Morphological variability of natural populations of *Aulacoseira granulata* (EHR.) SIMONS (Bacillariophyceae)

Morfologická variabilita přírodních populací *Aulacoseira granulata* (EHR.) SIMONS (Bacillariophyceae)

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Abstract

Measurements were carried out of cell height, valve diameter and cell number per filament during seasonal maxima of *A. granulata* for 24 hours at hourly intervals in the years of 1986-1988. Although, their cell length:width ratio corresponded to var. *angustissima*, the average width itself exceeded Hustedt's figures (1930).
Cell division in the populations was not synchronous. The cells had no tendency to maintain a constant volume - wider filaments contained longer cells. The populations differed in average valve diameter and cell heigh. The presumptive reasons of these differences were discussed.

Introduction

Massive populations of centric diatoms occur in shallow standing waters of the temperate zone, usually in spring and autumn seasons. *Aulacoseira granulata* (EHR.) SIMONS is an exception, because its temperature optimum is higher with seasonal maxima in the summer (LUND 1962). Recently, there has been much discussion about a decline in *Aulacoseira* and *Cyclotella* species due to eutrophication and their substitution by *Stephanodiscus* species (POULÍČKOVÁ & NOVOTNÝ 1999).
A total of 12 taxa belonging to the genus *Aulacoseira* according to the nomenclature by Krammer and Lange-Bertalot (1991) have been found on the territory of the Czech Republic and officially published (POULÍČKOVÁ & LHOTSKÝ in prep.).
Aulacoseira granulata, a species well distinguishable even in native preparations, is obviously one of the most frequent centric diatoms in Czech Republic (P. MARVAN, unpublished data). As in other centric diatoms, this species is characterized by incomplete knowledge on its morphological variability and life cycle. These traits have been studied in numerous centric diatoms with a special attention to variation in valve diameters in the course of a year and longer periods of time in cultures and nature populations. Changes

in valve diameters are related to reproduction. During the vegetative division the valve diameter of diatoms decreses, mostly following the rule by PFITZER (1896) & MACDONALD (1896). After some time, the original size is restored through the sexual reproduction, i.e. by auxospore formation. The changes in the average cell height may be caused by other factors (nutrient limitation, changes of pH, stress, GENSEMER et al. 1995).

The goal of this contribution was to confirm the existence and character of diurnal changes in selected morphological parameters of *A. granulata*.

Materials and methods

The biological material assessed - a population of *A. granulata* - was obtained from a shallow eutrophic fishpond called Opatovický located on the territory of the Třeboň Basin Biosphere Reserve (South Bohemia, Czech Republic). The ecosystem of Opatovický fishpond has been investigated in detail (KOMÁREK 1973, KOMÁRKOVÁ 1973, KOMÁRKOVÁ & PŘIBIL 1973, MARVAN 1973).

Morphological measurements of *A. granulata* were carried out in the years of 1986-1988 during its seasonal maxima, i.e, in September.

The samples were collected at 1-hour-intervals over 24 hrs in plastic bottles 20 cm below the water surface, and immediately fixed by formaldehyde to obtain a concentration of 3%. One hundred cells were measured in each sample, a total of 7,500 cells. The assessment was focused on the following parameters : cell height (i.e size along the pervalvar axis), valve diameter (i.e. filament width), and cell number per filament. Synchronization of the cell division was calculated according to KOMÁREK & SIMMER (1965).

Results

During 24-hour-measurements performed at hourly intervals in the period of the seasonal maxima of *A. granulata* in September 1986, 1987, and 1988 the assessment was made of cell height and cell number per filament (Figs 1, 2). We found only slight fluctuations in the cell height with no general trend. On the other hand there was an increase in the total number of cells per filament during morning hours in 1987. Based on the measurements of cell height during 24 hours period a degree of population synchronism was calculated (Fig. 3) which in no case showed the suggested synchronization in the cell division.

The overall morphological variability is summarized in Table 1. Figures 4 and 5 show the distribution of the valve diameter and cell height in the respective sampling days. Over the experimental period there was a reduction both in valve diameters and cell height. Figure 4 clearly demonstrates that in 1986 there was a prevalence of bigger valves and occurrence of the largest size categories (i.e. 8.75 and 10.00 μm). In the subsequent two years the peak

of the distribution curve got shifted towards smaller valves, whilst the largest size categories completely disappeared. Consequently, it cannot be expected to find out all of the size categories evenly spread across a locality at a time.
The cell height distribution diagrams (Fig. 5) show a remarkable difference between the three experimental years, but all the size categories are always represented. The most frequent size categories recorded in the years of 1986, 1987, and 1988 were 20-35, 15-30, and 20-35 µm, respectively.
Figure 6 gives a complete cell height distribution in filaments of different widths. As seen in this graph, narrower filaments contain lower cells, whilst there are more higher cells in wider ones. It may be concluded, that measured cells have no tendency to preserving a common volume.

Discussion

The observations on periodicity in the development of some algae, generally related to the diurnal light and darkness rhythm, together with the advances in laboratory culture of microorganisms led to the elaboration of methods enabling quantitative evaluation of laboratory cultures synchrony (CAMERON & PADILLA 1966, CAMPBELL 1957, ŠETLÍK et al 1972, TAMIYA 1966,). Later, some attempts were made to express a degree of synchrony of natural populations (LUKAVSKÝ 1973). The above papers dealing with synchronous cultures have confirmed that numerous important parameters change during the cell cycle, e.g. dry matter content per cell, chlorophyll content, rate of photosynthesis and respiration, amount of nucleic acids and storage substances. These parameters can then be used e.g. for estimation of fishpond phytoplankton populations. It seems obvious that the main synchronizing agent in nature is diurnal light rhythm. A synchronous population is characterized by the identical behaviour of cells in growth as well as cell and nuclear division. In non-synchronous populations the cells are randomly distributed in all existing phases of the cell cycle (ENGELBERG 1961). Real populations represent a compromise between these theoretical extremes. A universal method for caclulating a degree of synchrony suitable for comparing populations with various numbers of possible phases was proposed by KOMÁREK & SIMMER 1965. In principle, there are 3 criteria of synchrony related to natural populations:

1. linear size of a cell, diameter in global cells, length of filaments constant in diameter
2. cell volume
3. number of nuclei assessed e.g. by a fast fluorescence method.

There are some criteria, such as valve diameter and cell volume that cannot be used for diatoms, because they are dependent on the life cycle stages (PFITZER 1896, MAC DONALD 1896, MANN 1988). Consequently, cell height were used as a parameter to calculate the population synchrony. As seen in the final graph (Fig 3), there was no universal trend in the course of a 24-hour-cycle. The same was shown in the figure depicting a diurnal variability of the cell height (Fig. 1). These measurements have proved that the cell division in the *A. granulata* population under study was not accumulated in a shorter day interval, but it was randomly dispersed in time.

In earlier literature, the cell division synchronization has been described for synchronous cultures in laboratory conditions, particularly green algae (KOMÁREK & SIMMER 1965, LORENZEN 1964, MORIMURA et al. 1964, SULEK 1972) and natural populations of green algae and cyanobacteria (SIMMER & SODOMKOVÁ 1968, LUKAVSKÝ 1973). A lot of references about using this phenomen in practise and recent research of aquaculture systems can be found in literature (OTERO et al. 1998, OTERO & FÁBREGAS 1997).

There are several varieties within the scope of the species *Aulacoseira granulata* and two common in our waters, the most frequent being var. *angustissima* and the type variety. The variety *angustissima* is noted for its extraordinary long, narrow cells (width 3-5 µm, height many times as big as width up to the ratio of 10:1, HUSTEDT 1930, KRAMMER & LANGE-BERTALOT 1991). When collecting samples from Opatovický fishpond we only found the filaments whose cell length:width ratio corresponded to var. *angustissima*, the average width itself exceeded Hustedt's figures (1930).

STOERMER et al. 1985 revealed var. *angustissima* in older (more oligotrophic), and the type variety in younger (more eutrophic) sediment layers of Lake Ontario. On the other hand, some authors observed both types at the same locality (P. MARVAN, personal communication). Vodeničarov et al. (1985) performed measurements of populations originating from 5 localities different in trophy. Based on the results obtained he denied the existence of the varieties of the species *A. granulata* including var. *angustissima*, referring to them as ecoforms. KILHAM & KILHAM (1975) do not disclaimed the varieties *angustissima* and *granulata* based on culture observations.

TURKIA & LEPISTÖ (1999) studied the *Aulacoseira* species in Finnish lakes. The type variety of *A. granulata* was found in 8 lakes with a mean width of 10.4 - 16.8 µm and height of 19.8-33.2 µm. The variety *angustissima* was detected in six lakes measuring on average 2.3-5.7 µm in width and 25.2-30.2 µm in length. The population studied by DAVEY (1987) reached the average cell length 26.1-41.1 µm and width 8-21 µm indicating the type variety.

The filaments measured in Opatovický fishpond in 1986 were significantly wider (6-7,5 µm) than in the years 1987 and 1988 (4.8-6, and 4.5-6 µm, respectively). A slight reduction in the size was also evident on the average cell height over the years of 1986, 1987, and 1988 (29-34 µm, 22-29 µm, and 25-32 µm, respectively).

A decrease in the valve diameter is related to asexual reproduction. The whole cycle comprising gradual diminution followed by the enlargement up to the original size in the course of the sexual stage is characterized by different length of time in various diatom species.

Morphometric studies of diatom life cycles in wild populations in which periodic samples are taken for more than 1 year are rare. Such studies have been carried out on some planktonic freshwater diatoms (ROUND 1982, JEWSON 1992 a,b, POULÍČKOVÁ & NOVOTNÝ 1999), benthic or epipelic freshwater diatoms (STEINMAN & LADEWSKI 1987, MANN 1988) and marine species (MIZUNO & OKUDA 1985).

In most cases the cycle lasts several years depending not only on genetic dispositions, but also on ecological conditions (JEWSON 1992a, POULÍČKOVÁ & NOVOTNÝ 1999, RAO & DESIKACHARY 1970). NIPKOV (1927) reported *Melosira islandica* ssp. *helvetica* to have restored its size in 20 years under conditions of the lake Zurichsee.

However, MANN (1988) pointed out that earlier authors did not record large size classes simply because frequencies of these classes were too low. The low occurrence of large cells could be caused for instance by their faster sedimentation in the water column. It means, that the different vertical distribution of individual size classes could be expected. SCHLEGEL & SCHEFFLER (1999) described this situation in the case of *Cyclotella ocellata* in lake Dagow. Although *Cyclotella ocellata* was equally distributed in the epilimnion, preauxospores preferred 0 - 0,5m water depth and auxospores and initial cells were most abundant at 2 m depth.

Differences in the decline of the average cell size between the experimental years of 1986-1987, and 1987-1988 (Fig. 4) might be due to the fact that in the year with favourable conditions for a prolonged population development there were more divisions per season and a resulting decrease in the average cell size was higher than in the less favourable year. This suggestion is partly supported by TURKIA & LEPISTÖ (1999) having stated that in some *Aulacoseira* species a significant decrease in valve diameter was observed in the period of elevated abundance, growth rate and population density. Theoretically, another interpretation arises of the increasing amount of narrow cells based on a suggestion that sexual reproduction and auxospore formation are not only dependent on a certain minimum cell size, but also on suitable ecological conditions. Then the prevalence of small valves would mean that the conditions of a locality do not allow for auxospore formation. JEWSON (1992b) found that average cell diameters in the planktonic diatom *Aulacoseira subarctica* from Lough Neagh (Northern Ireland) were surprisingly stable throughout the year. JEWSON argued that the ability to maintain a constant mean population cell size is an adaptation of this planktonic diatom to the environment of a cool, turbid lake. DAVEY (1987) found only small differences in the filament width, but no significant seasonal variations in cell height except for some seasonal changes in filament length due to a different number of cells per filaments. The number of cells in the filaments may vary remarkably even

during the day as given in Fig. 2. In some diatoms, measurements of the valve diameter variability during the life cycle show that we cannot expect even distribution of the respective size categories of a given species in a locality all the time irrespective of the life cycle stage (MANN 1988, POULÍČKOVÁ & NOVOTNÝ 1999). On the contrary, the restoration of the original size through sexual reproduction does not probably occur fluently, but occasionally. The sexual reproduction actually can be a short-time contingency timing in specific season, for instance September (HEGEWALD & HINDÁKOVÁ (1997) - *Cyclotella ocellata*, POULÍČKOVÁ & NOVOTNÝ - *Stephanodiscus hantzschii*), or in winter (POTAPOVA & SNOEIJS 1997 - *Diatoma moniliformis*).
Size frequency curves of diatom natural populations sometimes clearly show the prevalence of either large or small valves, or they have double peaks as found e.g. in *Stephanodiscus hantzschii* (ROUND 1982, POULÍČKOVÁ & NOVOTNÝ 1999) and other species too (MANN 1988). On the other hand POTAPOVA & SNOEIJS (1997) did not find bi or multimodal size class distribution that are indicative of year classes representing annual periods of auxosporulation.

According to some diatomologists this phenomen should be considered particularly for taxonomy purposes in such cases when new taxa are being described on the basis of multiple-peak size frequency curves (MARVAN, personal communication). In the context of ecological studies it is necessary to keep in mind that the valve diameter and cell volume of diatoms is dependent on the stage of the life cycle, and thus it cannot be expected that all the stages will be always evenly represented in a population , i.e. at the moment of once-over sampling.
If TURKIA & LEPISTÖ (1999) assessed *Aulacoseira* cell diameters, height and volume following a once-over collection of samples from different lakes it seems probable that they could have found populations with different life cycle stages. The valve diameter and cell volume do not seem to have been a suitable criterion for the assessment of the direct dependence of trophy of the locality.

On the other hand, the changes in the average cell height might probably be related to more factors. Some authors showed morphological effects induced by phosphate and silicate limitation, aluminium addition, or pH changes (TILMAN et al. 1976, GENSEMER 1990, GENSEMER et al. 1995). GENSEMER et al. (1995) suggested that rapid cell size reduction may be a general response to any environmental stress.

DAVEY (1986) revealed the susceptibility of *A. granulata* to culture conditions. With the decreasing amount of nutrients the cells elongated, whilst they became shorter with increasing shaking. TURKIA & LEPISTÖ (1999) found shorter cells in the lakes with a higher phosphorus content, but longer ones in the localities rich in nitrogen. Based on the "nutrient hypothesis" gradual elimination of cell height in Opatovický fishpond over the 3 experimental years could be due to the continuing eutrophication of the locality. Unfortunately, this suggestion cannot be supported by concrete data about nutrient amounts.

A question arises, however, to which extent the cell hight is dependent on cell width, i.e. on its reproduction. Most probably, the cells of *A. granulata* population under study do not have a tendency towards preserving uniform volume, as seen in Fig. 6. Wider filaments contain longer cells. The observations on some diatoms showed that auxospore formation is preceded not only by decreasing valve diameters, but also by increasing cell height, i.e. their elongation along the pervalvar axis. This phenomenon was described e.g. in *Stephanodiscus hantzschii, Cyclotella ocellata* (KLING 1992, SCHLEGEL & SCHEFFLER 1999). According to POTAPOVA & SNOEIJS (1997), in the case of *Diatoma moniliformis* the size of the transapical and pervalval axix can be somehow regulated to accommode the best competitive proportions in a particular environment. In fact, the diatom girdle is more flexible than the thecae (ROUND 1972, CRAWFORD 1981). It should be pointed out that in a population of *A. granulata* this phenomenon has not been recorded yet. However, our observations of the population revealed neither auxospore formation nor enlargement of valve diameters which would have been a sign of the completed sexual process.

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Tab. 1

Variability in valve diameter and cell height of *Aulacoseira granulata* during observations in three subsequent years (minima, averages, maxima and standard deviations are presented)

Year	Valve diameter [µm]				Cell height [µm]			
	MIN	(AVG)	MAX	STD	MIN	(AVG)	MAX	STD
1986	3.75	(6.64)	10.00	1.19	18.75	(31.93)	62.50	8.84
1987	2.50	(5.22)	7.50	0.97	17.50	(24.69)	51.52	5.13
1988	2.50	(5.01)	7.50	1.10	16.25	(25.88)	47.25	4.35

Fig. 1
Diurnal fluctuation in the average cell height of *Aulacoseira granulata*.

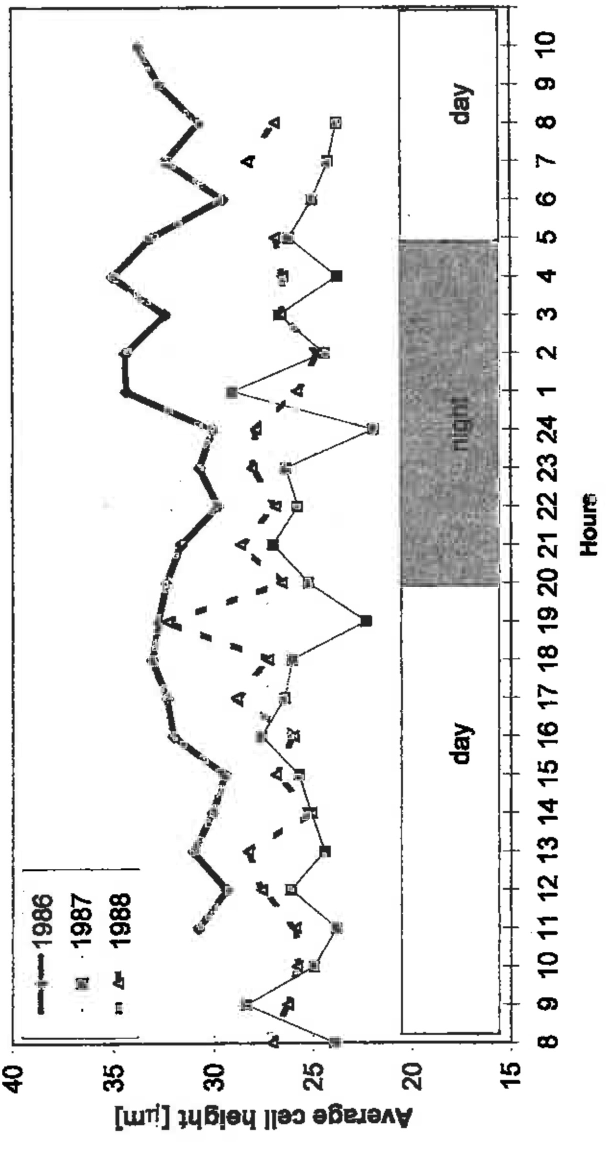


Fig.2
Diurnal fluctuation in the average cell number per filament of *Aulacoseira granulata*.

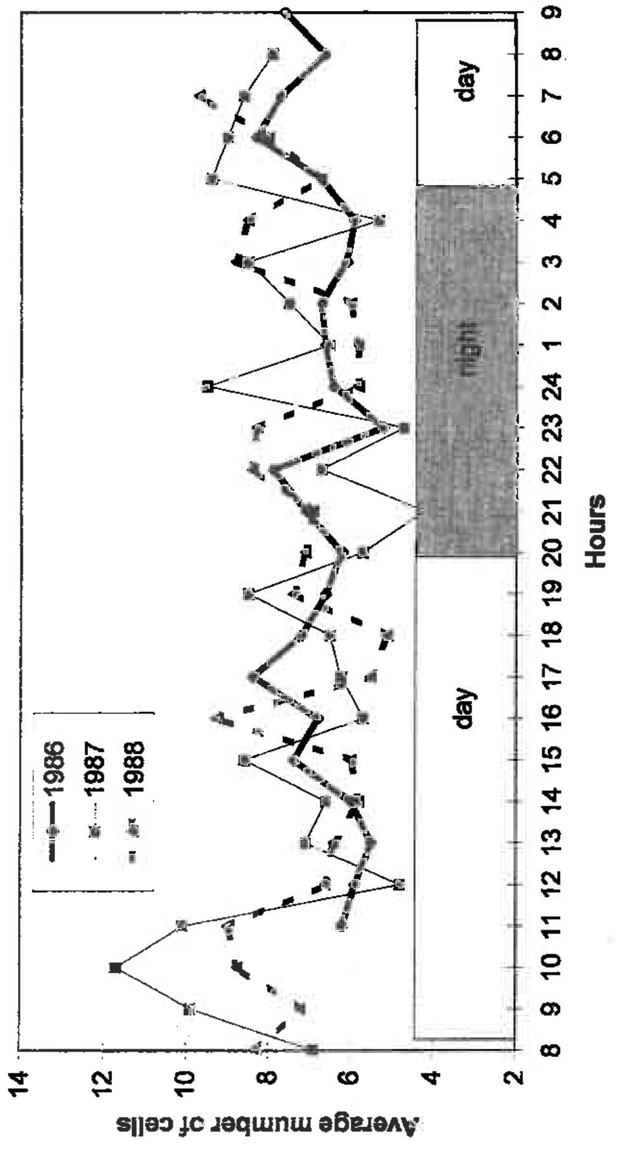


Fig.3
Diurnal changes in a degree of synchrony in a popoulation of *Aulacoseira granulata*

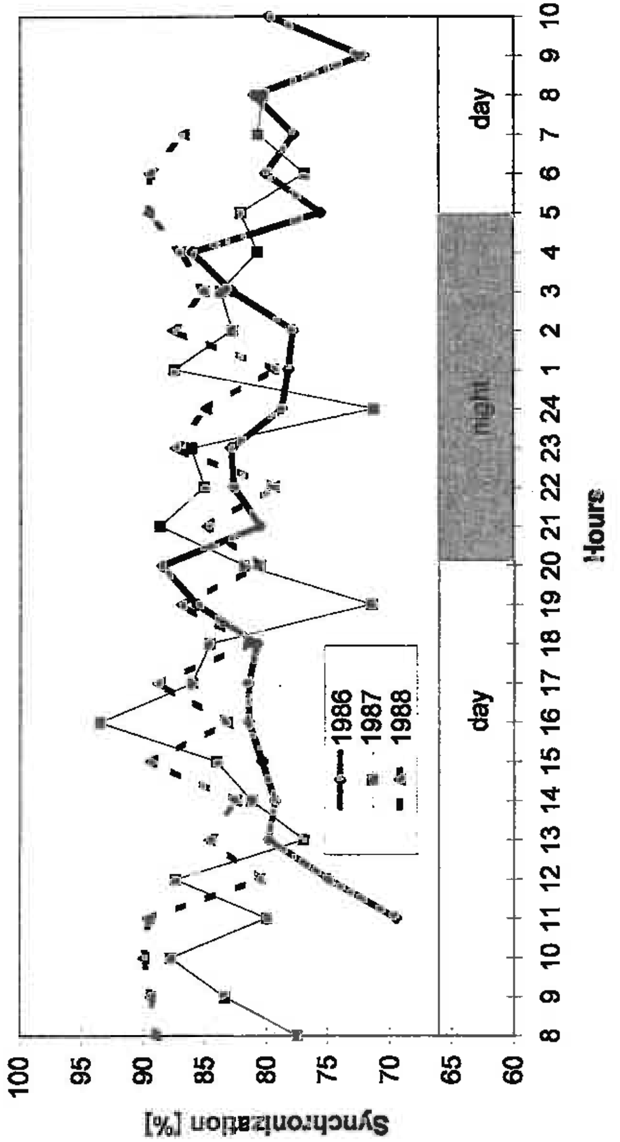
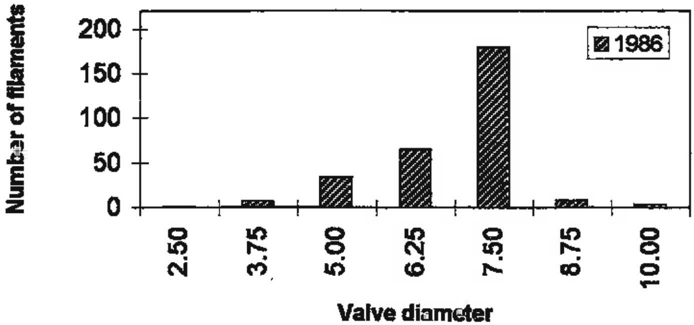
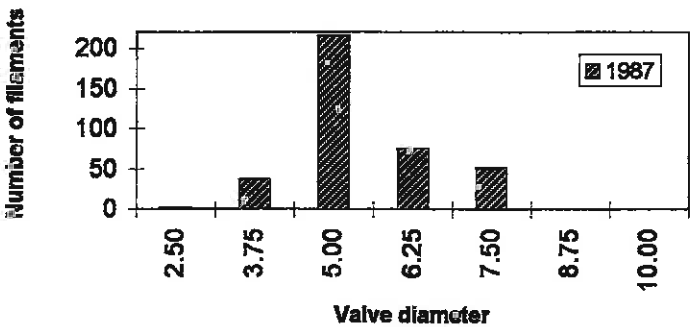


Fig.4
Distribution of valve diameters (in µm) of *Aulacoseira granulata* during observations in subsequent years. Frequency is expressed as the amount of filaments.





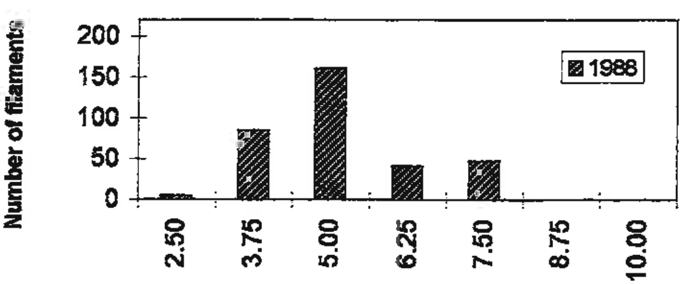
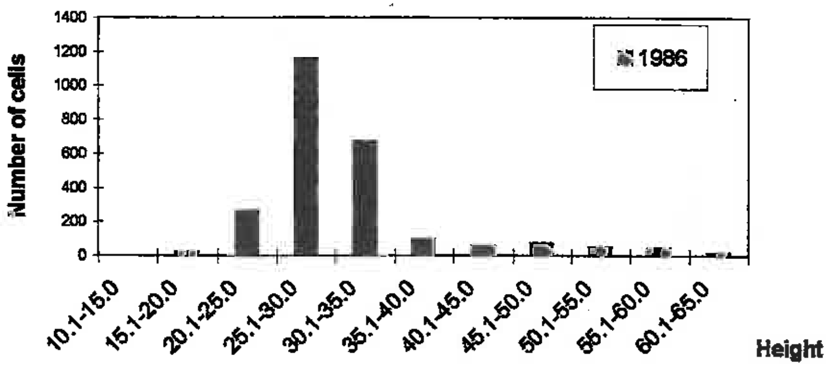
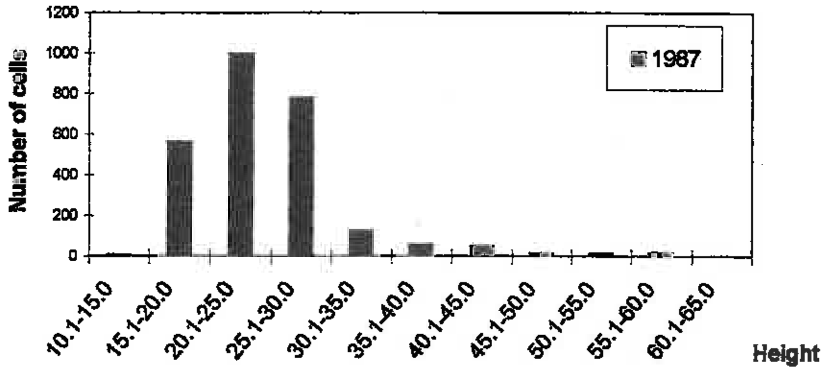


Fig.5. Distribution of cell heights (in µm) of *Aulacoseira granulata* during observations in three subsequent years. Frequency is expressed as the amount of cells.





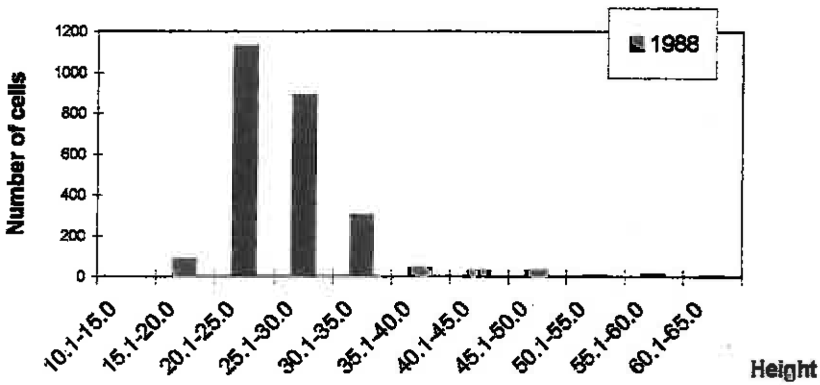


Fig.6: Distribution of cell height (in µm) among different filament widths (in µm). Frequency is expressed in %.