Annual Bacterioplankton Biomasses and Productivities in a Temperate West Coast Canadian Fjord

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Bacterioplankton numbers, biomasses, and productivities, as well as chlorophyll a concentrations and phytoplankton productivities, were assayed from 1 March 1984 to 12 August 1985 through a 250-m-deep seawater column in Howe Sound, a temperate fjord-sound on the southern coast of British Columbia, Canada. Primary production during this 18-month period was 845 g of C m⁻². Bacterial production was assayed over this same period as 193 g of C m⁻² (thymidine incorporation) and 77 g of C m⁻² (frequency of dividing cells). Bacterial productivities per cubic meter were usually greater in the euphotic zone than in deeper aphotic water, but when integrated through the water column, approximately half of the bacterial production occurred in the deeper aphotic portion. Bacterial production occurred throughout the year, although at reduced rates in late fall and early winter; primary production almost ceased during late fall and early winter. Because of this heterotrophic bacterioplankton production was a very large portion of the microbial (bacterial plus phytoplankton) production at this time. In mid-summer bacterial production was a small proportion of the microbial production. Because of this asynchrony in peaks and troughs of bacterial and phytoplankton production through the year, data comparison is best done over an annual cycle. On this basis the bacterial production in the Howe Sound water column was between 23 and 9% of the phytoplankton production when a bacterial C to biovolume ratio of 0.107 pg of C μm⁻³ was assumed; the corresponding values were 64 and 29% when a ratio of 0.300 pg of bacterial C μm⁻³ was assumed.

A variety of techniques have been suggested for determining the in situ growth rates of heterotrophic bacteria in natural waters. In general, these techniques have tended to be one of two approaches. One involves the incorporation of a common substrate into cell mass by all of the growing heterotrophic bacteria. The utilization rate of this substrate is then converted to bacterial production rate by use of an experimentally determined conversion factor. Such an approach is that of thymidine uptake by heterotrophic bacteria (9, 10). The second approach involves the determination of a bacterial cell component and relates it to the bacterial in situ growth rate. An example is the formation of a cell septum (usually assessed as the frequency of dividing cells; FDC), which Hagström et al. (12) have suggested for use as an assay of the growth rate of bacteria. These two assays have been used in a variety of both fresh and marine waters, and the bacterial productivities have often been expressed as a percentage of the phytoplankton production (Table 1). The activities and productivities of bacterioplankton in most marine and fresh waters depend mainly on the organic matter produced by phytoplankton, although there may also be bacterial use of allochthonous terrestrial organic matter. Therefore, bacterioplankton production would be expected to be a relatively constant portion of phytoplankton production. That it is not (Table 1) may indicate that (i) phytoplankton production is not always available for bacterial use, (ii) bacterial use of the phytoplankton may have been removed in time and space from the primary production, or (iii) there is significant concurrent use of allochthonous organic substrates.

Studies reported to date have emphasized bacterioplankton productivities within the euphotic zone and over relatively short time periods of several weeks or months to at best several contiguous seasons (however, see references 12 and 20). Heterotrophic bacterioplankton, however, are generally active throughout the year and through the water column, although these activities usually decrease in winter and diminish with depth. Active bacteria also tend to be productive cells. Therefore, we felt that to obtain a more complete estimate of bacterial, vis-a-vis primary, production in a water column, these considerations of time and space must be taken into consideration. We chose to study the bacterial and phytoplankton productivities throughout the photic (0 to 40 m) and aphotic (40 to 250 m) portions of a 250-m-deep coastal, temperate seawater column over an annual cycle.

MATERIALS AND METHODS

The site chosen for study was at approximately 49°34'N, 123°06'W within Howe Sound, a fjord-sound (26) on the west coast of British Columbia that is contiguous to the Strait of Georgia. While the southern part is a sound, the fjord portion (bounded by a sill of 30 to 70 m) extends from Anvil Island north to the Squamish River (Fig. 1). This results in an inner basin with a maximum depth of ca. 280 m, the deeper water of which tends to be poorly mixed for much of the year (21). The surface water (0 to 10 m) of this basin is mixed, with the main forcing factors being Squamish River discharge, wind, and tidal currents (21). Mean river discharge is substantial (x = 242 m³ s⁻¹), with maximum flow rates occurring between May and September (24). During periods of high discharge the silt content of the river water is generally high.

Water samples were retrieved from depths of 1, 5, 10, 20, 40, 75, 150, and 250 m at stations 1, 2, and 3, which were located within the fjord portion (Fig. 1), by using a Van Dorn sampler. Samples were retrieved from 1 March 1984 to 12 August 1985 at monthly or bimonthly intervals.

The chlorophyll a (Chl a) content of each sample was determined by filtering 1-liter water portions through glass fiber filters (nominal pore size, 1.2 μm; GF/C; Whatman, 1277
Inc., Clifton, N.J.) with a small amount of MgCO₃, which was added to prevent acidification. All filters were then frozen at −15°C until Chl α was analyzed (within 1 week) spectrophotometrically following acetone extraction. Extinction values were used to calculate Chl α concentrations by the equation given by Strickland and Parsons (25).

Water samples for total bacterial count were preserved with 3.7% formaldehyde (final concentration) at the time of sampling. Immediately before counting each sample was treated with 0.001 M Na₂HPO₄ (final concentration) for 30 min and then sonicated at 100 W for 20 s. This facilitated the detachment of bacteria from particulates and randomly distributed the cells in the suspending water and on the polycarbonate filters (28) on subsequent filtration. Bacterial numbers and mean sizes were obtained by using acridine orange-stained material and epifluorescent microscopy (14). Calculated biovolumes (based on the mean length and width of the cells) were converted to bacterial carbon values as described by Valdés and Albright (27).

Primary production and the thymidine-based bacterial production assays were initiated within 30 min of sample retrieval. Bacterioplankton productivities were estimated by using the thymidine incorporation technique (9, 10) and the FDC assay (12). Thymidine incorporation assays were performed on waters retrieved from depths of 1, 5, 7.5, and 250 m, whereas the FDC assay was used on waters removed from all eight depths. For the former assay two killed (3.7% formaldehyde; final concentration) and two live 10-mL portions of each water sample were each placed in a 30-mL syringe and treated with 0.15 nM of [³H]thymidine ([methyl-³H]thymidine; specific activity, 65 Ci M⁻³; New England Nuclear Corp., Boston, Mass.). Samples were then incubated in the dark for 60 min at the in situ temperature. Incubations were stopped by adding 10 ml of ice-cold 10% trichloroacetic acid (TCA). Samples were then filtered through a nominal pore size (0.22 μm) cellulose nitrate filter. Filters were washed twice with 5 ml of ice-cold 5% TCA and then dissolved in 2 ml of ethyl acetate. Ten milliliters of Scintiverse II (Fisher Scientific Co., Pittsburgh, Pa.) fluor was added, and the contents were radioassayed by using a scintillation spectrometer (LS8000; Beckman Instruments, Inc., Fullerton, Calif.). Quench corrections were done by the channels ratio method. The factor used to convert the rate of thymidine uptake to bacterial production rate was 1.2 \times 10^{-18}.

Samples examined for FDC were stained, and the bacteria were examined as described above, except that the PP and sonication steps were omitted. Dividing cells (i.e., cells that possessed a clear invagination of the cell wall) were counted, and the percentage FDC was calculated. To relate FDC to the bacterial growth rates, seven 100-mL portions of water from 5 m at station 1 were sampled on 4 October 1985 and treated with sterile yeast extract to final concentrations of 0, 1, 2.5, 5, 7.5, 10, or 20 mg liter⁻¹. Each portion was incubated in a 250-ml Erlenmeyer flask at 15°C (water temperature at the time of sampling was approximately 10°C) for 50 h. At ca. 10-h intervals the FDC and bacterial biomasses were determined for each water sample. From these data a ln µ (µ = growth rate) versus FDC plot was constructed. The regression of µ on FDC was determined as ln µ = −0.099 FDC − 0.518. Bacterial growth rates were estimated from the FDC values by use of this equation.

<table>
<thead>
<tr>
<th>Reference or source</th>
<th>Bacterial production as % of phytoplankton production (assay)</th>
<th>Water body</th>
<th>Range of bacterial production (mg of C m⁻³ day⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>This study</td>
<td>23 (thymidine)</td>
<td>Howe Sound</td>
<td>0.0-36.9 (March 1984-August 1985)</td>
</tr>
<tr>
<td>This study</td>
<td>9 (FDC)</td>
<td>Howe Sound</td>
<td>0.0-13.0 (March 1984-August 1985)</td>
</tr>
<tr>
<td>3</td>
<td>1 (FDC)</td>
<td>Lake Erken</td>
<td>0.4-7.6 (late April-early May 1983)</td>
</tr>
<tr>
<td>9</td>
<td>(thymidine)*</td>
<td>CEPEX</td>
<td>6.6-71 (August 1978)</td>
</tr>
<tr>
<td>9</td>
<td>1-93 (thymidine)</td>
<td>Coastal California</td>
<td>0.7-53 (March-August 1979)</td>
</tr>
<tr>
<td>12</td>
<td>14 (FDC)</td>
<td>Coastal Baltic Sea</td>
<td>10.7-74 (April-November 1982)</td>
</tr>
<tr>
<td>16</td>
<td>28 (thymidine)</td>
<td>Little Crooked Lake</td>
<td>13.7-38 (April-November 1982)</td>
</tr>
<tr>
<td>16</td>
<td>44 (thymidine)</td>
<td>Crooked Lake</td>
<td>13.7-38 (April-November 1982)</td>
</tr>
<tr>
<td>18</td>
<td>(thymidine)</td>
<td>Coastal Georgia</td>
<td>0.6-17.6 (April-May 1980)</td>
</tr>
<tr>
<td>20</td>
<td>50 (FDC and spectrophotometrically determined)</td>
<td>Lake Mendota</td>
<td>3.8-44 (April 1979-November 1980)</td>
</tr>
</tbody>
</table>

* = Primary production not assayed.

b CEPEX, Enclosed water column (Saanich Inlet).

![FIG. 1. Chart of Howe Sound showing sampling stations 1, 2, and 3.](http://aem.asm.org/Downloaded from jul8, 2017 by guest)
Growth rate ($\mu$) and bacterial biomass ($B$) values were then used to calculate bacterial productivity ($P$), where $P = \mu B$.

Phytoplankton productivities were assayed essentially by the standard $^{14}$CO$_2$ uptake technique as originally proposed by Steemann Nielsen (23). Water samples in two light and two dark 250-ml bottles were each treated with 60 $\mu$M NaH$^{14}$CO$_3$ (specific activity, 8.4 Ci M$^{-1}$) and incubated for periods of between 3 and 5 h (between 0900 and 1500 h) at the sampling depths. Reactions were stopped by adding ca. 25 ml of 37% formaldehyde and filtering the content of each bottle through a nominal pore size (0.22 $\mu$m) cellulose nitrate filter (diameter, 47 mm). The radioactivity that was retained on each filter was assayed as described above. Extracellular released organic matter was not assayed, and because of this the values (see Fig. 5) may be underestimates of primary production.

The bacterial and phytoplankton biomass and production data were plotted as computer-generated three-dimensional graphs (Fig. 2 to 7), with hidden lines removed by using the DISPLA program (Integrated Software Systems Corp., San Diego, Calif.). This program averages values between unevenly spaced data points to give a three-dimensional surface for each assayed parameter versus depth and sampling time. We modified the DISPLA program to compute the volume under each surface; in this way the bacterial and phytoplankton biomasses and productivities could be readily compared and computed over a given time interval or depth.

RESULTS

Bacterial concentrations in the 0 to 250-m water column at stations 1, 2, and 3 ranged from a high of 20.72 $\times$ 10$^{11}$ m$^{-3}$ (5-m depth, 15 May 1985) to a low of 2.81 $\times$ 10$^{11}$ m$^{-3}$ (10-m depth, 3 October 1984) (Fig. 2). The highest euphotic zone (0 to 40 m) concentrations occurred in the spring and summer, while the lowest concentrations occurred in the fall and winter. Bacterial concentrations in the aphotic zone varied over a markedly lower range. Maximum (9.32 $\times$ 10$^{11}$ bacteria m$^{-3}$, 75 m, 21 June 1985) and minimum (3.27 $\times$ 10$^{11}$ bacteria m$^{-3}$, 250 m, 19 December 1984) values were observed in spring-summer and fall-winter, respectively.

The bacterial biomasses ranged from 18.5 mg of C m$^{-3}$ (1-m depth) to 1.9 mg of C m$^{-3}$ (250-m depth), which were observed on 13 June 1983 and 19 December 1984, respectively (Fig. 3). In general, the higher biomasses were observed from mid-winter to early fall, whereas the lower values were observed during late fall to mid-winter. Bacterial biomass was generally greater in the euphotic zone throughout the year.

An annual cycle in Chl $a$ concentrations occurred; concentrations were high in the spring and summer and low in the fall (Fig. 4). The highest euphotic zone Chl $a$ concentration occurred at 5 m in spring (24 April 1985), while the lowest value (below the assay limit of 0.20 mg of Chl $a$ m$^{-3}$) occurred in waters sampled during October 1984 through February 1985. Significant concentrations of Chl $a$ were assayed in the aphotic water column on several occasions during the spring and summer 1984 (Fig. 4).

The phytoplankton had an annual production cycle (Fig. 5). Productivities were greatest during the summer and markedly reduced in the fall. In mid-winter (January 1985) primary productivities increased from the fall-early winter minimum and then showed variable values during each spring. Total primary production in the water column during the approximately 18-month period from 1 March 1984 to 12 August 1985 was 845 g of C m$^{-2}$.

We tested the assumption that 80% of the radioactive label of the cold TCA-insoluble material was in DNA (10). In Table 2 are listed representative data of one of these tests. In the one test that is listed most of the $^3$H label was indeed in
DNA when both DNA and protein were extracted. In samples removed from deeper water labels, however, distribution was less than 80%, with between ca. 64 and 35% of the macromolecular labeled material being DNA. Lovell and Konopka (16) determined a similar pattern of label distribution in the microflora of Little Crooked Lake, Ind., with the DNA containing 28% of the TCA-precipitable radioactivity in the hypolimnetic water sample. Hanson and Lowery (13) found similar results for oceanic bacterial populations from 500 and 2,000 m. R. D. Fallon and S. Y. Newell (University of Georgia Marine Institute, personal communication) also found that in a natural community of dead *Spartina alterniflora* the ratio of DNA: total macromolecular 3H label was 0.62, while in a model assemblage it was 0.39. We therefore calculated that 80% of the label in the TCA-precipitable material was in DNA in the 1- and 5-m samples and 35% in the 40-, 75-, 150-, and 250-m samples.

Several investigators have noted a diurnal variation in bacterial production in natural waters (e.g., Bell and Kuparinen [3]). To check for this possibility we assayed bacterial production at station 2 over an 18-h time period on 8 August 1984 (Table 3). We did not find a diurnal variation in bacterial production in aphotic water, although there was a slight increase in surface water at 1000 h.

Bacterial productivities (as determined by both the thymidine incorporation and the FDC methods) were greater in the euphotic than in the aphotic zone during any one sampling period (Fig. 6 and 7). Within the euphotic zone the greatest bacterial productivities usually occurred at 1 or 5 m. Bacterial productivities were greatest in the spring and summer and lowest in the late fall through early winter.

When assayed by the thymidine incorporation method, the highest observed bacterial production rate of 36.9 mg of C m\(^{-3}\) day\(^{-1}\) occurred at 5 m (13 June 1984), whereas no detectable bacterial growth was often found in deeper aphotic water during winter (Fig. 6). Bacterial productivities increased (and decreased) in the deeper aphotic water at approximately the same time that they increased (and decreased) in the euphotic zone. Total bacterial production during the approximately 18-month period of 1 March 1984 to 12 August 1985 was 193 g of C m\(^{-2}\).

Bacterial productivities determined by the FDC assay were lower in general than those determined by the thymidine incorporation method (Fig. 6 and 7). The highest value of 13.0 mg of C m\(^{-3}\) day\(^{-1}\) was recorded in water at a 1-m depth on 15 October 1984. Nonproductive bacteria were frequently observed in deeper water, particularly during the winter months. In most cases bacteria in the deeper portions of the aphotic zone were the least productive. The higher FDC values of production generally occurred in the photic zone during periods of primary production; the lower FDC values occurred in the winter (Fig. 7). Bacterial production (FDC assay) throughout the 250-m-deep water column at the three stations was 77 g of C m\(^{-2}\) during the period of 1 March 1984 to 12 August 1985.

**DISCUSSION**

The use of the thymidine incorporation (9, 10) and the FDC (12) techniques for determining bacterial productivities showed generally similar patterns of cell growth throughout the 250-m-deep water column over the 18-month period studied (Fig. 6 and 7). Both assays showed that bacterial productivities are (i) generally greater at the surface than in
deeper aphotic water and (ii) least in the winter months. However, the 193 g of bacterial C m⁻² produced over the 18-month period determined by the thymidine incorporation technique was significantly greater than the 77 g of bacterial C m⁻² determined by the FDC technique. We are uncertain why there is such a large discrepancy between the bacterial productivity values determined by the two techniques because both the thymidine uptake and FDC assays have apparently solid theoretical bases, although the former (9, 10) has a greater number of assumptions than the latter (12).

Taken over the entire 18-month period and when assayed by the thymidine incorporation method the portions of the water column at depths of 0 to 75 and 75 to 250 m had bacterial production values of 104 and 89 g of C m⁻², respectively. When assayed by the FDC technique the corresponding values were 31 and 46 g of C m⁻², respectively; i.e., between 46% (thymidine incorporation assay) and 60% (FDC assay) of the water column bacterial production occurred in this deeper water. These data emphasize that in this coastal water the deeper aphotic heterotrophic bacteria contribute significantly to the total water column bacterial production. What remains unresolved from our data is the mechanism(s) by which the heterotrophic bacteria remain productive in the aphotic zone because the main organic substrate source is the primary production of the surface water.

Bacterial concentrations and biomasses tended to change simultaneously with time throughout this water column, although the numbers were usually greater in photic than aphotic water (Fig. 2 and 3). A similar phenomenon was noted with Chl a concentrations (Fig. 4) and bacterial productivities (Fig. 6 and 7). Those data support the observations of other investigators (4, 15) that rapid movement of many biotic and abiotic materials from surface to deeper waters in coastal seawater columns may occur. The result is that a significant portion of the bacterial production occurred in the deeper, aphotic water.

The phytoplankton in this water column displayed three general periods of activities. From approximately midwinter to early summer they had generally moderate and variable primary productivities (Fig. 5). When the euphotic portion of the water column stabilized in June through September, primary productivities greatly increased and remained high. By October primary productivities greatly decreased and remained very low through December. The bacterial productivities which occurred through the water column during these time periods are illustrated in Fig. 6 and 7. Depending on the season there was quite a large variation in the ratios of bacterial to primary production (Table 4); i.e., during the active, inactive, and moderately active phytoplankton growth periods the bacterial productivities were 9, 189, and 71%, of the phytoplankton productivities, respectively, when assayed by the thymidine uptake technique. When assayed by the FDC technique the corresponding values were 4, 190, and 36%. Both assays showed the same trend (Table 4). They also showed that bacterial production continues throughout the fall and early winter months at a time when phytoplankton productivities had greatly diminished. During the approximately 2-month period (October and November) when phytoplankton had very low productivity, the bacteria were probably using microalgal-derived detritus and dissolved organic matter. The use of this phytoplankton debris may extend the growth season for some of the zooplankters beyond September by their use of the
microbial loop (2). One would also expect the microbial loop to be a relatively more important portion of this pelagic ecosystem during mid-winter to early summer than during summer because bacterial production is a greater portion of the total microbial (phytoplankton plus bacterioplankton) production during this time.

In a very general way bacterial productivities in this 250-m-deep water column were related to Chl a and productivities of the phytoplankton (cf. Fig. 4 to 7) because each of these values was low in the winter but higher during the phytoplankton growth season of January through September. This general relationship has been described previously by other investigators (10, 20). Within the phytoplankton growth season, however, bacterial productivities assessed by the thymidine incorporation assay decreased during the more productive period of June through September 1984, as compared with the more moderate phytoplankton growth period of March through May 1984. During the phytoplankton growth period of June through August 1985, bacterial production sharply increased and then fell when the thymidine incorporation assay was used (Fig. 6). Bacterial productivities assessed by the FDC assay had approximately the same values during both the moderately and highly productive phytoplankton growth seasons (Fig. 7). In addition, the thymidine incorporation assay showed an increase in bacterial production through the 250-m-deep water column during October 1984, when Chl a concentrations had substantially decreased and primary productivities were very low (Fig. 4 to 6). Bell and Kuparinen (3) noted a similar phenomenon in Lake Erken, Sweden, where bacterial production increased only slightly during the spring bloom and

![Diagram](image)

**FIG. 5.** Primary production versus sampling date and depth in Howe Sound (means from stations 1, 2, and 3).

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>% Label in: DNA</th>
<th>Protein</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>91.5</td>
<td>8.5</td>
</tr>
<tr>
<td>5</td>
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<tr>
<td>75</td>
<td>63.9</td>
<td>36.1</td>
</tr>
<tr>
<td>150</td>
<td>34.9</td>
<td>65.1</td>
</tr>
</tbody>
</table>

**TABLE 2.** Relative distribution of 3H label in DNA and protein of bacterial populations treated with [methyl-3H]thymidine on 8 August 1985

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>0600 h</th>
<th>1000 h</th>
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<th>1800 h</th>
<th>2100 h</th>
<th>2400 h</th>
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<tbody>
<tr>
<td>1</td>
<td>6.7</td>
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<td>5.9</td>
<td>6.8</td>
<td>5.9</td>
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</tr>
<tr>
<td>5</td>
<td>NA*</td>
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<td>4.9</td>
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<td>NA</td>
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<td>NA</td>
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<td>NA</td>
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</table>

* NA, Not assayed.

**TABLE 3.** Bacterial production in water removed from several depths at 6-h intervals at station 2 on 8 August 1984
FIG. 6. Bacterioplankton production (thymidine uptake method) versus sampling date and depth in Howe Sound (means from stations 1, 2, and 3).

FIG. 7. Bacterioplankton production (FDC method) versus sampling date and depth in Howe Sound (means from stations 1, 2, and 3).
greatly increased after the bloom had peaked. Lovell and Konopka (16) found bacterial production in the euphotic zone of Crooked Lake to decrease in summer when the phytoplankton were productive, while in Little Crooked Lake bacterioplankton productivities remained approximately the same before and after the summer phytoplankton bloom. However, in all four waters (i.e., Howe Sound and Erken, Crooked, and Little Crooked lakes) a peak in bacterial productivities occurred after the period of maximum phytoplankton production. This was probably due to bacterial use of organic materials released by senescent phytoplankton. As phytoplankters senesce they release organic materials to be metabolized by heterotrophic bacteria (1, 8, 11, 17), and as they die there is a further release of organic materials, many of which are rapidly metabolized by heterotrophic bacteria (1, 19). The result is that bacterial production occurs throughout the year, with late fall and early winter bacterial productivities largely depending on primary production which occurs earlier in the year.

Some investigators (7, 19, 22, 29) have suggested that allochthonous organic matter which originates from terrestrial sources may act as nutrients for both freshwater and heterotrophic marine microorganisms, and in many aquatic ecosystems this is probably so. In Howe Sound at stations 1, 2, and 3 the main allochthonous organic matter addition probably occurs by Squamish River discharge; discharge rates are high in summer and early fall and low in winter and spring (Fig. 8). A plot of bacterial production (assayed by thymidine incorporation in water sampled from a depth of 1 m) and Squamish River discharge versus time of sampling is shown in Fig. 8. The curves are not coincident, and there is no significant correlation between discharge rates and bacterial production (r = 0.254, n = 25). Although these data are not conclusive since allochthonous organic matter additions were not directly assayed, they do indicate that terrestrial organic nutrients are probably not a significant portion of the substrates for these heterotrophic bacteria.

We tabulated bacterioplankton production as a portion of phytoplankton production from data reported by us and others (Table 1). These percentage values ranged from 1 to 93%. Our observations (see above) indicate that one reason for this wide range in percent values may be that heterotrophic bacterial use of a portion of the phytoplankton production is displaced in time; i.e., the microalgae cells became available as bacterial substrates when they were senescent (1) or when they were ruptured by factors such as autolysis and herbivore grazers.

Our observations indicate that because of this apparent sequence of phytoplankton growth followed by bacterial production we should sum the respective productivities over at least an annual cycle when comparing one type of productivity with the other. In this way time-dependent variations in productivities would be minimized.

Our bacterial production values were calculated by using a carbon to biovolume ratio of 0.107 pg of C µm⁻³. However, the data reported recently by Bjornsen (5) and Brabak (6) indicate that bacteria may be significantly more dense than this. Brabak (6) calculated a mean ratio of 0.56 pg of bacterial C µm⁻³, whereas Bjornsen (5) suggested a ratio of 0.30 pg of bacterial C µm⁻³. If we assume that the bacterioplankton of Howe Sound have a ratio of 0.30 rather than 0.107 pg of C µm⁻³, then bacterial productivities would be 193(0.30/0.107) = 541 g of C m⁻² (thymidine uptake) and 77(0.30/0.107) = 216 g of C m⁻². These are 64 and 26% of the primary production, respectively. Based on a value of 0.107 pg of bacterial C µm⁻³, bacterial productivities were 23 and 9% of the phytoplankton productivities, respectively. Uncertainty in the correct bacterial C to biovolume ratios and observed discrepancies between the two assays of bacterial production make an accurate determination of bacterial to phytoplankton production percentages difficult.

ACKNOWLEDGMENTS

We appreciate the efforts of Jack Littlepage (vessel coordinator) and Don Horn (master) in arranging for use of MSSV John Strickland for this study. The technical assistance of Barbara May is appreciated.

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LITERATURE CITED


