panel (A), the line for BP_{auto} covers that of $autofrac_{DOC}$

our model differs for higher values of BP with a more abrupt plateau for BGE (Fig. 1B). This results in a lower maximum BGE of 0.43 compared to prior models with maxima of 0.73 (del Giorgio & Cole 1998) and 0.69 (Roland & Cole 1999). The latter models might better describe the relationship between BGE and BP in more productive waters, since the lakes we sampled had a low range of BP (up to 1 µg C l^{-1} h^{-1}) compared to high values in Roland & Cole (1999) (12 µg C $l^{-1}h^{-1}$) and del Giorgio & Cole (1998) (40 µg C $l^{-1}h^{-1}$). Indeed, the BGE values from this survey are in the lower range of previously reported measurements (del Giorgio & Cole 1998). They are, however, quite similar to results from other lakes with a similar range of chlorophyll concentration (Fig. 1A) (Biddanda et al. 2001).

In the survey, BP was correlated with chl *a* but not with DOC, even though DOC and chl *a* covaried. This suggests that BP is regulated by resources provided from phytoplankton production, even if terrestrially derived C may support a baseline level of BP. Correlations between BA and chl *a* (Bird & Kalff 1984) and BP and primary production (Cole et al. 1988) suggest that algal-derived C regulates bacterial growth.

Supersaturation of CO_2 was related to DOC concentration in the lakes (Table 3), suggesting that the high levels of CO_2 were a result of respiration of terrestrial C (Hope et al. 1996, Kelly et al. 2001). Several of these lakes have previously been shown to be net-heterotrophic (Schindler et al. 1997, Cole et al. 2000, Hansson et al. 2003). Thus, total respiration is in part supported by imported terrestrial C. Furthermore, there is direct evidence from stable carbon isotope analysis that bacterial biomass in Paul and Peter Lakes was to a large extent of allochthonous origin, although autochthonous DOC was preferentially utilized relative to terrestrial DOC (Kritzberg et al. 2004). The emerging picture appears to be counterintuitive, with a series of lakes where BP varies with system trophic richness (chl *a*) although lake metabolism is largely supported by allochthonous C. A similar pattern was found in a survey by del Giorgio et al. (1999), where phytoplank-

ton biomass and bacterial abundance were strongly related ($r = 0.75$, $p < 0.001$) although 18 out of 20 lakes were net-heterotrophic. How is this possible?

Adopting different values of P_{assim} and BGE_{allo} in the steady-state model produced different scenarios with regards to bacterial dependence on autochthonous versus allochthonous DOC. The interpretation of $P_{assim} > 1$ is that autochthonous DOC is more readily available to bacteria than DOC of allochthonous origin. This is a reasonable assumption considering that the allochthonous C has undergone some degradation and transformation before entering the pelagic environment (Hobbie 1988). Moreover, the majority of terrestrially derived C enters the lakes as humic substances, which are large and chemically complex compounds that are slow to degrade (McKnight & Aiken 1998). Although there is accumulating evidence that some phytoplankton-derived DOC is refractory to bacteria (Sundh 1992, Chen & Wangersky 1996), the availability of algal DOC is generally high. Both autochthonous and allochthonous DOC are mixtures of compounds with varying and overlapping availability to bacteria, and the factor P_{assim} refers to the average availability of the DOC sources.

It is also reasonable to assume that bacteria grow more efficiently on autochthonous than allochthonous DOC. In general, algal DOC has a higher nutritional value (C:N ≈ 12:1) compared to terrestrially derived DOC (~50:1) (Wetzel 2001) and these differences in nutrient composition may be reflected in the BGE. Indeed, BGE is often inversely related to substrate C:N (Kroer 1993, Cimberlis & Kalff 1998). Moreover, compounds of low molecular weight are known to be more efficiently incorporated into bacterial biomass (Amon & Benner 1996).

When applying equal growth efficiencies on autochthonous and allochthonous DOC, the model produced a scenario where both BP and respiration were heavily dependent on terrestrial C (Fig. 2A,B). When we instead assumed that bacteria grow more efficiently on phytoplankton-derived DOC, BP was mainly dependent on autochthonous C, while the total DOC consumed by bacteria was mainly of terrestrial origin (Fig. 2C,D). This is in line with the results from the survey, where BP is correlated with chl *a* even when ecosystems are net-heterotrophic and rely partially on terrestrial C.

Interestingly, availability of the different C sources does not affect the proportions of autochthonous and allochthonous C that support BP and respiration. It does, however, cause a depletion of autochthonous C in the DOC pool. Fig. 2B,D shows the result of $P_{assim} = 2$; that is, autochthonous DOC is 2 times more available to bacteria than allochthonous C. The resulting fraction of DOC that is autochthonous is 13%, which is in accordance with results from whole-lake isotope additions in Peter Lake the same summer (Bade 2004, Kritzberg et al. 2004). $P_{assim} = 2$ is an arbitrary number, but in correspondence with the observed difference in $autofrac_{bacteria}$ and $autofrac_{DOC}$ from the same study.

Bacterial biomass in Peter Lake was on average between 30 and 63% autochthonous (Kritzberg et al. 2004). Setting BGE_{allo} from 0.07 to 0.12 gives the same variation in dependence on autochthonous C for BP in the model. The resulting BGE_{auto} is between 0.18 and 0.37. In the survey, we measured BGE values <0.07. This does not necessarily contradict the results of the modeling, since BGE on a particular substrate probably depends on more factors than the origin of the substrate, including the concentration and forms of inorganic nutrients as well as temperature (del Giorgio & Cole 1998 and references therein). The number we use for percent extracellular release of phytoplankton production is not a direct measurement, but a literature-based value (Baines & Pace 1991). The release of DOC from phytoplankton may vary, but the conclusions made from the model are also the same if we apply a number equivalent to half or double the amount of photosynthetic release.

According to the model, the relative dependence on autochthonous and allochthonous C is most heavily dependent on the relative size of the input. Obviously bacterial dependence on autochthonous C for production will decrease with decreasing relative input of autochthonous C. Thus, for lakes with very low primary production compared to terrestrial DOC input, BP should be highly dependent on allochthonous C and covary with DOC concentration. This is in accordance with the positive relationship found between bacterial biomass and DOC (Tranvik 1988) and BP and DOC (Karlsson et al. 2001) in 2 sets of oligotrophic lakes.

Other studies imply that BP and BGE are strongly connected to phosphorus, e.g. TDP was found to be the best predictor of BP and BGE in a survey of a trophic lake gradient by Smith & Prairie (2004), and Pace & Cole (1996), reported increasing BP in response to P enrichment regardless of the response by phytoplankton. Although BP was better predicted by chl *a* in this set of lakes, BP could still be stimulated by P additions (and has been; Pace & Cole 1996), either indirectly by increasing the production of autochthonous DOC or directly by enhancing the growth on ambient DOC. Additions of P probably facilitate an increased utilization of both autochthonous and allochthonous C, as both have a lower P:C content than bacteria (Redfield et al. 1963, Fagerbakke et al. 1996). This is in agreement with the increased degradability of DOC upon fertilization with P (Schindler et al. 1992).

Our steady-state model which simulated the utilization of incoming DOC is simplistic, ignoring other loss

factors from the DOC pool such as flocculation, sedimentation and photooxidation. When assuming that IN_{allo} can be estimated from the difference between R and net primary production, we disregard many processes such as zooplankton respiring allochthonous particulate organic C. Nevertheless, the model explains how BP in net-heterotrophic systems can be primarily determined by and strongly correlated with primary production. It also suggests that little of the allochthonous C assimilated by bacteria is likely to reach higher consumers. This does not mean that allochthonous DOC is not of great significance to the aquatic food web. Terrestrial C may reach higher consumers by other pathways, such as zooplankton grazing on allochthonous particulate matter (Pace et al. 2004).

Acknowledgements. We thank D. Bade, D. Bastviken, and M. Van de Bogert for help in the laboratory and field. R. Hellenthal, J. Runde, G. Belovsky and J. Caudel facilitated work at the University of Notre Dame Environmental Research Center, WI, USA. Financial support was provided in part by the National Science Foundation (DEB-9509595), the Swedish Research Council (VR) contract no. B 5103-649, the Crafoord Foundation and Stiftelsen Längmanska kulturfonden.

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Editorial responsibility: Gerhard Herndl, Den Burg, Texel, The Netherlands

Submitted: March 31, 2004; Accepted: October 17, 2004
Proofs received from author: January 17, 2005