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SEASONAL AND YEAR-TO-YEAR VARIATION OF NUMBERS OF *CHIRONOMUS PLUMOSUS* L. AND TUBIFICIDAE IN A LOWLAND RESERVOIR: REGULARITIES, CAUSES, MECHANISMS

ABSTRACT: During 9 years of studies very regular *Chironomus* population dynamics was stated in a eutrophic, lowland dam reservoir. There were usually two peaks of the abundance: the higher one at spring (up to 80 thousands ind. m⁻²) and the much lower in autumn. The duration of the spring *Chironomus* generation was about 3 weeks. The constant presence of young larvae during the summer did not result in the high total abundance of larvae, mainly due to the strong predation of fish and swallows on various stages of *Chironomus*. The smaller predators pressure in the spring (due to fish breeding) and in the autumn (due to lower temperatures) resulted in the mentioned two peaks.

The spring peak abundance was positively correlated with the chlorophyll concentration in water (feeding resource for larvae) and negatively with the water flow. There was also negative correlation of the water flow and the chlorophyll concentration, as well as abundance of *Chironomus* and Tubificidae during the vegetation season (April–October). Tubificidae correlated strongly positively with the spring *Chironomus* numbers (with a month lag). The slight positive correlation of these benthic components abundance occurred for the whole vegetation season. Tubificidae occurred in generally high numbers up to 400 thousands m⁻², but various in different years, and with no regular changes during the season.

KEY WORDS: *Chironomus*, Tubificidae, population dynamics, long-term studies, dam-reservoir

1. INTRODUCTION

Chironomus plumosus and co-dominant Tubificidae are typical components of the benthos in eutrophic dam-reservoirs. Both these components are very important in the matter cycling and as the food for fish in eutrophic water bodies (Wiśniewski 1978, Sokolova 1983, Armitage *et al.* 1995). Both *Chironomus* and tubificids were examined during 9 years in the period 1982–2000 (see Figs 1 and 2) in the shallow central, broad part of the lowland, highly eutrophic reservoir (Central Poland). The numbers and biomasses of *Chironomus* in this reservoir belongs to the highest recorded ones – periodically values of more than 80 thousand ind. and up to 1 kg biomass (fresh weight) m⁻² were noted (Kuklińska 1989, 1992, Dusoge *et al.* 1999). This was one of the reasons for choosing this reservoir as the study site.

Various aspects of the reservoir ecology: general characteristics, chemistry, temperature, water flow, plankton, benthos, fish have been described earlier (Dusoge *et al.* 1985, 1999, Bubiń 1989, Kajak and Dusoge 1989, Kajak 1990a, b, Sych 1997).

Some field and laboratory experiments on the benthos have also been done. The results of these experiment showed that:

- Several times higher abundance of *Chironomus* could be achieved (in the same sediment, at the study site) by simple experimental trick of elevating the mud in the containers at a distance of 40–120 cm over the bottom. This indicates high importance of oxygen conditions (as a rule better over the bottom than at its very surface) for the survival and development of *Chironomus* larvae (Kajak and Dusoge 1996, Kajak 1997, Kajak and Prus 2001c).

- The amount of organic matter in the substrate is of secondary importance for *Chironomus*; the larvae fed mainly on freshly sedimented seston, which has high nutritive value (Kajak and Prus 2001a).

- Additional feeding (in laboratory conditions) can increase the survival and the development rate of *Chironomus* larvae in the sediment cores taken from the reservoir. Also the density-dependent regulation mechanisms in *Chironomus* populations in the laboratory were described (Kajak and Prus 2000, 2001b). Additional feeding in the natural conditions (field experiment) also increased (1.5–3 times) the survival and growth rate of *Chironomus* larvae (Prus unpublished).

The aim of the present study was to describe and to compare the varying *Chironomus* population dynamics and the diverse (different in particular years) population density in the reservoir. It was based on long-term series of data and also on the results of previous experiments, described above. The main goal of the paper is to find out factors and mechanisms causing various population levels and dynamics. Long-term series of data on: water temperature, flow, and chlorophyll concentration were correlated with the data on *Chironomus* and Tubificidae abundance. The data on the influence of oxygen conditions, mutual relations (within the *Chironomus* population and between *Chironomus* larvae and Tubificidae), and predators (mainly fish) pressure on the benthos in the reservoir were also taken into account.

2. STUDY AREA

The Zegrzyński reservoir (Fig. 1), formed by two large, lowland rivers: Bug and Narew (inflows to the Vistula river), is lo-

cated 30 km north from Warsaw (Central Poland). The length of the reservoir is 70 km, the surface area – about 33 km², average depth – 3–4 m (maximal at the dam – 9 m). The retention time at the low water flow during most of the vegetation season is 2–3 weeks, while at high water flow, mostly in the spring, it may be only 1 day. Detailed description of the Zegrzyński reservoir is given in previous papers (Kajak and Dusoge 1989, Kajak 1990a, b 1997).

The work was done in the central broad part of the reservoir (about 2 × 5 km), at the sites 3–5 m deep, with the slow water flow (Fig. 1).

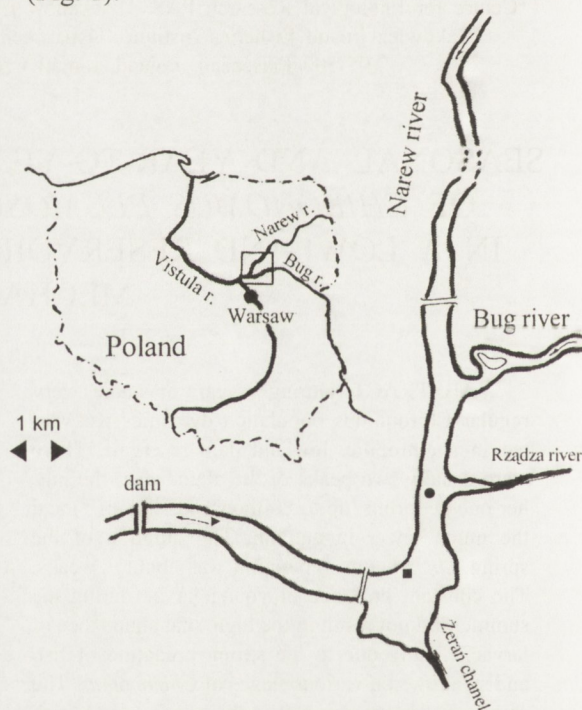


Fig. 1. The Zegrzyński dam-reservoir and its localization in Poland. Study sites: square – sampled in the years 1982, 1984, 1991, 1993, 1996, 1997, 2000, depths 5 m; circle – the year 1992, depths 3 m; triangle – the year 1999, depths 5 m. All sites located in a part of the reservoir with slight water flow and flat, muddy bottom.

3. METHODS

The studies were conducted since early 80-ties, during 9 years (1982, 1984, 1991, 1992, 1993, 1996, 1997, 1999, and 2000). Sampling was usually done during the vegetation season: since late April or early May till September–October in the central part of the reservoir with various frequency (usually every one-two weeks, at least monthly). Five

to ten samples with 20 cm² Kajak's core sampler were taken each time. They were sieved either immediately in the field or, within few hours, in the lab, on a 0.25 0.25 mm mesh sieve; the residue was preserved in the 4% formaline. The relatively small mesh size guaranteed quantitative estimation of all *Chironomus* individuals (above 2–3 mm of length) and also almost all the Tubificidae. *Chironomus* larvae were measured with the 1 mm accuracy, and classified into size classes ≤6, 7–12, 13–17 and ≥18 mm.

Statistical evaluation of the data on the benthos has been done for data since 1992 (until 1991 samples from each station were joined and sieved together). Data on the water flow, temperature and chlorophyll have been obtained from the Institute of Meteorology and Water Management, carrying out the monitoring program on the reservoir since 80-ties.

The simple regression method (Statistics software) was used for the correlation of environmental factors (temperature, water flow,

chlorophyll concentration) with *Chironomus* and Tubificidae numbers. This method was also used to correlate *Chironomus* and Tubificidae numbers (*Chironomus* as the independent variable).

4. RESULTS

4.1. *CHIRONOMUS* POPULATION DYNAMICS

Usually 2 peaks of *Chironomus* abundance occurred – the spring and summer/autumn one. Sometimes (years 1984, 1992, 1999) the summer/autumn peak was lacking (no data for the year 1991). Low (as for this reservoir) abundance i.e. almost zero to 2.5 thousands ind. m⁻² (practically only grown up larvae!) occurred in early spring, before the spring peak of the abundance (Fig. 2).

The size of spring peaks of abundance varied greatly – from about 5–6 thousands

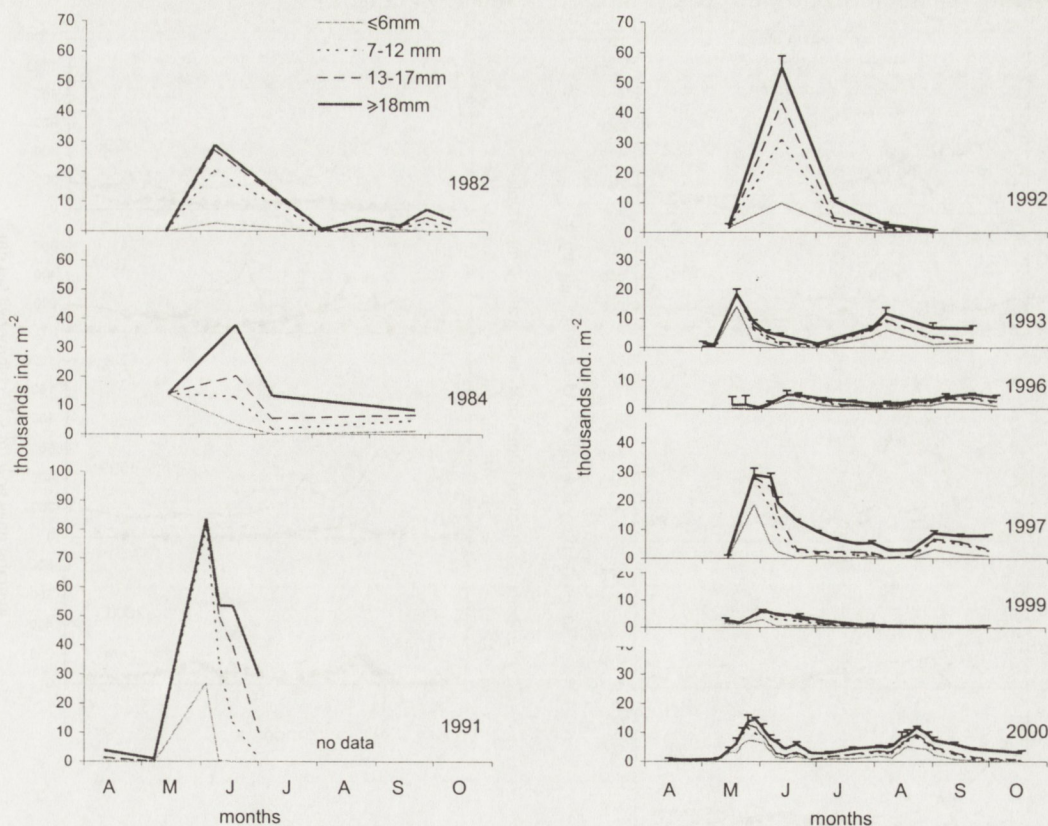


Fig. 2. The dynamics of *Chironomus plumosus* population and its size structure (9 years). Surfaces between lines – corresponds to numbers of particular size classes (as marked on the figure); whole surface below the top line – total numbers. \pm S.E. for total numbers is marked (excluding 1982, 1984 and 1991 when samples were coupled).

ind. m^{-2} in 1996 and 1999, to about 84 thousands ind. m^{-2} in 1991, that is about 17 times more. High peaks (>30 thousands ind. m^{-2}) occurred in 1982, 1984, 1991, 1992, 1997 that is 5 out of 9 years studied. Numbers below 20 thousands ind. m^{-2} occurred during four years (1993, 1996, 1999, 2000), and below 10 thousands ind. m^{-2} during 2 years (1996, 1999).

Spring peaks during all the years studied occurred within relatively short period, between middle May (in 1993) and middle June (in 1984), that is within 1 month; usually they occurred during even shorter period of two weeks (between last days of May and 12 June). Water temperatures of 18–24°C were noted during the time of spring peaks of abundance (Fig. 3). Usually there was a very pronounced peak of abundance of the youngest (≤ 6 mm) larvae and the next size class (7–12 mm), causing the peak of total numbers. Spring peak numbers decline rather rapidly. Already a month after the spring peak the numbers were several times lower, independently from the size of the peak (Fig. 2).

Very low (as for this reservoir) and relatively similar abundance (about 1–3 thousands ind. m^{-2}) occurred almost every year during few weeks – one month after the spring peak of the abundance. However during the rest of the time between spring and summer/autumn peaks, *Chironomus* numbers were relatively low, not exceeding several thousands ind. m^{-2} for several months. In the years 1984, 1992 and 1999, when the summer/autumn peak was lacking – such low numbers were noted to the end of the vegetation season (Fig. 2).

Summer/autumn peaks of *Chironomus* abundance were much more dispersed in time than spring ones – from August in 1993 till September–October in 1982, that is during three months, as opposed to less than one month in the spring. They were usually much lower than spring ones (Fig. 2). Summer/autumn peaks were similar to spring ones only in years 1993, 1996 and 2000, when spring peaks were moderate or low. Summer/autumn peaks were not observed in 1984 and 1999 (Fig. 2).

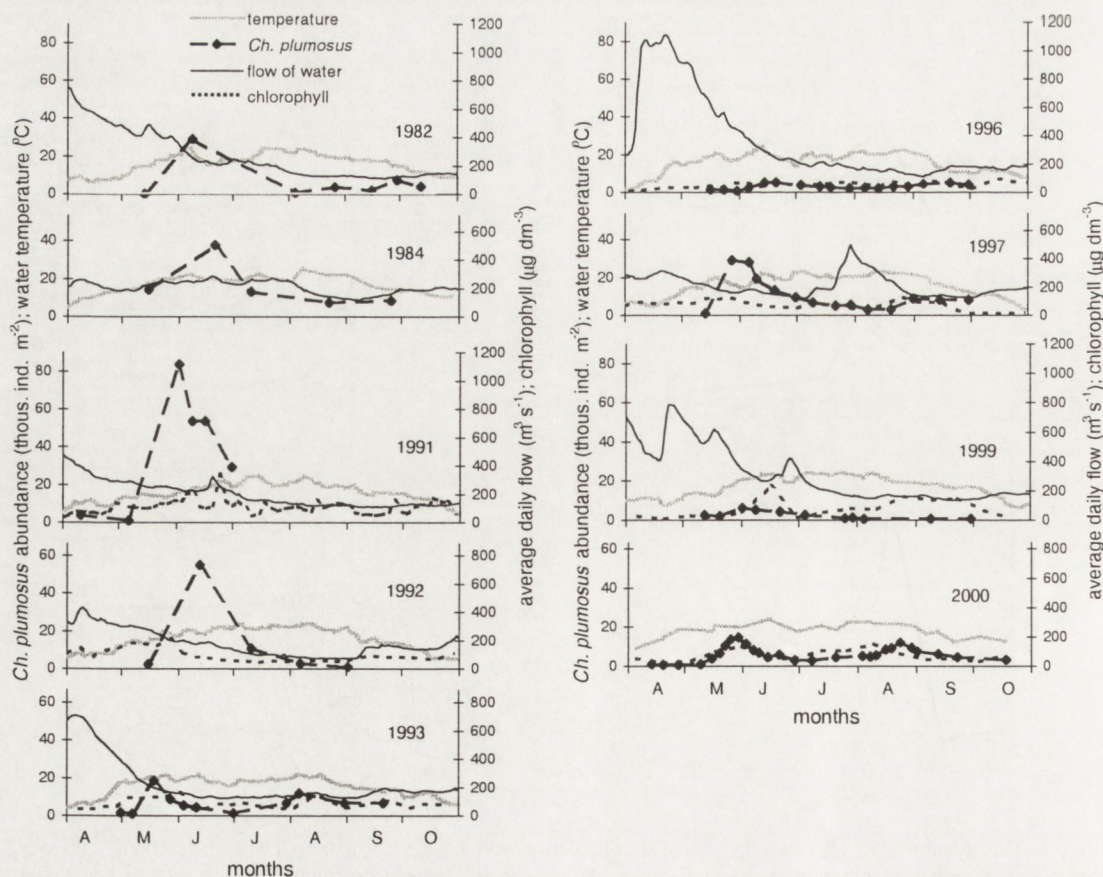


Fig. 3. The dynamics of the abundance of *Chironomus plumosus* on the background of the chlorophyll concentration, water flow and temperature (9 years). No data are available on chlorophyll concentration for 1982 and 84 and on water flow for 2000.

The youngest class (≤ 6 mm) of larvae did occur (although sometimes in very small numbers) practically during the whole vegetation season, including the period between spring and summer peaks, and also in the autumn.

4.2. CORRELATIONS BETWEEN *CHIRONOMUS* ABUNDANCE AND CHOSEN ENVIRONMENTAL FACTORS

There was some negative correlation ($P = 0.06$) between the spring *Chironomus* peak size and the water flow during 4 weeks before the peak (Table 1), as well as between the average seasonal *Chironomus* numbers and average seasonal water flow (Table 2). No correlation between the temperature (during one month before the spring peak) and the peak abundance was found (Table 1). The temperature was relatively high, usually above 18°C in this period (Fig. 3). There was also no relation between *Chironomus* numbers in the autumn and the spring peak size (Fig. 2). On the other hand there was the clear correlation ($P = 0.05$) between the *Chironomus* spring peak size and the chlorophyll concentration during a month period before the peak (Table 1, Fig. 3).

The correlation between the chlorophyll concentration and the water flow during four weeks before the spring peak *Chironomus* numbers ($P = 0.008$) as well as for the whole vegetation season ($P = 0.07$) was negative (Tables 1 and 2).

The size of summer/autumn peaks did not correlate with the temperature, water flow, and chlorophyll concentration during 10 days, as well as 4 weeks before the peak (Fig. 2).

4.3. TUBIFICIDAE

Tubificidae are, beside *Chironomus plumosus*, the second most important benthic component in the central part of the reservoir. The highest abundance found was 430 thousands ind. m^{-2} , the highest biomass (fresh weight) – about 300 g m^{-2} . Average annual abundance varied enormously – from 10 thousands ind. m^{-2} (in the year 2000) to about 180 thousands ind. m^{-2} (years 1992 and 1997). Average numbers for 8 years of studies were about 100 thousands m^{-2} . There was no seasonal regularity in changes of abundance during the year (Fig. 4).

Juvenile forms (not determinable to species) were dominant, *Limnodrillus* consisting on the average 77%, and *Tubifex* – 18% of total numbers of Tubificidae.

Fifteen species altogether have been found; the dominant ones constituted the following percent share of Tubificidae (mature individuals determinable to species): *Limnodrillus hoffmeisteri* (Clap.) – 55; *L. claperedeanus* (Rat.) – 25; *L. profundicola* (Verril.) – 12; *Potamothrix hammoniensis* (Mich.) – 8. Maximal share of adults in the whole population took place in May and July about 10%, in other months – 1.5 – 6.0%. Adults were found and breeding was going on all over the year (Badetek unpublished).

There was a significant, positive correlation between spring peak of *Chironomus* abundance and Tubificidae numbers during one month after the *Chironomus* spring peak. A weak correlation was also found between spring peak *Chironomus* abundance and average (April–October) numbers of Tubificidae (Table 3). There was also a strong negative correlation ($P = 0.03$) between average water flow (for a vegetation season April–October) and average Tubificidae

Table 1. Correlation (simple regression) between *Chironomus plumosus* spring peak numbers, chlorophyll concentration, water flow and temperature (averages for 28 days before the *Chironomus* peak) and between chlorophyll concentration and the water flow (for the same period); n – number of replicates (years). Chlorophyll contents – in $\mu\text{g m}^{-3}$; *Chironomus* abundance – individuals m^{-2} ; water flow – sum of inflow from Bug and Narew rivers ($\text{m}^3\text{ s}^{-1}$).

Parameters	n	Correlation coefficient	r^2 %	P
<i>Chironomus</i> –chlorophyll	7	0.75	57	0.05*
<i>Chironomus</i> –water flow	8	–0.69	47	0.06*
<i>Chironomus</i> –temperature	9	–0.38	14.4	0.31
Chlorophyll–water flow	6	–0.92	86	0.008*

*significant correlation.

Table 2. Correlation between average (for the vegetation season April–October) chlorophyll contents, water flow, abundance of *Chironomus* and abundance of Tubificidae; n – number of replicates (years), chlorophyll contents – in $\mu\text{g m}^{-3}$; *Chironomus* and Tubificidae abundance – individuals m^{-2} ; water flow – sum of inflow from Bug and Narew rivers ($\text{m}^3 \text{s}^{-1}$).

Parameters	n	Correlation coefficient	r ² %	P
Chlorophyll–water flow	6	–0.78	60	0.07*
<i>Chironomus</i> –water flow	7	–0.83	68	0.04*
Tubificidae–water flow	7	–0.87	75	0.03*

*significant correlation.

Table 3. Correlation between *Chironomus plumosus* and Tubificidae abundance (individuals m^{-2}); n – number of replicates (years)

Parameters	n	Correlation coefficient	r ² %	P
<i>Chironomus</i> (spring peak numbers)				
Tubificidae (during a month after <i>Chironomus</i> peak)	8	0.77	60	0.02*
<i>Chironomus</i> (spring peak numbers)				
Tubificidae (seasonal average)	8	0.69	48	0.06*

*significant correlation.

numbers for this period (Table 2). Similar negative correlation was found between *Chironomus* abundance and water flow and a weak correlation between chlorophyll concentration and water flow (average values for vegetation season).

5. DISCUSSION

5.1. GENERAL REGULARITIES IN *CHIRONOMUS* OCCURRENCE

The Zegrzyński reservoir (the area of this study) has almost ideal conditions as a habitat for *Chironomus plumosus*: it is shallow, hypertrophic, with usually slow water flow. This flow of water guarantees generally good oxygen conditions and the permanent supply of river seston, with dominant small diatoms, the favorite food item of *Chironomus* (Johannson and Beaver 1983, Rasmussen 1984; Johnson *et al.* 1989, Goedkoop and Johnson 1996, Goedkoop *et al.* 2000). That is why *Chironomus* attains occasionally and periodically high numbers and biomass in this reservoir: up to more than 80 thousands ind. and 1000g m^2 (Fig. 2, Kuklińska 1989, 1992, Kajak

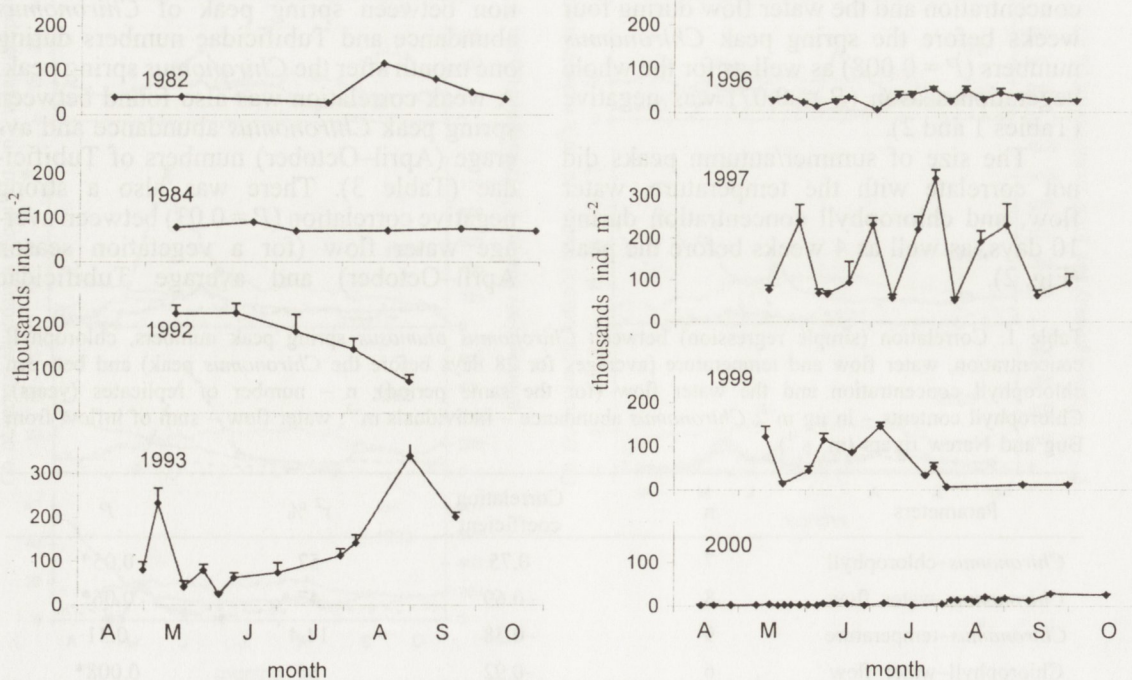


Fig. 4. The dynamics of the abundance of Tubificidae (8 years). + S.E. is marked (excluding 1982 and 84, when samples were coupled).

1990b, Dusoge *et al.* 1999). This is among the highest amounts noted in the literature. Numbers in nature are extremely differentiated: from less than 100 ind. m⁻² to the mentioned enormous ones. They can also differ many (several to more than twenty) times in the same water body in various years (Jonasson 1977, Sokolova 1983, Toderaš 1984, Kajak 1987, Kangur 1989, Linedegaard *et al.* 1993, Wolnomiejski 1994, Armitage *et al.* 1995, Kangur *et al.* 1998).

There are usually two peaks of *Chironomus* numbers in the season: May–June and August–September. The highest numbers occur at the spring peak. Such two peaks were noted at various densities of larvae, and in different types of water bodies (Janković 1971, Matěna 1989, Ružičkova 1987, Ivakuma *et al.* 1993). Summer/autumn peaks are usually much lower, sometimes similar (only when spring peaks are low) but never higher than spring ones.

Numbers in the summer, between spring and summer peak, are low as for the studied reservoir (about one to few thousands ind. m⁻²), probably due to the heavy fish pressure. These numbers are however quite high when compared to most situations in other water bodies (Sokolova 1983, Armitage *et al.* 1995), where few hundreds or even few dozens individuals m⁻² are common.

Usually at the study area there is no other peak of *Chironomus* abundance as high as this one noted in May–June. The summer/autumn peak is as a rule much lower than the spring one; sometimes it does not develop at all. However usually there is some (often very low) amount of the youngest larvae all over the summer and autumn (Fig. 2). Such situation happens in various water bodies (Yamagishi and Fukuhara 1971, Gower and Buckland 1978, Frank 1982, Sokolova 1983, Ivakuma 1992, Ivakuma *et al.* 1993, Drake and Arias 1995). There are good reasons for the high numbers of young larvae in the summer: the abundance of grown up larvae during the summer is much higher than in the spring, the emergence of imago and the egg-laying is going on all over the summer. It should lead to high numbers of eggs and young larvae. However obviously during most of the summer the strong mechanisms reducing the abundance of *Chironomus* are operating, resulting in the low level of the offspring (see the chapter 5.2, this paper). Summer peaks appears usually from late August till October (Fig. 2), when

mechanisms decreasing *Chironomus* abundance (mainly the fish and swallows pressure) are lower, due to lower temperatures. Perhaps it is also partially due to better food conditions, as the share of small diatoms in the sedimenting phytoplankton increase in autumn (Bubień 1989).

The decline of *Chironomus* numbers after the late summer/autumn peak of its abundance (as a rule much lower than the spring one) is much weaker than that after the spring peak. This smaller reduction of numbers late in the season, is probably due to the lower pressure of fish and birds (at lower temperatures) as well as to the higher supply of eggs due to the same reason.

The regularity of *Chironomus* occurrence in the studied reservoir, described above, raises a number of questions: 1) Why can the spring maximum be so high only in some years? 2) Why numbers decline so strongly and rapidly after the spring maximum? 3) What is the reason of the summer minimum, sometimes quite low and long lasting? 4) Why usually the decline of the late summer/autumn maximum is so small, especially if compared to that of the spring one? 5) Do the two maxima mean two generations, and if so – why not more? 6) Are the occasional oxygen deficits important? These questions will be discussed below, basing on the results of long-term studies conducted in the Zegrzyński reservoir.

The emergence of imago begins as early as 3–4 weeks after the spring peak of abundance. It was found in laboratory cultures of intact cores of the sediments with their benthos (Kajak and Prus 2000) taken just after the spring peak, and also endorsed by the analysis of field materials (Kajak and Prus in press). Such quick development has been found also by some other authors in laboratory cultures (Kalugina 1971) and in freshly flooded fish ponds. On the other hand many authors suppose the generation time as long as 1.5–2.0 or even 3–4 months within the epilimnion in the relatively high temperature zone (Janković 1971, Kalugina 1971, Frank 1982, Sokolova 1983); however the materials are not always sufficiently convincing.

The length of the generation time in summer is not clear. The emergence (and consequently the recruitment) goes on all the time, but at unknown rate. Perhaps the development of larvae is limited by the competition, and the pressure of predators

(Macchiusi and Baker 1992, Ball and Baker 1995), including just “frightening” larvae as well as destroying larval tubes by fish, which decrease the amount of time spent by larvae on feeding. It can also be hampered by the occasional covering of the bottom surface with a layer of mud carried by the flow of water or resedimenting after strong winds. Such situation forces larvae to lose their energy for rebuilding the tubes what undoubtedly slows down their development.

It is common in the literature that peaks of *Chironomus* abundance are treated as the appearance of the new generations. In the reservoir under study it certainly is so with the spring generation. But its high abundance is due mainly to the low pressure of predators. The summer/autumn peak results probably also from the decreased pressure of predators. It enables the increase of hatching and survival of larvae, leading to their high abundance. Young larvae do occur all the summer, but in small numbers. It seems that there can be up to several generations (that is life cycles finishing with imagos) during the summer (Kajak and Prus in press). The peaks of the abundance however, do not occur due to the strong pressure of predators on various stages of *Chironomus*. That is why it is very difficult to distinguish particular generations.

5.2. FACTORS LIMITING *CHIRONOMUS* POPULATION ABUNDANCE

Assuming 10 mm² of the surface area of one larval tube (3.5 mm of the diameter) there is the space for about 100 thousands of tubes of grown up larvae (but of course for much more of smaller ones) on 1 square meter. This enables the abundance of 50 thousands of larvae per square meter (2 tube openings of 1 larva), which is almost maximal number observed in nature. After the spring maximum the numbers drop to a level many times lower. The larvae during the maximum and soon after are relatively small, so it is not the space limitation which may cause the observed, great decline of the population. On the other hand the larvae penetrate the area around the tubes, probably the more intensively the younger they are (Kajak and Prus 2001a, b). This activity and resulting frequent contacts of larvae make their competition one of the reasons of the decline of the abundance (Kajak 1987), apart from the pressure of predators, water flow and other factors.

In years with very high spring numbers of larvae, bottom surface is composed exclusively of apertures and walls of larval tubes touching each other, without free space between them. They form the compact, spectacular “carpet”, which undoubtedly counteracts the mixing and resuspension of the mud, assuring stable and comfortable conditions for larvae. At the lower abundance of larvae tubes apertures were often not seen, being frequently covered by sediments brought by movements of water or by the activity of fish (Kajak and Prus in press).

The different size of the spring peaks of numbers of larvae strongly negatively correlates with the flow of water during few weeks before the peak in particular years. The flow of the water above some critical value (in the studied reservoir about 400–500 m³ s⁻¹ – Fig. 3), could lower *Chironomus* peaks, by carrying out both the egg-masses and the youngest larvae. Such a high flow can also destroy larval tubes, by covering them with high amounts of mud transported by rivers, which sediments to the reservoir bottom. This forces larvae to spend more time and energy on rebuilding their tubes (instead of feeding), what can slow down their development and increase the mortality.

Despite the relative shallowness of the study sites (about 3–5 m) and constant water flow in this part of the reservoir, some short-lasting oxygen deficits are noted in the near-bottom water layers (Kajak and Dusoge 1989, Kajak 1997). These deficits can decrease survival and development rate of *Chironomus* larvae, especially young individuals which are less resistant to oxygen depletions than older ones (Armitage *et al.* 1995).

The importance of the oxygen conditions for larvae was confirmed in field experiments (Kajak and Dusoge 1996, Kajak 1997, Kajak and Prus 2001a, c). In experimental trays (with the natural *Chironomus* population) located 0.4–1.2 m over the bottom, *Chironomus* abundance was several times higher than in the bottom. For the youngest larvae (≤ 6 mm lengths) this difference was much greater – up to 50–70 times. The abundance in trays also declined after the spring peak, but remained much higher than in the bottom (Kajak and Dusoge 1996, Kajak 1997, Kajak and Prus 2001a, c). So, much higher numbers of *Chironomus* larvae can live in this environment, at the same food conditions and fish pressure, but in improved oxygen

conditions, which are undoubtedly better above than at the very bottom.

The importance of the food for *Chironomus* development and abundance is well documented (Sokolova 1983, Graham and Burns 1983, Kajak 1987, Armitage *et al.* 1995, Nakazato and Hirabayashi 1998). Some authors indicate that the number of generations may depend on the food situation (Nakazato and Hirabayashi 1998). Analyzing 2.5 thousands of guts of larvae of various size we found them always full; only much less than 0.1% were partly or completely empty (Kajak and Spodniewska unpublished). Also the great amount of sedimenting riverine seston of high nutritive quality, not decomposed due to the shallowness of the studied reservoir, indicates that food conditions are not limiting in this environment (Dusoge *et al.* 1985, Bubień 1989). Of course, full guts of larvae do not prove that they eat as much as they would like to. The guts can be full because they are not emptied if the new portions of food are not taken. The intake of the food can be limited for a number of reasons, like mentioned relations (physical contacts) of neighboring larvae resulting in less time spent for the collection of the food. The same effect can be caused by fish penetrating the environment; physical damaging of tubes by other larvae and by fish as well as by water movements (destroying tubes and covering them with layer of mud) is also possible. The various degree of the disturbance of larvae is probably one of reasons of their rapid differentiation in size after the spring maximum, when they were fully or relatively uniform in size (Kajak and Dusoge 1996, Kajak and Prus 2001a, b; and in press).

The seston was always abundant in the reservoir due to its transport by rivers and also the resuspension from the bottom; however its nutritive value could differ significantly, being the highest in spring, when small diatoms are most abundant. The exclusive nutritive value of diatoms, due to the high content of unsaturated fatty acids, and the variation of the food value during the year is stressed by a number of authors (Johansson and Beaver 1983, Rasmussen 1984, Johnson *et al.* 1989, Goedkoop and Johnson 1996, Ahlgren *et al.* 1997, Goedkoop *et al.* 2000). The importance of seston as the main food source for *Chironomus* in the studied reservoir was also confirmed in field experiments by similar larval numbers

obtained on a fully mineral substrate and on sediments containing up to 83% organic matter (Kajak and Prus 2001a).

Chironomus abundance at the spring peak strongly correlated with phytoplankton concentration (in rivers supplying the reservoir) during four weeks before this peak. This indicates high importance of feeding conditions for the development of spring *Chironomus* generation. A strong negative correlation between water flow and chlorophyll concentration was also stated for the four-weeks period preceding the spring peak of *Chironomus* abundance as well as for the whole vegetation season (April–November). So the high flow of water could influence *Chironomus* abundance both directly by washing out egg masses and small larvae, and indirectly by decreasing the chlorophyll concentration (Tables 1 and 2, Fig. 3).

The predation by fish on various stages of *Chironomus* (egg masses, larvae, pupae, emerging and egg-laying imagos) is a very important factor decreasing its abundance. In the studied reservoir fish are very abundant. Dominant fish species are: bream, white bream, roach, perch, and ruff (Boroń and Grudniewski 1990, Grudniewski and Boroń 1990, Terlecki *et al.* 1990). The total biomass was estimated to 400–600 kg per ha (Sych 1997).

It is possible that the spring peak of *Chironomus* numbers results from lower fish pressure. Before and during the peak the fish are busy with the spawning; only some time after the *Chironomus* peak they become interested in benthos; also the new fish generation begins soon with feeding on *Chironomus* larvae and pupae. Probably the fish pressure, apart from some "competition" of growing larvae, can cause the decline of the high spring *Chironomus* abundance. Fish can also lower *Chironomus* numbers by eating egg masses or even egg laying females as well as emerging imagos. Within a number of benthophagous fish, there is especially abundant population of ruff considered as a very voracious consumer of chironomids (Boroń and Grudniewski 1990, Grudniewski 1990, Wolnomiejski 1994). This fish was frequently found in the study site, even in the traps for sedimenting tripton, and those for catching migrating benthic invertebrates (Prus and Kajak 1999). Egg laying females and emerging imagos can also be eaten by swallows, great numbers of which, hunting for imagos, were observed at the reservoir.

5.3. THE TUBIFICIDAE

The abundance of *Tubificidae* was on the average high, but very differentiated both during the season and between years; occasionally it was very high – more than 400 thousands ind. m⁻² (Fig. 4). There was the clear positive correlation between the spring *Chironomus* peak and *Tubificidae* numbers during a month period after this peak, and also some slight correlation between these two groups during the whole vegetation season (Table 3). This probably was the reaction of *Tubificidae* for the “manuring” of the environment by *Chironomus* dying abundantly after its spring peak. The same phenomenon has been observed in the laboratory experiment (Kajak and Prus in press). Some authors do indicate strong quantitative dependence between these groups of animals both negative at very high densities (Yashouv 1970, Bakanov 1978, Marian and Pandian 1985) as well as positive (Kangur 1989, Wolnomiejski 1994).

Basing on correlations found between tubificidae abundance and *Chironomus* numbers and water flow a general regularity can be stated as follows: higher *Tubificidae* numbers correlate with high *Chironomus* abundance in spring and moderate water flow during whole vegetation season (Tables 2 and 3).

The pressure of fish on *Tubificidae* can be expressed by the ratio: individuals without the tail part of the body to total numbers of individuals (Kajak and Wiśniewski 1966). This ratio was very high in the studied reservoir – on the average about 80% of the population (fluctuating during the year between 60–90%). In several Masurian Lakes the similar ratio was found (up to 70–80%) in the littoral and sublittoral, but much lower (about 20%) in the deeper profundal where fish pressure was low (Wiśniewski 1978). The data on *Tubificidae* species composition, adults share and pressure of fish were supplied by R. Badałek (unpublished).

6. CONCLUSIONS

1. *Chironomus* numbers in the Ze-grzyński reservoir are often extremely high at the spring maximum caused by the new generation, in May–June. The high differences in the level of this peak observed in particular years (6–80 thousands ind. m⁻²) are probably

determined by the phytoplankton concentration (positive correlation with *Chironomus* abundance) and water flow (negative correlation) during few weeks before the appearance of the new *Chironomus* generation. Very high numbers of the spring peak are possibly also due to good oxygen conditions and to the relatively low fish pressure during a spawning period.

2. As a rule there is the second summer/autumn peak of abundance, usually much lower than the spring one. The main reason of this relatively low abundance is probably the much higher pressure of fish on *Chironomus* than in the spring. The strong fish pressure in this period has been confirmed in the field experiment (Prus unpublished). Also the oxygen conditions are usually worse in late summer than in spring.

3. The high spring *Chironomus* abundance undergoes the severe reduction (to the summer low numbers), probably mainly due to the increasing pressure of the mentioned biological factors. The reduction of summer-autumn peak is smaller, probably due to lower fish and birds predation and better oxygen conditions in the autumn than in mid-summer.

4. Two peaks of abundance do not mean two generations, as often interpreted by many authors. There are rather several generations impossible to delimitate due to the permanent presence of all instars, permanent emergence of imagos and egg laying, and the continuous strong pressure of predators. Summer/autumn peaks of abundance seem rather to result from the smaller pressure of predators and improved environmental conditions at the time they occur.

5. *Tubificidae* occur in very different numbers both during the year and between years. Their numbers correlate negatively with the flow of water during the season. *Tubificidae* react very positively on the “manuring” of the environment by dead *Chironomus* larvae after the high spring peak *Chironomus* numbers.

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7. SUMMARY

The abundance of *Chironomus plumosus* in the Zegrzyński Reservoir (Fig. 1) attains sometimes extraordinarily high values – up to 80 thousands ind. m⁻² and 1000 g m⁻². However it differs greatly in particular years (Fig. 2). The spring peak numbers, due to the mass appearance of the new generation, occur usually in June; in 9 years of studies they ranged from 6 to 80 thousands ind. m⁻². These high numbers are probably due to the comfortable environmental conditions like high oxygen concentrations due to flow of water and the shallowness of the reservoir (the efficient wave action), and abundant seston (with the high share of small diatoms) brought in by rivers, sedimenting to a great extent in the reservoir. The spring peak of *Chironomus* abundance was positively correlated with the chlorophyll concentration in the water and negatively with the flow of water (Table 1, Fig. 3). Water flow is favorable for *Chironomus* (assuring good oxygen conditions) at relatively low values, but disadvantageous above some critical value. Similar negative correlation of water flow and *Chironomus* numbers was also found for the whole vegetation season April–October (Table 2).

The spring peak of *Chironomus* abundance drops rather rapidly during June/July, probably due to predation by fish and intensifying mutual relations of growing larvae. For the same reason and perhaps also due to the short-term (up to few hours) oxygen deficits, numbers in the summer are relatively low, up to few thousands ind. m⁻². Young larvae are present all over the vegetation season proving the continuous reproduction; their numbers in summer are however relatively low. Their increase in the autumn is probably due to weaker predators pressure and better oxygen conditions, resulting from the lowered temperature. These increased numbers are however incomparably lower than that in June (Fig. 2), due to still existing pressure of fish and worse feeding (lower phytoplankton biomass – Fig. 3) and oxygen conditions in late summer/autumn than in spring.

The other main benthos component in the study area, the Tubificidae, show very different level of abundance as well as very different patterns of its changes in particular years (Fig. 4). Their average seasonal numbers negatively correlated with the average water flow (Table 2). The main correlation between *Chironomus* and Tubificidae abundance is the increase of abundance of the latter probably due to the “manuring” of the environment by abundantly dying *Chironomus* larvae, after their spring peak abundance (Table 3).

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