Revisited phytoplanktonic carbon dependency of heterotrophic bacteria in freshwaters, transitional, coastal and oceanic waters

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Abstract
Positive relationships between heterotrophic bacteria and particulate phytoplankton production (respectively, BP and PPP) have been reported for several areas, suggesting that material produced by phytoplankton was a major substrate for bacterial growth. Since then, thousands of simultaneous measurements of both PPP and BP have been performed. A review of these data showed that BP may exceed PPP considerably (median ranged between 132% and 484%) in all aquatic systems with the lowest PPP. In oceanic waters, BP did not seem to be temporally synchronized with PPP and the median BP : PPP ratio is 15% with moderate PPP, but the immediate bacterial carbon (C) demand (including bacterial respiration) was greater than the corresponding total primary production (i.e. dissolved and particulate primary production) for > 80% of both volumetric and areal datasets. In freshwaters, the strong covariation observed between BP and PPP seemed mainly due to a common response to sudden nutrient inputs into enclosed systems, leading to a similar range of production rates and temporal synchronities. Indeed, phytoplanktonic exudates contributed directly to only 32% (median) of BP when C-tracking experiments were performed in freshwaters. Therefore, because direct C dependency of bacteria on phytoplankton is questionable, other C sources might be more significant for bacterial growth.

Introduction
Phytoplankton and heterotrophic bacteria are major components of the biological carbon (C) cycle in aquatic systems. Phytoplankton (including photoautotrophic bacteria, i.e. cyanobacteria), using light as energy for growth, are primary producers, whereas heterotrophic bacteria (including Archaea and hereafter referred to as bacteria), incorporating dissolved organic matter for growth, are both mineralizers and prey for upper trophic-level organisms.

Positive relationships between bacteria and phytoplankton production or biomass have been reported for diverse geographical areas (Cole et al., 1988), with no consistent difference between marine and freshwater systems (Williams, 1981; Cole et al., 1988). Such general cross-system relationships suggest a coupling between phytoplankton and bacteria, i.e. phytoplankton or material produced by phytoplankton is an important substrate for bacterial growth. Bacterial production (BP) is thus classically considered as secondary production, averaging 20% of the planktonic primary production (Cole et al., 1988). The annual depth-integrated BP was estimated at 54–110% of the global primary production estimates in the euphotic zone, with oceanic areas undersampled at that time (Ducklow & Carlson, 1992). More recent findings suggest that the potential use of phytoplankton-produced dissolved organic C (DOC) by bacteria should only be expected in areas far from the influence of coastal inputs of dissolved organic matter (Morán et al., 2002). However, this suggestion was challenged by recent observations where DOC produced by phytoplankton was clearly not enough to support the bacterial C demand (BCD) in some oligotrophic tropical areas (Rochelle-Newall et al., 2008). Therefore, phytoplankton-produced substrate may not be sufficient for BCD in oligotrophic oceanic areas where net CO2 production (i.e. respiration prevailing) was estimated (del Giorgio et al., 1997). This implies that bacteria require more C that phytoplankton may provide. Morán et al. (2002) also
suggested that weaker phytoplankton–bacteria C coupling could be expected in coastal waters relative to more open waters. This suggestion is apparently inconsistent with the assumption of a strong C coupling between bacteria and phytoplankton, explaining the positive relationships between bacteria and phytoplankton production rates observed in some productive aquatic systems, such as estuaries (Cole et al., 1988). These latter authors proposed an alternative explanation that both bacteria and phytoplankton may also grow in response to common factors, i.e. nutrient load. If bacteria use C sources other than those directly provided by phytoplankton, the functional role of bacteria and phytoplankton is thus considered to be similar, i.e. providing organic matter to higher trophic levels in the aquatic ecosystems.

Since the review proposed by Cole et al. (1988), thousands of simultaneous measurements of phytoplankton and BP, associated or not with biomass measurements, have been performed in more diverse areas, especially through the implementation of several international programmes such as the Joint Global Ocean Flux Study (JGOFS) and the Bermuda Atlantic Time-Series BATS Study focused on oceanic waters. Data were retrieved from available JGOFS databases and papers published from additional studies performed in diverse geographical locations.

The objective of this paper is primarily to investigate and reformulate the observed comparative relationships between bacteria and phytoplankton production from different aquatic systems, and secondly, to revisit the theoretical concept of C dependency between heterotrophic bacteria and phytoplankton in aquatic systems.

Covariation between phytoplankton and bacteria production revisited

The relationships between bacteria and phytoplankton have been investigated extensively by looking at the covariation between chlorophyll a concentrations, as a proxy of phytoplankton biomass, and bacterioplankton abundance reported from diverse environments. The examination of several published relationships showed no systematic differences in these relationships among systems (Gasol & Duarte, 2000). Analyses of these relationships also showed that bacterial abundance is the highest, relative to phytoplankton, in phytoplankton-poor systems. Therefore, these authors suggest that bacteria are fuelled by allochthonous C subsidies in oligotrophic ecosystems. In contrast, bacterial abundances are too low for the available primary production at high chlorophyll concentrations, suggesting that bacteria experience greater losses by grazing or viral mortality (Li et al., 2004).

In the present review, because temporal dynamics of chlorophyll and bacterial abundance are not robust indicators of organic matter flux, the relationships between phytoplankton and bacteria were explored by retrieving paired measurements of bacterial and phytoplankton production rates performed in the euphotic zone, from seven international programme databases (JGOFS Canada Gulf of St. Lawrence 1993–1994, DYNAPROC 1995, FRUELA 1995–1996, PROSOPE 1999, U.S. Arabian Sea Process Study 1994–1996, U.S. JGOFS EqPac 1992, U.S. Southern Ocean JGOFS program 1996–1998), the Bermuda Atlantic Time-Series Study 1990–2008 (http://www.bios.edu/research/bats.html) and 25 studies from other geographical areas published between 1982 and 2009 (Table 1). The latter were selected from ISI Web of knowledge using the following keywords ‘bact* and (phyt* or primary) and production and (aquat* or mar* or fresh* or water*)’. In our database, four different aquatic systems were distinguished as oceanic, coastal, transitional waters and freshwaters, according to the sampling site description. Oceanic and coastal waters were distinguished by the limit of 200 km to the shore from the sampling site ( < 200 km: coastal waters, > 200 km: oceanic waters). Transitional waters were defined as waters strongly influenced by freshwaters occasionally or permanently (i.e. river plume, estuaries) with salinity below 30.

Volumetric data were converted into areal unit when depth profiles were available. Data expressed in areal units only in some studies were not converted into volumetric units in order to avoid the addition of assumptions and error propagation, but these data were discussed as a BP: PPP ratio.

We converted and expressed all the data into one single unit (µg C L⁻¹ day⁻¹ and mg C m⁻² day⁻¹). When only daylight hourly values were available, the daily BP was assumed to be 24 times the hourly rate and that primary production was 10 times the hourly rate, similar to the previous review published by Cole et al. (1988). The data reported in the present paper were obtained using different methods and conversion factors. Concerning the BP methods used, the groups of bacterioplankton may have different abilities to take up thymidine and leucine, leading to underestimation of BP rates. This was recently illustrated by Pérez et al. (2009) from freshwater bacterioplankton groups where 80–90% of the Betaproteobacteria group took up leucine while only 10% used thymidine. Concerning the bacterial conversion factors, although the BP estimates may vary by 100% when comparing the different conversion factors used (Ducklow & Carlson, 1992), no attempt at standardization was made considering that the authors used conversions factors specific to their respective studied area. However, common conversion factors (i.e. 2 × 10⁸ cells mol⁻¹ and 20 fg C per cell) were used when estimation of BP was expressed in mol of incorporated ³H-thymidine. Estimates of BP based on simultaneous incorporation of ³H-thymidine, ³H-leucine and ¹⁴C-leucine may differ only by a
Table 1. References of bacterial and phytoplankton production rates used for the database of the present investigation

<table>
<thead>
<tr>
<th>References used</th>
<th>Studied sites</th>
<th>Type of aquatic systems</th>
<th>Type of data</th>
<th>Bacterial production method used</th>
<th>Phytoplankton 14C production method</th>
<th>n</th>
<th>Range of salinity</th>
<th>Sampling depth</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ameryk et al. (2005)</td>
<td>Gulf of Gdansk</td>
<td>Transitional waters</td>
<td>Hourly values</td>
<td>$^3$H-thymidine</td>
<td>4-h incubation, in situ light</td>
<td>70</td>
<td>7–12</td>
<td>0.5–20 m</td>
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<td>Azam et al. (2003)</td>
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<td>Hourly (bact) and daily (phyto) values</td>
<td>$^3$H-thymidine</td>
<td>24-h incubation, in situ light</td>
<td>148</td>
<td>34–37</td>
<td>1–90 m (profiles)</td>
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<td>Barber et al. (2003a)</td>
<td>Equatorial Pacific</td>
<td>Oceanic waters</td>
<td>Hourly (bact) and daily (phyto) values</td>
<td>$^3$H-thymidine</td>
<td>24-h incubation, in situ light</td>
<td>347</td>
<td>34–36</td>
<td>0–120 m (profiles)</td>
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<td>Barber et al. (2003b)</td>
<td>Ross Sea</td>
<td>Oceanic waters</td>
<td>Hourly (bact) and daily (phyto) values</td>
<td>$^3$H-thymidine</td>
<td>24-h incubation, in situ light</td>
<td>138</td>
<td>33–35</td>
<td>2–100 m (profiles)</td>
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<td></td>
<td>Bermuda Atlantic Ocean</td>
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<td>Hourly (bact) and daily (phyto) values</td>
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<td>24-h incubation, in situ light</td>
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<td>Cho et al. (2001)</td>
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<td>Coastal waters</td>
<td>Hourly values</td>
<td>$^3$H-thymidine</td>
<td>2-h incubation, simulated in situ light</td>
<td>26</td>
<td>31–33</td>
<td>8–32 m</td>
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<tr>
<td>Chrost &amp; Siuda (2006)</td>
<td>Polish Lakes</td>
<td>Freshwaters</td>
<td>Averaged daily values</td>
<td>$^3$H-thymidine</td>
<td>4-h incubation, in situ light</td>
<td>95</td>
<td>0</td>
<td>0.2–2.7 m</td>
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<td>Chrzanowski &amp; Hubbard (1988)</td>
<td>Lake Arlington, Texas (USA)</td>
<td>Freshwaters</td>
<td>Depth-integrated daily values</td>
<td>$^3$H-thymidine</td>
<td>1–2-h incubation, simulated in situ light</td>
<td>15</td>
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<td>0–2.5 m (profiles)</td>
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<td>Covney &amp; Wetzel (1995)</td>
<td>Lawrence Lake, SW Michigan, (USA)</td>
<td>Freshwaters</td>
<td>Daily values</td>
<td>$^3$H-thymidine</td>
<td>4-h incubation, in situ light</td>
<td>104</td>
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<td>Hill et al. (2002, 2004)</td>
<td>Western Arctic</td>
<td>Transitional waters</td>
<td>Daily values</td>
<td>$^3$H-leucine</td>
<td>24-h incubation, simulated in situ light</td>
<td>368</td>
<td>24–36</td>
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<td>Hoppe et al. (2002)</td>
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<td>33–38</td>
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<td>Iriarte et al. (2003)</td>
<td>Urdalbai estuary, North Spain</td>
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<td>16</td>
<td>1–38</td>
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<td>Jugnia et al. (2006)</td>
<td>Sep Reservoir, France</td>
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<td>Hourly values</td>
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<td>3-h incubation, in situ light</td>
<td>9</td>
<td>0</td>
<td>1 m</td>
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<td>Kamjunke et al. (2005)</td>
<td>Acidic, iron-rich mining Lakes, Germany</td>
<td>Freshwaters</td>
<td>Daily values</td>
<td>$^{14}$C-leucine</td>
<td>3-h incubation, in situ light</td>
<td>39</td>
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<td>Kirchman et al. (2009)</td>
<td>Sub-Arctic Pacific Ocean</td>
<td>Oceanic waters</td>
<td>Depth-integrated daily values</td>
<td>$^3$H-leucine</td>
<td>Simulated in situ light</td>
<td>89</td>
<td>N/A</td>
<td>0–80 m (profiles)</td>
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<td>Kopacek et al. (2004)</td>
<td>Acidified mesotrophic Plesni Lake, Czech Republic</td>
<td>Freshwaters</td>
<td>Daily values</td>
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<td>4-h incubation, in situ light</td>
<td>26</td>
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<td>Hourly values</td>
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<td>12-h incubation, simulated in situ light</td>
<td>9</td>
<td>32–35</td>
<td>1 m</td>
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<td>Larsson &amp; Hagstrom (1982)</td>
<td>Baltic Sea, Sweden</td>
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<td>Depth-integrated daily values</td>
<td>FDC</td>
<td>4-h incubation, in situ light</td>
<td>48</td>
<td>5.3–7.4</td>
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Table 1. Continued.

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<th>References used</th>
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<th>Range of salinity</th>
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<td>Legendre et al. (2003)</td>
<td>St. Lawrence Gulf, Canada</td>
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<td>Daily values</td>
<td>³H-thymidine</td>
<td>24-h incubation, simulated in situ light</td>
<td>129</td>
<td>27–34</td>
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<td>McManus &amp; Peterson (1988)</td>
<td>Upwelling off central Chile</td>
<td>Coastal Waters</td>
<td>Hourly values</td>
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<td>Simulated in situ light</td>
<td>17</td>
<td>N/A</td>
<td>surface</td>
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<td>Morán et al. (2001)</td>
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<td>Oceanic and coastal waters</td>
<td>Hourly values</td>
<td>³H-leucine</td>
<td>6-h incubation, artificial light</td>
<td>18</td>
<td>34–35</td>
<td>5–80 m (profiles)</td>
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<td>Morán &amp; Estrada (2002)</td>
<td>Gerlache and Bransfield Straits, Antarctic Peninsula</td>
<td>Coastal waters</td>
<td>Hourly values</td>
<td>³H-leucine</td>
<td>6-h incubation, artificial light</td>
<td>20</td>
<td>33–38</td>
<td>5–10 m</td>
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<td>Moutin &amp; Van Wambeke (2003)</td>
<td>Mediterranean Sea</td>
<td>Coastal waters</td>
<td>Hourly (bact) and daily (phyto) values</td>
<td>³H-leucine</td>
<td>24-h incubation, in situ light</td>
<td>20</td>
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<td>13–130 m (profiles)</td>
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<td>Pedrós-Alió &amp; Varela (2003)</td>
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<td>Coastal waters</td>
<td>Daily values</td>
<td>¹⁴C-leucine</td>
<td>24-h incubation, simulated in situ light</td>
<td>68</td>
<td>33–37</td>
<td>5–60 m (profiles)</td>
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<td>Hourly values</td>
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<td>58</td>
<td>25–31</td>
<td>Surface</td>
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<td>³H-thymidine</td>
<td>1-h incubation, artificial light</td>
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<td>35–36</td>
<td>Surface</td>
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<td>Riemann (1983)</td>
<td>Lake Tystrup, Denmark</td>
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<td>Daily values</td>
<td>FDC</td>
<td>24-h incubation, in situ light</td>
<td>14</td>
<td>0</td>
<td>N/A</td>
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<td>Rochelle-Newall et al. (2008)</td>
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<td>Hourly values</td>
<td>³H-thymidine</td>
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<td>50</td>
<td>35–36</td>
<td>3 m</td>
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<td>Rosenstock &amp; Simon (2001)</td>
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<td>Hourly values</td>
<td>¹⁴C-leucine</td>
<td>4-h incubation, in situ light</td>
<td>32</td>
<td>0</td>
<td>3 m</td>
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<td>Simon &amp; Tilzer (1987)</td>
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<td>Freshwaters</td>
<td>Depth-integrated daily values</td>
<td>¹⁴C-protein hydrolysate</td>
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<td>41</td>
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<td>Teira et al. (2003)</td>
<td>North Atlantic Subtropical Gyre</td>
<td>Oceanic waters</td>
<td>Hourly values</td>
<td>³H-thymidine</td>
<td>2-h incubation, simulated in situ light</td>
<td>38</td>
<td>36–37</td>
<td>0–120 m (profiles)</td>
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<td>Turley et al. (2000)</td>
<td>Western and Eastern Mediterranean Sea</td>
<td>Coastal waters</td>
<td>Daily values</td>
<td>³H-leucine</td>
<td>10–12 h incubation, in situ light</td>
<td>74</td>
<td>37–39</td>
<td>0–150 m</td>
</tr>
<tr>
<td>Vadstein et al. (1989)</td>
<td>Eutrophic Lake Nesjovatn, central Norway</td>
<td>Freshwaters</td>
<td>Depth-integrated daily values</td>
<td>FDC</td>
<td>4-h incubation, in situ light</td>
<td>15</td>
<td>0</td>
<td>0.2–5 m (profiles)</td>
</tr>
</tbody>
</table>

N/A, not available.
maximum of 31% (Chin-Leo & Kirchman, 1988; Riemann et al., 1999). Furthermore, the conversion of primary production from hourly rates to daily rates may result in maximally a 60% underestimation of daily rates (Moutin et al., 1999). Because BP and particulate phytoplankton production (PPP) values ranged over five and seven orders of magnitude, respectively, errors due to the different methods used will have minor effects on any relationship between BP and PPP.

BP rates were plotted against the PPP rates on a log–log scale for oceanic waters, coastal waters, transitional waters and freshwaters (Fig. 1a–d, respectively). The lowest BP were reported in marine waters (oceanic and coastal waters), where values varied over three orders of magnitude compared with variation of five orders of magnitude for PPP (Fig. 1a and b). The values of BP in oceanic and coastal waters were rarely above 10 μg C L⁻¹ day⁻¹. A reduced range of bacterial abundance values relative to a larger range of chlorophyll values was also reported in oceanic systems (Ducklow, 1999; Gasol & Duarte, 2000; Li et al., 2004). The capacity for PPP and PPP-derived substrates to support BP, based on the flux of utilizable organic matter from phytoplankton production and cellular maintenance efficiency, seems to be highly constrained in the open ocean (Gasol & Duarte, 2000; Li et al., 2004). A reduced availability of labile organic substrates for bacteria in oceanic waters may also explain the low range of BP values reported here. In contrast, BP reached values > 100 μg C L⁻¹ day⁻¹ in transitional waters and freshwaters (Fig. 1c and d), where dissolved organic matter inputs from rivers occur regularly. In contrast to oceanic, coastal and transitional waters, where PPP poorly explained BP values (R² < 0.5), a positive and significant log–log relationship (R² = 0.83) was clearly observed only for freshwaters, suggesting a close relationship between BP and PPP in these waters.

The apparent weak relationship in marine and transitional waters may reflect the lack of synchronicity and long delays between the phytoplankton and bacteria blooming periods, as suggested for oceanic waters by Kirchman (1997) and del Giorgio et al. (1997), while these two microbial communities may be highly synchronized in freshwaters. We evaluated the synchronicity or time delay between the maximal BP and PPP values (volumetric and areal values) reported from 21 time-series studies and for each year recorded at the BATS station (18 years). Most of these studies were performed in freshwaters probably because of an easier access to the field for frequent in situ or simulated BP and PPP incubations over a long period of time. We referred to the author statement when the synchronicity was clearly noted in the studies, and when not stated, we visually evaluated the synchronicity from time delay between the maximal BP and PPP values. The maximal BP and PPP values obtained in oceanic waters appeared out of phase (Ducklow et al., 2002) or delayed by > 1 month (from 28 to 186 days) for most of the years observed at the BATS station (13 out of 18 years). In the coastal waters, we identified two studies where maximal BP and PPP rates were not synchronized (Renaud et al., 2005; Lamy et al., 2006) and four studies with a time delay between 3 days and 3 months (Lancelot & Billen, 1984; Billen & Fontigny, 1987; McManus & Peterson, 1988; Krstulović et al., 1995). In transitional waters, two studies displayed synchronicity (Ducklow & Kirchman, 1983; Laanbroek et al., 1985) and three no synchronicity (Larsson & Hagström, 1982; Poremba et al., 1999; Iriarte et al., 2003). In freshwaters, six out of nine studies displayed synchronicity (Riemann, 1983; Simon & Tilzer, 1987; Chrzanowski & Hubbard, 1988; Coveney & Wetzel, 1995; Rosenstock & Simon, 2001; Kopácek et al., 2004) and three studies showed short time delays (< 1 month: Lovell & Konopka, 1985; Vadstein et al., 1989; Jugnia et al., 2006).

The apparent shift from no synchronicity or long time delays to synchronicity between maximal BP and PPP values from oceanic regions to freshwaters, reported here, is consistent with the shift from a clear synchronicity observed in the upper Delaware estuary, to the time lag reported in the lower estuary observed earlier by Hoch & Kirchman (1993) from production temporal variations. Therefore, bacteria would not be dependent on immediate phytoplankton C exudation in marine waters. The strong advection and patchiness observed in open waters combined with the general low reduced inorganic nutrient (e.g. ammonia) and organic matter availability measured in marine waters, limiting BP and inducing competition between bacteria and phytoplankton (Church 2008), may explain the lack of synchronicity and the low maximal BP values reported in such waters. This is supported by the drastic increases in BP reported during organic and inorganic nutrient enrichment microcosm experiments (Church et al., 2000; Zohary et al., 2005; Van Wambeke et al., 2007) and mesoscale iron enrichment experiments (Cochlan, 2001; Oliver et al., 2004) performed in different oceanic waters, where BP became synchronized with PPP.

Based on a general cross-system relationship between BP and PPP, Cole et al. (1988) showed that BP averaged 20% of PPP, considering that BP derived only from primary production. Because no general cross-system relationship was found from our present database (Fig. 1), the ratio between BP and PPP was therefore highly variable for the different aquatic systems considered (Table 2). Furthermore, this ratio is probably meaningless for some waters, due to the lack of synchronicity between temporal variations of BP and PPP reported in the present review. Indeed, BP may largely exceed PPP in oceanic waters when PPP < 0.1 μg L⁻¹ day⁻¹ and < 100 mg m⁻² day⁻¹, where BP in areal and volumetric units was in median 158% (interquartiles 69% and 347%,


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of PPP, respectively. The large BP:PPP ratios found at lower PPP rates do not seem to relate to technical issues of measuring PPP at low rates, as the variance in BP:PPP ratios estimated from interquartiles and determined at low-
est PPP rates was not significantly greater (Table 2). In contrast, BP was < 20% of PPP (in both volumetric and areal unit) in the highest productive waters of each system (Table 2). Therefore, PPP and derived substrates may not directly support BP in oceanic unproductive waters, whereas BP should be a rather small component of the total secondary production in high productive waters.

C flowing from phytoplankton to bacteria

The degree of C coupling between bacteria and phytoplankton may be evaluated by comparing phytoplankton exudate production (i.e. dissolved phytoplankton production: DPP) and the total phytoplankton production (TPP) to the bacterial C requirement (i.e. BP and respiration). There is no clear definition of the degree of C coupling; however, Morán et al. (2002) suggested a shift from a weak to a strong C coupling when DPP varied from accounting for as low as 7% (shelf locations) to 104% (offshore location) of the BCD. We therefore suggest that a high degree of C coupling (i.e. strong C coupling) is defined as DPP or total PPP rates fully satisfying the bacterial C requirement, and a low degree of C coupling (i.e. weak C coupling) as DPP or total PPP rates satisfying < 10% of the bacterial C requirement.

The DPP is classically measured using trace addition of radiolabelled compounds assimilated by phytoplankton (H\(^{14}\)CO\(_3\)) and size fractionation (0.2 um), followed by measurement of radiolabelled phytoplankton exudates in the dissolved fraction after a short-time incubation (ca. 4 h) of an enclosed natural community. Because bacteria may incorporate recently produced \(^{14}\)C-exudates during the incubation period, DPP is usually underestimated (i.e. net DPP). Few studies evaluated gross DPP (GDPP), corrected to bacterial incorporation, using time courses of radiolabelled C incorporation or bacterial inhibitors. Published log-transformed GDPP values from different aquatic systems were plotted against the corresponding log-transformed values of PPP (Fig. 2, \(n = 196\)), and a linear model was fitted with a slope of 0.90 significantly lower than 1. The contribution of GDPP to PPP ranged between 6% and 32%

In the regression equation, the value within brackets is the 95% confidence interval of the regression parameter.

Fig. 2. Relationship between the PPP and GDPP reported from dissolved phytoplankton production rates corrected by bacterial uptake and obtained from four different aquatic systems by Lancelot (1979), Cole et al. (1982), Coveney (1982), Larsson & Hagstrom (1982), Riemann et al. (1982), Wolter (1982), Møller-Jensen (1983), Brock & Clyne (1984), Bell et al. (1989), Carillo et al. (1999). In relatively high productive waters (PPP > 10 μg C L⁻¹ day⁻¹ and > 1000 mg C m⁻² day⁻¹), the TPP may supply the BCD through the bacterial incorporation of phytoplankton-derived C from sloppy feeding, viral infection or cell apoptosis.

Comparison of BCD and GDPP rates did not provide measurements of the actual bacterial use of phytoplanktonic exudates for their growth. Very few studies (mainly carried out in freshwaters, as far as we know) reported measurements of both bacterial uptake rates of phytoplanktonic exudates for their growth. Very few studies (mainly carried out in freshwaters, as far as we know) reported measurements of the actual bacterial use of phytoplanktonic exudates for their growth.

Table 2. Median (interquartiles and data number) of ratios between BP and PPP expressed in %, for each log intervals of PPP in volumetric and areal units reported from the four different aquatic systems

<table>
<thead>
<tr>
<th>Units</th>
<th>PPP range</th>
<th>Oceanic waters</th>
<th>Coastal waters</th>
<th>Transitional waters</th>
<th>Freshwaters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Volumetric values (μg L⁻¹ day⁻¹)</td>
<td>10⁻¹–10⁻²</td>
<td>419 (317–750, n = 18)</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>10⁻²–10⁻¹</td>
<td>288 (145–844, n = 162)</td>
<td>–</td>
<td>168 (52–336, n = 7)</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>10⁻¹–10⁰</td>
<td>70 (33–136, n = 531)</td>
<td>51 (35–63, n = 28)</td>
<td>27 (16–45, n = 79)</td>
<td>225 (141–289, n = 6)</td>
</tr>
<tr>
<td></td>
<td>10⁻²–10¹</td>
<td>14 (7–26, n = 1366)</td>
<td>33 (14–52, n = 125)</td>
<td>8 (4–13, n = 253)</td>
<td>46 (36–99, n = 50)</td>
</tr>
<tr>
<td></td>
<td>10⁻¹–10²</td>
<td>8 (4–16, n = 387)</td>
<td>12 (2–31, n = 105)</td>
<td>6 (2–13, n = 240)</td>
<td>30 (19–38, n = 94)</td>
</tr>
<tr>
<td></td>
<td>10⁻²–10³</td>
<td>–</td>
<td>1 (0.6–7, n = 35)</td>
<td>12 (0.6–18, n = 61)</td>
<td>12 (6–21, n = 56)</td>
</tr>
<tr>
<td></td>
<td>10⁻¹–10⁴</td>
<td>–</td>
<td>0.4 (0.2–1, n = 7)</td>
<td>–</td>
<td>7 (5–10, n = 75)</td>
</tr>
<tr>
<td></td>
<td>10⁻²–10⁵</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>4 (3–5, n = 12)</td>
</tr>
<tr>
<td>Areal values (mg m⁻² day⁻¹)</td>
<td>10⁻¹–10⁰</td>
<td>484 (428–556, n = 4)</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>10⁻²–10¹</td>
<td>173 (98–251, n = 6)</td>
<td>–</td>
<td>132 (95–348, n = 3)</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>10⁻¹–10²</td>
<td>145 (39–188, n = 17)</td>
<td>34 (28–38, n = 4)</td>
<td>8 (6–18, n = 26)</td>
<td>93 (36–189, n = 12)</td>
</tr>
<tr>
<td></td>
<td>10⁻²–10³</td>
<td>16 (9–23, n = 303)</td>
<td>3 (2–7, n = 15)</td>
<td>6 (3–12, n = 105)</td>
<td>25 (14–46, n = 51)</td>
</tr>
<tr>
<td></td>
<td>10⁻¹–10⁴</td>
<td>14 (11–18, n = 25)</td>
<td>0.5 (0.4–1, n = 3)</td>
<td>1 (0.5–2, n = 20)</td>
<td>15 (7–19, n = 21)</td>
</tr>
</tbody>
</table>

33%. GDPP values were thus estimated using the regression equation obtained from the relationship between GDPP and PPP (Fig. 2) and applied to the whole PPP dataset (n = 3707). Comparison between GDPP and BP values (Fig. 3a) shows that rates of GDPP, ranging over several orders of magnitude across different aquatic systems, can generally meet BP.

However, the rates of GDPP do not meet the bacterial C respiration rates (BR) in all studied systems, except in high productive freshwaters (Fig. 3b). A weak C coupling is clearly observed in low productive waters where GDPP rates are much lower than 10% of the BR rates.

When considering the bacterial carbon demand (BCD = BP + BR) and compared with the total phytoplankton production (TPP = PPP + GDPP), the whole volumetric and areal primary production do not meet the immediate BCD in low productive oceanic waters (Fig. 3c). This suggests that bacteria used other C sources such as semi-labile or refractory DOC with a low turnover rate in marine oligotrophic waters. This is supported by some findings showing that open-ocean bacteria (eastern North Pacific) assimilate both modern (< 10 year old) and older (> 1000 year old) components of DOC, while estuarine bacteria exclusively assimilate the modern component of bulk DOC (Cherrier et al., 1999). In relatively high productive waters (TPP > 10 μg C L⁻¹ day⁻¹ and > 1000 mg C m⁻² day⁻¹), the TPP may supply the BCD through the bacterial incorporation of phytoplankton-derived C from sloppy feeding, viral infection or cell apoptosis.

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exudates using tracking C experiments (i.e. mainly direct determination of $^{14}$C in the bacterial fraction using size fractionation) and BP (Cole et al., 1982; Coveney, 1982; Larsson & Hagstrom, 1982; Bell et al., 1983; Brock & Clyne, 1984; Vadstein et al., 1989; Chröst & Siuda, 2006). The comparison of the rates of bacterial uptake of phytoplankton exudates and the BP rates may be considered as a proxy of the direct and immediate C dependency of bacteria on phytoplankton.

Results from all these early studies showed that bacterial uptake of phytoplankton exudates averaged only 39% (median 32%, $n = 83$) of BP over a large range of PPP values (from 3 to 9200 µg C L$^{-1}$ day$^{-1}$). This suggests that most of the C needed for bacterial growth is supplied by other C sources (e.g. sloppy feeding by micrograzers, viral lysis or external DOC inputs), although an apparent strong C coupling between PPP and BP was hypothesized in freshwaters. Therefore, the significant positive relationship between phytoplankton and bacteria and the synchronicity of their temporal variations reported in freshwaters could be more related to a common response to environmental conditions such as nutrient load rather than a direct C dependency.

From all these results, it appears that direct C dependency of bacteria on phytoplankton is rather questionable for all aquatic systems. A dependence-type relationship in general ecology means that one organism absolutely needs another one for its growth and survival. In this sense, we believe that bacteria are not immediately and directly dependent on phytoplankton, although bacteria can use phytoplankton-derived production in the large time scale, as well as the chemoautotroph-derived production. In other terms, other C sources might be more significant for bacterial growth.

**Toward a new aquatic ecological concept: nondependence of bacteria on phytoplankton**

Most of the aquatic ecology concepts derive from general concepts of ecology that are mainly influenced by terrestrial ecology. In the general conception of terrestrial ecology, food web functioning is based on terrestrial plant production, where bacteria favour the plant assimilation of nutrients. Aquatic ecology adapted this concept by replacing terrestrial plants with unicellular phytoplankton as the basis of the aquatic system functioning. Acceptance of this concept resulted in the recognition that all other aquatic organisms are directly or indirectly dependent on phytoplankton and their primary production. Therefore, it was widely accepted that bacteria should directly or indirectly be dependent on the phytoplankton activities in order to be able to produce its biomass. However, in aquatic systems, and most importantly in the marine system, there is a huge...
Phytoclanktonic carbon dependency of heterotrophic bacteria

pool of DOC that bacteria can assimilate. A fraction of this DOC results ultimately from phytoplankton activities, but was produced along various scales of time and space (Carlson, 2002). The synchronicity or short-time delays between the temporal variations of bacteria and phytoplankton production (or biomass) observed in some areas and for certain periods are rather related to a common response to forcing factors (e.g. nutrient inputs, temperature), and bacteria in marine systems seem to be able to maintain their activities independent of immediate phytoplankton activities. This ecological independence of bacteria from phytoplankton places bacteria in a special place within the aquatic food web. In addition to their remineralizing role, bacteria play the same role as phytoplankton in the aquatic system by producing biomass comparable to that of phytoplankton, but using allochthonous rather than autochthonous C in the oceans. Indeed, Gasol et al. (1997) calculated that the bacterial biomass in areal units increases twofold from coastal waters to oceanic waters (from $541 \pm 63$ mg C m$^{-2}$, $n = 82$ to $1132 \pm 71$ mg C m$^{-2}$, $n = 206$), while phytoplankton biomass decreases from $2921 \pm 335$ mg C m$^{-2}$ ($n = 163$) to $1966 \pm 126$ mg C m$^{-2}$ ($n = 279$).

In oligotrophic waters, functioning of the food web is based on the microbial loop and the microbial food web (Legendre & Rassoulzadegan 1995), where bacteria act not only as remineralizers but also as prey, like phytoplankton. In this way, both bacteria and phytoplankton, assimilating allochthonous DOC and DIC, respectively, transfer their C production directly to the higher trophic levels.

The nondependence of BP on phytoplankton production in aquatic systems leads us to highlight the specific functional role of bacteria in these systems, where bacteria and phytoplankton, using two different metabolic C ways, provide a comparative amount of biomass and energy for all other organisms at higher trophic levels. The interactions between bacteria and phytoplankton through the dissolved C matter in aquatic ecosystems do not seem to be wholly based on a dependence-type relationship.

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