



# Bacterioplankton growth

  
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## Key Message

Bacterioplankton decompose organic matter and transform chemical compounds leading to significant growth of bacterial biomass in the sea. This bacterioplankton metabolism accounts for about half of the remineralisation of pelagic organic matter and thereby oxygen consumption. The deep water bacterioplankton growth is dependent on and thus also reflects the sedimentation of plankton and associated nutrients from the surface layer. Thus, bacterioplankton growth below the photic zone is an indicator of the trophic status of the sea.

The bacterial growth in the offshore, deep waters of the Bothnian Bay and Bothnian Sea indicate a good trophic status. Both bacterial growth and calculated oxygen consumption in the Gulf of Bothnia is higher than at similar depths in the oligotrophic areas of the Atlantic Ocean, but assessed to be due to expected higher productivity closer to the coast. A weak increasing trend can be seen in the Bothnian Bay over a longer time period, but has ceased during the past 10 years. No statistically significant long-term trends can be shown for the Bothnian Sea indicating stable trophic status.

## Results and Assessment

### Relevance of the indicator for describing developments of the environment

Bacterioplankton community growth rate<sup>1</sup> (briefly “bacterial growth”, BG) is a relatively unambiguous indicator of the flux of organic matter in aquatic ecosystems (Billen et al. 1990). This fact is backed up by observations in many types of aquatic environments, including both oligotrophic, eutrophic, fresh and saltwater (Cole et al. 1988). BG is the product of the factors specific growth rate (i.e., average per cell growth rate, abbreviated  $\mu$ ) and abundance (or mass). As bacterioplankton biomass show moderate variation, both BG and growth rate per cell reflects the substrate supply to the bacterial community (Wikner and Hagström 1999). In other words, although many variables affect BG such as temperature, zoo- and phytoplankton excretion, bacteriophages, and supply of riverine dissolved organic carbon, bacterioplankton growth sensitively indicates trophic status (Billen et al. 1990).

Additionally, bacterial respiration associated with degradation of organic matter consumes oxygen corresponding to half of marine pelagic oxygen consumption in the deep water without active phytoplankton. By using BG, we can calculate a rough estimate of pelagic oxygen consumption (Del Giorgio and Cole 1998). If the rate of oxygen consumption exceeds the rate of oxygen supply, oxygen deficiency can occur in the water column.

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<sup>1</sup> Bacterioplankton community growth rate is an ecological quantity synonymous with “bacterial production” often used in systems ecology. The latter term is applied due to the contribution of bacterial growth to secondary production of biomass. Here the term “growth” is preferred, specified on the organism level for clarity, as bacteria, apart from biomass and cells, can produce pili, enzymes, signal molecules, and many other structures on both individual, population and community level.

## Results

The BG in the Bothnian Bay deep water (40-100 m) show a significant increasing trend for the time period exceeding 22 years by the applied ARIMA model (Fig. 2, Table 1). A Mann-Kendall trend analysis did, however, not confirm a significant trend calling for taking this result with some caution. No trend could be demonstrated during the past 10 years by an ARIMA analysis and has therefore ceased. No significant trend is found in the Bothnian Sea during any time period analysed (Fig. 3). A synchronized month-long peak in growth was observed in both basins and all stations during the winter 2020 to 2021. The cause remain unclear.

The BG was on average  $0.99 \mu\text{g C dm}^{-3} \text{ day}^{-1}$  in the Bothnian Bay, while being 7 % higher in the Bothnian Sea with  $1.05 \mu\text{g C dm}^{-3} \text{ day}^{-1}$  (ANOVA, total df=955,  $p=0.026$ ). The higher value in the Bothnian Sea was in accordance with the higher carbon fixation of this basin (Larsson et al. 2010). This difference was still low considering that the level of phytoplankton production is two times higher in the Bothnian Sea. The relatively high BG in the Bothnian Bay is explained by the higher load per volume of organic matter from rivers (Sandberg et al. 2004).

The ability of bacterial community production to measure changes in trophic status was shown by the seasonally recurrent variation in the deep water by a factor of 3 (data not shown). Highest values occurred in June, when also the highest sedimentation from the spring bloom is expected. Lowest growth rate was observed in February.

The BG in the Bothnian Bay and Bothnian Sea corresponded to a bacterial oxygen consumption of 2.0 and  $2.1 \mu\text{mol O}_2 \text{ dm}^{-3} \text{ day}^{-1}$ , respectively, assuming a bacterial growth efficiency relationship according to del Giorgio and Cole (1998). The oxygen consumption can be assessed relative to the average oxygen concentrations of 377 and  $237 \mu\text{mol dm}^{-3}$ , respectively, for the Bothnian Bay and Bothnian Sea (mean values in deep water 2014-2020). Assuming bacterioplankton to account for one third of the total respiration (Robinson and Williams 2005), average daily oxygen consumption would then correspond to 1.6 and 2.6 % of the average oxygen pool  $\text{day}^{-1}$ , respectively.

## Assessment

The bacterioplankton community growth rates in the deep water of the Bothnian Bay and Bothnian Sea have been assessed as representing a good trophic state. This indicates that the export of organic matter by sedimentation to the deep water occurs within allowable limits.

The status classification is based on comparison the level of BG and pelagic respiration found in oceanic water. Most relevant comparison is an estimate of BG from the 50-100 m layer in the Barents Sea of  $0.30 \mu\text{g C dm}^{-3} \text{ day}^{-1}$  (Børsheim and Drinkwater 2014). A similar level of  $0.24 \mu\text{g C dm}^{-3} \text{ day}^{-1}$  was reported from the oligotrophic equatorial Atlantic in (Dufour and Torreton 1996), while rates up to  $5.5 \mu\text{g C dm}^{-3} \text{ day}^{-1}$  can be found during a spring bloom in the euphotic zone of the N Atlantic (Ducklow 2000). The low BG observed in the Gulf of Bothnia is in accordance with that phytoplankton production levels are in the oligotrophic interval in the area (Wasmund et al. 2001).

Another way to compare with reference values is to evaluate total oxygen consumption from BG, assuming 50 % of plankton respiration to be due to bacterioplankton. The level of calculated oxygen consumption in the Gulf of Bothnia was 3 times higher ( $4 \mu\text{mol dm}^{-3} \text{ day}^{-1}$ ) than the mean oxygen consumption measured at the same depth interval in the ocean ( $1.3 \mu\text{mol dm}^{-3} \text{ day}^{-1}$ ) (Robinson and Williams 2005). This as in good accordance with the difference found between status value and reference value for BG. The deep water oxygen consumption also corresponded to the lower end of the range observed by direct measurements of plankton respiration in a coastal estuary in the Bothnian Sea, defined there as baseline respiration (Vikström et al. 2020).

Higher productivity, and thereby oxygen consumption, is expected in coastal waters compared to oceanic, so it is not obvious that the higher rates of bacterial growth measured in the Gulf of Bothnia

are above allowable limits. The lack of a significant decrease of oxygen levels in the Bothnian Bay since the beginning of the 1970's (Lindberg 2016), corroborate that oxygen supply to the deep water has been and remained sufficient to account for total respiration. This supports that the deep-water oxygen consumption and thereby BG is within allowable limits (Fig. 2). A decline in oxygen concentration has, however, been observed in the Bothnian Sea during the past 40 years, making the classification for this basin more difficult. However, no increase in bacterial growth occur that could explain decreasing oxygen levels (Fig. 3). It also seems unlikely that the only 7 % higher BG in the Bothnian Sea than the Bothnian Bay alone could explain the observed difference in oxygen status between the basins. Instead, temperature increase and import of oxygen deficient water from the Baltic Proper probably explain the decline in oxygen concentration in the Bothnian Sea (Ahlgrén et al. 2017).

A management consequence of the stable and low BG observed is that it will be extraordinarily difficult to reduce oxygen consumption further by nutrient reductions. Another reason is the fact that that riverine discharge of dissolved organic carbon can be a significant carbon and energy source driving pelagic respiration in estuaries of the Gulf of Bothnia (Vikström et al. 2020).

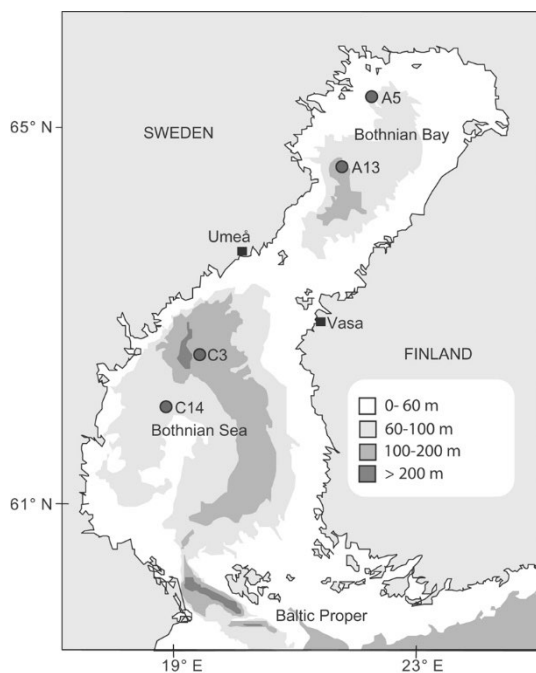
## Metadata

### Data description

#### Values

The bacterioplankton community growth rate estimates are based on uptake of the nucleotide thymidine into the DNA (i.e., chromosome) of the bacteria. The original method is published in international scientific journals and has been used in many marine research studies since the beginning of the 1980s. The method is included in the Manual for Marine Monitoring in the COMBINE program of HELCOM (part C, Annex C-11, [Manual-for-Marine-Monitoring-in-the-COMBINE-Programme-of-HELCOM.pdf](#)).

Values were averaged for the depths sampled within the 40-100 m water layer chosen (median, n=4). Typically, values are based on 8-20 samplings distributed over the year. Data is collected within the Swedish national marine monitoring program, funded by the Swedish Agency for Marine and Water Management and the Swedish Environmental Protection Agency. Sampled stations are shown in Figure 1. Data collection is done by the technical staff at Umeå Marine Sciences Centre at Umeå University, Sweden, with logistic support by the Swedish Coastguard.



**Figure 1.** Sampling stations for pelagic indicators in the Gulf of Bothnia.

### Statistics

Linear interpolation replaced missing values and data was averaged to yield monthly time series, as required for the seasonal decomposition. About 24% of the values in the analysed time series were interpolated. The average seasonal variation was removed from the time series by a multiplicative model and endpoints weighted by 0.5 in the software SPSS® v.28.

The seasonally decomposed time series were typically serially autocorrelated by one lag and therefore analysed for trends by a first order autoregression (SPSS®). This uses a least-square technique where errors follow a first order autoregression.

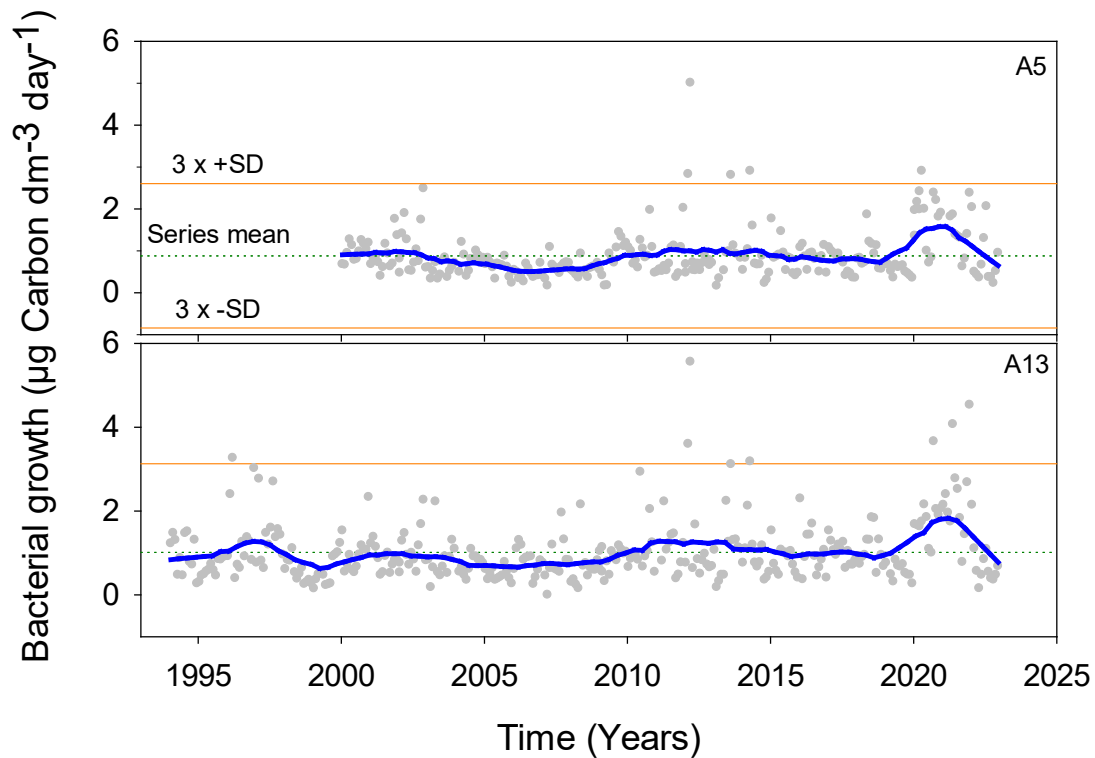
A non-parametric test for trend analysis was also performed using Multitest (Department of Computer and Information Science, Linköping University), an Excel-based software for Mann Kendall tests with monotonic trends (Helsel 2005) (result not shown).

To show the general trends in the time series, a negative exponential smoother was applied. This is a local smoothing technique using polynomial regression and weighted values computed from the Gaussian density function (SigmaPlot v. 15.0®).

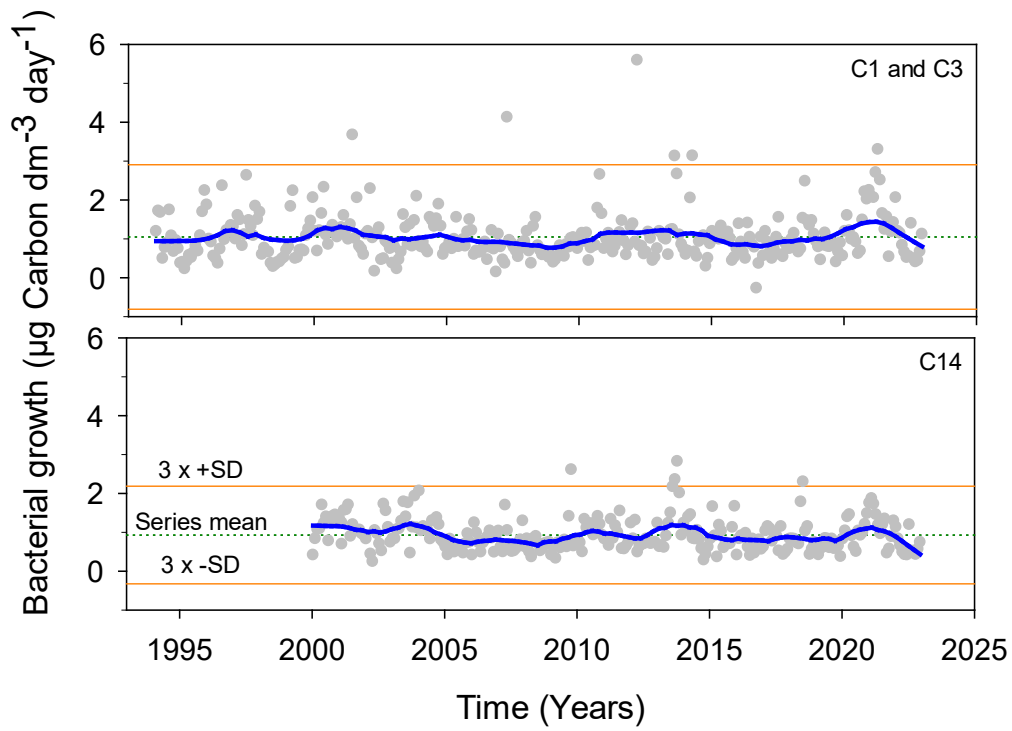
The statistical power of the time series was estimated from the standard deviation of the autoregression (Root Mean Square Error), the non-centrality parameter and the non-central t-distribution. As a guidance to assess significant changes, a difference of 25 % in 2 years can be detected with 80 % probability.

The difference between the Bothnian Bay and Bothnian Sea was determined from marginal means in an ANOVA on primary BG data, where area, year and month were fixed factors.

## Figures



**Figure 2.** The bacterioplankton community growth rate at stations A5 and A13 below the stratified layer (40-100 m) in the Bothnian Bay. A negative exponential smoother is shown (blue line) together with seasonally adjusted data (grey dots). The 3 x SD lines represent the upper and lower 99% confidence limits of the smoothed time series, suggested as action limits for the quality factor. Year ticks are located on the 1st of January each year.



**Figure 3.** The bacterioplankton community growth rate at stations C14 and C1/C3 below the stratified layer (40-100 m) in the Bothnian. Symbols defined as in Figure 2.



## Tables

**Table 1.** Bacterioplankton community growth rate (BG) below the pycnocline level shows a significant trend (bold face) only in the Bothnian Bay and for a longer period than 22 years. The 95% confidence interval (C. I.) of the trend is shown. The significance ( $\alpha$ ) shows the risk of being wrong if stating that there is a trend, which should be below 0.05 for a statistically significant statement. The series mean of BG is shown on the far right.

Sea area	Station	Years	Period	Trend (% year <sup>-1</sup> )	±95%CI (% year <sup>-1</sup> )	$\alpha$ (-)	BG mean ( $\mu\text{g C dm}^{-3} \text{ day}^{-1}$ )
Bothnian Bay	A5	10	2013-2022	4.0	7.4	0.287	1.0
Bothnian Bay	A13	10	2013-2022	4.5	7.1	0.205	1.2
Bothnian Sea	C3	10	2013-2022	1.6	6.8	0.655	1.1
Bothnian Sea	C14	10	2013-2022	-2.8	6.0	0.359	0.9
Bothnian Bay	A5	23	2000-2022	<b>1.8</b>	1.8	<b>0.039</b>	0.9
Bothnian Bay	A13	23	2000-2022	<b>1.1</b>	0.8	<b>0.014</b>	1.0
Bothnian Sea	C3	23	2000-2022	0.3	1.5	0.740	1.1
Bothnian Sea	C14	23	2000-2022	-0.8	1.5	0.264	0.9
Bothnian Bay	A13	29	1994-2022	<b>0.7</b>	0.6	<b>0.032</b>	1.0
Bothnian Sea	C1/C3	29	1994-2022	0.3	1.1	0.651	1.1

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