The dependence between bacterial production and environmental conditions in the Gulf of Gdańsk

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Abstract

Bacterial production, primary production and a number of other environmental factors were measured during six cruises in the Gulf of Gdańsk conducted in various seasons from 1995 to 2001. Bacterial production (BP) in the epipelagic layer ranged from 1.5% (April) to 80% (July) of the gross primary production (PP). Significant differences were observed between the BP/PP ratios in estuarine and open-water areas. The highest values were recorded in the coastal area and near the mouth of the river Vistula. It suggests that allochthonous organic matter has a great influence on BP. The correlations between particular parameters and regression analyses indicated that BP in the Gulf of Gdańsk depended on temperature, organic nitrogen concentration, PP, chlorophyll a concentration, organic phosphorus concentration, salinity and biochemical oxygen demand. Of all the independent variables, the temperature had the greatest impact on BP ($R^2 = 0.62$). There was an inverse parabolic relationship between bacterial production and temperature. It appears that above a temperature of 12°C bacterial production depended on substrates

The complete text of the paper is available at http://www.iopan.gda.pl/oceanologia/

to a higher degree than on temperature. The negative correlation between BP and concentrations of mineral nitrogen and phosphorus in the annual cycle were probably due to an indirect dependence. A multiple regression equation, which included temperature and organic phosphorus concentrations, explained 78% of the variation in BP.

Increasing BP resulted in an increasing biomass of bacterivorous nanoflagellates and of bacterivorous ciliates, which is indicative of bottom-up control in this segment of the trophic chain.

1. Introduction

Heterotrophic bacteria play a special role in pelagic communities. They are responsible for the decomposition and mineralisation of organic matter and are the only group of organisms that reintroduce dissolved organic substances into the carbon cycle. Phytoplankton primary production is considered the main source of energy for bacterioplankton. Heterotrophic bacteria also require certain amounts of inorganic nutrient salts for their development (Lignell et al. 1992, Kuparinen & Heinänen 1993), and they may have to compete for them with phytoplankton during strong blooms. Williams (1981) and Cole et al. (1988) reported that bacterial secondary production constitutes an average of 20% of the primary production in both lakes and oceans. However, this may differ in estuaries, where inputs of allochthonous organic matter can be high.

The second largest river draining into the Baltic Sea is the Vistula, which flows into the Gulf of Gdańsk and drains 11.6% of the Baltic Sea catchment area (HELCOM 1990). Annually, the Vistula discharges approximately 30 km^3 of water into the Baltic Sea along with 85×10^3 t of total nitrogen, 5×10^3 t of total phosphorus (Dojlido et al. 1994), and about 445×10^3 t of organic carbon (Pempkowiak & Kupryszewski 1980). The Gulf of Gdańsk is a partially sheltered, relatively deep basin (max depth 118 m). A characteristic feature of the water column in the gulf is the stable salinity gradient (7–12 PSU), starting from about 70 m depth downwards. This stratification is characteristic of the Baltic Proper, where the deeper water layer originates from the more saline North Sea waters. There is riverine stratification in the Gulf of Gdańsk, too, but this is detectable only in the thin surface layer, and the location of the river plume is very variable. The western and the southern parts of the Gulf of Gdańsk belong to Poland, the eastern part to Russia. In the Polish part of the gulf, two administrative water districts are differentiated – internal sea waters and territorial waters. The line separating the internal and territorial waters runs south-eastwards from the Hel Peninsula (Fig. 1). This purely conventional division reflects the character of the area well. The typically estuarine, internal part is strongly influenced by the waters of the Vistula.

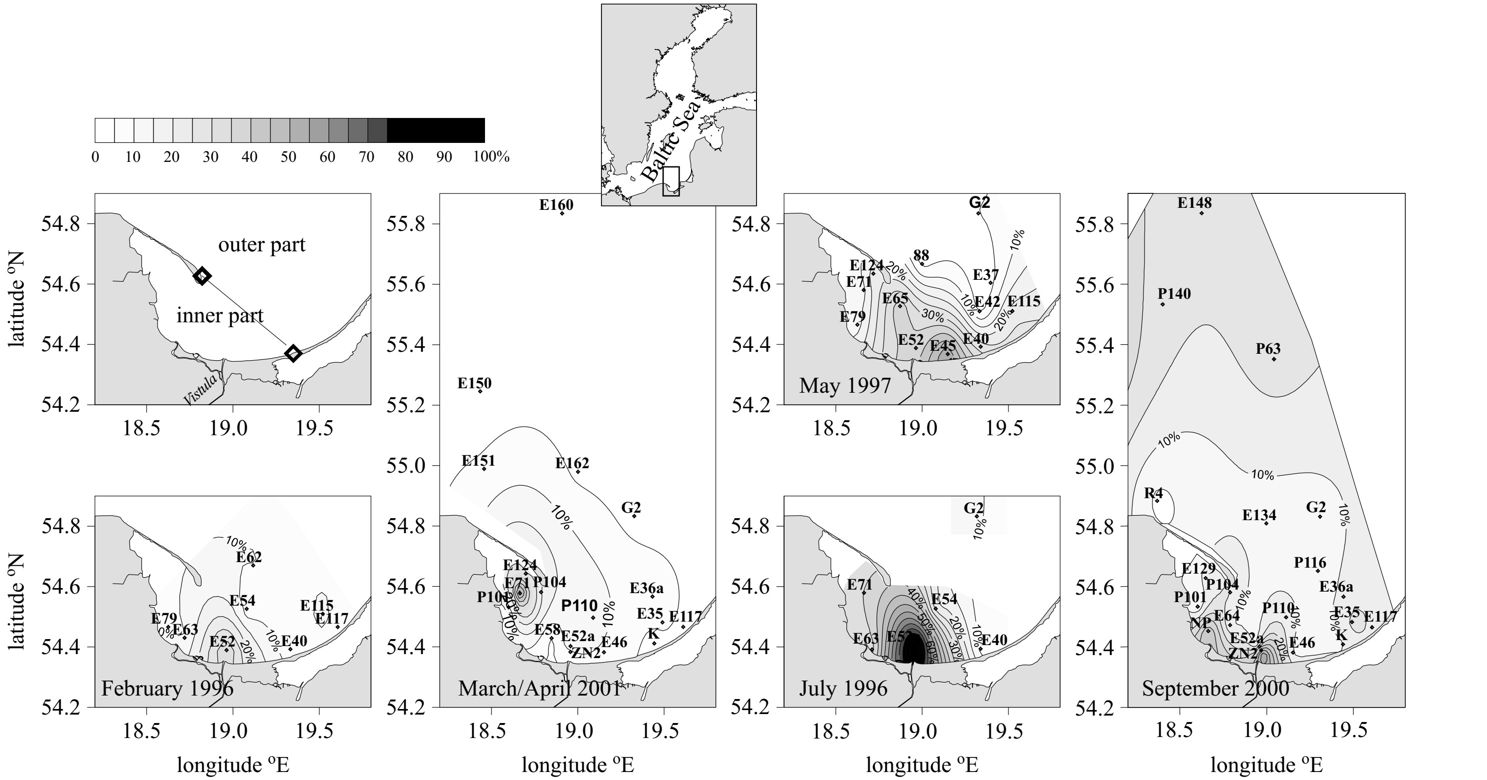

Fig. 1. Bacterial production in relation to primary production [%] in the epipelagic layer of the Gulf of Gdańsk during different cruises

The outer part is similar in character to the open sea (Cyberska & Lauer 1990, Trzosińska & Łysiak-Pastuszak 1996). Conditions in the Gulf of Gdańsk are favourable to the transformation or accumulation of terrigenous matter (Trzosińska & Łysiak-Pastuszak 1996, Carman & Rahm 1997, Kruk-Dowgiałło 1998, Witek et al. 2003). Our knowledge of the microbiological processes occurring in this basin, which are very important for the functioning of the entire Baltic Sea ecosystem, is still insufficient (Mudryk et al. 1991, Maciejowska & Boćwińska 1996, Witek et al. 1997a, b, Mudryk 2003).

The aim of this work was to determine the proportions between bacterial and primary production in the estuarine area of the Gulf of Gdańsk, and to investigate whether the riverine discharge of allochthonous organic matter modifies these proportions. An additional aim was to derive some empirical formulas enabling the bacterial production to be calculated on the basis of certain routinely measured environmental factors.

2. Material and methods

The studies were performed during the course of six cruises in the Gulf of Gdańsk in August 1995, February and July 1996, May 1997, September 2000 and from late March till April 2001. Several parameters were measured during the cruises: temperature, salinity, bacterial abundance and production (BP), primary production (PP), chlorophyll *a* concentration, nutrient concentrations, pelagic community respiration, biochemical oxygen demand (BOD), as well as protozooplankton composition and biomass. The last two parameters were estimated only during the first four cruises. Water temperature and salinity were measured with a Niels Brown CTD probe.

BP was determined by measuring the bacterial uptake of tritium-labelled thymidine with an activity of 1.7–1.8 TBq mmol^{-1}. The thymidine was diluted four times, after which 20 μl were added to the sample to produce a final concentration of 11–12 nM (Fuhrman & Azam 1982, Riemann et al. 1987). Samples were incubated at the *in situ* water temperature for two hours when this was $< 10°$C, and for one hour when it was $> 10°$C. Thymidine activity was measured using a Beckman LS 6000 IC scintillation counter. BP was calculated using the thymidine conversion factor 11×10^7 cell pmol^{-1} (Rieman et al. 1987), a cellular carbon content of 27×10^{-2} pg C μm^{-3} (Kuparinen 1988) and the average bacteria volume. This last was obtained from microscope measurements. Both abundance and the average bacteria cell volume were determined by direct counting and by measuring the length and width of bacteria (dyed with acridine orange) under Olympus BX50 and BX60 epifluorescence microscopes (Hobbie et al. 1977, Bergström et al. 1986, Bjørnsen 1986).

PP, chlorophyll *a*, hydrochemical and protozoological measurements were conducted by the staff of the Sea Fisheries Institute in Gdynia; the data were available in the form of either publications or working materials (see Acknowledgements).

Primary production was determined using the C^{14} method (Steemann-Nielsen 1952, Evans et al. 1987, HELCOM 1988), and the chlorophyll *a* concentration was determined with the fluorimetric method (Evans et al. 1987). Primary production and chlorophyll *a* data from the cruises performed in 1995–1997 have been published by Renk et al. (2000).

Chemical analyses ($PO_4{}^{3-}$, P_{tot}, $NO_3{}^-$, $NO_2{}^-$, $NH_4{}^+$, N_{tot}) were conducted according to the standard methods used in the Baltic Monitoring Programme (Grasshoff et al. 1983, UNESCO 1983, HELCOM 1988). Mineral nitrogen was determined by summing the values obtained for individual inorganic nitrogen forms: $N_{miner} = NO_3{}^- + NO_2{}^- + NH_4{}^+$. Organic nitrogen and phosphorus were derived by subtracting the values of the mineral forms from those of total nitrogen and phosphorus: $N_{org} = N_{tot} - N_{miner}$ and $P_{org} = P_{tot} - PO_4{}^{3-}$. Oxygen content during measurements of pelagic community respiration and biochemical oxygen demand were determined by the Winkler method using an autoburette (Titrino 702 SM).

The abundance of heterotrophic nanoplankton flagellates (1–8 μm) was determined using the epifluorescence method (Caron 1983). The composition and abundance of ciliates were analysed under a reverse microscope (Utermöhl 1958).

The studies and analyses presented in this paper refer to the epipelagic layer, which is understood here as the layer between the surface and a depth of 20 m. Samples for bacterioplankton abundance, biomass and production, biochemical oxygen demand, pelagic community respiration, and protozooplankton composition and biomass were taken at depths of 0.5, 10 and 20 m (or near the bottom), while those for PP, chlorophyll *a* and nutrient concentrations were taken at depths of 0.5, 2.5, 5, 10, 15 and 20 m. Because of wave mixing, such parameters as temperature, salinity, concentrations of substances and microorganisms as well as bacterial production and pelagic community respiration were usually evenly distributed within the epipelagic water column. The only exception was primary production, which was strongly dependent on light intensity and decreased exponentially with increasing depth. In order to investigate temporal or horizontal rather than vertical variability in the variables studied, weighted averages of all the parameters measured from the surface to 20 m depth, or at shallower stations from the surface to the bottom, were used in all the correlations and regressions.

Student's t-test was applied to verify the hypothesis that assumes the proportions of BP and PP to differ in both the inner and outer parts of the Gulf of Gdańsk. The logarithm of the BP/PP ratio yielded normal distributions (W Shapiro-Wilk test) and homogeneity of variances (Levene's test) of the transformed variables. Multiple linear regression analysis was used to determine the dependence of the BP on various factors, forward stepwise regression to select the best model, and the least squares method to estimate the model parameters. In order to obtain regression model linearity, logarithmic transformations were applied to the data, describing BP, PP, chlorophyll a concentration, heterotrophic nanoflagellate biomass, bacterivorous ciliates, pelagic community respiration, biochemical oxygen demand, as well as concentrations of organic and inorganic nitrogen and phosphorus. In order to determine the model significance, variance analysis was used in the regression (F Fisher-Snedecor test) (Stanisz 2000).

3. Results

The values of bacterial abundance, biomass and BP were strongly correlated with temperature, and the highest values of all these parameters were recorded in July 1996, the lowest in February 1996. Winter weather conditions prevailed at the very beginning of the March–April 2001 cruise; however, during the cruise, conditions improved sufficiently for a typical spring phytoplankton bloom to occur. Bacterial abundance and biomass were highest in coastal waters, especially near the Vistula mouth. BP was highest in the surface layer and at a depth of 10 m, and lowest at 20 m.

In the present study, there was a significant difference in the BP/PP (%) ratio between the inner and outer parts of the gulf (t-test, $t = 5.08$; $df = 67$; $p = 3 \times 10^{-6}$) (Fig. 2). In the inner part, BP in the epipelagic layer ranged from 3 to 80% of the gross PP (average 22%, $n = 31$), with the highest values being recorded in July 1996 and the lowest in early April 2001. BP/PP ratios were highest near the Vistula mouth (Fig. 1). The influence of riverine waters is well illustrated by the relation between BP/PP and salinity (Fig. 3). Only in March–April 2001 was the situation different (Fig. 1). In spring 2001, BP/PP ratios reached a maximum in the western part of the Gulf of Gdańsk (Fig. 1). In the outer gulf these values varied within a smaller range – from 1.5% in April 2001 to 23% in May 1997 (average 8%, $n = 38$).

Analysis of the relations between BP and several environmental factors showed that the latter could be divided into two groups: factors independent of BP and factors dependent on BP. The independent factors were temperature, PP, chlorophyll a concentration, biochemical oxygen demand, concentrations of organic nitrogen and phosphorus, and salinity. The depen-

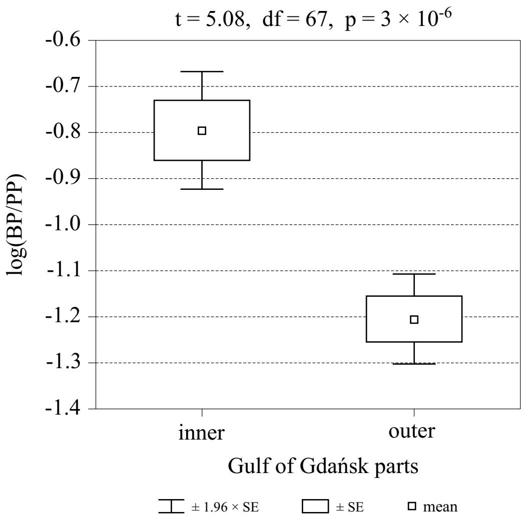

Fig. 2. The ratio of bacterial production to primary production (BP/PP) in the waters of the inner and outer Gulf of Gdańsk (Student's t-test for equal variance). The normal distribution was determined by finding the logarithms of BP/PP

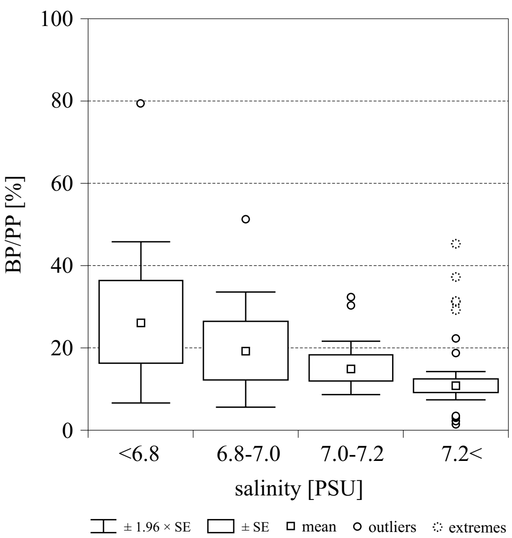

Fig. 3. Relationship between the bacterial production to primary production (BP/PP) ratio and salinity

dent factors were heterotrophic nanoflagellate biomass, bacterivorous ciliate biomass and pelagic community respiration. The determination coefficients in the regression analysis in the first group of factors were highest for organic nitrogen ($R^2 = 0.52$), PP ($R^2 = 0.51$), chlorophyll a ($R^2 = 0.46$),

Table 1. Single regression analysis of the relationship between bacterial production (log transformed) [mg C m^{-3} d^{-1}] and particular factors. Mean values from 0 to 20 meters were used

Independent variables (X)	b_0 **(intercept)**	b_1 **(slope)**	R^2	F	SE	p	N
log $\mathbf{N}_{organic}$	–6.1 (±0.7)	4.8 (±0.5)	0.52	83	0.413	7×10^{-14}	79
log **PP**	–0.90 (±0.15)	0.91 (±0.11)	0.51	71	0.390	4×10^{-12}	69
log **chl** *a*	–0.105 (±0.073) ns	1.189 (±0.149)	0.46	64	0.427	1×10^{-11}	77
temperature	–0.216 (±0.082)	0.060 (±0.008)	0.45	62	0.443	2×10^{-11}	79
log $\mathbf{P}_{organic}$	1.20 (±0.14)	2.83 (±0.40)	0.41	49	0.461	1×10^{-9}	72
salinity*	7.78 (±1.57)	–1.05 (±0.22)	0.23	23	0.524	9×10^{-6}	79
log $\mathbf{BOD}_{21}$	0.70 (±0.17)	705 (±304)	0.15	5	0.645	3×10^{-2}	32
Dependent variables (Y)	b_0 **(intercept)**	b_1 **(slope)**	R^2	F	SE	p	N
log **biomass HNF**	0.85 (±0.03)	0.64 (±0.04)	0.86	215	0.194	1×10^{-16}	38
log **biomass BC**	0.147 (±0.068)	0.768 (±0.088)	0.68	77	0.388	2×10^{-10}	38
log **PCR**	–1.35 (±0.04)	0.37 (±0.06)	0.33	35	0.277	1×10^{-7}	72
Indirectly dependent variables (Y)	b_0 **(intercept)**	b_1 **(slope)**	R^2	F	SE	p	N
log $\mathbf{P}_{mineral}$*	–0.66 (±0.06)	–0.60 (±0.09)	0.38	47	0.453	2×10^{-9}	78
log $\mathbf{N}_{mineral}$*	0.31 (±0.06)	–0.54 (±0.09)	0.30	33	0.494	2×10^{-7}	79

PP – primary production [mg C m^{-3} d^{-1}]; chl *a* – chlorophyll *a* concentration [mg m^{-3}]; BOD_{21} – biochemical oxygen demand [mg O_2 m^{-3} 21 d^{-1}]; HNF – heterotrophic nanoplankton flagellates (1–8 μm) [mg m^{-3}]; BC – bacterivorous ciliates [mg m^{-3}]; PCR – plankton community respiration [dm^3 O_2 m^{-3} d^{-1}]; * – reversibly proportional correlation; b_0, b_1 – coefficients of regression equation $Y = b_0 + b_1X$; Y-log BP for independent variables; X-log BP for dependent variables; the values of the standard errors of particular factors are in parentheses; R^2 – determination coefficient; F – ratio (Fisher-Snedecor test); SE – standard error of estimation; p – level of significance; N – number of measurements; ns – no significant intercept at $p = 0.05$; $N_{organic}$, $P_{organic}$, $P_{mineral}$, $N_{mineral}$ [mmol m^{-3}]; temperature [°C]; salinity [PSU].

temperature ($R^2 = 0.45$) and organic phosphorus ($R^2 = 0.41$) (Table 1, Figs 4 and 5). The lowest values, though still significant, were obtained for the salinity and biochemical oxygen demand. Nevertheless, a quadratic relationship (eq. (1)) provided a better correlation ($R^2 = 0.62$) between BP and temperature than a linear one ($R^2 = 0.45$) (Fig. 4b):

$$\log \mathrm{BP} = -0.674 + 0.251 \times temp - 0.010 \times temp^2$$
$$(R^2 = 0.62,\ N = 79,\ F = 61,\ SE = 0.372), \tag{1}$$

where R^2 is the determination coefficient, F – ratio (Fisher-Snedecor test), SE – standard error of estimation, p – level of significance, N – number of measurements.

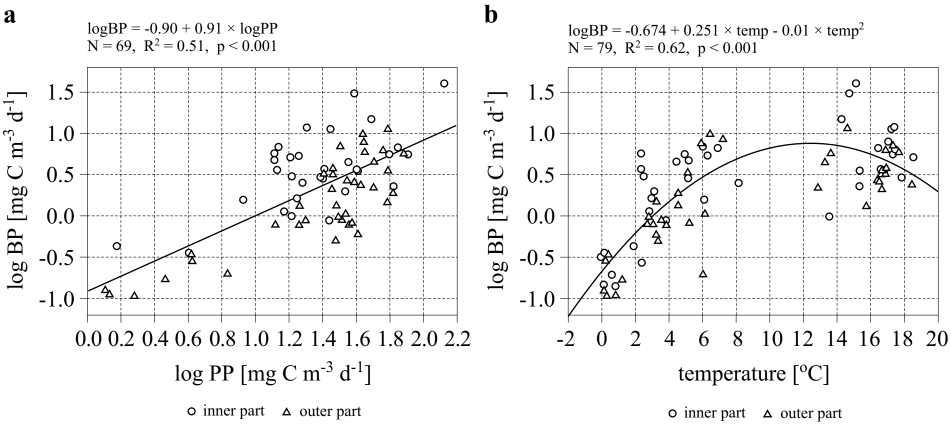

Fig. 4. Relationship between bacterial production (BP), and primary production (PP) (a), and temperature (b) in the epipelagic layer of the Gulf of Gdańsk

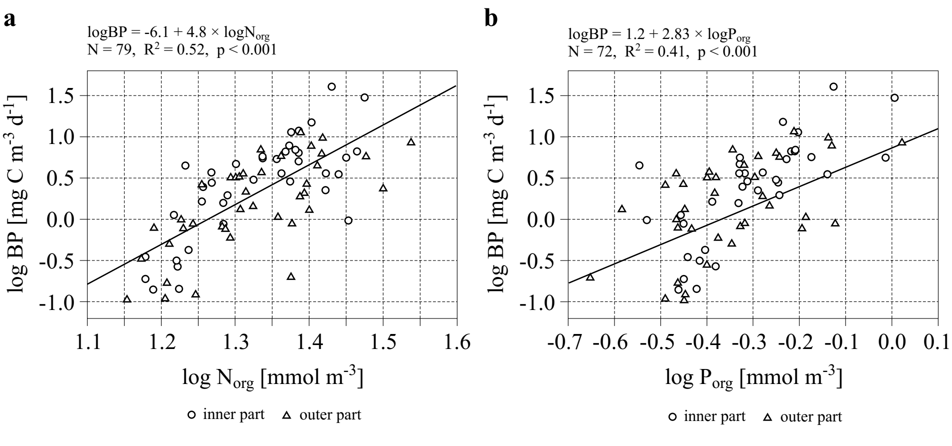

Fig. 5. Relationship between bacterial production (BP), and organic nitrogen (N_{org}) (a); organic phosphorus (P_{org}) (b) in the epipelagic layer of the Gulf of Gdańsk

In the group of factors dependent on BP, the highest values of the determination coefficient (R^2) were obtained for the heterotrophic nanoplankton flagellate biomass (0.86) and bacterivorous ciliate biomass (0.68) (Fig. 6). The following genera and species of bacterivorous ciliates, which, according to the literature, feed on bacterioplankton, were observed in the samples: *Cyclidium, Euplotes, Prorodon, Vaginicola, Vorticella, Lohmanniella oviformis* and *Mesodinium pulex* (Fenchel 1968, 1969, Farmer

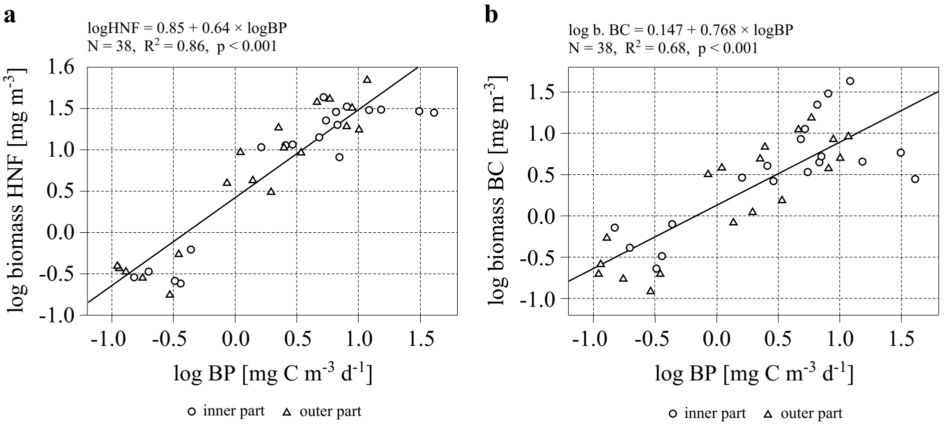

Fig. 6. Relationship between the biomass of heterotrophic nanoplankton flagellates (HNF) and bacterial production (BP) (a); relationship between the biomass of obligatory bacterivorous ciliates (BC) and bacterial production (BP) (b) in the epipelagic layer of the Gulf of Gdańsk

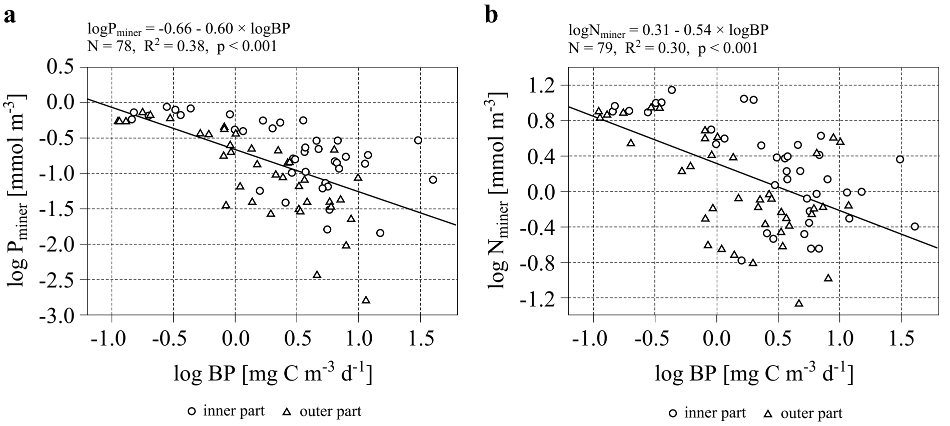

Fig. 7. Relationship between concentrations of mineral phosphorus (P_{miner}) and bacterial production (BP) (a); relationship between concentrations of mineral nitrogen (N_{miner}) and bacterial production (BP) (b) in the epipelagic layer of the Gulf of Gdańsk

Table 2. Multiple regression between the log of bacterial production [mg C m^{-3} d^{-1}] and particular factors (with $p < 0.001$ in the single regression analysis)

Independent variables (X)	b_0 (intercept)	b_1 (slope)	b_2 (slope)	b_3 (slope)	R^2	F	SE	N
Two-factor model								
$\mathbf{X_1}$-*temp*	0.184	0.179	1.973	–0.007	0.78	80	0.287	72
$\mathbf{X_2}$-log $\mathbf{P}_{organic}$	(±0.153)	(±0.031)	(±0.278)	(±0.002)				
$\mathbf{X_3}$-*temp*^{2}	ns							
$\mathbf{X_1}$-log **chl** *a*	–0.610	0.746	0.151	–0.006	0.73	66	0.305	77
$\mathbf{X_2}$-*temp*	(±0.090)	(±0.124)	(±0.032)	(±0.002)				
$\mathbf{X_3}$-*temp*^{2}								
$\mathbf{X_1}$-log $\mathbf{N}_{organic}$	–2.885	1.871	0.183	–0.007	0.65	46	0.359	79
$\mathbf{X_2}$-*temp*	(±0.862)	(±0.724)	(±0.042)	(±0.002)				
$\mathbf{X_3}$-*temp*^{2}								
$\mathbf{X_1}$-log **PP**	–0.846	0.669	0.030	–	0.61	51	0.353	69
$\mathbf{X_2}$-*temp*	(±0.140)	(±0.115)	(±0.008)					
	ns							
Three-factor model								
$\mathbf{X_1}$-log **PP**	0.039	0.419	1.775	0.035	0.75	60	0.285	64
$\mathbf{X_2}$-log $\mathbf{P}_{organic}$	(±0.196)	(±0.108)	(±0.305)	(±0.007)				
$\mathbf{X_3}$-*temp*	ns							

temp – temperature [°C]; PP – primary production [mg C m^{-3} d^{-1}]; chl *a* – chlorophyll *a* concentration [mg m^{-3}]; log $N_{organic}$, log $P_{organic}$ [mmol m^{-3}]; b_0, b_1, b_2, b_3 – coefficients of regression equation $Y = b_0 + b_1X_1 + b_2X_2 + b_3X_3$ where Y-log BP; R^2 – determination coefficient; F – ratio (Fisher-Snedecor test); SE – standard error of estimation; N – number of measurements; ns – no significant intercept at $p = 0.05$; the values of the standard errors of particular factors are in parentheses.

1980, Gast 1985, Pratt & Cairns 1985, Albright et al. 1987, Sanders 1988, Turley et al. 1988). The taxonomic composition was typical of the Gulf of Gdańsk and was not different from compositions observed in previous studies in this region (Witek 1998).

Inversely proportional relationships were found between BP and concentrations of mineral forms of nitrogen and phosphorus (Fig. 7). Decreasing concentrations of nutrient salts with increasing BP may suggest bacterial consumption of inorganic nutrients. It is also possible, however, that indirect relations existed.

Multiple regression analysis was performed for the factors significantly influencing BP (PP, chlorophyll *a* concentration, temperature, and organic nitrogen and phosphorus concentrations) (Table 2). The biochemical oxygen demand parameter did not satisfy the significance condition in the multiple regression. The highest values of the determination coefficient and the F coefficient were observed for temperature and organic phosphorus, those of temperature and chlorophyll *a* concentration were somewhat less. The three-factor model did not explain the variability of BP in any greater detail than did the two-factor model with temperature and organic phosphorus.

4. Discussion

Heterotrophic bacteria in coastal areas have two sources of organic matter at their disposal – local ones comprising excreta and the remains of phyto- and zooplankton and external ones in the form of terrigenous allochthonous organic matter. The importance of the first source was indicated by the relationship between BP and PP.

Derived in this work, eq. (2) is less satisfactory in explaining the variability of the BP than eq. (3), published by Cole et al. (1988). Both equations exhibit similar relationships between the variables, although the values of the coefficients differ slightly. The higher R^2 in the equation of Cole et al. (1988) could have been due to the broader spectrum of values originating from different environments as compared to the single system examined here.

$$\log \mathrm{BP} = -0.90 + 0.91 \times \log \mathrm{PP} \;\; (R^2 = 0.51,\ N = 69,\ F = 71), \qquad (2)$$

$$\log \mathrm{BP} = -0.63 + 0.86 \times \log \mathrm{PP} \;\; (R^2 = 0.77,\ N = 30,\ F = 92) \quad \text{(Cole et al. 1988)}, \qquad (3)$$

where R^2 is the determination coefficient, N – number of measurements, F – ratio (Fisher-Snedecor test).

With reference to regression (2), BP increases with increasing PP. This dependence can have two causes: a direct one, i.e. phytoplankton itself, or excreted products that are important food substrates for bacteria (Larsson & Hagström 1979), or an indirect one, i.e. bacteria and phytoplankton are similarly dependent on different factors (temperature, nutrient concentrations, etc.). It is most likely, however, that both mechanisms occur simultaneously. Bacteria utilise only a small amount of the large pool of dissolved organic matter (DOM) present in the aquatic environment, principally monosaccharides and aminoacids, which are excreted mainly by phytoplankton (Larsson & Hagström 1982, Norrman et al. 1995). Findings from the coastal zone of the Gulf of Gdańsk showed that amounts of dissolved organic substances excreted by phytoplankton were about half the level of bacterial food requirements (Witek et al. 1997a). This indicated that DOM excretion by phytoplankton, though an important source of food for bacteria in the area studied, was not the most important source for BP. Matter derived from decaying flora and fauna cells and allochthonous matter were more important sources. According to Wikner & Hagström (1999), bacteria do not depend on the impact of phytoplankton in certain situations. These authors observed a separation in the dependence between BP and PP in the Gulf of Bothnia, where there was a significant external source of dissolved organic carbon (from inflows of dissolved organic carbon with winter discharges from hydroelectric power plants) and residence times were long.

Biochemical oxygen demand (BOD) is commonly used as an indirect measure of the amounts of biodegradable organic matter and could therefore reflect the quantity of phytoplankton-derived organic matter in the water as well as the amount of allochthonous organic matter. The results of single regression indicated that BOD explained only 15% of the variability of BP. The highest BOD values are measured in cold seasons, when bacterial production is strongly inhibited by low temperatures and organic matter cannot be fully utilised by bacteria.

Depending on season and sampling location, BP ranged from 1.5% to 80% of the PP with an average of 14.3% (N = 69). Similar mean values were reported by Witek et al. (1999) for the Gulf of Gdańsk (17.7%), and by Kuosa & Kivi (1989) and Lignell (1990) for the northern Baltic Sea (15% and 14.4%, respectively). Average BP/PP ratios reached 22% in the inner part of the Gulf of Gdańsk but only 8% in the open waters. Such a low ratio in the open waters, as compared to the figure of 20% given by Cole et al. (1988) as an average for lakes and oceans, could be due to the low temperature in the Baltic Sea. However, Kuosa & Kivi's (1989), and Lignell's (1990) values came from the Baltic Sea, too. Their measurements were made in coastal waters, where BP could have been higher. Moreover, in their studies PP was measured with a long incubation time (24 h and 6–7 h) and may therefore have represented the net primary production, whereas in this study (with an incubation time of 2–4 h) the gross primary production was measured. The higher BP or lower (net) PP will have influenced the greater magnitude of the BP/PP ratio noted by our Finnish colleagues. The Gulf of Gdańsk receives almost half a million tons of organic carbon annually from the river Vistula (Pempkowiak & Kupryszewski 1980, Niemirycz et al. 1989). In the vicinity of the river mouth, high values of BP in relation to PP, ranging from 37 to 80%, were reported in May 1997, July 1996 and September 2000. It is likely that bacteria utilised allochthonous organic matter to a significant degree. Also, a negative dependence between the BP/PP ratio and salinity (Fig. 3) indicated indirectly that the Vistula waters had an impact on the increase in BP.

Temperature alone explained 62% of the variability in BP. Considering the Arrhenius equation (a 10° increase in temperature doubles the speed of chemical reactions), one may expect that temperature has an impact on BP as an independent variable. In comparison with the results obtained by Joint & Pomroy (1987) in the euphotic zone of the Celtic Sea, the data presented in this work have a higher R^2 as well as higher F statistics. As regards the increase in R^2 of the two- and three-factor regression, temperature explained most of the variability in BP. However, the temperature and BP relationship was positive only within a certain range of temperature. BP decreased at temperatures exceeding 12°C (Fig. 4b), which might be an indication of the greater importance of other factors once the temperature rises above 12°C. A decrease in BP at temperatures in excess of a certain value was also noted by Autio (1992) in the Baltic Sea, Shiah et al. (1999, 2000, 2003) in the East China Sea and Li & Harrison (2001) in the North Atlantic. According to Shiah et al. (1999, 2000), during spring, temperature controlled BP to a higher degree than did the substrates. In the present material, very high values of the determination coefficient were obtained for organic forms of nitrogen and phosphorus. Organic phosphorus was of much greater importance in both the two- and the three-factor multiple regressions. Organic forms of nitrogen and phosphorus can originate from different sources. In multiple regression equations, BP depended to a greater degree on organic phosphorus than on chlorophyll *a* and PP. This indicated that other substrate sources are available for bacterioplankton uptake in addition to the phytoplankton.

Analysis of the regression results indicates that the highest values of the determination coefficient were between bacterial production and the heterotrophic nanoflagellate biomass, and between bacterial production and the biomass of bacterivorous ciliates (log-log relationship). The positive relationship between BP and the nanoflagellate or ciliate biomass (the greater the value of BP, the greater the bacterivore biomass) indicates bottom-up control (bacterivores depend on the amount of food). This means that bacterivores are regulated by bacteria to a greater degree than bacteria by bacterivores. Similar dependences between bacteria and heterotrophic flagellates were reported by Heinänen et al. (1995) in the Baltic Sea.

In the Gulf of Gdańsk BP and concentrations of inorganic nutrients were negatively correlated. Being the main decomposers, bacteria are responsible for the recycling of organic matter and can be regarded as a source of nutrients. However, the negative proportion may suggest that bacteria take up inorganic nutrients. Kuparinen & Heinänen (1993) and Zweifel et al. (1993) described the situation where mineral forms of nitrogen and phosphorus limited BP. In the present study, the negative correlation between BP and inorganic nitrogen and phosphorus was probably the effect of an indirect dependence. Low BP and high nutrient concentrations were observed in winter. In summer, when values of BP were high, nutrient uptake by phytoplankton resulted in low concentrations of mineral forms of nitrogen and phosphorus. In certain situations, mineral phosphorus limits PP in the Gulf of Gdańsk (Trzosińska & Łysiak-Pastuszak 1996, HELCOM 2002).

5. Conclusions

In the Gulf of Gdańsk the highest BP/PP_{gross} ratio was noted in the inner part of the gulf whereas the lowest values were noted in the outer part. As a result of the river Vistula's discharge, BP in the inner part depended more on allochthonous organic matter. In the outer part of the gulf autochthonous organic matter provided the main source for bacterial production.

The parameters that appeared to have the greatest impact on BP were temperature, organic nitrogen and organic phosphorus, PP and chlorophyll *a* concentration. There was an inverse parabolic relationship between bacterial production and temperature. Above a temperature of 12°C bacterial production apparently depended on substrates to a greater degree than on temperature.

It appears that the connection between mineral nitrogen, mineral phosphorus and BP was generally indirect, and was related to the seasonal dynamics of temperature, nutrient concentrations, PP and BP. In combination with other factors, inorganic phosphorus may play a certain role in explaining BP variability.

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