Papers

OCEANOLOGIA, 28, 1990
PL ISSN 0078-3234

Plankton
Spring bloom
Ecosystem

Short-term changes in pelagic biocenosis in the near-surface layer at station G-2 (Gdańsk Deep, southern Baltic) during the spring bloom

ZBIGNIEW WITEK
Sea Fisheries Institute,
Gdynia

ELLEN ALLIKAS
Institute of Thermo- and Electrophysics,
Academy of Sciences of the Estonian SSR,
Tallinn

Manuscript received August 2, 1988, in final form July 25, 1989.

Abstract

The aim of the study was to find out what factors have played a major role in bringing about short-term quantitative changes in various components of the biocenosis. The level of 5 m was chosen for the study as representing the near-surface layer. The composition of the biocenosis and the biomass of its major components were studied; most important trophic relations between them were indicated. Observations of quantitative changes in some of the components were carried out in the sea, with measurements taken at the same site, in regular time intervals, within a period of three days. This permitted to determine the scope of changes and ascertain whether they occur in a diurnal cycle. In order to eliminate distortions caused by advection of water masses and migrations of organisms themselves, observations of quantitative changes were carried out on organisms with the shortest life cycle (bacteria and algae) in enclosed systems, exposed *in situ*. In this way, the rate of growth of certain taxa was determined. In addition, the rate of growth of individual zooplankton groups, possible under the given feeding conditions, as well as mortality of algae and zooplankton caused by grazing, were estimated.

1. Introduction

The spring phytoplankton bloom was a subject of studies in various areas of the Baltic. As a result of these studies, regional differences and similarities in succession of phytoplankton taxa were revealed (Niemi, 1975; Smetacek, 1977; Larsson *et al*, 1986). Size of primary production, dependence of the course of the

bloom on abiotic conditions, long-term and regional changes, were described (Renk, 1973, 1974; Niemi, 1975; Kaiser *et al*, 1981; Smetacek *et al*, 1984; Smetacek, 1985; Larsson *et al*, 1986). Observations of zooplankton development during the bloom were carried out (Smetacek, 1981; Hernroth, 1983; Larsson *et al*, 1986). Experiments were conducted in enclosed systems, in which selected relations between elements of the ecosystem were studied (Mc Kellar and Hobro, 1976; Nöthig, 1986). Because a bloom is a very dynamic phenomenon and is controlled to a large degree by easily measurable physical factors, it has become an attractive object of mathematical modelling (Sjöborg and Wilmot, 1977). Recently, during the spring bloom, large-scale international investigations PEX '86, directed at explaining the phenomenon of patchiness, were carried out. They provided very numerous and extensive data on temporal and spatial changes in the ecosystem (Dybern, 1986; *PEX General Report*, 1988). The following elements were distinguished in materials from the PEX '86 experiment as main factors resulting in quantitative changes and shaping a picture of microdistribution of biocenotic components: growth, mortality, succession, sedimentation, vertical migrations, and a variety of physical factors. The aim of this study was to find out which of these factors played the most important role with respect to individual components of the biocenosis in the near-surface layer, where primary production was taking place. In order to achieve this goal, the following studies were undertaken:

(i) determination of composition and biomass of major components of the biocenosis and indication of major trophic relations between them,

(ii) observations of quantitative changes in some components of the biocenosis in the sea, by taking measurements at the same spot in regular intervals over a period of three days. This allowed to determine the scope of the changes and to establish whether they occur in a diurnal cycle,

(iii) in order to eliminate disturbances caused by advection of water masses and migrations of the organisms themselves, observations of quantitative changes were carried out on organisms with the shortest life cycle (bacteria and algae) in enclosed systems, exposed *in situ*. In this way, the rate of growth of some taxa could be determined,

(iv) estimations were carried out of the rate of growth of individual zooplankton groups, possible under the given feeding conditions, and mortality of algae and zooplankton caused by grazing.

2. Material and method

The study was carried out at station G-2 (54°50′N, 19°20′E) located in the Gdańsk Deep. The level of 5 m was chosen as representative for the near-surface water layer. Between 00.00 hours on May 1 and 00.00 hours on May 4, 1987, water temperature at a depth of 5 m, measured in 6-hour inervals, ranged from 2.94 to 5.01°C. At 00.00 hours on May 1, an approximately 30-litre water sample was collected with a Van Dorn water sampler; various methods, depending on the kind of plankton, were used to analyse the composition of the biocenosis. Phytoplankton was preserved in Lugol solution and analysed under an inverted

microscope, the material being sedimented in chambers with a volume of 10 and 2 ml. Protozooplankton was preserved and analysed by the same method, the only difference being a 100 ml sedimentation chamber. Metazooplankton (*ie*, multicellular animal organisms) was concentrated by filtering 26 l of water through a planktonic net with a mesh size of about 60 μm. This material was preserved in formalin and analysed in a Bogorov chamber by means of a stereoscopic microscope. Bacterioplankton was analysed on a Synpor membrane filter, with pores of 0.22 μm, through which 20 ml of water were filtered. The filter with bacteria was stained with erythrosine and analysed under an optical microscope with oil immersion. Chlorophyll "a" concentrations were measured by a spectrophotometric method (Edler, 1979), filtering 2 l of water through a Whatman GF/F membrane filter. Calculations of chlorophyll "a" concentrations were based on the formulae of Jeffrey and Humphrey (Edler, 1979). Measurements of volume of planktonic organisms were carried out by measuring their main body dimensions and using formulae for the volume of simple geometric solids. After measuring 10–20 specimens of a given taxon, its mean volume was calculated. The volume was converted into carbon units with the help of the following conversion factors: for phytoplankton and protozooplankton – after Edler (1979) and Smetacek (1977); for metazooplankton – after Parsons *et al* (1977) and Vinogradov and Shuskina (1987); for bacterioplankton – a factor of 0.1 g C/cm^3 after Zimmermann (1977).

Between 00.00 hours on May 1 and 00.00 hours on May 4, every six hours, subsequent samples of phytoplankton, bacterioplankton, and chlorophyll "a" were collected from a depth of 5 m according to the method described above, and – every 12 hours – metazooplankton samples. At the same time, when samples from the sea were being collected, samples of phytoplankton, bacterioplankton, and chlorophyll "a" were taken every six hours from two polyethylene bags placed in the sea, containing about 100-litre water portions taken from the level of 5 m. Bag N was placed there at 00.00 hours on May 1, its exposition being terminated at 18.00 hours on May 3, while bag D was placed at 12.00 hours on May 1, its exposure being terminated at 12.00 hours on May 3. The bags were suspended at a depth of 4.3 m in order to compensate for absorption of light by their walls. This adjustment of depth was determined on the basis of measurements of light absorption by the bag walls in a green spectrum. In planktonic samples collected over that period only the abundance of major taxa was analysed, according to methods described above.

3. Calculations

Numerous measurements of abundance enabled a direct determination of the rate of changes in abundance. The rate constant k of these changes was calculated by a least squares method according to the linear equation

$$\ln N_t = \ln N_0 + kt, \tag{1}$$

where N_0 is the initial abundance and N_t is abundance after time t.

The rate constant of growth b depending on feeding conditions was calculated

from the formula

$$b = \ln\left(\frac{B_0+P}{B_0}\right)\Big/t = \ln\left(1+\frac{P}{B_0}\right)\Big/t, \tag{2}$$

where B_0 is initial biomass and P is production for a period of time t. Production is a part of the food consumed, used for growth, and may be calculated from the equation

$$P = K_1 \cdot F \cdot B_p \cdot B_0 \tag{3}$$

in which:
K_1 – the gross growth efficiency,
F – feeding rate *per* biomass (*ie* speed of penetration of environment in search of food),
B_p – food biomass.
Thus, substituting equation (3) into equation (2) we obtain:

$$b = \ln(1+K_1 \cdot F \cdot B_p)/t. \tag{4}$$

Constant of mortality due to grazing d was calculated from the formula:

$$d = \ln\left(\frac{B_0}{B_0-E}\right)\Big/t = -\ln\left(1-\frac{E}{B_0}\right)\Big/t, \tag{5}$$

in which E is elimination by grazing:

$$E = B_0 \cdot \sum_{i=1}^{n} (B_{d_i} \cdot F_{d_i}), \tag{6}$$

where B_{d_i} and F_{d_i} are the biomass of consumers from group i and their feeding rate, respectively. Substituting equation (6) into equation (5) we obtain

$$d = -\ln\left[1-\sum_{i=1}^{n} (B_{d_i} \cdot F_{d_i})\right]. \tag{7}$$

3.1. Selection of parameters

Coefficient K_1 may change within quite a wide range. It mostly depends on the kind of food and costs of the organism metabolism. According to Parsons *et al* (1977), the most often encountered values for invertebrates range from 0.1 to 0.4. Similar numbers are obtained from formula $K_1 = U^{-1} \cdot K_2$, where U^{-1} is assimilation efficiency and K_2 is the net growth efficiency. Estimates of U^{-1} range from 0.6 to 0.9 (Parsons *et al*, 1977), estimates of K_2 being 0.2 – 0.6 (Parsons *et al*, 1977; Winberg, 1971; for protozoans – Klekowski, 1981). In further calculations the values adopted in this paper are: $K_1 = 0.25$, $U^{-1} = 0.75$.

The feeding rate is relatively well-known in the case of filtrators (Jorgensen, 1983; Jorgensen *et al* 1984; Peters and Downing, 1984; Fenchel, 1986a). According to Fenchel (1986a), there is an allometric relationship here:

$$F' = \gamma \cdot V^{\lambda}, \tag{8}$$

where:
V – the volume of the organism,
γ, λ – coefficients,
F' – the filtration rate *per* animal.
Coefficient λ of this relationship, equalling 0.75, is very similar to such a coefficient in the relationship between respiration rate and body size. Coefficients γ of regression (8) found in Figure 31 in Fenchel (1986a) allow to write down approximate relative filtration rate F'' (multiple of body volume in 24 hours) at a temperature of 20°C:

– for copepods: $1.3 \cdot 10^7 \cdot V^{-0.25}$,
– for ciliates: $2.5 \cdot 10^7 \cdot V^{-0.25}$,
– for bacterivorous ciliates: $3.5 \cdot 10^6 \cdot V^{-0.25}$,
– for zooflagellates: $7.5 \cdot 10^6 \cdot V^{-0.25}$,

where the body volume V is expressed in μm^3. In order to take into account the effect of temperature on the filtration rate, the van't Hoff temperature coefficient *ht* may be applied. It has the following form:

$$ht = Q_{10}^{0.1(T-D)}, \tag{9}$$

where:
T – present temperature,
D – standard temperature (20°C),
Q_{10} – relative increase in rate of the process accompanying an increase in temperature by 10°C.
Q^{10} has a greater value within the range of low temperatures than in the range of high ones (Winberg, 1971). There are no direct data on the effect of temperature on the filtration rate. With respect to the growth of various species of protozoans, Fenchel (1968) believed that within a temperature range of 8 – 20°C, Q_{10} ranges from 3.5 to 2.3. In this paper Q_{10} was assumed to be 3.0 and $T = 4$°C.

Since equation (4) may be applied only when food concentration allows for covering minimum costs of metabolism ($M_{\min}$), we should know the minimum food concentration $B_{p\,\min}$:

$$B_{p\,\min} = M_{\min}/(U^{-1} \cdot F). \tag{10}$$

Metabolism rate M is connected with the body size by an allometric equation

$$M = \alpha W^{\beta}, \tag{11}$$

where W is body weight, α and β are coefficients. According to Fenchel (1986b), the relationship between metabolism rate and body size for filtering ciliates and heterotrophic flagellates during their intense growth (close to maximum) is the same as that given by Hemmingsen (1960) for heterothermal metazoans. This relationship, after conversion of units according to Appendix (p. 212) in the paper by Vinogradov and Shuskina (1987), has the following form (at 20°C):

$$M' = 10 \cdot (V \cdot Cc)^{-0.25}, \tag{12}$$

where:
M' – the relative metabolism rate and has dimension d^{-1},
V – the volume of specimen [μm^3],
Cc – the relative carbon content in the body, *eg* pgC/μm^3.

Since differences in the results of measurements of the metabolism rate of filtering ciliates in various stages of their development range from the values described by (12) to the values lower by one order of magnitude (Klekowski, 1981; Fenchel, 1980a, 1986b), we may assume that at least for filtering ciliates $M'_{\min}$ equals about 1/10 M'. Hence, equation (10) may be written in the following form:

$$B_{p\,\min} = \frac{0.1 \cdot 10 \cdot (V \cdot Cc)^{-0.25}}{U^{-1} \cdot \gamma \cdot V^{-0.25}} = \frac{Cc^{-0.25}}{U^{-1} \cdot \gamma}. \tag{13}$$

4. Results

Abundance, body size, and biomass of components of the pelagic biocenosis in the near-surface layer were analysed in samples collected at midnight on May 1 (Table 1). Total phytoplankton biomass was 350 mg C/m^3. Main components were dinoflagellates, diatoms, and monads as well as the autotrophic ciliate *Mesodinium rubrum*, constituting about 10% of the phytoplankton biomass. Approximately 1/3 of the biomass consisted of pico- and nanoplanktonic algae. Estimation of picoplankton biomass is probably largely erroneous due to an

Table 1. Composition of pelagic biocenosis at a depth of 5 m in samples collected at station G-2 at 00 hour on May 1*

Biocenosis components	V [μm^3]	Cc	N [m^{-3}]	B [mg/m^3]	Bc [mg C/m^3]
1	2	3	4	5	6
Picoplankton 1–2 μm	1	0.11	$40 \cdot 10^9$	40	4.4
Pyramimonas sp.	50	0.11	$394 \cdot 10^6$	19.7	2.2
Cryptomonas sp.	200	0.11	$77 \cdot 10^6$	15.4	1.7
Monads, 2–5 μm	25	0.11	$3.3 \cdot 10^9$	82.8	9.1
Monads, 5–10 μm	150	0.11	$736 \cdot 10^6$	110.4	12.1
Dinoflagellata sp. 1 (*Scripsiella*), 17–27 μm	$3.7 \cdot 10^3$	0.13	$175 \cdot 10^6$	647	84.1
Dinoflagellata sp. 2, 30–40 μm	$20 \cdot 10^3$	0.13	$250 \cdot 10^3$	5	0.7
Dinoflagellata sp. 3, 60–70 μm	$100 \cdot 10^3$	0.13	$440 \cdot 10^3$	44	5.7
Gonyaulax catenata	$40 \cdot 10^3$	0.13	$10.8 \cdot 10^3$	435	56.6
Chaetoceros spp.	130	0.08	$6 \cdot 10^9$	800	63.8
Skeletonema costatum	150	0.077	$362 \cdot 10^6$	54.3	4.2
Thalassiosira decipiens	$8 \cdot 10^3$	0.05	$71.6 \cdot 10^6$	573	28.7
Thalassiosira baltica	$50 \cdot 10^3$	0.033	$2.7 \cdot 10^6$	130	4.3
Achnanthes taeniata	$6.7 \cdot 10^3$	0.077	$72.4 \cdot 10^6$	485	37.3
Diaphanoeca sp.	50	0.11	$56 \cdot 10^6$	2.8	0.3
Protoperidinium bipes	$1 \cdot 10^3$	0.13	$6.5 \cdot 10^6$	6.5	0.8
Protoperidinium sp. 1	$12 \cdot 10^3$	0.13	$3.1 \cdot 10^6$	37	4.8
Protoperidinium sp. 2	$30 \cdot 10^3$	0.13	$542 \cdot 10^3$	16.3	2.1
Gyrodinium sp.	$30 \cdot 10^3$	0.13	$125 \cdot 10^3$	3.8	0.5
Ebria tripartita	$3 \cdot 10^3$	0.11	$4.05 \cdot 10^3$	12.2	1.3
Mesodinium rubrum < 25 μm	$3 \cdot 10^3$	0.11	$6.5 \cdot 10^6$	19.4	2.1
Mesodinium rubrum > 25 μm	$30 \cdot 10^3$	0.11	$10.2 \cdot 10^6$	306.0	33.7
Cyclidium sp.	$1 \cdot 10^3$	0.11	$4.86 \cdot 10^6$	4.9	0.5

Table 1 continued

1	2	3	4	5	6
Holotricha, 10–17 μm	$1.1 \cdot 10^3$	0.11	$2.43 \cdot 10^6$	2.7	0.3
Holophrya sp. ~ 16 μm	$1.5 \cdot 10^3$	0.11	$150 \cdot 10^3$	0.2	0.02
Holophrya sp. ~ 26 μm	$12 \cdot 10^3$	0.11	$480 \cdot 10^3$	5.8	0.6
Holotricha, ~ 25 μm	$8 \cdot 10^3$	0.11	$60 \cdot 10^3$	0.5	0.06
Holotricha, 40–50 μm	$30 \cdot 10^3$	0.11	$140 \cdot 10^3$	4.2	0.5
Holotricha, ~ 60 μm	$100 \cdot 10^3$	0.11	$40 \cdot 10^3$	4.0	0.4
Lacrymaria sp. 1	$60 \cdot 10^3$	0.11	$450 \cdot 10^3$	27.0	3.0
Lacrymaria sp. 2	$15 \cdot 10^3$	0.11	$460 \cdot 10^3$	7.0	0.8
Didinium sp. 50–60 μm	$100 \cdot 10^3$	0.11	$50 \cdot 10^3$	5.0	0.6
Didinium sp. 100 μm	$400 \cdot 10^3$	0.11	$40 \cdot 10^3$	16.0	1.8
Strombidium "*delicatissima*"	$1.5 \cdot 10^3$	0.11	$510 \cdot 10^3$	0.8	0.1
Strombidium spp. 30–40 μm	$25 \cdot 10^3$	0.11	$720 \cdot 10^3$	18.0	2.0
Strombidium spp. 15–25 μm	$5.3 \cdot 10^3$	0.11	$300 \cdot 10^3$	1.6	0.2
Strombidium sp. 60 μm	$80 \cdot 10^3$	0.11	$170 \cdot 10^3$	13.6	1.5
Strombidium sp. 30 μm	$10 \cdot 10^3$	0.11	$300 \cdot 10^3$	3.0	0.3
Lohmaniella "*oviformis*"	$4 \cdot 10^3$	0.11	$210 \cdot 10^3$	0.8	0.1
Lohmaniella sp. ~ 25 μm	$8 \cdot 10^3$	0.11	$60 \cdot 10^3$	0.5	0.06
Lohmaniella sp. ~ 50 μm	$40 \cdot 10^3$	0.11	$50 \cdot 10^3$	2.0	0.2
Tintinnopsis beroidea	$5 \cdot 10^3$	0.11	$1.95 \cdot 10^6$	9.8	1.1
Tintinnopsis "*lobiancoi*"	$30 \cdot 10^3$	0.11	$70 \cdot 10^3$	2.1	0.2
Euplotes sp.	$6 \cdot 10^3$	0.11	$10 \cdot 10^3$	0.1	0.01
Pleurobrachia pileus juvenes	$16 \cdot 10^6$	0.003	$1.3 \cdot 10^3$	20.8	0.06
Synchaeta baltica	$3.7 \cdot 10^6$	0.05	$1.2 \cdot 10^3$	4.4	0.22
Synchaeta spp.	$1 \cdot 10^6$	0.05	$15.3 \cdot 10^3$	15.3	0.77
Acartia sp. nauplii	$0.9 \cdot 10^6$	0.06	$9.6 \cdot 10^3$	8.6	0.52
Acartia sp. copepodites I–III	$5.6 \cdot 10^6$	0.06	$1.9 \cdot 10^3$	10.6	0.64
Acartia sp. copepodites IV–V	$11.3 \cdot 10^6$	0.06	$0.7 \cdot 10^3$	7.9	0.47
Acartia bifilosa ad.	$22.5 \cdot 10^6$	0.06	60	1.4	0.08
Pseudocalanus elongatus naupli	$2.1 \cdot 10^6$	0.06	$16.2 \cdot 10^3$	34.0	2.04
Temora longicornis naupli	$0.2 \cdot 10^6$	0.06	$1.7 \cdot 10^3$	0.4	0.02
Temora longicornis copep. IV–V	$45 \cdot 10^6$	0.06	60	2.7	0.16
Eurytemora sp. copep. IV–V	$22.5 \cdot 10^6$	0.06	60	1.4	0.08
Bivalvia larvae	$0.2 \cdot 10^6$	0.06	$1.2 \cdot 10^3$	0.3	0.02
Fritillaria borealis	$0.4 \cdot 10^6$	0.03	$0.2 \cdot 10^3$	0.1	0.003
Bacteria	0.3	0.1	$2.18 \cdot 10^{12}$	655	65.5

*V–body volume; Cc–relative carbon content; N–abundance;
B–biomass, at density = 1 g/cm^3; Bc–biomass in carbon units.
Dimensions given refer to body diameter or width

inaccurate calculation of its size and underestimated abundance of these very small cells, obtained by the sedimentation method. In the zooplankton, whose total biomass was less than 30 mg C/m^3, unicellular organisms (protozooplankton) constituted about 80% – mainly various – species of ciliates and heterotrophic dinoflagellates. Data on the occurrence of zooflagellates are incomplete in this paper since the study method adopted did not allow a distinct differentiation between heterotrophic and autotrophic forms, with the exception of characteristically-structured *Choanoflagellata*. For this reason the group of "monads" in Table 1 comprises, in addition to autotrophic forms, some heterotrophic forms as well. Among multi-cell zooplankton (metazooplankton), copepods and rotatoria predominated. The biomass of bacterioplankton was about 65 mg C/m^3.

The structure of the biocenosis, with body size of its components taken into account, is presented schematically in Figure 1. Organisms were grouped according to their systematic affiliation and, in the case of zooplankton, the manner of feeding. Food relationships between functional groups formed in this way, based on the literature, are presented in Figure 2. Kind of food and manner of feeding for filtering flagellates were adopted after Fenchel (1982, 1986a), Sherr *et al* (1983);

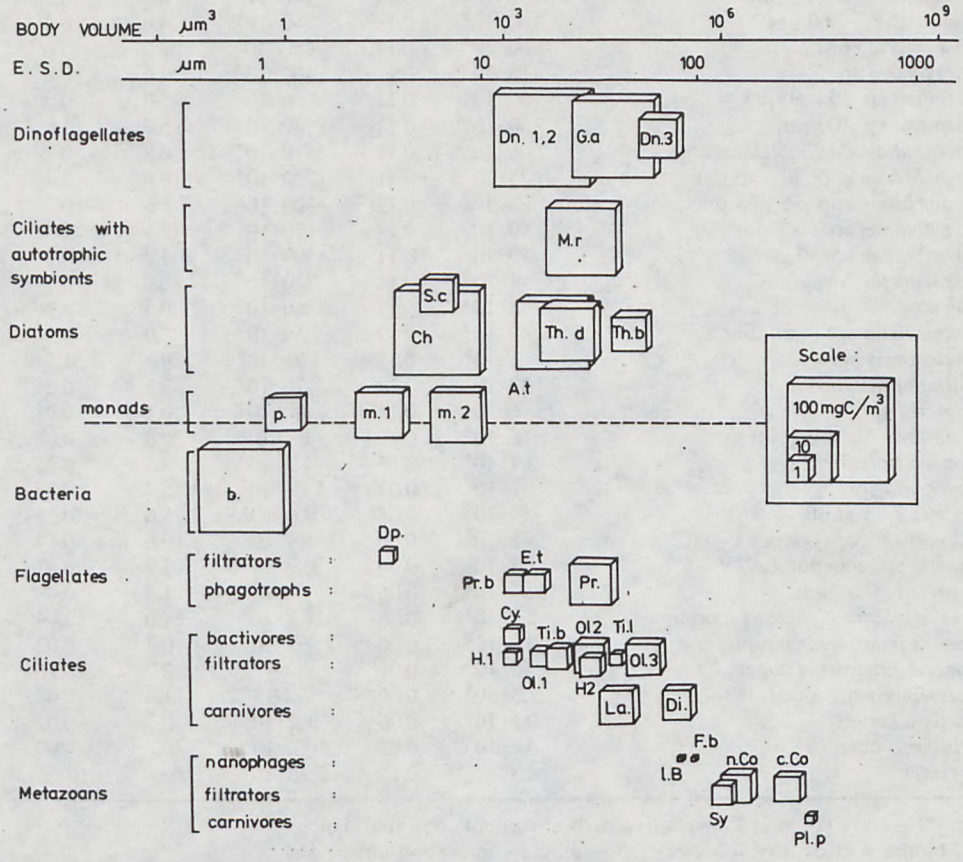

Fig. 1. Structure of pelagic biocenosis at a depth of 5 m
Species (groups of species) are listed according to body size (upper scale) and their systematic and functional affinity (categories enumerated in the left-hand part). Volume of cubes is proportional to biomass. E.S.D. – equivalent sphere diameter. Dn. 1, 2 – *Dinoflagellata* sp. 1, 2; G.c. – *Gonyaulax catenata*; Dn. 3 – *Dinoflagellata* sp. 3; M.r. – *Mesodinium rubrum*; S.c. – *Skeletonema costatum*; Ch. – *Chaetoceros* spp.; A.t. – *Achnanthes taeniata*; Th.d. – *Thalassiosira decipiens*; Th.b. – *Thalassiosira baltica*; p. – picoplankton; m.1 – *Pyramimonas* sp. and monads 2 – 5 µm; m. 2 – *Cryptomonas* sp. and monads 5 – 10 µm; b. – bacteria; Dp. – *Diaphanoeca* sp.; Pr.b. – *Protoperidinium bipes*; E.t. – *Ebria tripartita*; Pr. – *Protoperidinium* sp. 1, 2 and *Gyrodinium* sp.; Cy. – *Cyclidium* sp.; H.1 – *Holophrya* sp. and Holotricha 10 – 17 µm; Ol.1 – *Strombidium* "*delicatissima*", *Strombidium* spp. 15 – 25 µm, *Lohmaniella* "*oviformis*" and *Lohmaniella* sp. 25 µm; Ti.b. – *Tintinnopsis beroidea*; Ol.2 – *Strombidium* spp. 30 – 40 µm H.2 – *Holophrya* sp. and Holotricha 25 – 50 µm; Ti.l. – *Tintinnopsis* "*lobiancoi*"; Ol.3 – *Strombidium* sp. 60 µm and *Lohmaniella* sp. 50 µm; La. – Lacrymaria sp. 1, 2; Di. – *Didinium* spp. i Holotricha 60 µm; l.B. – larvae of Bivalvia; F.b. – *Fritillaria borealis*; Sy. – *Synchaeta* spp.; n.Co. – nauplii of Copepoda; c.Co. – copepodites of Copepoda; Pl.p. – *Pleurobrachia pileus*

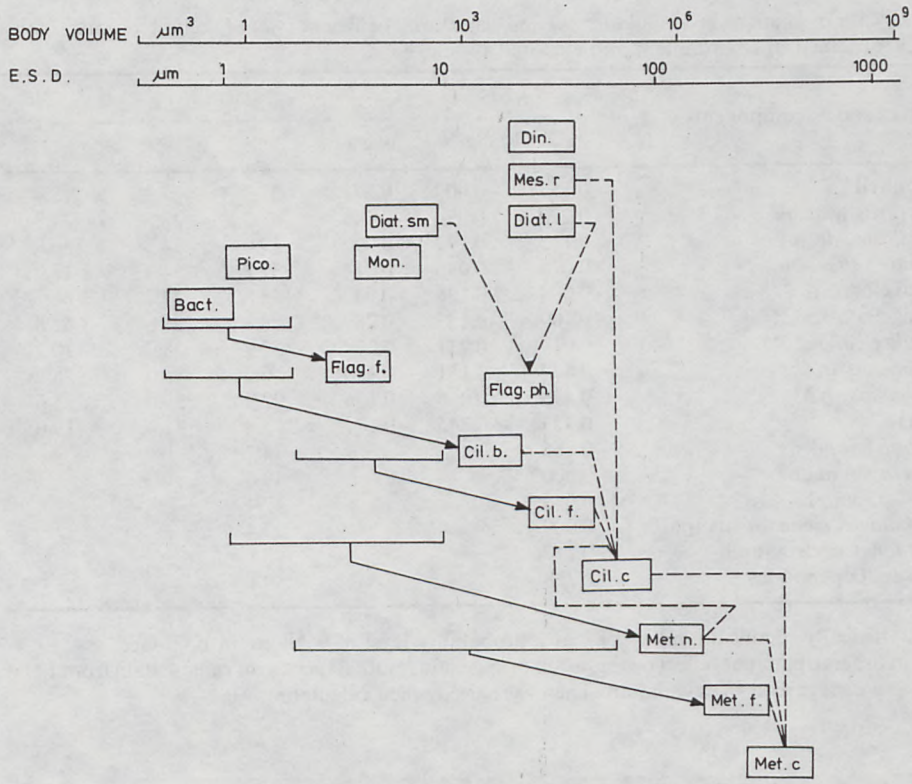

Fig. 2. Trophic relations among functional groups presented in Figure 1
Solid line arrows signify food collection by filtration, broken line arrows – raptorial mode. Braces indicate size range of particles retained when feeding by filtration. E.S.D. – equivalent sphere diameter. Din. – autotrophic dinoflagellates; Mes.r. – *Mesodinium rubrum*; Diat.sm. – small diatoms; Diat.l. – large diatoms; Pico. – picoplankton; Mon. – monads; Bact. – bacteria; Flag.f. – filtrating flagellates; Flag.ph. – phagotrophic flagellates; Cil.b. – bacterivorous ciliates; Cil.f. – filtrating ciliates; Cil.c. – carnivorous ciliates; Met.n. – nanophagous metazoans; Met.f. – filtrating metazoans; Met.c. – carnivorous metazoans

for phagotrophic flagellates – after Gaines and Taylor (1984), Jacobson and Anderson (1986); for ciliates – after Capriulo and Carpenter (1980), Fenchel (1980a,b, 1986a,b), Heinbokel (1978), Jonsson (1986), Rassoulzadegan (1982), Smetacek (1984); for metazooplankton – after Berk *et al* (1977), Conover (1978), Johansson (1983), Jorgensen (1983), Jorgensen *et al* (1984), Lindholm (1985), Reeve (1980), Schnack (1982), Taylor *et al* (1971).

Changes in abundance of plankton taking place in the environment and the enclosed systems, observed during the three-day measurements, are presented in Figures 3 – 5. Table 2 shows coefficients k of the rate of these changes and coefficients of variation. The changes in the environment were as follows: chlorophyll "a" concentration at a depth of 5 m in the first half of the observation period remained at a level of about 13 mg/m^3, in the second half – at a level of 8 – 9 mg/m^3. The scatter of values measured by the variation coefficient, was

Table 2. Rate of changes in abundance (k) and variation coefficient (v.c) of some biocenosis components, observed in environment and enclosed systems*

Biocenosis components	k			v.c. [%]		
	sea	bag N	bag D	sea	bag N	bag D
Chlorophyll "a"	−0.157	−0.009	**0.271**	21.2	7.2	15.4
Chaetoceros wighami	−0.275	0.094	−0.048	47.2	28.5	24.3
Thalassiosira decipiens	−0.112	0.279	0.092	49.9	34.5	30.9
Achnanthes taeniata	−0.074	0.085	0.014	37.2	34.4	16.9
Dinoflagellata sp. 1**	−0.004	−0.196	0.530	148.8	79.7	66.1
Dinoflagellata sp. 2**	0.409	−0.123	0.289	88.8	31.6	51.8
*Gonyaulax catenata***	−0.019	**0.231**	0.370	52.9	28.7	30.2
Pyramimonas sp.**	**0.607**	0.131	−0.130	70.2	26.0	28.8
Cryptomonas sp.**	**0.495**	0.055	0.136	92.9	29.0	25.6
Bacteria	**−0.423**	−0.245	−0.177	53.4	31.4	19.6
Pleurobrachia pileus	−0.865	·	·	74.2	·	·
Synchaeta sp. nauplii	−0.0002	·	·	49.6	·	·
Acartia sp. nauplii	−0.043	·	·	47.4	·	·
Pseudocalanus elongatus nauplii	0.009	·	·	27.4	·	·
Temora longicornis nauplii	0.117	·	·	43.1	·	·
Acartia sp. copepodites	0.238	·	·	80.1	·	·

* statistically significant values of k at a probability level of 95% are in bold-face

** in order to eliminate effect of migration of flagellata (motile) species on value k, data from 12.00 hours were disregarded in calculation. They were used when calculating v.c.

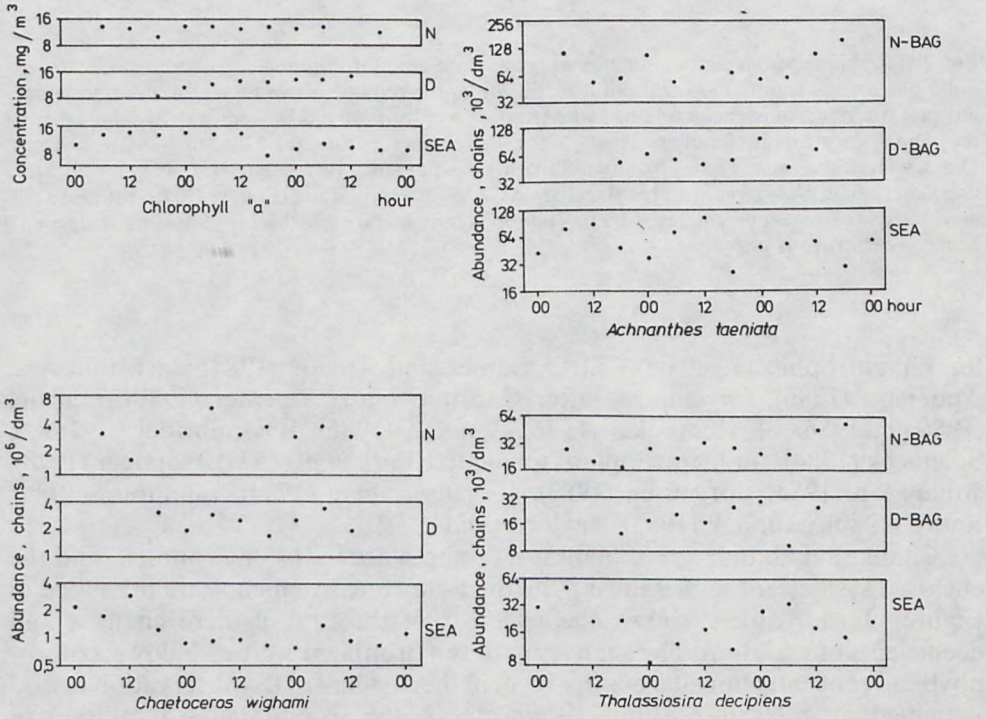

Fig. 3. Changes in chlorophyll "a" concentration and abundance of diatoms at a depth of 5 m and within enclosed systems (N and D)
Concentration and abundance in a logarithmic scale

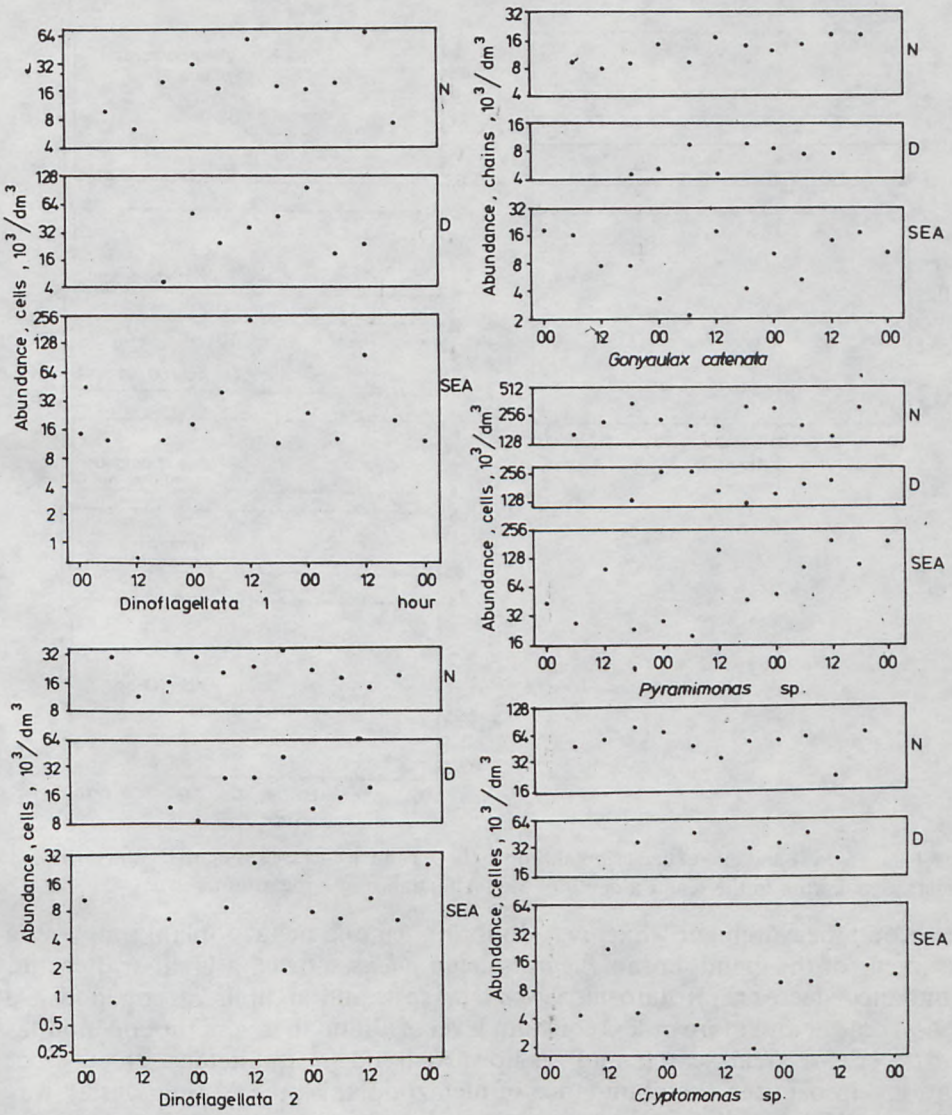

Fig. 4. Changes in abundance of dinoflagellates and flagellates in the sea at a depth of 5 m and within enclosed systems (N and D)
Abundance in a logarithmic scale

small. Individual species of diatoms exhibited a slightly greater scatter in abundance. The abundance of species with the greatest share in the biomass of diatoms decreased during the studied period. Dinoflagellates exhibited great fluctuations in abundance, with extreme values (most frequently maximum ones) usually recorded at noon. The abundance of Dinoflagellata sp. 2 increased whille that of the remaining dinoflagellates did not change. The flagellates *Cryptomonas* sp. and *Pyramimonas* sp. distinguished themselves – besides fluctuations – with a maximum at noon, they exhibited a constant increase in abundance. In the case of bacteria, their abundance decreased and its scatter was modest, if we disregard

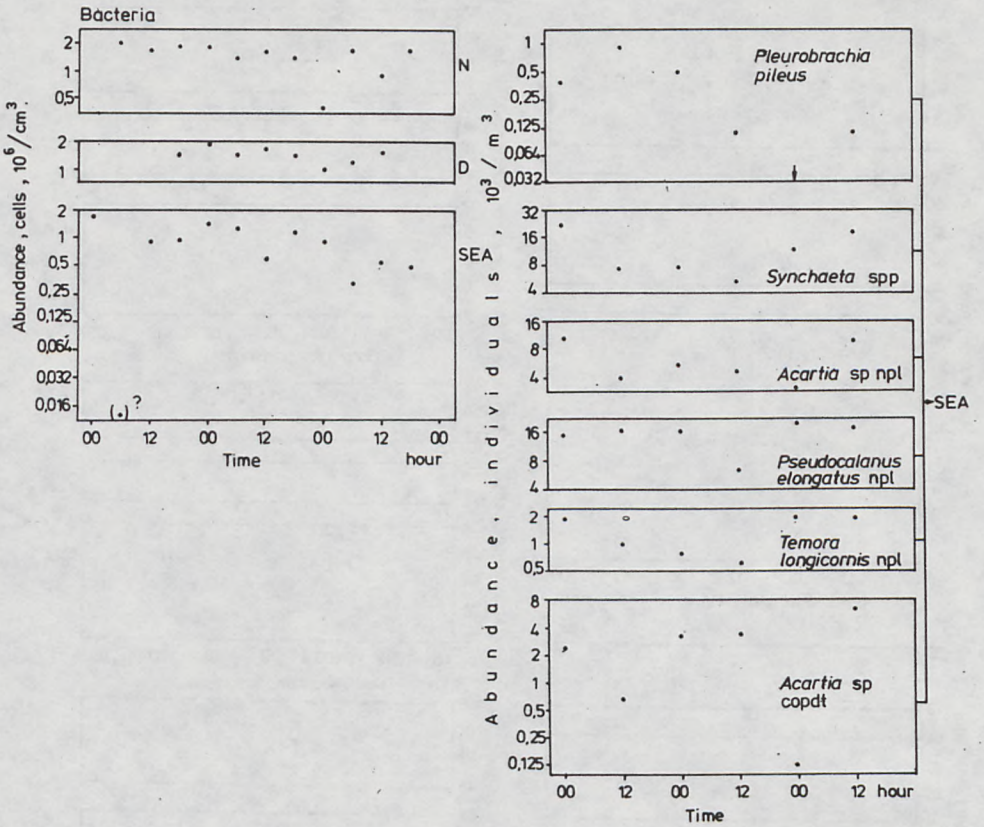

Fig. 5. Changes in abundance of bacterioplankton in the sea and in enclosed systems (N and D) as well as metazooplankton in the sea at a depth of 5 m. Abundance in a logarithmic scale

the second measurement which was doubtful. Among metazooplankton, young specimens of the ctenophoran *Pleurobrachia pileus* showed a great scatter and abundance decrease, Rotatoria *Synchaeta* spp. and nauplii of copepods—a modest scatter and more or less constant level of abundance, and the copepodites *Acartia* sp.—a great scatter and an upward trend in abundance. No distinct relationship between the abundance of metazooplankton and time of day was observed. Among all the changes observed in the environment, statistically significant at a 95% probability level were a decrease in abundance of bacteria (with a rate of -0.42) and an increase in abundance of the flagellates *Pyramimonas* sp. and *Cryptomonas* sp., calculated without taking into account the values from 12.00 hours (with a rate of 0.61 for *Pyramimonas* sp. and 0.50 for *Cryptomonas* sp.).

The enclosed systems differed one from another mainly in that due to the differences in the amount of phytoplankton in the sea when the bags were filled, phytoplankton in bag N was much richer at the beginning of exposure than in bag D. In the enclosed system in bag N chlorophyll "a" concentration remained at a constant level of about 13 mg/m^3 and the scatter of values was very small. Individual species of diatoms showed a small scatter of abundance around a constant or slightly increasing level. A great scatter of abundance values was

characteristic of Dinoflagellata sp. 1, whose greater abundance levels were noted at noon. The abundance of Dinoflagellata sp. 1 and 2 exhibited a downward trend while *Gonyaulax catenata* – a statistically significant increase, with a rate of 0.23. The flagellates *Pyramimonas* sp. and *Cryptomonas* sp. exhibited fluctuations in abundance with a period of 24–30 hours, and a minimum at noon. The abundance of bacteria, stable at first, with time exhibited greater differences and a downward trend.

In the enclosed system in bag D, chlorophyll "a" concentration increased during the observation period in a statistically significant manner, from a value of about 8 mg/m^3 to about 14 mg/m^3, with a mean rate of 0.27. The rate of concentration increase, high at first, gradually decreased. The abundance of individual species of diatoms was stable or increased slightly, its scatter being small. Dinoflagellates exhibited a great scatter and an upward trend in abundance. Similar fluctuations in abundance as in bag N were characteristic of flagellates, though with a shift in phase. Bacteria also exhibited small fluctuations in abundance, with a downward trend.

Recapitulating the above observations, one may note that changes in abundance of the species studied were greater in the environment than in the enclosed systems. Motile algae (dinoflagellates and the flagellates *Pyramimonas* sp. and *Cryptomonas* sp.) exhibited greater differences in abundance, both in the environment and in the enclosed systems, than diatoms. Fluctuations in abundance of dinoflagellates and flagellates were related to the time of day, while changes in abundance of metazooplankton did not exhibit such a relationship. Mean abundance of individual species of algae in bag N was higher than in bag D. Chlorophyll "a" concentration in the environment decreased, in bag N it remained at the same level, while in bag D was on the increase. In the environment and bag N the abundance of some species increased while that of others decreased. In bag D the abundance of dinoflagellates increased. The abundance of bacteria, both in the environment and in the enclosed systems, was on the decrease.

Approximate growth rate, possible under the given feeding conditions, and mortality caused by grazing calculated for some of the biocenosis components, are presented in Table 3. Calculations for carnivorous ciliates were made under the assumption that their feeding rate is the same as that for filtering ciliates, which – after having studied mechanisms of food collection described by Fenchel (1986b) – seems quite probable. Because of a lack of direct data, a similar procedure was adopted in the case of carnivorous metazooplankton and nanophages, assuming for them the same values of feeding rate as for typical filtrators – copepods. The manner of food collection by thecate heterotrophic dinoflagellates was described only very recently (Gaines and Taylor, 1984; Jacobson and Anderson, 1986) and seems so peculiar that further studies are needed before estimation of feeding rate and efficiency will be possible. The cost of metabolism in these organisms is little known, so calculations of b were not made for this group. However, in order to bring mortality values of diatoms, which constitute the food of heterotrophic dinoflagellates, close to actual ones, it was assumed that the relative feeding rate of the latter is $1 \cdot 10^7 \cdot V^{-0.25}$, this value being located in the middle of the range of such values for other groups of zooplankton.

It may be seen from Table 3 that growth conditions were most favourable in the case of filtering metazooplankton, which – with a growth rate of about 0.1

Table 3. Growth rate under given feeding conditions (b) and mortality due to predation (d) for some biocenosis components

Biocenosis components	b	d
Picoplankton	·	0.002
Monads	·	0.031
autotrophic dinoflagellates	·	0.006
Mesodinium rubrum	·	0.027
Diatoms, small	·	0.044
Diatoms, large	·	0.019
Bacteria	·	0.002
zooflagellates, filtrators	0.074	0.031
dinoflagellates, phagotrophs	·	0.006
ciliates, bacterivores	$< = 0$	0.020
ciliates, filtrators	0.087	0.015
ciliates, carnivores	0.023	0.007
metazoans, nanophages	0.046	0.008
metazoans, filtrators	0.103	0.001
metazoans, carnivores	0.040	

and minimum mortality due to grazing—could double its biomass (time of doubling $\mu = \ln 2/(b-d)$) almost every seven days. Filtering ciliates could double their biomass every ten days, which is not a high growth rate for these organisms with a potentially fast growth. The relatively small growth rate of heterotrophic flagellates was largely compensated by mortality. According to our calculations, bacterivorous ciliates were not able to find sufficient concentrations of food to enable growth, but a diversity in food concentration would be enough to maintain a positive growth rate of a part of their population. The remaining groups of zooplankton exhibited a slight predominance of growth over mortality caused by grazing, which, with mortality due to other reasons at a low level, could be sufficient to maintain the biomass at a constant level. Grazing on phytoplankton was small. Grazing was relatively largest on small diatoms and flagellates, as well as *Mesodinium rubrum*, if the assumption that it may constitute the food of carnivorous ciliates is true. Mortality of bacterioplankton due to grazing of bacterivorous organisms considered here was very small.

Recapitulating this part of the results, it may be said that food concentrations for individual groups of zooplankton were sufficient to maintain their moderate growth. The conditions were relatively most favourable for the development of filtering metazooplankton. Mortality of phytoplankton and bacterioplankton due to grazing by zooplankton was small, similarly to mortality of zooplankton, which was generally lower than their growth rate.

5. Discussion

As is evident from its structure, the pelagic biocenosis was at a stage of an advanced spring bloom of phytoplankton. This stage is characterized by a large biomass of diatoms and dinoflagellates, a relatively large biomass of protozooplankton, and a low biomass of metazooplankton (Smetacek *et al*, 1984). Of

course, the near-surface layer, to which the present study was limited, is only a part of the ecosystem; its main characteristic is that primary production is taking place there. It seems that, at least in the studied period, there was a strong spatial separation between autotrophic and heterotrophic components of the biocenosis. Besides bacteria, the heterotrophic part of the biocenosis in the near-surface layer had small biomass and, as may be calculated from mortality of algae caused by grazing, daily eliminated not more than 5 mg C/m^3, which constituted 1.4% of the phytoplankton biomass, and about 5% of primary production (particulate), determined by Woźniak and Kaczmarek (personal communication) at about 100 mg C/m^3 *per* day at a depth of 5 m. Since in the environment no increase in the general amount of phytoplankton was observed at this depth (an increase in the amount of dinoflagellates was probably compensated for by a decrease in the amount of diatoms), the part of primary production not used up for respiration by algae and not utilized by zooplankton must have left the near-surface layer and been utilized at a greater depth. First of all diatoms sedimented into deeper layers. This is evident from their decreasing abundance in the environment, while in both of the enclosed systems their abundance either remained at a stable level or was on the increase. The absence of a diurnal cycle in the changes of metazooplankton abundance at a level of 5 m and its small biomass indicate that metazooplankton of deeper layers did not directly reach the production layer in its vertical migrations (over 90% of primary production was taking place in the upper 5–7 m (Woźniak and Kaczmarek, personal communication) and did not exert pressure to eliminate the phytoplankton inhabiting it, as could be believed from a paper by Ciszewski *et al* (1984), where the authors describe strong fluctuations in zooplankton biomass in the 0–15 m layer, with a maximum at midnight. The reason for the differences may originate in different behaviour of zooplankton during the study by Ciszewski *et al* (1984) (it took place in July 1974) or in the fact that integration of the whole 0–15 m layer could obscure during their study the true picture in the upper part of this layer.

An interesting example of diurnal fluctuations in abundance was revealed by the flagellates *Pyramimonas* sp. and *Cryptomonas* sp. and dinoflagellates. Their abundance was sometimes several times greater at 12.00 hours than six hours earlier, which excludes the possibility of reproduction. According to Banse (1982), for algae with a volume of 100 μm^3 (*eg* flagellates), the maximum diurnal growth rate is 0.9–2.3, while a fourfold increase in abundance within six hours would suggest an unreal growth rate of 5.5.

The only explanation is vertical migration of these algae, most likely an escape from the near-surface layer caused by its excessive illumination, which is additionally supported by the fact that the phenomenon concerned only flagellate forms. Some traces of these fluctuations in the enclosed systems might have been a result of migrations between the walls or the bottom of the bag and the centre of its volume. The ability of dinoflagellates to undertake vertical migrations was mentioned by Sournia (1974), while diurnal fluctuations in phytoplankton abundance, interpreted as a result of growth, were described by Renk *et al* (1984, 1985). In their study, the fluctuations had a smaller amplitude, reaching a maximum in the near-surface layer before noon. Diurnal growth rate calculated on the basis of these changes for various species was 0.3–2.

Changes in abundance in the sea, unrelated to the diurnal cycle, point to a non-uniform distribution of plankton in the horizontal plane. Phenomena of a different scale may be mentioned here. Figure 3 shows how in the middle of the study period chlorophyll "a" concentration changed in the spot where the ship was anchored. These changes may be assigned a spatial dimension in the order of several kilometres. However, even over a period of one sample collection, the changes were sometimes so great that when at 12.00 hours samples were collected from the environment, chlorophyll "a" concentration at a depth of 5 m was 13.7 mg/m^3, that is it did not significantly depart from that measured six hours earlier and six hours later, while a quarter after 12.00 hours, when bag D was being filled, chlorophyll "a" concentration was about 8 mg/m^3, thus introducing a significant change in initial conditions of the experiment. The differences, though smaller than in the open sea, were also visible in the bags, whose contents were not mixed and the result of measurement could be dependent on the spot from which the sample was taken in the bag. Thus, we see here changes ranging from days and kilometres to minutes and centimetres.

The diversity of the environment enables intense local growth of algae. An example of this may be the situation discussed above – when filling bag D, water with a lower chlorophyll "a" concentration was encountered at the 5 m level. The planktonic community enclosed in the bag exhibited then a rapid, especially in the initial phase, increase in chlorophyll "a" concentration to values even exceeding those observed at this depth in the environment and in bag N. A possible explanation for this may be the supposition that the water portion enclosed in bag D had been pushed upwards from greater depths and contained relatively small amounts of phytoplankton, while at the same time containing higher concentrations of dissolved nutrients. An increase in chlorophyll "a" concentration inside bag D was accompanied by an increase in the abundance of dinoflagellates.

It is difficult to account for a decrease in the abundance of bacterioplankton, observed both in the environment and in the enclosed systems, despite the seemingly low mortality due to grazing by zooplankton. It is possible that feeding requirements of bacteria themselves or secretion of substances toxic for bacteria by algae played a role here. The decrease in the abundance of bacteria in the environment might have been connected with a change of the water mass in the middle of the studied period, though the decrease in their abundance in the enclosed systems must have had other causes; it is also possible that because of the existing scatter of results, the values of k in Table 2 are of little significance.

6. Conclusions

(i) The pelagic biocenosis was at the stage of an advanced spring bloom, which in the near-surface layer is characterized by a large biomass of diatoms and dinoflagellates, a relatively large biomass of protozooplankton, and a low biomass of metazooplankton.

(ii) At a depth of 5 m, an increase in the amount of algae in the enclosed systems took place at a rate of 0.23 – 0.27 *per* day (in statistically significant cases).

(iii) According to estimates, feeding conditions of zooplankton were most favourable for filtering metazooplankton and filtering protozooplankton, enabling them growth at a rate of about 0.10 and 0.09 *per* day, respectively.

(iv) Mortality due to grazing by zooplankton was low for all the biocenosis components studied; according to estimates, it did not exceed 0.05 *per* day. At a depth of 5 m zooplankton eliminated slightly over 1% of phytoplankton biomass and about 5% of primary production.

(v) Changes in zooplankton abundance in a diurnal cycle, which could be a sign of vertical migrations, were not observed at a depth of 5 m. Such changes were visible in motile algae – dinoflagellates and other flagellates.

(vi) No increase in the abundance of phytoplankton in the environment at a depth of 5 m, with production processes exceeding elimination due to grazing, indicates that a considerable part of algae, especially diatoms, sedimented into deeper layers.

(vii) Irregular changes in the abundance of the biocenosis components, most likely connected with non-homogeneity of the environment, were observed on a temporal scale ranging from minutes to days.

Acknowledgments

The authors wish to thank dr. S. Apine for analyses of bacterioplankton abundance, dr. A. Kosakowska for determinations of chlorophyll "a" concentrations, and Mr. A. Dargiewicz, Mr. S. Kaczmarek, M.Sc., and the crew of r/v "Oceania" for their help during work at sea.

References

Banse K., 1982, *Cell volumes, maximal growth rates of unicellular algae and ciliates, and the role of ciliates in the marine pelagial*, Limnol. Oceanogr., 27 (6), 1059 – 1071.

Berk S. G., Brownlee D. C., Heinle D. R., Kling H. J., Colwell R. R., 1977, *Ciliates as a food source for marine planktonic copepods*, Microb. Ecol., 4, 27 – 40.

Capriulo G. M., Carpenter E. J., 1980, *Grazing by 35 to 202μm microzooplankton in Long Island Sound*, Mar. Biol., 56, 319 – 326.

Ciszewski P., Ochocki S., Pytel H., Renk H., 1984, *Diel changes in zooplankton distribution at the Gdańsk Deep*, Pol. Ecol. Stud., (3), 361 – 372.

Conover R. J., 1978, *Feeding interactions in the pelagic zone*, Rapp. P.-v. Reun. Cons. Int. Explor. Mer., 173, 66 – 76.

Dybern W., 1986, *The Patchiness Experiment in the Baltic in April – May 1986*, ICES Paper C.M. 1986/E: 3a.

Edler L., 1979, *Recommendations on methods for marine biological studies in the Baltic Sea*, The BMB Publ., 5.

Fenchel T., 1968, *The ecology of marine microbenthos III. The reproductive potentials of ciliates*, Ophelia, 5, 123 – 136.

Fenchel T., 1980a, *Suspension feeding in ciliated Protozoa: feeding rates and their ecological significance*, Microb. Ecol., 6, 13 – 25.

Fenchel T., 1980b, *Suspension feeding in ciliated Protozoa: functional response and particle size selection*, Microb. Ecol., 6, 1 – 11.

Fenchel T., 1982, *Ecology of heterotrophic microflagellates. I. Some important forms and their functional morphology*, Mar. Ecol. Prog. Ser., 8, 211 – 223.

Fenchel T., 1986a, *Protozoan filter feeding*, Progress in Protistology, 1, 65 – 113.

Fenchel T., 1986b, *The ecology of Protozoa*, Springer Verl.

Gaines G., Taylor F. J. R., 1984, *Extracellular digestion in marine dinoflagellates*, J. Plankton Res., 6 (6), 1057 – 1061.

Heinbokel J. F., 1978, *Studies on the functional role of tintinnids in the Southern California Bight. I. Grazing and growth rates in laboratory cultures*, Mar. Biol., 47 (2), 177–190.

Hemmingsen A. M., 1960, *Energy metabolism as related to body size and respiratory surfaces, and its evolution*, Rep. Steno. Hosp., Copenh., 9, 1–110.

Hernroth L., 1983, *Marine pelagic rotifers and tintinnids—important trophic links in the spring plankton community of the Gullmar Fjord, Sweden*, J. Plankton Res., 5 (6), 835–846.

Jacobson D. M., Anderson D. M., 1986, *Thecate heterotrophic dinoflagellates: feeding behavior and mechanisms*. J. Phycol., 22, 249–258.

Johansson S., 1983, *Annual dynamics and production of rotifers in an eutrophication gradient in the Baltic Sea*, Hydrobiologia, 104, 335–340.

Jonsson P., 1986, *Particle size selection, feeding rates and growth dynamics of marine planktonic oligotrichous ciliates (Ciliophora: Oligotrichina)*, Mar. Ecol. Prog. Ser., 33, 265–277.

Jorgensen C. B., 1983, *Fluid mechanical aspects of suspension feeding*, Mar. Ecol. Prog. Ser., 11, 89–103.

Jorgensen C. B., Kiorboe T., Mohlenberg F., Riisgard H. V., 1984, *Ciliary and mucus-net filter feeding with special reference to fluid mechanical characteristics*, Mar. Ecol. Prog. Ser., 15, 283–292.

Kaiser W., Renk H., Schulz S., 1981, *Die Primarproduktion der Ostsee*, Geod. Geoph. Veröff., 4 (33), 27–52.

Klekowski R. Z., 1981, *XI. Ecology of aquatic organisms. 3. Animals. Size dependence of metabolism in protozoans*, Verh. Internat. Verein. Limnol., 21, 1498–1502.

Larsson V., Hobro R., Wulff F., 1986, *Dynamics of a phytoplankton spring bloom in a coastal area of the northern Baltic proper*, Contrib. Askö Lab. Univ. Stockholm, 30, 32.

Lindholm T., 1985, *Mesodinium rubrum—a unique photosynthetic ciliate*, Adv. Aquat. Microbiol., 3, 1–48.

Mc Kellar, Hobro R., 1976, *Phytoplankton—zooplankton relationships in 100-liter plastic bags*, Contrib. Askö Lab. Univ. Stockholm, 13.

Niemi A., 1975, *Ecology of phytoplankton in the Tvärminne area, SW coast of Finland. II. Primary production and environment conditions in the archipelago and the sea zone*, Acta Bot. Fennica, 105.

Nöthig E. M., 1986, *Tank experiments with natural plankton: the influence of light and zooplankton grazing on pelagic system structure*, Ophelia, Suppl., 4, 179–190.

Parsons T. R., Takahashi M., Hargrave B., 1977, *Biological oceanographic processes*, Pergamon Press, Oxford.

Paulsen H., Kiorboe T., Munk P., 1983, *Growth and survival of fish larvae in stratified contra mixed food environments*, ICES paper C.M. 1983/L: 36.

Peters R. H., Downing J. A., 1984, *Empirical analysis of zooplankton filtering and feeding rates*, Limnol. Oceanogr., 29 (4), 763–784.

PEX General Report, 1988, ICES (Draft).

Rassoulzadegan F., 1982, *Feeding in marine planktonic protozoa*, Ann. Inst. Oceanogr., Paris, 58 (1), 191–206.

Reeve M. R., 1980, *Comparative experimental studies on the feeding of chaetognaths and ctenophores*, J. Plankton Res., 2 (4), 381–393.

Renk H., 1973, *Produkcja pierwotna toni wodnej południowego Bałtyku*, Stud. i Mater. MIR, A 12.

Renk H., 1974, *Primary production and chlorophyll content of the Baltic Sea*. Part III. *Primary production in the Baltic*, Pol. Arch. Hydrobiol., 21, 191–209.

Renk H., Ochocki S., Pytel H., 1984, *Short-term fluctuations of primary production and chlorophyll "a" concentration at the Gdańsk Deep*, Pol. Ecol. Stud., 9 (3), 341–360.

Renk H., Borysiak M., Nakonieczny J., Ochocki S., 1985, *Dobowe fluktuacje biomasy fitoplanktonu*, Stud. i Mater. Oceanolog., 46, 151–180.

Schnack S. B., 1982, *The structure of the mouth parts of copepods in Kiel Bay*, Meeresforsch., 29, 89–101.

Sherr B. F., Sherr E. B., Berman T., 1983, *Grazing, growth and ammonium excretion rates of a heterotrophic microflagellate fed with four species of bacteria*, Appl. Environ. Microbiol., 45 (4) 1196–1201.

Sjöberg S., Wilmot W., 1977, *System analysis of a spring phytoplankton bloom in the Baltic*, Contrib. Askö Lab. Univ. Stockholm, 20.

Smetacek V., 1977, *Die sukzession des Phytoplanktons in der Westlichen Kieler Bucht*, Sonderforschungsbereich 95, Univ. Kiel.

Smetacek V., 1981, *The annual cycle of protozooplankton in the Kiel Bight*, Mar. Biol., 63. 1–11.
Smetacek V., 1984, *Growth dynamics of a common Baltic protozooplankton: the ciliate genus Lohmanniella*, Limnologica (Berlin), 15 (2), 371–376.
Smetacek V., 1985, *The annual cycle of Kiel Bight plankton: a long-term analysis*, Estuaries, 8 (2A), 145–157.
Smetacek V., v. Bodungen B., Knoppers B., Peinert R., Pollehne F., Stegmann P., Zeitzschel B., 1984, *Seasonal stages characterizing the annual cycle of an inshore pelagic system*, Rapp. P.-v. Reun. Cons. Int. Explor. Mer., 183, 126–135.
Sournia A., 1974, *Circadian periodicities in natural population of marine phytoplankton*, Adv. Mar. Biol., 12, 325–389.
Taylor F. J. R., Blackburn D. J., Blackburn J., 1971, *The red-water ciliate Mesodinium rubrum and its "incomplete symbionts": a review including new ultrastructural observations*, J. Fish. Res. Bd. Canada, 28 (3), 391–407.
Vinogradov M. E., Shuskina E. A., 1987, *Funkcyonirovanye planktonnych soobshcestv epipelagiali okeana*, Nauka, Moskva.
Winberg G. G., 1971, *Methods of the estimation of production of aquatic animals*, Acad. Press, London.
Woźniak B., Kaczmarek S., *Krzywe świetlne fotosyntezy w morzu*, (in press).
Zimmermann R., 1977, *Estimation of bacterial number and biomass by epifluorescence microscopy and scanning electron microscopy*. [In:] G. Rheinheimer (Ed.), *Microbial ecology of a brackish water environment*, Ecol. Studies, 25, 103–120.