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ABUNDANCE AND PRODUCTIVITY OF ESTUARINE NEUSTONIC AND PLANKTONIC BACTERIA

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Abstract

The paper presents the results of the study of abundance and secondary production of neustonic and planktonic bacteria inhabiting estuarine Lake Gardno. The obtained data indicate that numbers of bacterioneuston were only slightly higher than of bacterioplankton. The rate of secondary production of bacteria was higher in the film layer than in the surface layer and subsurface water. Bacterial abundance and production were changing with seasons. Differences among studied bacteriological parameters were determined among sites across Lake Gardno.

Key words: estuarine lake, bacteria, abundance, productivity

INTRODUCTION

Estuaries are commonly regarded as intermediate transition zones linking freshwater and marine systems. They belong to the most complicated aquatic ecosystems (Monaco and Ulanowicz 1997, Attrill and Rundle 2002, Elliott and McLusky 2002) and are characterized by mixing of seawater with freshwater, strong gradients and fluctuations of salinity, and large quantities of chemically diverse dissolved organic matter (DOM) and particulate organic matter (POM) (Hopkinson et al. 1998, Almeida et al. 2001).

Provided with marine and fresh waters, and greatly influenced by human activities, estuaries are characterized by a constant inflow of nutrients; therefore they belong to the most productive water bodies with the highest accumulation of DOM and POM (Raymond and Brauer 2000, Revilla et al. 2000, Harvey and Mannino 2001). High concentrations of DOM and POM generate optimal conditions for the development of bacteria resulting in their numbers and production being much higher than in the seas and inland waters (Saňudo-Wilhelmy and Taylor 1999, Schultz and Ducklow 2000, Almeida et al. 2001). Bacteria in estuaries play a key role in the processes of maintaining biological balance by actively participating in energy flux and metabolic conversions of various organic compounds (Goosen et al. 1995, Raymond and

Bauer 2000). Thus, elucidating the major determinants of bacterial abundance and production in various estuaries and coastal waters is a significant ecological issue (Hyun and Kim 2003, Murrell 2003).
Unfortunately, we know relatively little about bacterial abundance and secondary productivity in surface water layers in estuarine ecosystems. Hence, the aim of the present paper was to determine spatial and seasonal dynamics of the changes in the abundance and production of bacteria in the surface and subsurface water layers of estuarine Lake Gardno.

MATERIALS AND METHODS

Description of the study area

The study was carried out in estuarine Lake Gardno situated in the World Biosphere Reserve – Słowiński National Park (Poland). The lake is very shallow (1.3 m of average depth) but covers a large area (2 500 ha). Lake Gardno is characterized by conditions intermediate between marine and inland environment, as it is supplied by fresh waters of the Łupawa River while being connected with the Baltic Sea by a 1.3 km channel (Fig. 1). Because large quantities of sea water can penetrate into the

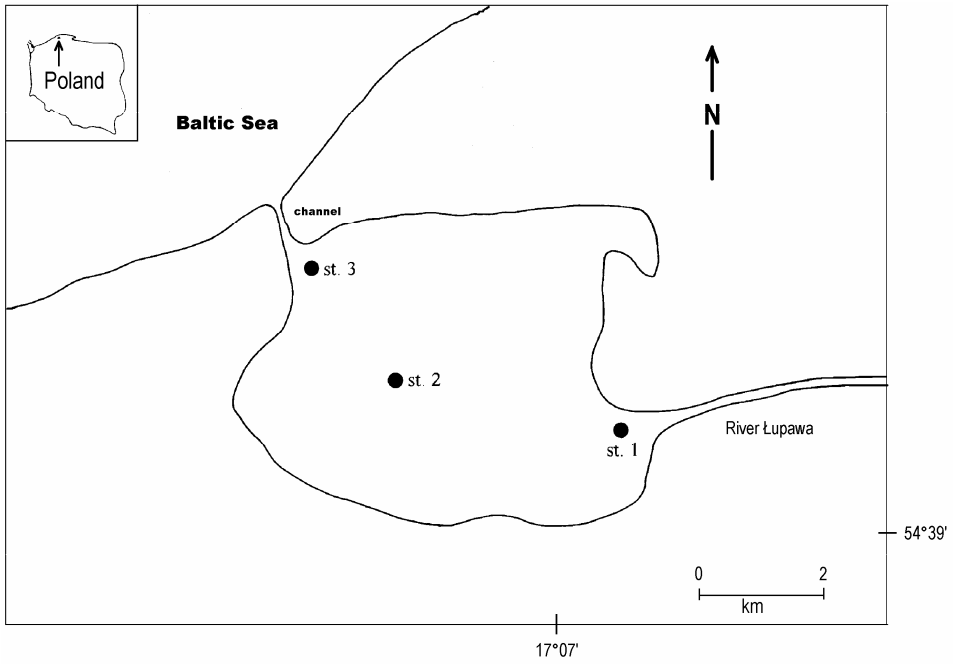

Fig. 1. Lake Gardno, northern Poland, with location of sampling sites

lake, its waters – or parts of them – acquire seawater properties, with the salinity of 2-5‰. Consistently with the Venetian system, Lake Gardno can be classified as belonging to the mixo-oligohaline type (0.5-5.0 PSU) (Dethier 1992).
The studied estuary is a polymictic water basin with no thermal or oxygen stratification, and with a considerable level of eutrophication. This high eutrophication level together with a high concentration of nutrients (Mudryk et al. 2003) create perfect conditions for the development of phytoplankton, whose bloom lasts practically from spring to autumn (Strzelecki and Półtorak 1971).
This shallow and productive estuarine lake is characterized by an extensive growth of macrophytes. The emergent macroflora covers 4% of the lake surface forming a 20-100 m wide offshore belt, a home for many bird species. The main macrophytes are: *Typha angustifolia, Phragmites australis, Scirpus lacustris* and *Schoenoplectus lacustris.*

Sampling

Water samples were taken in 1996-1999 in spring, summer and autumn from three sites (Fig.1): site 1, near the River Łupawa inflow (freshwater zone); site 2, in the mid-lake (mixed water zone); site 3, close to the inflow of the sea-water (seawater zone). At each site, three layers of water were sampled. Film layer samples (FL, thickness of 90 μm) were taken with a 30 x 30 cm glass plate (Harvey and Burzell 1972), and surface layer (SL) samples (thickness of 240 μm) were collected with a 40 x 50 cm Garrett net (24 mesh net of 2.54 cm length) (Garrett 1965). Prior to sampling, the glass plate and polyethylene net were rinsed with ethyl alcohol and distilled sterile water. The water from subsurface layer (SUB) was sampled at the depth of about 10-15 cm. All water samples were placed in sterile glass bottles and stored in an ice-box at a temperature lower than 7^0C. The time between collection of the samples and their analysis usually did not exceed 6-8 h.

Bacterial abundance and biomass

The total bacterial number (TBN) was established with the acridine orange direct method (AODC) according to Hobbie et al. (1977). Aliquots of 10 ml were preserved with formaldehyde at a final concentration of 1% and stored. Within a few days, a 2 ml sample was filtrated using black-stained polycarbonate filtres (Millipore) (0.2 μm pore size, 12 mm diameter) and stained for 2 min with acridine orange at a final concentration of 0.01%. The filters were mounted on microscopic slides in non-fluorescence immersion oil (Olympus Optical Co., LTD). Counting and sizing was performed at 1250x magnification using Nikon Eclipse E 400 epifluorescence microscope (equipped with a 50-W Hg lamp and filter set for blue and green excitation) using a calibrated ocular grid with cell sizes of 4 x 4 μm. Bacteria were counted in 50 different fields, with a minimum of 200 cells. Bacterial biomass (BB) was calculated from cell numbers by assuming a mean carbon content of 20 fg C $cell^{-1}$ (Lee and Fuhrman 1987).

Bacterial production

The secondary production of bacteria (BP) in the water samples was determined by measuring the rate of incorporation of [methyl - [^{3}H] thymidine ([^{3}H]TdR) into the bacterial DNA (Furhman and Azam 1982, Simon and Azam 1989). In order to determine this parameter, 20 µl [^{3}H]TdR (NEN Life Science Products 60 Ci/nmol specific activity) was added to 10 ml water samples in three replications with final concentration of 20 nM. Samples were incubated for 30 min at 20^{0}C. After this period, the incubation was stopped by adding 200 µl of 37% formaldehyde to the samples. A prekilled sample was used as a blank. Samples were then filtered with a Millipore sampling manifold on to 0.2 µm nitrate cellulose filters (Sartorius) (25 mm diameter). Filters were rinsed twice with 5 ml 10% ice-cold TCA and then dissolved in 1 ml of ethyl acetate before counting and placed in scintillation vials (Packard) with 10 ml LCS-cocktail (Packard, Filter-Count). After 24h, the samples were radio--assayed in a Packard TRI-CRAB 2100TR liquid scintillation counter. The calculation of bacterial production was based on the thymidine incorporation (TdR) using a factor of $1.25 \cdot 10^9$ cells nmol^{-1} thymidine (Chróst et al. 1988). Bacterial growth rates (µ) were calculated from bacterial production/bacterial biomass and their doubling times (D) from ln2/µ (Dixon and Turley 2001).
The obtained data have been subjected to suitable statistical analyses. Statistical characteristics (standard deviation – SD, coefficient of variation – CV, coefficient of dispersion – CD) were based on Velji and Albright (1986). Simple linear regression was used to calculate general correlation between studied parameters. Data on the total bacterial number and bacterial production were natural-log transformed to equalise the variance. The significance of differences between layers, sites and seasons in bacterial abundance and production was assessed using ANOVA according to Almeida et al. (2001).

RESULTS

The total number of bacteria (TBN) in the water of Lake Gardno varied from 7.98 to 9.77 $10^8 \cdot$ cells dm^{-3}, while their biomass oscillated from 20.73 to 39.77 µg C dm^{-3} (Tab. 1). Data on the total number of bacteria in estuarine Lake Gardno indicate that the bacterial abundance were only slightly higher in the neuston (FL, SF) than in plankton (SUB) (Fig. 2a). The maximum values of TBN were noted in the film layer in the seawater zone (site 3) and in the surface layer in the mixed water zone (site 2). The lowest numbers of bacteria were determined in the subsurface water near the Łupawa River inflow (site 1) and in the mid-lake (site 2).
The total number of bacteria in the surface and subsurface water layers (Fig. 3a) and at the sampling sites (Fig. 3b) changed with the changing seasons. Data presented in Fig. 3a show that in all the studied water layers maximum values of TBN were determined in the spring 1997. Minimum numbers of bacteria in the film layer were noted in the spring 1998, in the surface layer in the autumn 1997, and in the subsurface layer in the summer 1997.

Table 1

Total number bacteria (TBN), bacterial biomass (BB), thymidine incorporation (TdR), bacterial production (BP), bacterial growth rates (μ) and doubling times (D) in different sites in lake Gardno

Sites	Statistic parameters	TBN (10^8 · cells dm^{-3})	BB (μg C dm^{-3})	TdR (pmol · dm^{-3} h^{-1})	BP (μg C dm^{-3} d^{-1})	μ (d^{-1})	D (d)
site 1	mean	7.98	20.73	0.67	398.85	19.24	0.04
	min	0.35	0.70	0.01	7.44	10.69	0.06
	max	14.99	77.0	2.68	1593.60	20.70	0.03
	SD	4.33	14.39	0.69	413.41	28.73	0.02
	CD	235.0	9.99	0.72	0.74	0.07	9.31
	CV(%)	54.25	69.43	103.65	103.65	1.49	0.46
site 2	mean	9.21	34.71	1.45	865.20	24.93	0.03
	min	0.29	0.59	0.00	2.40	4.10	0.17
	max	29.60	240.00	8.42	5016.00	20.90	0.03
	SD	7.54	52.45	2.09	1245.76	23.75	0.03
	CD	58.13	79.27	3.01	3.11	0.04	17.64
	CV(%)	81.83	151.14	143.93	143.99	0.95	0.73
site 3	mean	9.77	39.77	1.78	862.40	21.68	0.03
	min	0.10	0.20	0.05	27.84	139 0	0.05
	max	34.48	450.00	8.97	4382.64	9.74	0.07
	SD	8.20	85.31	2.42	1118.26	13.11	0.05
	CD	68.90	183.01	3.28	2.52	0.01	50.38
	CV(%)	83.98	214.5	135.5	129.7	0.60	1.15

Horizontally, seasonal maxima of TBN in the mid-lake zone (site 2) and in the sea--water zone (site 3) were determined in the spring 1997, while minimum values were observed there in the autumn 1997. In the freshwater zone (site 1), the highest numbers of bacteria were noted in the autumn and spring, while the lowest numbers were observed in the summer 1997 (Fig. 3b).

The rate of thymidine incorporation (TdR) in the water of Lake Gardno varied from 0.67 to 1.78 pmol dm^{-3} h^{-1}. Bacterial production (BP) estimated from the rate thymidine incorporation oscillated from 398.85 to 865.20 μg C dm^{-3} d^{-1}. The rate of secondary production of bacteria was higher in the film layer than in the surface layer and subsurface water. Average bacterial growth (μ) changed in the range of 19.24 to 24.93 d^{-1}, and doubling time (D) from 0.03 to 0.04 d (Tab. 1). The highest rates of secondary bacterial production in estuarine Lake Gardno were noted in the film layer in the sea-water zone (site 3); minimum values of this parameter were noted in the surface layer in the sea-water zone (site 3) and in the subsurface layer in the fresh water zone (site 1) (Fig. 2).

In the studied water layers large fluctuations of the seasonal dynamics of the changes in the level of bacterial production were determined (Fig. 4a). Maximum values of bacterial production were noted in the film and surface layers in the summer 1997, while in the subsurface layer – in the spring 1997.

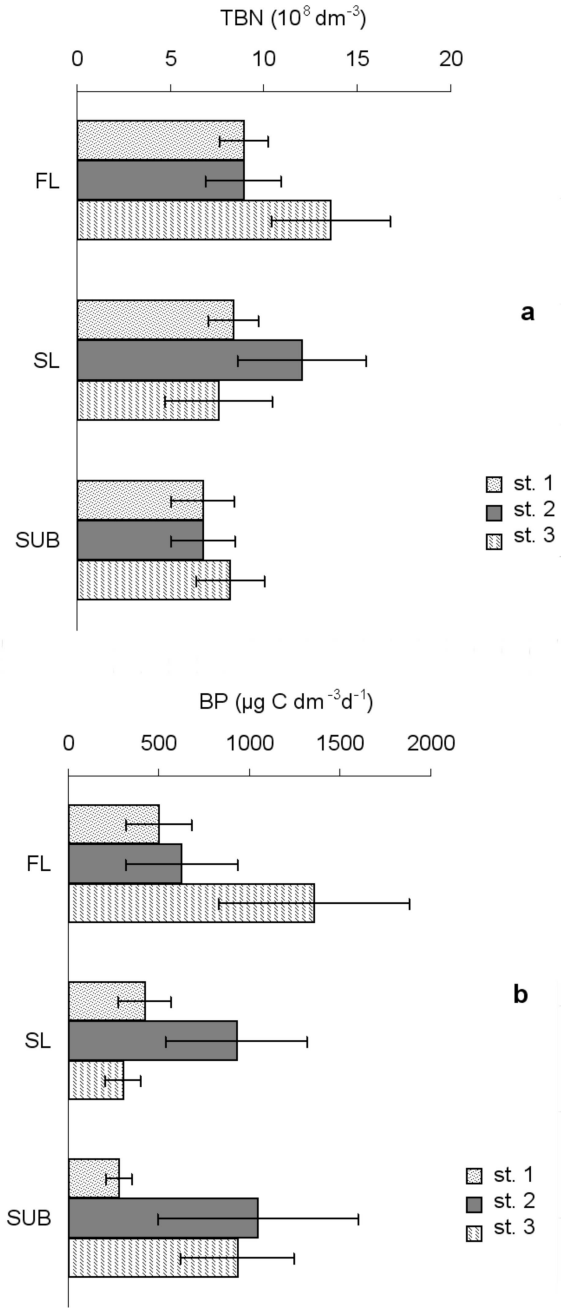

Fig. 2. Vertical profiles of the total bacteria number (a) and bacterial production (b) in the film layer (FL), surface layer (SL) and subsurface water (SUB) (data derived from the pooled data of all seasons). Vertical bars represent standard errors

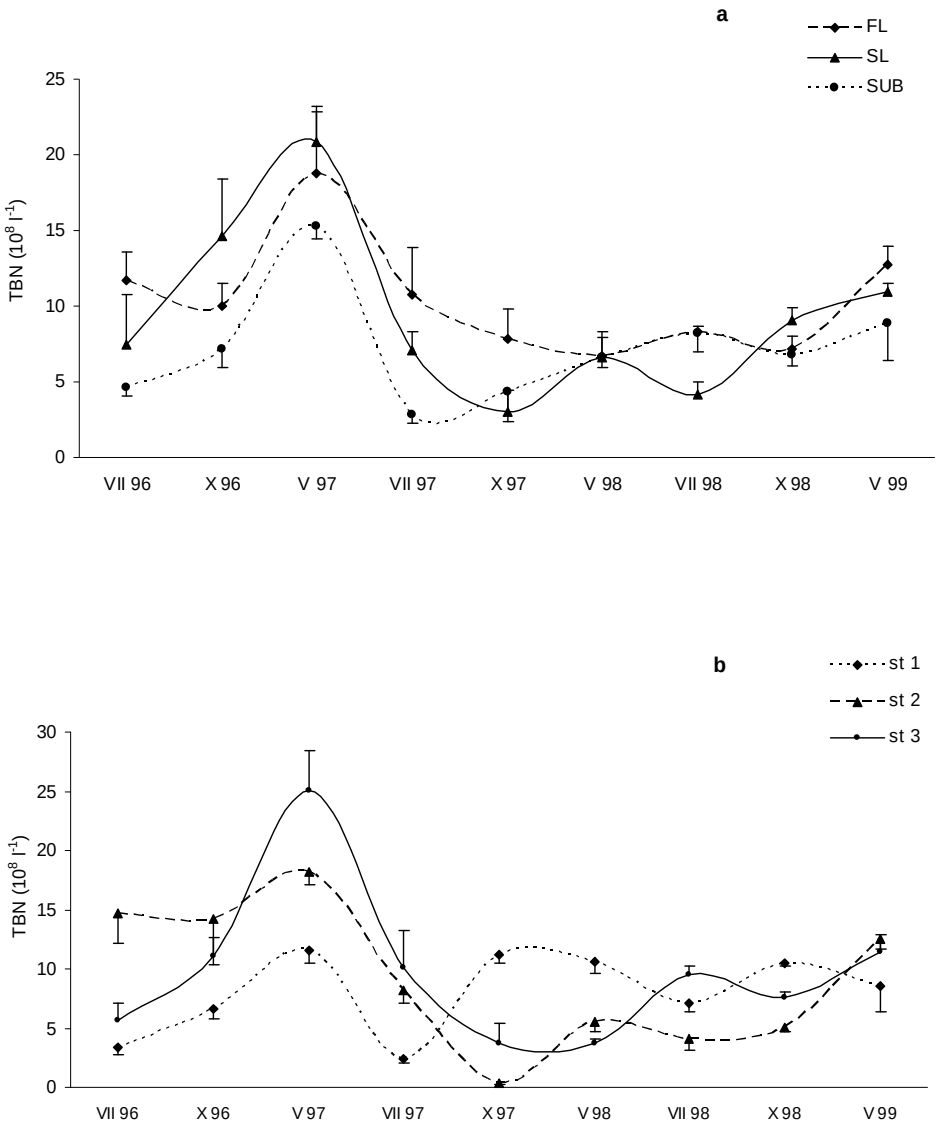

Fig. 3. Seasonal variations in the total bacteria number in three water layers (a) (data derived from the pooled data of all sites) and sites (b) (data derived from the pooled data of all water layer) during the study period. Vertical bars represent standard errors

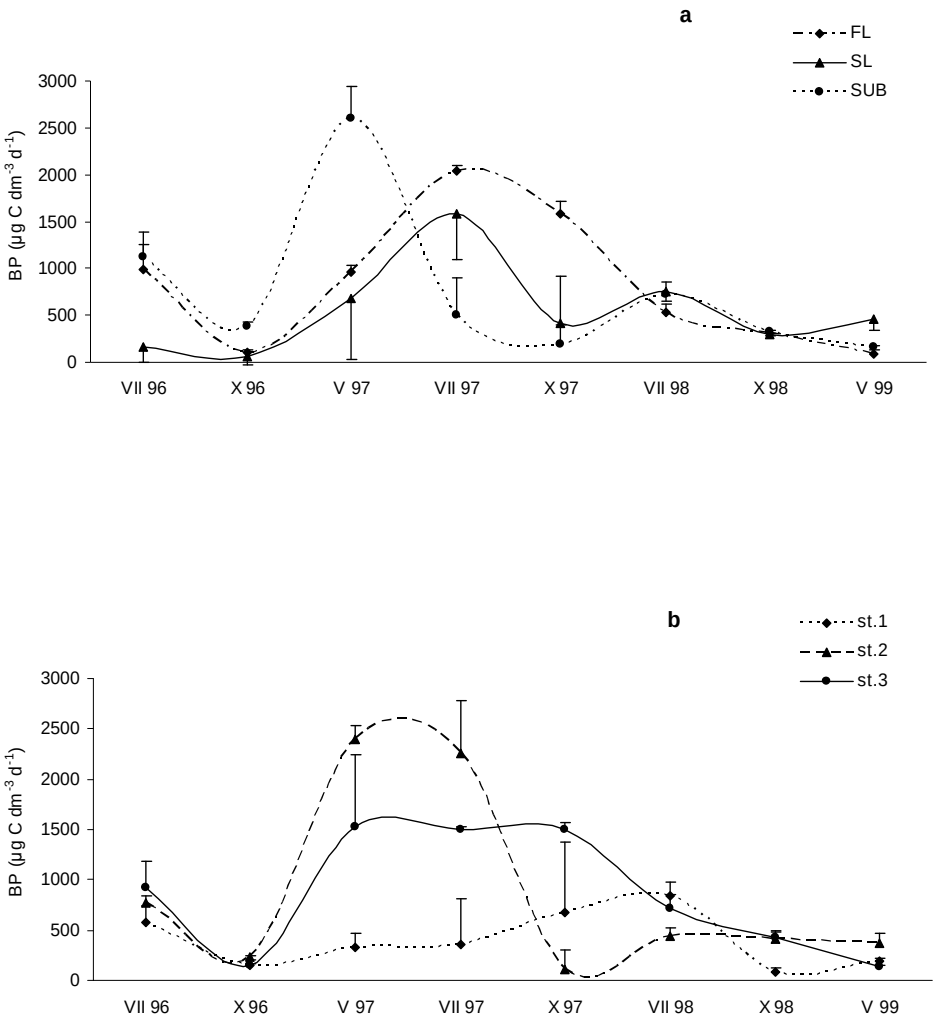

Fig. 4. Seasonal fluctuation of bacterial production in three water layers (a) (data derived from the pooled data of all sites) and sites (b) (data derived from the pooled data of all water layer) during the study period. Vertical bars represent standard errors

In the studied zones of Lake Gardno, differences in the level of bacterial production were determined (Fig. 4b). In the mid-lake (site 2), the maximum rate of bacterial production was observed in the spring and summer 1997. Similarly in the sea-water zone (site 3), in the period from the spring to autumn 1997, the value of this parameter remained at a constant high level. In the region of the inflow of the River Łupawa

(site 1), the level of bacterial production was the lowest, and throughout the study period remained at a rather constant level.

Correlations and linear regressions were carried out considering all observations in order to determine the relationship between the total bacteria number (TBN) and bacterial production (BP) (Fig. 5). Linear regression shows that in Lake Gardno in all studied water layers TBN was positively and significantly correlated with the BP. The highest correlation ($R^2 = 0.283$, $p < 0.01$) was found between TBN and BP in the surface layer (SL).

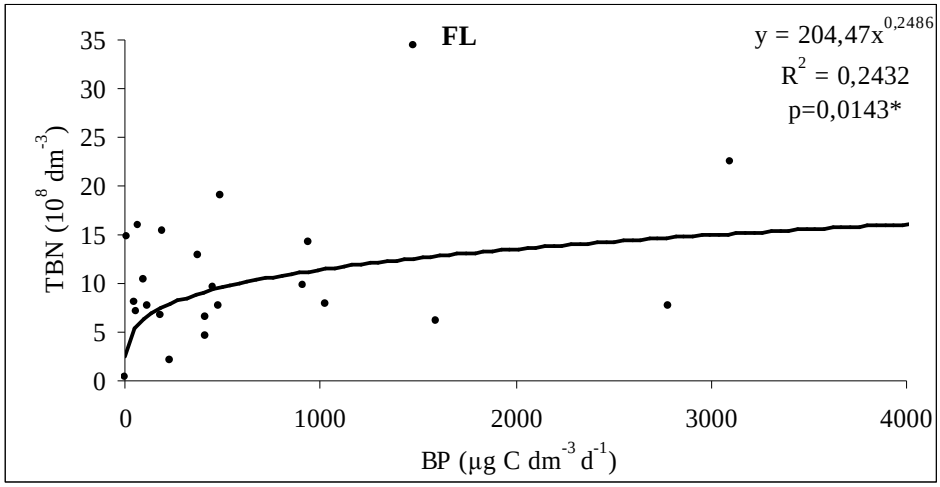

Fig. 5. Relationship between the total bacteria number and bacterial production in the film layer (FL), surface layer (SL), and subsurface water (SUB). Solid line represents linear regression including all data. Significance (p) is indicated by asterisks * $p<0.05$, ** $p<0.01$, *** $p<0.001$

By grouping the results by seasons, layers and sites, a factorial ANOVA test was carried out for the total bacteria number and bacterial production (Tab. 2). Bacterial productivity rates were found to be significantly different between seasons, but not between sites and layers. The analyses showed no significant differences for the total bacteria number among grouped data using two-way ANOVA.

Table 2

Analyses of 2-way-ANOVA of variance in the total bacteria number and bacterial productivity, due to layer, site and season. Significance (p) is indicated by asterisks ** p<0.01, n.s. non-significant

Source	TBN				BP			
	df	MS	F	p	df	MS	F	p
site	2	0.01	0.05	0.95	2	0.42	0.98	0.38
layer	2	0.39	1.48	0.24	2	0.14	0.32	0.72
season	2	0.73	2.77	0.07	2	2.23	5.18	0.009**
site x layer	4	0.25	0.96	0.44	4	0.40	0.92	0.46
site x season	4	0.44	1.67	0.17	4	0.51	1.19	0.33
layer x season	4	0.11	0.42	0.79	4	0.26	0.61	0.65
site x layer x season	8	0.09	0.34	0.95	8	0.14	0.32	0.95

Explanations:
df – degrees of freedom
MS – mean squares
F – Fisher test
p – significance level

DISCUSSION

Bacterial abundance in estuarine Lake Gardno varied from 7.98 to 9.77 10^8 · cells dm^{-3}. This range was consistent with ranges reported in other estuaries, such as the Delaware River estuary (6.5 10^8 · cells dm^{-3}) (Hoch and Kirchman 1993), in Massachusetts estuaries (7.0 10^8 · cells dm^{-3}) (Wright and Coffin 1983) and in Hudson River estuary (5-16 10^8 · cells dm^{-3}) (Findlay et al. 1992), but lower than values obtained in York River estuary (1.4-7.9 10^9 · cells dm^{-3}) (Schultz and Ducklow 2000), Ria de Averio estuary (0.2-8.5 10^9 · cells dm^{-3}) (Almeida et al. 2001) and in Pensacola Bay estuary (2.5-15.3 10^9 · cells dm^{-3}) (Murrell 2003).
Many authors (Mudryk et al. 1991, Plusquellec et al. 1991, Maki and Hermansson 1994, Münster et al. 1998, Donderski et al. 1999) demonstrated that the greatest

abundance of bacteria in water basin occurred in the surface layer, and decreased with depth. Those results do not correspond with the data obtained in the present study, which indicated that in estuarine Lake Gardno total number of bacteria in surface and subsurface water layers were almost identical. This absence of vertical bacterial gradients can be according to Maki (1993), explained by the occurrence in estuarine surface microlayers of the considerable fluctuations of environmental factors such as wind, solar radiation, temperature, pH and mainly salinity which can have an impact on inhibiting growth of neustonic bacteria.

Studies carried out by Saňudo-Wilhelmy and Taylor (1999), Andrade et al. (2003) and Murrell (2003) have shown that maximum numbers of bacteria in water bodies are generally observed in the summer, when phytoplankton blooms are also often noted. For bacteria, extracellular algal excretions constitute a source of easily assimilable nutrients, stimulating increased bacterial abundance. In spite of the fact that in Lake Gardno intensive algal blooms also occur in the summer, maximum bacterial numbers were observed in the spring. The reason for this can be that algal blooms exert not only a stimulating effect on bacterial growth, but also a bacteriostatic or even bacteriocidal effect (Teuscher et al. 1992). When blooming, many algae, especially blue-green algae and green algae, exert into water biologically active secondary metabolites belonging to polyketides, amides, alkaloides, which show antibacterial activity (Kreitlow et al. 1999). Because blue-green algae and green algae predominate in the taxonomic composition of the phytoplankton of Lake Gardno (Strzelecki and Półtorak 1971), it cannot be excluded that during summer blooms their metabolites could significantly reduce the numbers of bacteria in this water body.

Additionally, according to Laybourn-Parry et al. (1997) and Takacs and Priscu (1998), the numbers of bacteria in water bodies can be significantly reduced by bacteriovory organisms, especially heterotrophic nanoflagellates, rotiferes, ciliates and zooplankton. Painchaud et al. (1987) suggest that in estuaries organisms capable of bacteriovory may be a major factor controlling bacterial abundance. Bacteriovory zooplankton, very abundant in Lake Gardno in the summer (Paturej and Jabłońska 2001), can reduce the numbers of bacteria.

Generally, a gradient of decreasing bacterial numbers with increasing salinity has been observed in different estuaries (Painchaud et al. 1987, Prieur et al. 1987, Almeida et al. 2001). In Lake Gardno, a reverse regularity has been determined. Maximum numbers of bacteria were noted in the salty sea-water zone, while minimum numbers were observed in the fresh-water part of the lake, near the inflow of the Łupawa River. The main factor causing an increase of bacterial numbers close to the inflow of the sea-water is the presence of a holiday town Rowy located in this part of the lake. From this town, considerable amounts of organic pollutants in the form of sewage are carried into the lake, generating an increase in the number of bacteria. Studies of del Giorgio and Scarborough (1995) and Almeida et al. (2001) also showed positive correlation between the number of bacteria and concentration of organic matter in highly productive estuaries. Minimum numbers of bacteria determined near the inflow of the Łupawa River to Lake Gardno, i.e. in the freshwater

zone, can result from halophobic riverine bacteria undergoing osmotic shock in contact with brackish water of the lake (Painchaud et al. 1987).

There is a general agreement that bacterial production is a major pathway of the flow of matter in many aquatic ecosystems (Wiebinga et al. 1997, Hyun and Kim, 2003, Lemée et al. 2003). Among various kinds of water bodies, the highest level of bacterial secondary productivity has been noted in estuaries (Hoch and Kirchman 1993, Goosen et al. 1997, Harvey and Mannino 2001).

In Lake Gardno secondary production of bacteria varied from 398.85 to 865.20 μg C $dm^{-3}d^{-1}$. This was higher than bacterial carbon production in the Scheldt estuary (7.2-273.6 μg C dm^{-3} d^{-1}) (Goosen et al. 1995), in Guanabara Bay estuarine systems (4.8-316.2 μg C $dm^{-3}d^{-1}$) (Andrade et al. 2003), in estuarine system Rio de Aveiro (16.8-340.8 μg C dm^{-3} d^{-1}) (Almeida et al. 2001) and was similar to values obtained in Loire Estuary (803.0 μg C dm^{-3} d^{-1}) (Ducklow and Shiah 1993).

In Lake Gardno, the highest level of bacterial production was determined in the film layer. It seems that increased phytoplankton exudation is the main factor generating this high level of bacterial production (Williams et al. 1986). In addition, higher bacterial productivity in the film layer could be stimulated by photochemical transformation of recalcitrant dissolved organic matter into labile compounds that may stimulate locally and transiently the growth of active bacteria. Photodegradation generates low molecular weight organic compounds such as primary amines, amino acids, combined amino acids and urea that are readily assimilated by bacterioneuston (Jorgensen et al. 1998, Bushaw-Newton and Moran 1999, Raymond and Brauer 2000). In deeper water, a higher degree of turbidity blocks light penetration and reduces photodegradation and phytoplankton exudation. These observations suggested that in the film layer of eutrophic estuarine Lake Gardno, solar radiation may be instrumental in making additional sources of nutrients available to bacterial growth, as has been pointed out by Almeida et al. (2001).

According to Kirchman and Rich (1997) and Becquevort et al. (2002), gradient of organic matter concentration explained most of the variation in bacterial production over the longitudinal transect in an estuary. Presence of organic matter of allochthonnous origin particularly in estuarine systems generates bacterial production (Goosen at al. 1997). Similarly, in Lake Gardno the highest level of bacterial production was determined in the mid-lake and in the seawater zone, to which high load of organic matter in the form of urban organic waste is discharged from the town Rowy.

This paper has shown that the control of bacterial numbers and their productivity in an estuary is a complex problem. Thus, the pattern of bacterial numbers and their production in estuaries should be examined as a result of the interaction between the sources and rates of supply of natural substrates, physiological dispersion growth, mortality and predation processes. However, estimating the rates of those processes is difficult. Consequently, the overall dynamics of estuarine bacteria and the processes that control their distribution and productivity are still poorly documented and understood.

CONCLUSION

The above considerations give the ground to formulate the following conclusion:
- The total numbers of bacterioneuston were only slightly higher than of bacterioplankton.
- The level of bacterial production was higher in the film layer than in the surface layer and subsurface water.
- In the studied zones of Lake Gardno differences in the level of total number of bacterioneuston, bacteriplankton and bacterial production were determined.

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LICZEBNOŚĆ I PRODUKTYWNOŚĆ ESTUARIOWYCH BAKTERII NEUSTONOWYCH I PLANKTONOWYCH

Streszczenie

W pracy przedstawiono wyniki badań dotyczących oznaczenia ogólnej liczby i produkcji wtórnej bakterioneustonu i bakterioplanktonu zasiedlającego estuariowe przymorskie jezioro Gardno zlokalizowane na terenie Słowińskiego Parku Narodowego. Badania mikrobiologiczne prowadzono w trzech warstwach wody (film, błona powierzchniowa, woda podpowierzchniowa). Uzyskane wyniki badań wykazały, że ogólna liczba bakterii neustonowych była nieznacznie większa niż bakterii planktonowych. Poziom produkcji bakteryjnej w filmie powierzchniowym był wyższy niż w błonie powierzchniowej i podpowierzchniowej warstwie wody. Wykazano znaczące różnice wartości badanych parametrów bakteriologicznych w różnych częściach badanego jeziora. Stwierdzono znaczącą dynamikę zmian sezonowych liczebności bakterii i ich produktywności.