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The magnitude of spring bacterial production in the North Atlantic Ocean

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Abstract

Dissolved organic carbon (DOC), a major reservoir in the ocean carbon cycle, is produced by a profusion of plankton sources and processes but is consumed mainly by bacterioplankton. Thus bacterial metabolism regulates the entry of DOC into the longer scale global carbon cycle. Bacterial production (BP) is the routinely measured quantity for evaluating the roles of bacteria in carbon cycling. However BP cannot be measured directly and instead is estimated from related metabolic processes requiring the use of poorly constrained conversion factors. BP, and thus the total carbon utilization, are potentially uncertain by a factor of two or more. In the North Atlantic Bloom Experiment (NABE), BP was estimated to be about 30% of the simultaneous particulate primary production (PP), with some daily estimates exceeding 50%. Here we reassess these estimates, synthesizing knowledge and understanding of plankton dynamics gained since the 1989 NABE study. Daily BP derived from six different conversion factors averaged 20% of PP but ranged from 3 to 68%. The coupling of BP to PP was not consistent with either short-term cycling of labile DOC (hours) nor with much longer term cycling of semilabile DOC (seasons). Trophodynamic processes, including release of DOC from phytoplankton, by themselves could have maintained BP at about 15% of PP. Use of decomposing POC or previously accumulated semilabile DOC could each have supported some additional increment of BP for brief periods. Both reconsideration of observations and model results indicated that higher estimates of BP exceeding 20% of PP could not be supported without extraordinary and prolonged inputs of allochthonous carbon. Recent assertions of high BP in the tropics and other oceanic regimes should be considered carefully, especially if external subsidies are not obvious.

Export of carbon from the surface to deep ocean via sinking particles or dissolved organic matter (DOM) depends on the balance between processes that generate these export products and processes that recycle them. The bacterioplankton are key players in this recycling, consuming low-molecular weight (LMW) DOM, respiring considerably more than half, and converting the rest into bacterial biomass (Azam and Hodson 1977; Carlson et al. 1999; del Giorgio and Cole 1998). Not all organic matter supporting bacterial secondary production originates as LMW-DOM, however. Both particle-associated and free-living bacteria can hydrolyze particulate matter, colloids, and large macromolecular polymers, producing smaller molecular weight DOM for subsequent consumption by themselves or other bacteria (Smith et al. 1992). Thus bacterioplankton are major actors in the play of ocean biogeochemistry, performing in the carbon cycle by regulating the entry of primary production into the large oceanic pool of dissolved organic carbon (DOC) and by de-composing the vertical flux of particles (Cho and Azam 1988).

Measurements of bacterial production (BP) conveniently, though not necessarily most accurately, help to quantify these manifold roles of bacterioplankton in the sea (Ducklow and Carlson 1992). It is important to realize in this context that bacterial respiration, but not BP, is constrained by the supply of carbon from primary producers (Anderson and Ducklow 2001). Rather, the ratio of BP to primary production will depend on the conversion efficiency and the degree of recycling and can theoretically exceed 1.0 when recycling is intense. A more informative measure of the bacterial role in the carbon cycle would therefore be bacterial respiration (BR), which can be inferred from BP if the bacterial growth efficiency (BGE) is known. The bacterial growth efficiency links observed BP to the total bacterial carbon demand (BP + BR = BCD). Early studies suggested BGE was high (50–90%), which led to relatively low BCD, which could be accommodated within flow analyses (Williams 1981). But more recent estimates for BGE are much lower, averaging about 15% (del Giorgio and Cole 1998; Carlson et al. 1999). If BGE is lower, BCD associated with a given BP is larger, and either extra sources of carbon may need to be postulated or BP estimates revised downward in order to balance carbon sources and sinks. BP:PP ratios are therefore useful indicators of the magnitude of the bacterial sink for organic carbon, but care has to be taken when interpreting them to

take account of recycling of organic matter by bacteria and potential sources of dissolved organic carbon (DOC) other than primary production (PP) and grazing (Anderson and Ducklow 2001). Such sources include phytoplankton excretion of extracellular organic carbon, temporal imbalances such as supply via a degrading organic matter pool that had accumulated earlier in the season, and allochthonous inputs.

The North Atlantic bloom experiment (NABE) provided some of the first estimates of BP during the conspicuous, basin-scale spring bloom event. During the main part of NABE in April–May, 1989, carbon-based, euphotic zone BP was reported as averaging about 30% of the integral daily *particulate* primary production (defined hereafter as PP) near latitude 47°N in the eastern and western basins (range, 14–80%: Ducklow et al. 1993; Li et al. 1993; Lochte et al. 1993). Net bacterial uptake of inorganic plus organic nitrogen was also high, ranging from 20 to 90% of the net primary production, expressed in nitrogen units (i.e., ^{14}C-PP divided by 6.7: Kirchman et al. 1994). At the time, the high values of BP compared to PP were not considered remarkable for a large phytoplankton bloom, when abundant organic matter was stored for possible later consumption. In addition, the mean BP : PP value was consistent with reviews of that ratio (Cole et al. 1988) as well as with earlier flow analysis models of BP (e.g., Williams 1981). However, many subsequent studies have reported lower values of BP : PP. For example, in most other open ocean locations studied in JGOFS, BP was seldom greater than 20% of PP (Ducklow 1999). In the North Atlantic, only the BATS data provide a long-term annual average (14% of PP). In the Antarctic, BP is low in absolute and relative terms, seldom exceeding 5% of the PP during the growing season (Bird and Karl 1999). Recently Zubkov et al. (2001) reported that BP was 4–14% of the daily PP along 20°W throughout the North and South Atlantic in July 1996. The difference in seasons made a direct comparison with the earlier measurements inconclusive. Most recently Hoppe et al. (2002) reported BP data from a long transect across the North and South Atlantic basins, similar to that occupied by Zubkov et al. (2001), finding BP : PP values of 1–10% north of 30°N in the North Atlantic but exceeding 40% in the tropics. They suggested that in the tropical Atlantic BCD > PP, suggesting that external subsidies of organic matter may be required. Thus BP : PP remains uncertain, with important considerations for regional and basin-scale carbon balance.

Modeling approaches can be used to yield new insights and help to add confidence to BP estimates by providing ecological context. Application of models incorporating ecosystem data from each specific study can be used to constrain the possible BP rates for a given set of conditions. Fasham et al. (1999) addressed the same region in the period just before that considered here, forcing a linear flow, difference equation model with observed primary and bacterial production. One implication of their model was that observed bacterial production and community respiration required large inputs of DOC, either from an existing pool or from (unmeasured) phytoplankton exudation. Anderson and Ducklow (2001) developed a steady-state flow analysis model to estimate BP : PP given the observed PP, a value of BGE (Carlson et al. 1999; Del Giorgio and Cole 1998), and rea-

sonable assumptions about zooplankton and phytoplankton ecology, including exudation rates of DOC from phytoplankton (PER). Their model indicates that if BGE is as low as 0.1–0.2 then, at least at steady state, fluxes of DOC arising directly or indirectly from PP would be expected to generate BP : PP in the range 5–20% depending on recycling parameters and the magnitude of phytoplankton exudation. Fasham et al. (1999) took the BP estimates as given and did not consider uncertainty in them. In this paper we reconsider the original NABE BP data and the derivations of the NABE BP estimates. We show that the higher BP : PP estimates cannot be sustained by rapidly cycling labile DOC produced by trophic processes and consider possible alternate sources of DOC, for example via supply of semilabile material (particulate organic carbon, POC or DOC). We conclude that the supply of DOC produced by foodweb processes is not sufficient to support the original estimates of BP made for NABE, even when subsidized by a drawdown of a previously accumulated DOC or POC. Revised BP estimates are discussed.

Methods and materials

[3]H-thymidine (TdR) and ^{3}H-leucine (Leu) incorporation were measured daily at the NABE site (nominally 47°N, 20°W) between 18 and 31 May 1989 throughout the upper 200 m, as described in Ducklow et al. (1993). Thymidine and leucine incorporation measure DNA synthesis and protein synthesis, respectively, and are complementary aspects reflecting bacterial division and growth processes. Rates were integrated through the euphotic zone (EZ) following the depths sampled for in situ ^{14}C incorporation measurements of particulate PP (Martin et al. 1993), interpolating between sampled depths where depth of the base of the EZ was not sampled for BP. The bacterial data as well as PP data and other environmental data were retrieved from the U.S. JGOFS database (http://usjgofs.whoi.edu/jg/dir/jgofs/nabe/atlantisII/).

BP was derived from the incorporation rate measurements using empirical factors obtained during four, 40-h incubation experiments described in Ducklow et al. (1992). Several different factor values were derived using the two precursors and two different algorithms (Table 1). The modified derivative method (Kirchman and Ducklow 1993; Kirchman et al. 1982) was used to derive the BP estimates in the original NABE report (Ducklow et al. 1993). This approach calculates a factor value (CF; Tdr-1 and Leu-1 in Tables 1, 3) that equals the product of the abundance, N, and an independently estimated specific growth rate, μ (usually from changes in cell abundance over time), divided by the incorporation rate, T:

$$CF = [\mu \times N]/T \qquad (1)$$

assuming exponential growth of the enclosed population. Li et al. (1993) and more recently Zubkov et al. (2001) used the cumulative approach of Bjørnsen and Kuparinen (1991) in which the successive abundance estimates made during an incubation are plotted against the cumulative incorporation rate, integrated over time:

Table 1. Empirical conversion factors* employed for estimating BP in US NABE.

May date	TdR-1	TdR-2	Leu-1	Leu-2
	10^{18} cells produced mole^{-1} incorporated			
24	2.03			
26	2.26	0.67	0.14	0.044
28	3.69	0.67		
30	2.65	1.5	0.22	0.13
Mean	2.66	0.95	0.18	0.087
	kg C produced mole^{-1} incorporated (factors above multiplied by 2×10^{-14} gC cell^{-1})			
24	40.6			
26	45.2	13.4	2.8	0.9
28	73.8	13.4		
30	53.0	30.0	4.4	2.6
Mean	53.1	18.9	3.6	1.7

* TdR-1 and Leu-1 were derived by the modified derivative method; TdR-2 and Leu-2 were derived with the cumulative method; *see text for details.*

$$\sum_0^i (N_i - N_0) = \mathrm{CF} \int_0^i \mathrm{TdR} + b \qquad (2)$$

where the i are successive time intervals (sampling points in the time course) and the CF is the slope of the plot (TdR-2 and Leu-2 in Tables 1, 3). This is an empirical approach that makes no assumption about the form of growth. Unless growth is closely balanced, i.e., increases in T exactly mirror increases in N, the cumulative approach tends to give lower values than the modified derivative method (e.g., Table 1).

BP estimated using either approach also requires another factor to derive biomass production (usually as carbon). Various literature values for the mass of carbon per cell have been employed for this purpose (Caron et al. 1995; Christian and Karl 1994). Li et al. (1993) and Ducklow et al. (1993) both used 20 fgC cell^{-1} (1 fg = 10^{-15} g), and that value is used here for consistency. More recently, lower carbon per cell values have been used (Carlson et al. 1999; Zubkov et al. 2001), thus again yielding a different biomass production rate for the same incorporation rates. An alternative avoiding the use of *two* possibly poorly constrained CF is the theoretical factor directly relating leucine incorporation and carbon biomass production (Simon and Azam 1989), with a value of 3–1.5 kgC mole^{-1} incorporated. These two theoretical values were also employed to estimate BP (Leu-3 and Leu-4, respectively).

Results

BP and PP estimates—During the second U.S. JGOFS NABE cruise, the euphotic zone (EZ, 0.1% of surface irradiance) averaged 50 m in depth, and EZ Chl *a* stocks peaked near 100 mg m^{-2} then declined (Table 2). Irradiance varied by a factor of five (Table 2) as several low pressure cells passed over the study area, and PP varied accordingly (Fig. 1; Martin et al. 1993). Event-scale variations in PP appeared to be a key factor governing C flows in this system, as discussed below. ^{3}H-thymidine and ^{3}H-leucine incorporation rates varied by a factor of 2–3, out of phase with PP (Fig. 1B,C). Thymidine incorporation rates were higher later in the cruise (Fig. 1B), and bacterial stocks rose by a factor of 2 (Table 2).

Six different conversion factor values were used to derive BP estimates from the original incorporation data (Table 1, Fig. 2A). TdR-1,2 and Leu-1,2 are the empirical factors for thymidine and leucine, respectively (Ducklow et al. 1992). In addition, the theoretical leucine factors specified by Simon and Azam (1989), 3 and 1.5 kgC mole^{-1}, were also used (Leu-3 and Leu-4 in Table 3). With these CF, an array of BP estimates was calculated (Table 3), ranging from 65 (23 May, Leu-4) to 503 mgC m^{-2} d^{-1} (25 May Leu-1). The overall mean BP, taking all estimates into account, rose throughout most of the cruise (Fig. 1D) and was 208 ± 53 mgC m^{-2} d^{-1}, about 19% of the mean PP (Table 3, Fig. 2A,B). The estimate derived from the Leu-4 (theoretical)

Table 2. Euphotic zone depth, irradiance, primary production, standing stocks, and bacterial precursor incorporation rates for the NABE region 47°N, 20°W, 18–31 May 1989. nd, no data.

| May date	EZ (m)	PAR (E m^{-2} d^{-1})	PP (mgC m^{-2} d^{-1})	Chl (mg m^{-2})	POC (mgC m^{-2})	Cells (10^{13} cells m^{-2})	TdR	Leu
							(pmol m^{-2} d^{-1})	
18	48	26.1	1,173	56	7,438	6.1	289	4,243
19	63	38.8	1,360	82	nd	5.2	147	3,328
20	63	12.2	712	57	6,499	4.7	223	2,743
21	nd	10.0	650	nd	nd	nd	nd	nd
22	49	39.5	1,366	74	8,867	4.6	331	nd
23	53	48.4	1,562	72	7,261	5.9	172	1,802
24	54	30.6	1,251	95	7,696	5.4	152	4,452
25	45	13.5	876	94	7,481	4.8	163	5,825
26	45	16.5	890	78	6,123	6.1	169	5,107
27	45	13.0	658	75	7,237	7.5	329	2,267
28	45	14.5	821	85	8,407	8.0	244	4,359
29	45	50.1	1,230	52	6,284	9.3	232	4,242
30	45	39.0	1,362	42	6,753	11.0	261	4,435
31	45	34.5	1,259	53	7,254	12.0	321	3,894
Avg.	50	27.6	1,084	70	7,275	7.0	233	3,891
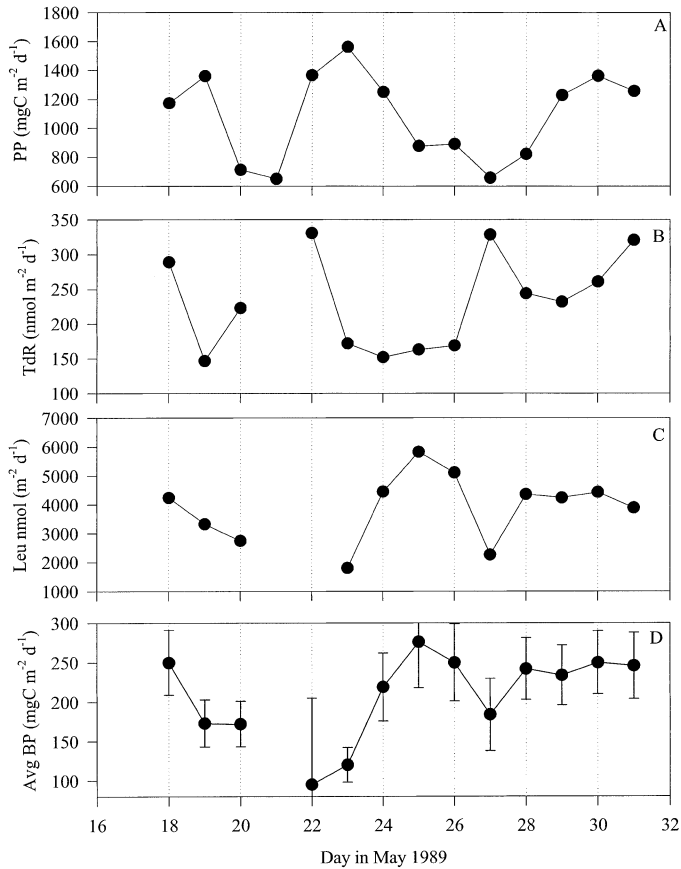
Fig. 1. Time series of (A) primary production, (B) euphotic zone ^{3}H-thymidine (TdR) incorporation rate, (C) euphotic zone ^{3}H-leucine (Leu) incorporation rate, and (D) average bacterial production rate derived from TdR and Leu estimates (± standard error; *see text for details*).
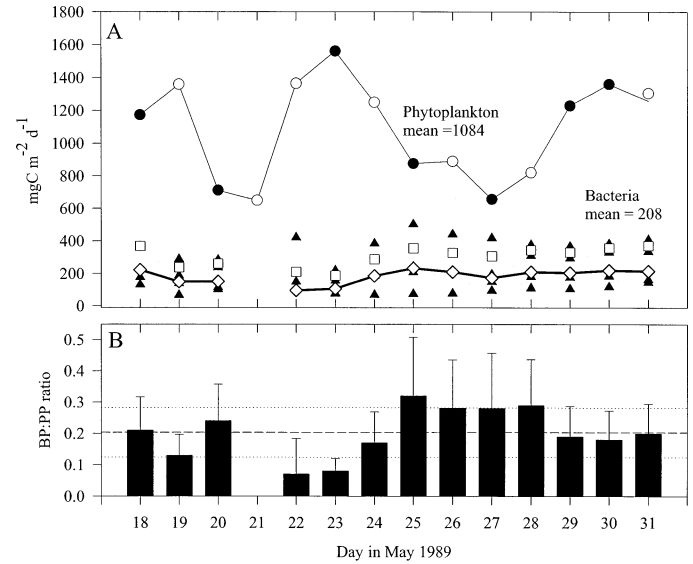

Fig. 2. (A) PP and BP estimates at NABE site. BP: heavy line with open diamonds is mean of all six estimates given in the last column of Table 3. The two thin dotted lines are the estimates using the theoretical Leu factor values (1.5 and 3 kgC mole^{-1}). PP: closed circles, in situ ^{14}C incubations; open circles, estimated from PAR after Martin et al. (1993). (B) mean BP:PP ratio derived from mean BP and PP estimates. Error bars are the standard deviations of all six estimates (Table 3). The reference lines indicate the overall means ±1 SD of the daily BP:PP estimates.

factor (1.5 kgC mole^{-1}) closely approximated the overall average from all six factors (Fig. 2A) but was significantly different from the mean of the four empirical factors (Table 3, *t*-test, $p < 0.001$). The mean rate for the four empirical estimates, 227 mgC m^{-2} d^{-1}, was not significantly different

Table 3. Bacterial production near 47°N, 20°W in the U.S. JGOFS NABE cruise, May 1989, based on ^{3}H-thymidine (TdR) and ^{3}H-leucine (Leu) incorporation rates using various conversion factors (*see Methods and Table 1*). The Leu-3 and Leu-4 factors were derived using the values 3 and 1.5 kgC mole^{-1} recommended by Simon and Azam (1989).

May date	TdR-1	TdR-2	Leu-1	Leu-2	Mean*	Leu-3	Leu-4	Mean†
	(mgC m^{-2} d^{-1})							
18	368	131	367	177	261	306	153	250
19	187	67	288	139	170	240	120	173
20	284	101	237	115	184	197	99	172
21								
22	421	150			285			95
23	219	78	156	75	132	130	65	120
24	193	69	385	186	208	321	160	219
25	208	74	503	243	257	419	210	276
26	215	77	441	213	236	368	184	250
27	418	149	196	95	214	163	82	184
28	311	111	377	182	245	314	157	242
29	295	105	367	177	236	305	153	234
30	332	118	383	185	255	319	160	250
31	409	146	336	163	263	280	140	246
Mean	297	106	336	163	227	280	140	208
SD	84.5	30.1	96	47	42	80	40	53
BP:PP	0.27	0.10	0.31	0.15	0.21	0.26	0.13	0.19

* Mean of the four empirical estimates.
† Mean of all six estimates.

from the overall mean ($p > 0.05$). The mean of the original BP estimates, derived from Tdr-1 and Leu-1 (Ducklow et al. 1993) was significantly greater than the overall mean BP from all the estimates ($p < 0.001$). The overall mean BP was more uniform over time than the individual estimates, in part because TdR and Leu incorporation tended to vary out of phase with each other (Fig. 1B,C). Mean BP : PP estimated from the various alternative values for BP ranged from <10 to >30% (Fig. 2B), with individual estimates (Table 3) ranging from 0.03 (Leu-2, May 23) to 0.68 (Leu-3, 25 May).

Sustenance of BP—TdR and Leu-based EZ-BP were not correlated with PP, even accounting for response lags (Figs. 1, 2, 3). The absence of any relationship suggests a lack of direct coupling between photosynthesis and BP, at least over a scale of a few days. Variations in photosynthesis, and the resulting fluxes of DOM to bacteria were not reflected in BP variations over the time scale of the cruise. The time series of average BP (Figs. 1C, 2A) was more uniform, with daily variations of 20–60 mgC m^{-2} d^{-1}, or about 5% of the mean PP. It seems possible that recent products of photosynthesis entered a more slowly cycling pool that buffered the BP (and BP : PP) variability. Nonetheless we show that mean BP was about 20% of PP during May 18–20 and May 29–31 (Fig. 2). Following a storm on May 21, PP almost tripled, with a decline in BP : PP to 5–15%. Then as PP declined, BP : PP increased to about 30% for 4 d before returning to the mean value toward the end of the cruise. This pattern suggests a coupling timescale of about 4 d, consistent with the event-scale passage of storms at this time. But lack of correlation between BP and PP forces us to focus on the mean fluxes for the cruise rather than trying to explain the short-term variability.

Reliable DOC data do not exist for JGOFS-NABE, preventing a comparison of variations in the dissolved semilabile pool, which accumulates and degrades on seasonal timescales (e.g., Anderson and Williams 1998), with BP (Fasham et al. 1999). We compared mean euphotic zone BP with mean POC concentrations (POC stock divided by the EZ depth) to remove the variation in stock contributed by changing EZ depth (Fig. 4A,B). POC concentrations and the mean BP varied roughly in phase and were significantly correlated (Fig. 4C), which suggests that the flux of organic matter into bacteria was controlled by variations in POC. POC concentrations varied daily by ~20–60 mgC m^{-3} d^{-1}, an amount approximating the daily PP in the upper 20 m. The magnitude of POC variation greatly surpassed the daily variations in BP, which suggests that POC decomposition might have supported some of the BCD. The bacterial contribution to the POC pool itself was low (Ducklow et al. 1993).

Discussion

The true ratio of BP : PP varies as a consequence of differences in foodweb structure and the consequent magnitude and composition of organic matter fluxes, bacterial growth efficiency, and temperature (Pomeroy and Wiebe 2001). There are several reasons for variations in BP : PP estimates besides those inherent to ecological space–time variability.
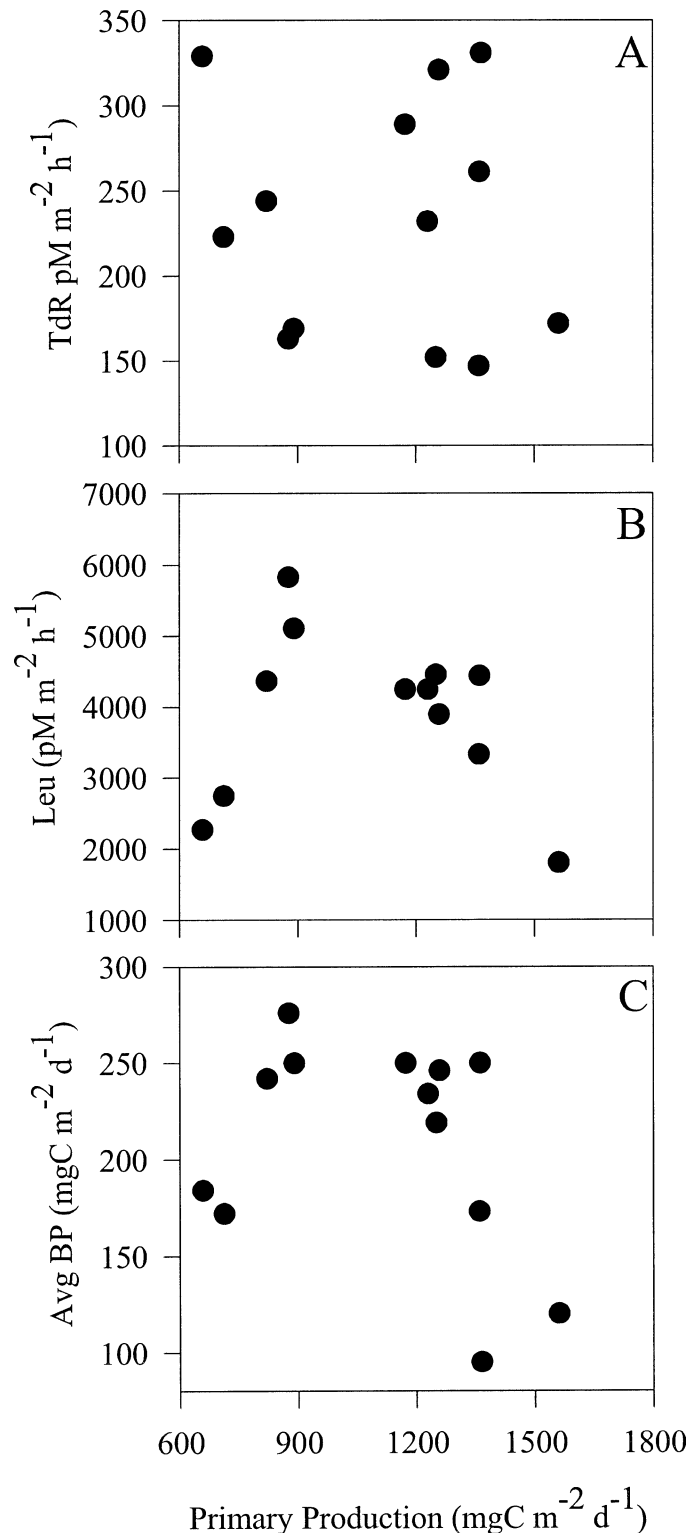

Fig. 3. Bacterial incorporation data vs. PP. (A) Thymidine incorporation; (B) leucine incorporation; (C) overall mean BP derived from the TdR and Leu rates (*see text for details*).
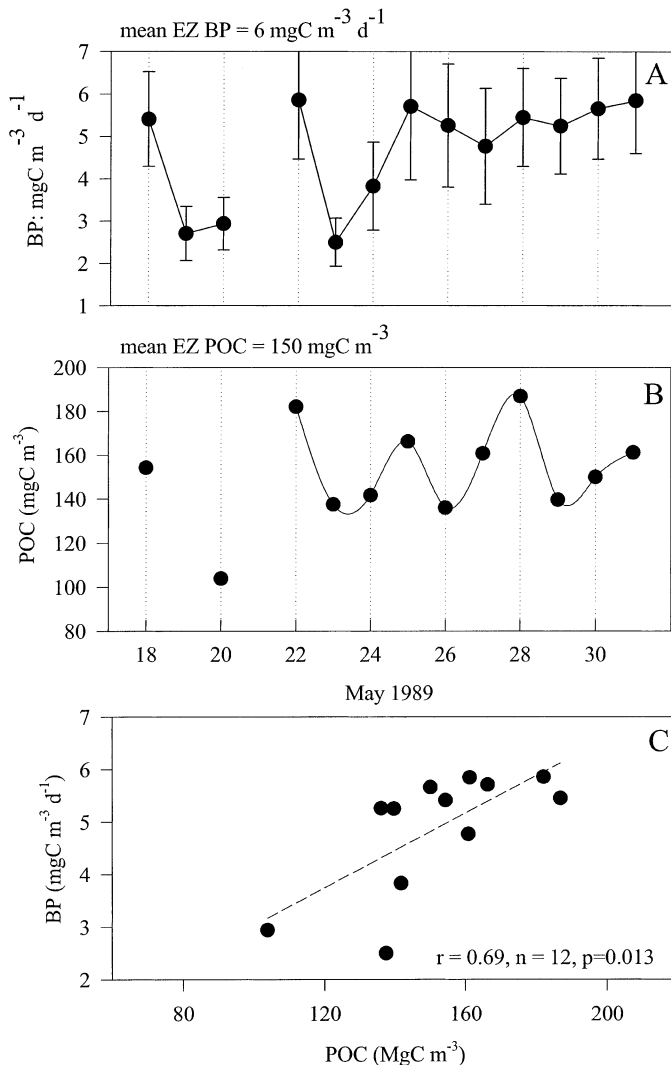
Fig. 4. (A) Mean euphotic zone BP (mean BP divided by EZ depth $\pm$ standard error) and (B) mean EZ POC stock. Note day to day variability in POC could support high BP, but BP and POC vary in phase; i.e., increases in BP do not coincide with decreases in POC. (C) Relationship (no lag) between BP and POC.

different algorithms to derive CF for their simultaneous studies in different regions of the North Atlantic, resulting in different estimates of BP from the same range of precursor incorporation rates. Containment affects the microbial populations enclosed in bottles during experimental incubations, resulting in metabolic and taxonomic shifts that could also impact the CF values. To minimize containment effects, BP incubations are usually much shorter than PP incubations (1–2 h), and the disparity in time scales for the two measurements also complicates comparison. Others have made the point that the magnitude of bacterial production estimates depends critically on indirect measurements and poorly constrained conversion factors (Ducklow and Carlson 1992). Empirical factors derived over the course of the NABE cruise for two different precursors (thymidine and leucine) yielded a wide range of values and an overall average BP : PP of about 20% (Table 3, Fig. 2). The 13 daily estimates of BP varied by a factor of 3–7, with a mean coefficient of variation of 0.52 (Table 3).

The majority of BP in the euphotic zone is usually thought to be sustained by the flux of fresh DOM released through physiological processes and trophodynamic encounters (Nagata 2000). Thus BP would be expected to fluctuate in response to production of labile DOC by the plankton ecosystem, e.g., fluctuations resulting from short-term changes in PP. Here, we estimate the flux of fresh DOM supporting BP using flow analysis (Anderson and Ducklow 2001). We then examine possible additional sources of organic matter to support BP, such as degrading stocks of previously accumulated POC or DOC, as a means of explaining the BP : PP estimates higher than levels that can be supported by short-term production of fresh DOC by foodweb processes. The approach is complementary to the top-down strategy used by Fasham et al. (1999), who forced a linear flow analysis model of the NABE observations with measured BP and community respiration estimates and determined what levels of gross primary production (GPP) and phytoplankton exudation (PER) were required to support the observations. Our bottom-up method starts by generating the DOM supply from foodweb processes and asking what BP : PP it would support, given various levels of BGE and PP. Fasham et al. (1999) concluded that either a large amount of phytoplankton exudation (drawn from increased GPP, a fresh DOC scenario) or use of a large preexisting DOC pool (older DOC alternative) was required to simulate the observed respiration levels. The lack of reliable DOC measurements precluded evaluation of these two alternative scenarios. Their older DOC scenario resulted in a 17 gC m^{-2} decline in DOC stocks over 20 d, or about 3 μMC d^{-1} in the upper 35 m, not an unreasonable rate. But they noted that DOC is more commonly observed to increase, rather than decline, during a bloom and favored the fresh DOC scenario—even though it required rather large rates of phytoplankton exudation and respiration (i.e., high GPP).

Phytoplankton exudation (PER) was not measured in NABE and is not routinely measured during in situ ^{14}C incubations, but many other data are available, allowing us to consider what values for PER are acceptable or excessive. Baines and Pace (1991) reviewed 16 studies and 225 measurements of PER in marine and freshwater systems and

First, there might be errors in the estimates of PP. PP in NABE was measured by 12 and 24 h in situ incubations with Carbon-14 (Martin et al. 1993). Although such determinations can vary between values closer to either net or gross primary production, they appeared to be reasonable estimates of net PP in NABE (Chipman et al. 1993). If the ^{14}C estimates were closer to GPP, a given BP value would yield a lower BP : PP than if the PP estimate were closer to net PP. BP itself cannot be measured directly and empirical or theoretical conversion factors (CF) are required to translate measured precursor incorporation rates (^{3}H-thymidine and ^{3}H-leucine incorporation) into BP in mass units (e.g., mgC m^{-2} d^{-1}; Kirchman et al. 1982). CF values have units of cells produced per mole of precursor incorporated and vary depending on the experimental conditions and design employed to determine them (Ducklow et al. 1992). For example Ducklow et al. (1993) and Li et al. (1993) employed
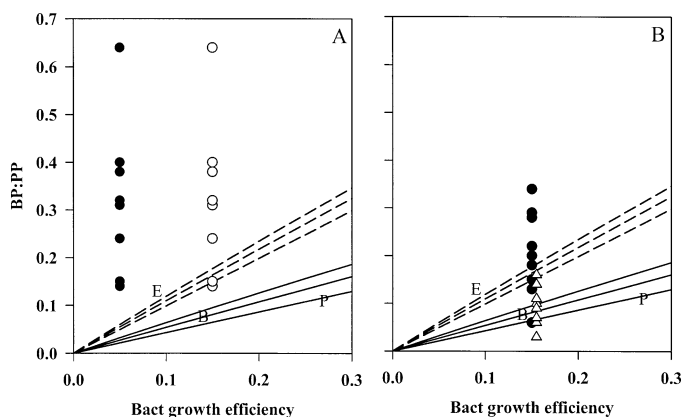
Fig. 5. (A) Model predictions of BP:PP assuming phytoplankton extracellular DOC release (PER) of 10% (solid lines) and 40% (dashed lines). Symbols: original BP estimates using TdR-1 factor (Tables 1, 2), assuming 5% BGE (solid circles, as originally determined by Kirchman et al. 1991) and 15% BGE (open circles). E, P, B (obscured by lines) show means for EQPAC, BATS, and Sta. P observations as in Anderson and Ducklow (2001). The three lines in each set indicate model sensitivity to zooplankton release and excretion of DOC (parameter K_c). (B) Comparison of modeled BP: PP (as in A) and revised BP:PP calculated using the Leu-2 factor (open circles) and overall mean BP:PP (closed circles). *See also Tables 1, 2.*

found that PER averaged 13% of particulate PP (95% confidence intervals 2–50%). Recently Teira et al. (2001) made a comprehensive series of measurements along a productivity gradient off the Spanish Coast, finding PER was a mean of 7% of PP in the coastal upwelling area and 28% in offshore, oligotrophic waters. Thus recent data sets as well as earlier reviews suggest that while values upward of 40% do occur, mean values are usually in the range of 10–20% of the particulate production rates normally measured with ¹⁴C.

Here we use the flow analysis model of Anderson and Ducklow (2001) to provide estimates of the baseline BP, resulting from the production of labile fresh DOC from trophodynamic processes (the recent products of photosynthesis and grazing). The flow analysis is used to set a lower limit for BP:PP without subsidies of previously produced and stored DOC or externally supplied DOC. Although the marine ecosystem as a whole is not in a steady state during the spring bloom period, the rapid processing of labile DOM by the microbial loop means that fluxes of fresh labile DOC at any one instant can nevertheless be approximated using the steady-state equations. If BGE < 0.3 then the model indicates that BP:PP in the range 0.05–0.15 could be supported with low exudation of DOC from healthy phytoplankton (PER ~10%) and additional DOC production by grazers. The allowable BP:PP would increase to 0.15–0.35 at high PER ~40% (Fig. 5). At low PER, grazer-mediated processes would contribute the major fraction of labile DOC, whereas at higher PER, phytoplankton excretion would contribute around half the DOC supply (Anderson and Ducklow 2001). Kirchman et al. (1991) originally estimated that BGE during NABE was very low, around 5%, but this figure represented growth on semilabile DOC. The original NABE BP:PP estimates (Ducklow et al. 1993) are plotted against the pre-

dicted BP:PP in Fig. 5A (closed circles). It is clear that none of these values could be sustained on the supply of recently produced DOC alone, even with a PER of 40%, an unlikely but not impossible value for healthy phytoplankton. Even raising the BGE to 15% to bring it into line with other estimates (del Giorgio and Cole 1998; Carlson et al. 1999) leaves most of the original values outside the permissible range (Fig. 5A, open circles). But other CF values (Table 1) produce lower BP:PP estimates (Table 3, Fig. 2), which are accommodated within the model range. For example, the Leu-2 factor yielded a low set of BP:PP estimates that fall largely within the envelope specified by the steady-state model (Fig. 5B). The overall mean estimates, as expected, span a range for which only the lower values seem permissible without a DOC subsidy. The overall average BP:PP of 20% cannot be supported at BGE of 0.15 unless PER is very high (>40%), as suggested by Fasham et al. (1999). Since such a high PER for the entire period seems unlikely, we consider that even the mean BP estimates are unacceptably high.

It appears unlikely that the higher estimates of BP generated by some CF values could be valid unless bacteria could exploit previously accumulated POC or semilabile DOC, in addition to the fresh DOC generated by recent food-web processes. We now examine scenarios for POC and DOC subsidies. High BP:PP can be explained by invoking use of accumulated organic matter (POC or DOC) from an earlier period (Ducklow et al. 1993; Fasham et al. 1999). Mean euphotic zone POC varied daily by up to 4 gC m⁻² (cf. Table 2, Fig. 4B), which implies potentially large fluxes of POC-derived organic matter to bacteria, if the apparent losses were due to decomposition or dissolution into labile DOC. Particulate aggregates can support intense enzymatic activity and release DOC for consumption by free bacteria (Smith et al. 1992). Of course, not all the apparent POC losses suggested in Fig. 4 were due to in situ decomposition. The export of POC via sedimentation out of the upper euphotic zone (35 m) was estimated from a thorium-234 balance because the shallowest sediment traps were deployed at 150 m, well below the euphotic zone. The thorium-derived export was 240–924 mg C m⁻² d⁻¹ during 19–30 May 1989 (Buesseler et al. 1992), up to half the daily variability in POC. Thus, of 15 gC m⁻² produced during the study period, about half (13 d × 500 mgC m⁻² d⁻¹) was lost to sedimentation. Since POC stocks did not increase over the study period (Fig. 4), the rest of the production must have been grazed, advected away, or else dissolved or decomposed in situ. Advection is probably not important because the NABE study was conducted within the Lagrangian frame of a mesoscale eddy (Lochte et al. 1993), which retained water column constituents within the study region. These considerations suggest that although there were several large day to day excursions in the POC stock, production was closely balanced by a combination of grazing and sedimentation, leaving little of the ambient standing stock available for decomposition-mediated fluxes from POM to DOM to the dominant free-living bacterial assemblage. Still, grazer-mediated DOC release from grazing on the POC pool could have supported some additional BP. If half the maximum daily change in POC (~2000 mgC m⁻² d⁻¹) were due to

Table 4. Microbial carbon demand budget for NABE region, 47°N, 20°W, 18–31 May 1989 (*see text for details*).

Budget term	mgC m^{-2} d^{-1}
PP	1,134
Export	500
Bacterial carbon demand (using BGE = 0.15)*	
High, from BP (Leu-3)	2,240
High, from BP (TdR-1)	1,980
Mean, from mean BP	1,387
Low, from BP (Leu-2)	933
Low, from BP (TdR-2)	707
Carbon sources to support BGE	
Foodweb DOC flux, PER = 10%†	605
Foodweb DOC flux, PER = 40%†	1,285
Particle decomposition‡	384
Total	990–1,670

* From BP estimates in Table 3 using BCD = BP/BGE.
† Calculated from Eq. 2 in Anderson and Ducklow (2001).
‡ Hoppe et al. (1993), *see text for details.*

removal by grazers, the resulting DOC production would be ~800 mgC m^{-2} d^{-1} (~40% of ingestion; Anderson and Ducklow 2001), supporting an additional BP of (ignoring recycling by the microbial loop) 120 mgC m^{-2} d^{-1} at BGE = 15%, or 8% of the PP. Clearly use of the POC pool could not support much additional BP.

During the period immediately preceding the studies reported here, and in a different part of the eddy field, Hoppe et al. (1993) estimated hydrolytic enzyme activity, an index of particle breakdown. They estimated breakdown of the PON pool (450 mg N m^{-2}) to be 56 mg N m^{-2} d^{-1} in the upper 30 m, or about 0.1 per day. Converted to carbon using C:N of 7.9 (Ducklow et al. 1993), the breakdown rate translates to 384 mg C m^{-2} d^{-1}. At a conversion efficiency of 15%, this flux could have supported BP of about 58 mg C m^{-2} d^{-1}, or about 25% of the overall mean BP (Table 3).

The other potential carbon subsidy is semilabile DOC, which could have accumulated as observed elsewhere in the North Atlantic (Carlson et al. 1994). As a simple illustration of the potential of semilabile DOC to support additional BP, consider a semilabile pool of 25 μM C in the euphotic zone. In NABE, the mean BP was 20% (Table 4) of PP of ca. 1,200 mgC m^{-2} d^{-1}, or ~8 mg C m^{-3} d^{-1} in a 50-m euphotic zone. If BGE = 20%, the bacterial carbon demand (BCD) would be roughly equivalent to the PP (24 mg C m^{-3} d^{-1}). A 25 μM C (600 mg m^{-3}) DOC pool undergoing first-order decay at 0.1 d^{-1} yields a flux of 29 mg C m^{-3} d^{-1} declining to zero over about 25 d. Thus semilabile DOC use could initially supply about 100% of the BCD, for BP:PP and BGE = 20%. A larger DOC pool (50 μM C) decaying at 0.01 d^{-1} would yield a flux of 6 mg C m^{-3} d^{-1} or about 25% of the PP. Greater values for BP:PP or smaller values of the BGE demand greater fluxes from the semilabile DOC pool. The size of the semilabile pool in the North Atlantic study area is presently unknown. Maximum accumulations near Bermuda, where productivity is lower, reach about 30 μM C (Carlson et al. 1994). Decay rates are poorly studied and not well constrained and appear closer to 1% than 10% d^{-1}

(Anderson and Williams 1999; Carlson and Ducklow 1996; Zweifel et al. 1996) but can be higher (Gasol et al. 1998). Thus it seems that subsidies of previously stored DOC might be 50–100% of the PP (supporting BP:PP of 5–15%) for brief periods but are unlikely to be much greater and if they should become greater, then it would not be for very long. It is clear that some of the larger individual observations of BP:PP shown in Fig. 5 need extraordinary subsidies to be maintained over any period and are probably unrealistic estimates.

The high growth rates of bacteria and their protozoan grazers mean that any labile DOC that becomes available for bacterial consumption is rapidly used and cycled through the microbial loop, with concentrations of labile material remaining low, i.e., fluxes in the loop are controlled by bottom-up factors. We therefore expected BP to be coupled to instantaneous DOC supply, i.e., fluxes within the microbial loop to be in approximate steady state, assuming that bacteria are limited by carbon (Carlson and Ducklow 1996). But BP was not closely coupled to variations in PP (Figs. 1–3). The lags between high BP and high PP (Figs. 1, 3) are not consistent with either the relatively instantaneous transfer of labile LMW compounds from planktonic sources to bacteria or with the production and use of semilabile DOM. The former processes are coupled over minutes to hours, whereas the latter processes are coupled over much longer (seasonal–interannual) time scales. Event-scale variations in PP generated intermittent fluxes through the foodweb resulting in transient bursts of BP, at least as detected by TdR and Leu incorporation (Fig. 1), which are not easily explained by use of either labile of semilabile DOM. One possibility is that during conditions driving the 2–3-fold variations in PP, DOM of intermediate lability with turnover times of 1–10 d was produced. Another explanation is that modulation of the labile DOM flows by poorly understood dynamic foodweb processes generated the observed BP:PP variability. Even simple time-dependent models (e.g., Fasham et al. 1999) are inadequate to examine this process much further than we attempt here. More complex, time-dependent models and new observations are needed to advance further in understanding these trophic interactions.

By way of conclusion, we summarize in Table 4 an overall carbon budget for the NABE region, 47°N, 20°W, 18–31 May 1989 during the waning phase of the phytoplankton bloom. Grazing and foodweb processing of primary production plus extracellular release from phytoplankton (PER) produced a DOC flux of 600–1,200 mgC m^{-2} d^{-1}, i.e., most of the daily PP passed through the dissolved pool. Particle breakdown may have added an additional 300–400 mgC m^{-2} d^{-1}. At a BGE of 0.15, estimated BP required 700–2,700 mgC m^{-2} d^{-1} of DOC from all internal and external sources. Thus the estimated DOC production rates were sufficient to support only the lower estimates of BP derived for the NABE region, unless DOC exudation was extremely high. Very high exudation rates and/or large external subsidies are necessary to support the mean BP:PP of 20% (i.e., BCD = 1,387 mgC m^{-2} d^{-1} or 128% of PP). Our analysis suggests that breakdown of a previously accumulated DOC pool could not support high BCD for more than a few days. No horizontal gradients in DOC concentration have been doc-

umented to support external inputs to the open sea (Williams and Bowers 1999).

The lower BP estimates were derived from two conservative conversion factors, the cumulative factor for thymidine incorporation (Bjørnsen and Kuparinen 1991) and the lower value proposed by Simon and Azam (1989) for leucine incorporation. Empirically derived factors such as those used here (Table 1) can be used to justify high values for BP. But there are biochemical and molecular constraints of conversion factor values, which have been evaluated, and can be used to assess the factors leading to very high estimates. For example Simon and Azam (1989) proposed a leucine conversion factor of 1.5 kgC produced per mole of leucine incorporated, based on consideration of cellular protein composition and isotope dilution. BP values much greater than those yielded by this factor should be viewed skeptically.

We cannot explain the higher individual BP : PP values given in Table 3, nor the large short-term excursions in BP : PP. Data from the study region do not exist for making more complicated models than those used by Fasham et al. (1999) or Anderson et al. (2001). Only the lower BP and resulting BCD estimates are consistent with our current knowledge of DOC flux and BP estimation.

Recent assertions of net heterotrophy in oceanic systems remote from external sources of DOC (Del Giorgio et al. 1997; Duarte and Agusti 1998; Geider 1997; Williams 1998; Williams and Bowers 1999) highlight the importance of understanding BP : PP, as attempted here. Since bacteria often account for a large fraction of community respiration, accurate evaluation of metabolic balance depends on accurate assessment of BP, BGE, and BR. Here we suggest that BP : PP in excess of about 15% is difficult to account for. Proponents of net heterotrophy driven by high BP invoke large subsidies of organic matter from previously existing pools or transport from remote sources (Hoppe et al. 2002). These subsidies have not yet been convincingly demonstrated. More precise and direct estimates of BP are needed, but so are better and more comprehensive models and approaches to synthesizing pertinent ecosystem data for evaluating DOC flows to and from and within ocean ecosystems.

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