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TIME OF *CHIRONOMUS PLUMOSUS* (L.) GENERATIONS IN NATURAL CONDITIONS OF LOWLAND RESERVOIR

ABSTRACT: The time of *Chironomus plumosus* generation in the field conditions (shallow, eutrophic dam reservoir) was estimated to be about 3 weeks in the spring. This estimate has been possible due to simultaneous mass appearance of young larvae (the new generation) and the lack of older larvae at this time. Later in the season usually there was some amount of the youngest larvae, indicating the permanent emergence of imagos and the egg-laying, but without clear peaks of numbers and boundaries between successive generations. This regularity and the relatively low total numbers of larvae during the summer indicate the heavy fish pressure on the benthos, not allowing for the mass appearance of young larvae and the estimate of the generation time. Fish pressure is probably weak in spring, during a spawning period, but then increase in the summer.

The generation number could be theoretically as high as 5 during the vegetation season (May–October), assuming about 3 weeks for full larval development, as it was estimated at optimal feeding and oxygen conditions and low fish pressure in the spring. However some limiting factors like: oxygen deficits, the annoyance by fish and bestrewing of larval tubes with the mud transported by the water flow (range 150–500 $m^3 s^{-1}$ of the total inflow) increase in the summer. These factors can slow down larval development, resulting in observed lower generation number: 3 to 4 during a year.

KEY WORDS: *Chironomus*, population dynamics, generation time, growth limiting factors

1. INTRODUCTION

The aim of the studies has been to estimate the time of *Chironomus plumosus* development from the egg to the imago and also the number of generations during the vegetation season (April–October) in the field conditions of a lowland, eutrophic dam reservoir. *Chironomus plumosus* is one of the most important species in eutrophic water bodies outside littoral. It is relatively big (larva' length up to 30 mm) and it is important as a favourite food item for fish. Also its role in the exchange of substances between bottom deposits and the overlaying water is great, as far as larvae pump the water through their tubes in the surface layer of bottom deposits. These tubes are usually 10 cm deep, but sometimes as deep as 30 cm and more. The abundance of *Chironomus* waries enormously in different water bodies: from dozens individuals to about 100 thousands individuals m^{-2} (Sokolova, 1983, Armitage *et al.* 1995). Such high abundance occurs in the study area (the Zegrzyński dam-reservoir, Central Poland), making it the convenient place of the study on this species (Ooklińska 1989, 1992; Kajak and Dusoge 1996; Kajak 1997; Prus and Kajak 1999; Kajak and Prus 2000, 2001a,b, 2003).

The time of the development and the life-span of the generation, and consequently – the rate of the production of this important species is a subject of the discussion. Often the time of the generation is determined basing on number of peaks of the abundance. It is not the best method, as far as the peaks may result from various causes, like temperature and oxygen conditions, water flow, food availability, and predators pressure (Kajak and Prus 2003). In the present paper this problem will be more precisely discussed.

In this study two relatively original steps were taken to estimate the time of the generation: frequent sampling, and precise measurements of the length of larvae. Both are not often used in benthic studies.

2. STUDY AREA AND METHODS

The material was collected during 5 years (1993, 1996, 1997, 2000, 2001) in the centre of the middle, broad part of the Zegrzyński dam reservoir (Central Poland, 30 km from Warsaw), at the station about 5 m deep. The water flow in this part of the reservoir is slow, but occurs permanently, even at low total inflow to the reservoir (about 150 $m^3 s^{-1}$).

The reservoir is highly eutrophic or even hypertrophic, fed by two rivers (Bug r. and Narew r.) bringing continuously a lot of nutritious seston, sedimenting to a great extent in the reservoir (Kajak 1990a, b). One of the dominant (especially in colder periods of the year) components of the seston were small diatoms (Bubień 1989) – the favourite food for *Chironomus plumosus* (Armitage *et al.* 1995). The reservoir is polymictic due to its shallowness, and relatively large size (about 2×4 km) of its broad part, where the study site was located. This guarantees generally good oxygen conditions at the bottom. Nevertheless short periods (few hours) with some oxygen deficit happen occasionally, especially at nights in the summer, after a period of a very hot and calm weather (Kajak 1997).

In the studied reservoir fish stock is very abundant. Dominant fish species are: bream, *Abramis brama* (L.), white bream, *Blicca bjoerkna* (L.), roach, *Rutilus rutilus* (L.), perch, *Perca fluviatilis* L., and ruff, *Gymnocephalus cernuus* (L.) (Boroń and Grudniewski, 1990; Grudniewski, 1990; Terlecki *et al.* 1990; Szlakowski and Wiśniewolski, 2001). The total fish biomass was estimated to be about 400–600 kg ha^{-1} (Sych 1997; Szlakowski and Wiśniewolski, 2001).

Samples were taken weekly (in 2000 and 2001 sometimes 2 times per week), or every 2–3 weeks (compare Figs 1–5). Each time 5–10 samples were taken with 20 cm^2 Kajak's core sampler. Samples were sieved on 0.25 × 0.25 mm mesh size sieve; this practically guaranteed the catching of all *Chironomus* larvae, including the youngest ones. After sieving the material was preserved in the 4% formaline solution (1993, 1996) or in 70% ethanol (1997, 2000, 2001). Larvae were measured with 1 mm accuracy.

3. RESULTS

In the early spring (April – early May) only grown up, big larvae occurred and only sporadically very few small ones, which probably overwintered. From these low numbers of larvae and consequently of imagos, the spring peak of larvae of the new generation appears in late May – early June. This peak is usually well pronounced, with numbers of larvae being the highest in the vegetation season. After the spring mass appearance the larvae grow rapidly and differentiate in size. The population soon becomes composed of larvae of various lengths (Figs 1–5).

The period between the spring peak of the youngest larvae and the time of the appearance of grown up larvae (above 20––22 mm), can be taken as the time of the generation, that is the time of the development from the egg to the imago. Pupae are very short living and most easily caught by fish, so they are only sporadically found in the collected material and can not be used as the indicator of the emergence time. Due to the relatively great size of the spring peak of the youngest larvae numbers, the clear timing of this peak, and practically lack of bigger larvae at that moment, one can roughly estimate the time of the generation. This estimation is based on the assumption that the pupation and emergence go undoubtedly simultaneously with the occurrence of the grown up larvae. Soon after the peak of the appearance of the youngest larvae the size composition of the population becomes to complicate, as far as the young ones grow in the differentiated rate, and the new young larvae continue to appear. This however does not hinder to estimate the time of the pronounced spring generation. In particular years the following estimates of the time of this generation could be done.

In the year 1993 (Fig. 1) the peak of young larvae was registered on 19 May their appearance probably began earlier (e.g. 12 May), as far as on 19 May quite big individuals (≥ 10 mm) in substantial numbers were noted. On previous dates of sampling

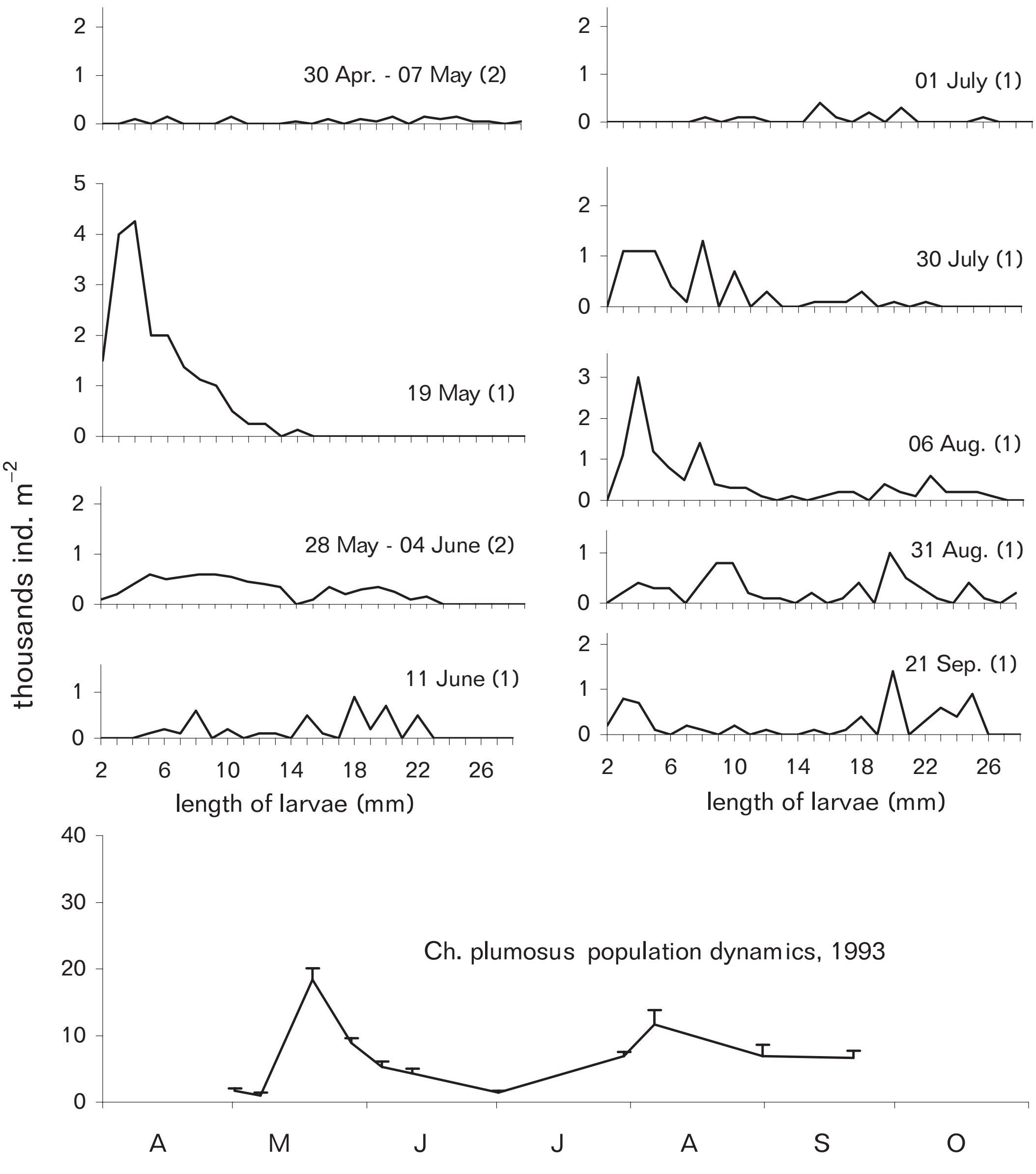

Fig. 1. Size structure of *Chironomus plumosus* larvae population in the Zegrzyński dam reservoir during the vegetation season (April–October) of the year 1993. The successive figures represent the periods with similar size structure of larvae (number of data series in brackets). At the bottom – the population dynamics of *Ch. plumosus* in 1993 is given (total numbers + standard error).

(the end of April and the beginning of May) only single specimens of this size (probably the ones from the previous autumn) occurred sporadically. Big specimens (≥ 20 mm), present at these dates, were completely absent on 19 May, obviously due to previous emergence. The first big specimens (≥ 20 mm) of the new generation were noted on 28 May, that is in less than 3 weeks since 12 May. So at least for the great part of the population the generation time would be about 3 weeks.

In the year 1996 (Fig. 2) the spring peak of young larvae numbers was noticed on 5 June. First young larvae could appear few days earlier: between 30 May and 5 June. Big larvae (>20 mm) were registered on 3 July but they began to appear between 20 June and 3 July (e.g. 27 June). So the time of generation would be 3.5 weeks.

In the year 1997 (Fig. 3) the spring peak of the youngest larvae was registered on 28 May. It undoubtedly began not later than 21 May (till 28 May some larvae reached already the size of 12 mm). The biggest larvae (up to 25 mm) appeared on 20 June that is after a month, but big ones (> 20mm) occurred between 6 and 10 June. It means that the time of the full development of larvae, which grew most rapidly, could be not longer than 3 weeks.

In the year 2000 (Fig. 4) the distinct peak of young larvae appeared on 15 May with the biggest larvae 8 mm, so the real peak appearance of the youngest larvae could be a bit earlier – e.g. 10–12 May. The big larvae (≥ 20 mm) began to appear since 28 May, that is a bit more than 2 weeks since the appearance of first young ones. The generation time again was probably about 3 weeks.

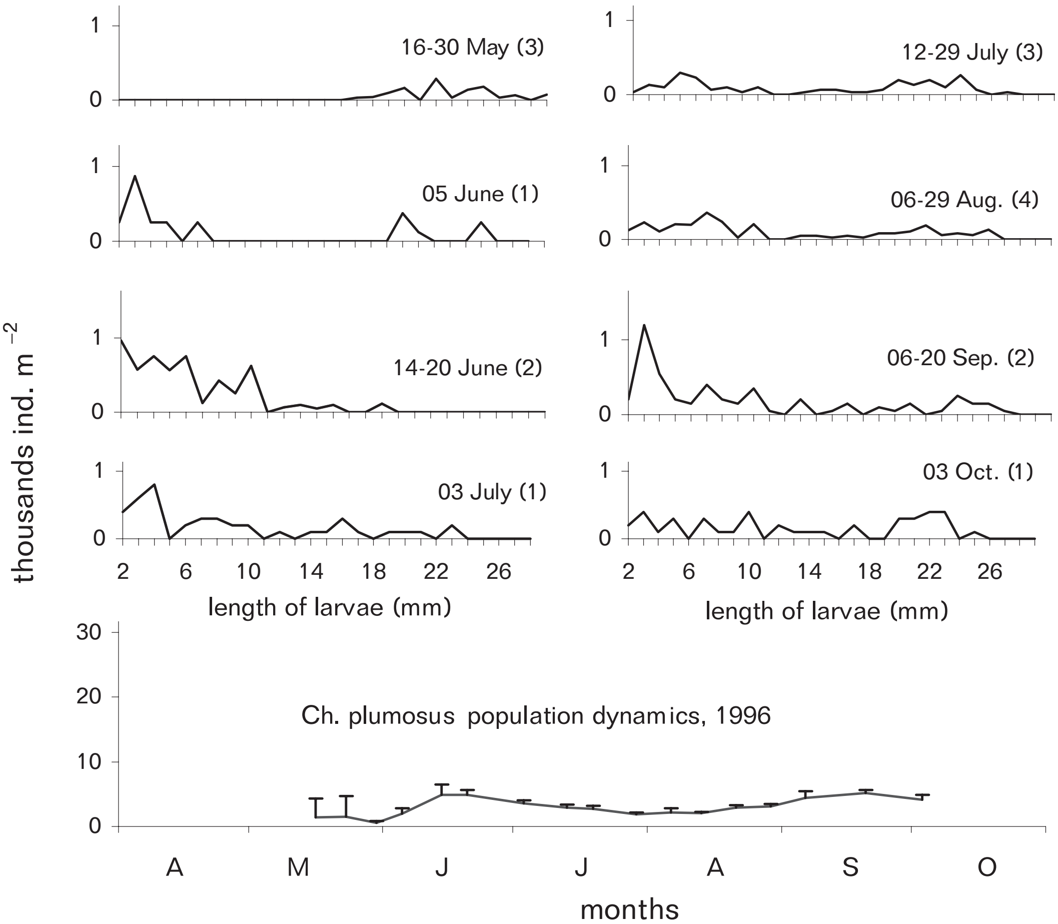

Fig. 2. Size structure of *Chironomus plumosus* larvae population in the Zegrzyński dam reservoir during the vegetation season (April–October) of the year 1996. Further explanations – see Fig. 1.

In the year 2001 (Fig. 5) the distinct peak of young larvae (2–3 mm) appeared on 17 May. The real appearance of the youngest larvae could began few days earlier (e.g. 14 May), because on 17 May some larvae of about 7–8 mm length were present. First big (≥ 20 mm) larvae from the new generation were registered on 31 May that is in about two weeks since the appearance of the new generation, but high abundance of grown-up larvae was registered on 12 June. It means that the time of the full development of larvae, which grew most rapidly, could be again not longer than 3 weeks. It must be stressed, that in the year 2001 the spring generation of larvae was very abundant, reaching over 40 thousands indiv. m^{-2} at the beginning of June. The mass appearance of the young larvae lasted from 17 May till 12 June, and than stopped, what coincided with the rapid decline of population numbers: from about 25 thousands indiv. m^{-2} on 12 June to about 7 thousands indiv. m^{-2} on 3 July (Fig 5).

Every year, after about 3–4 weeks since the spring peak of larval abundance, numerous pupal exuviae on the water surface and egg-carrying females above the water were seen. These observations confirm the above estimates of the generation time in spring, based on size structure of the *Chironomus* population.

During the summer larvae of all sizes occur all the time, making impossible to delimit particular cohorts. Distinctly more young larvae appear in the late sum-

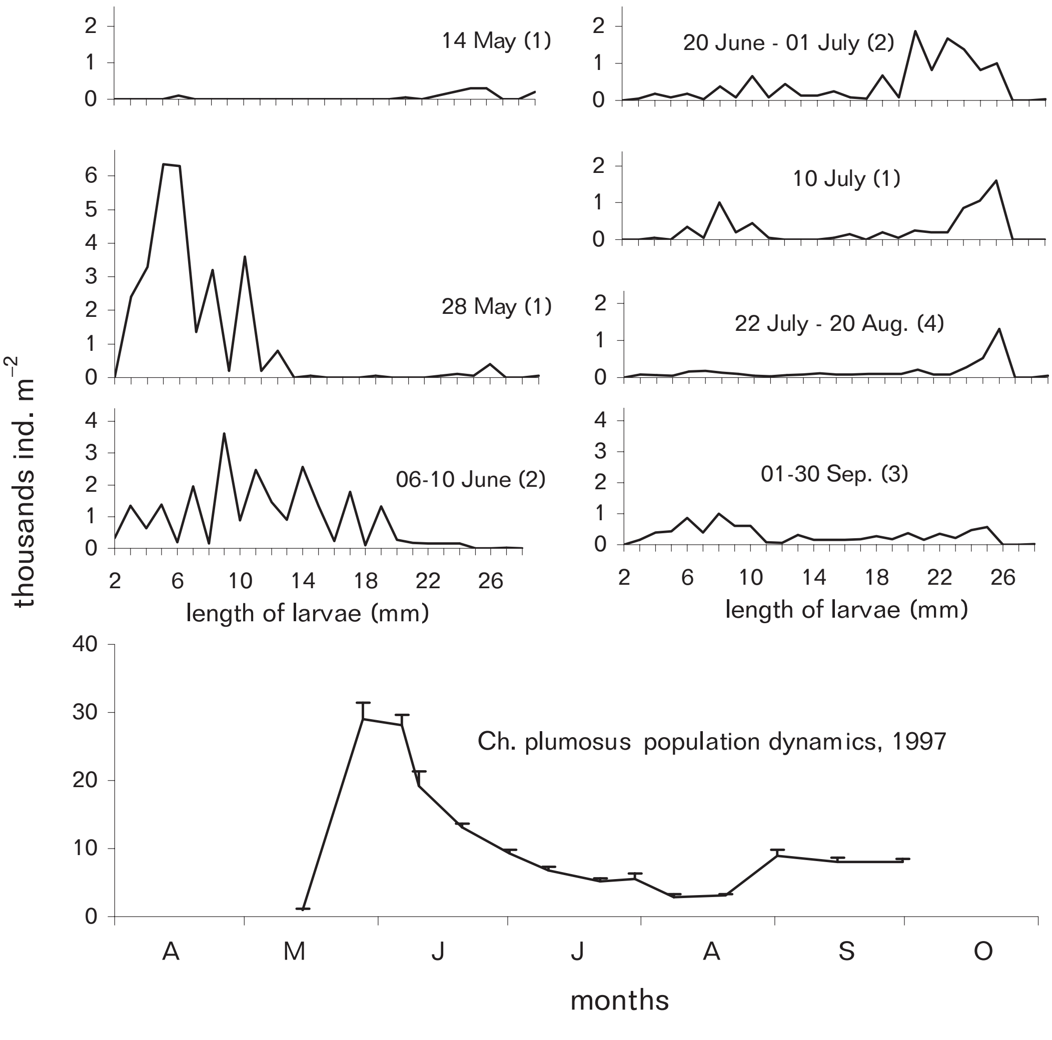

Fig. 3. Size structure of *Chironomus plumosus* larvae population in the Zegrzyński dam reservoir during the vegetation season (April–October) of the year 1997. Further explanations – see Fig. 1.

mer/autumn period, but here also, as in the summer, larvae of all sizes co-occur (Figs 1–4). The only exception from this regularity was the year 2001, when very low total numbers of larvae occurred from August till the end of October, with no late summer/autumn peak of abundance (Fig. 5). In this year there was also possible to delimit some cohorts of larvae during the summer. Young larvae occurred abundantly till 12 June, but the recruitment stopped between 18 and 29 June, and on 3–12 July almost only grown-up (18–26 mm) larvae were found. On 26–30 June two cohorts occurred simultaneously: grown-up ready to emerge larvae

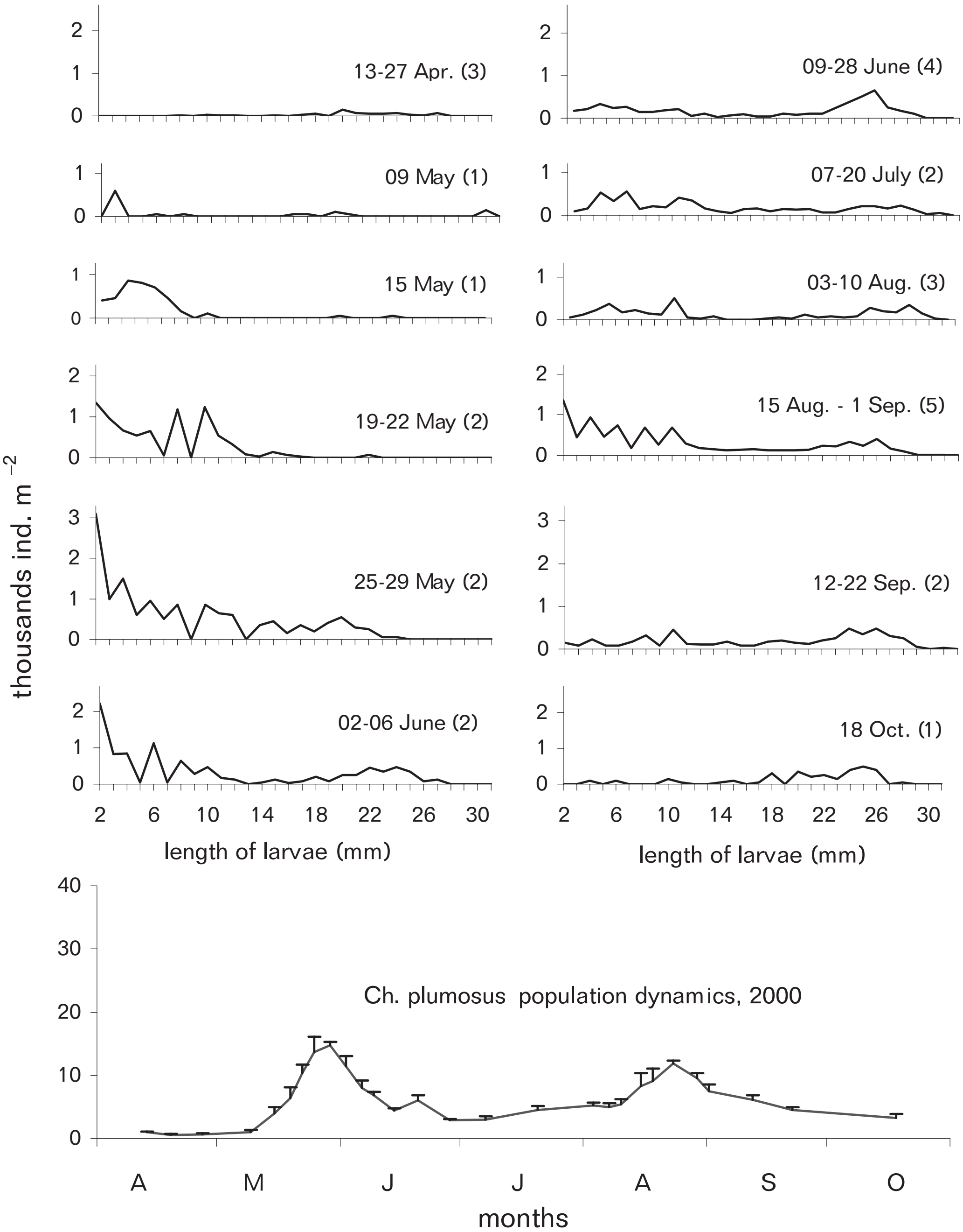

Fig. 4. Size structure of *Chironomus plumosus* larvae population in the Zegrzyński dam reservoir during the vegetation season (April–October) of the year 2000. Further explanations – see Fig. 1.

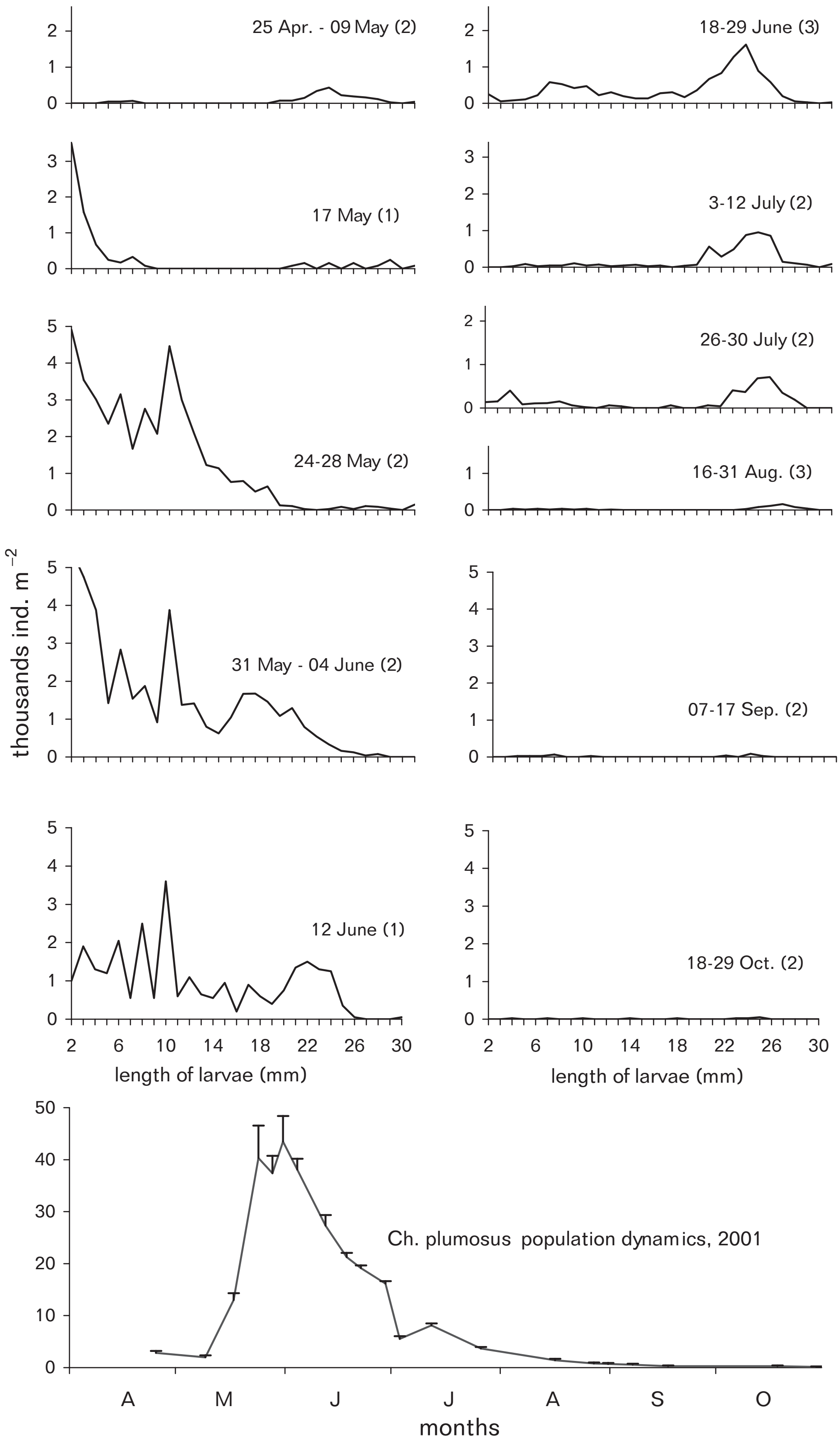

Fig. 5. Size structure of *Chironomus plumosus* larvae population in the Zegrzyński dam reservoir during the vegetation season (April–October) of the year 2001. Further explanations – see Fig. 1.

(20–27 mm) and young ones (≤ 10 mm) (Fig. 5). This indicates that emergence of the big larvae of the second generation started between 12 and 26 July, what allows to estimate the time of this generation to be about 5–6 weeks (since 12 June till 20–26 July). In the next 3 sampling dates (16–31 August) only big larvae (≥ 23 mm) were noted in very low numbers (Fig. 5). These larvae could be assumed as the third generation, which appeared about 20–26 July, and the time of their development could be estimated to about 5 weeks, as in the case of the second generation, described above. In September and October of 2001 the numbers of larvae were extremely low, what not allows to delimit generation time or any cohorts (Fig. 5).

The continuity of the occurrence of young larvae (up to about 10 mm) differed between years. In 1996 and 2000 these larvae occurred relatively abundantly during whole vegetation season (although the level of absolute numbers differed significantly between these years). It means that emergence and egg laying occurred also in the whole vegetation season (Figs 2, 4). In 1993 there were periods with no young larvae in July and August (Fig. 1), and in 1997 and 2001 during all the July and August young larvae did not occur or occurred in negligible numbers (Figs 3, 5). So obviously the intensity of reducing mechanisms differed essentially both between years and during the vegetation season. The continuance of the occurrence of young larvae during the vegetation season was noted in years with the low spring peak abundance of *Chironomus i.e.* in 1996 and 2000 (Figs 2, 4). The disrupted occurrence of young larvae was noted in years with the relatively high spring abundance of the population i.e. in 1993, 1997 and 2001 (Figs 1, 3 and 5).

4. DISCUSSION

The estimation of the rate of development and the generation time is relatively easy in laboratory conditions. Its transposition to field situation can be however the subject of criticism, as far as conditions in the field and in the laboratory (including feeding and physical – chemical ones, biocenotic influences etc.) undoubtedly differ seriously (Kajak and Prus 2000). Field circumstances are practically impossible to be fully simulated. That is why the estimate of the generation time in the field is so important. It is relatively easy in natural, field conditions under permanently low temperatures like in deep waters and in shallow ones of cold regions, where new generations appear simultaneously and the individuals grow slowly and relatively uniformly (Sokolova 1983; Armitage *et al.* 1995). This task is much more difficult in shallow habitats in temperate and warm climate. Usually the estimate of the time of the development in the field is based either on peaks of abundance of imagos or larvae, and on the materials not too frequently sampled. Only exclusively age/size structure of larval populations is taken into account (Sokolova 1983; Armitage *et al.* 1995). These approaches are often misleading, because numbers of larvae and imagines depend not only on numbers of eggs laid and the amount of emergences but also on many factors and mechanisms like: water flow, feeding and oxygen conditions, predation, other mortality factors and migrations (Kajak, 1997; Prus and Kajak, 1999; Kajak and Prus 2003).

The time of generation in the reservoir under study in the spring was estimated as close to three weeks. This occurred in almost optimal environmental conditions. Water temperature was as a rule high enough (about 20°C), the water flow not too high (about 200–300 $m^3 s^{-1}$ of the total inflow to the reservoir), but sufficiently refreshing the environment (Kajak and Prus 2003). The amount of sedimenting seston was also high and the percentage of small diatoms (the preferable food of *Chironomus*) in seston was higher than in the summer (Bubień 1989).

Later in the vegetation season the estimate of the generation time from the age structure has been usually impossible due to the permanent presence of larvae of various size. Also pupae and imagos were usually permanently present and egg laying females and egg masses were observed. The exception was the year 2001, when some estimates of the generation time in summer were possible due to interrupted occurrence of young larvae. Permanent, or at least frequent occurrence of the youngest larvae (as well as pupae and imagos) in relatively shallow (few meters) sites is common, although the youngest larvae often occur in very small numbers. This happens both at very low and very high total abundance (Giziński and Wiśniewski 1971; Malej 1974; 1977; Wiśniewski 1980; Matěna 1990; Iwakuma 1992; Nakazato and Hirabayashi 1998). Apart of that, usually one to three peaks of abundance are more or less distinctly visible.

Such peaks are often interpreted as the new generations however without the sound documentation (Giziński and Wiśniewski 1971, Janković 1971). It is possible that the number of generations, without clear peaks of abundance, can be higher. It may well be that long periods with low numbers of larvae (including the youngest ones) result rather from the strong fish pressure on various stages of *Chironomus* (larvae, pupae, imagos, eggs) in summer than from the prolongation of larval development, the lack of the emergence and egg laying. Peaks of numbers are often observed in the spring and autumn, sometimes even in winter (Frank 1982, Giziński and Wiśniewski 1971, Wiśniewski 1980), that is in periods with the weaker fish pressure and usually also the lower temperature. It would however be strange to expect that the lower temperature as such would stimulate the survival of the young larvae and the increase of the abundance.

Most important factors influencing the rate of the development of larvae and their generation time like the temperature and the food, were similar in the summer to that in the spring. The percentage of small diatoms in the summer was slightly lower than in the spring (Bubień 1989), however still high: about 50% of the phytoplankton biomass. The oxygen regime in summer could be worse than in the spring. Due to higher temperatures, the lower flow of water and occasional lack of wind, short time oxygen deficits in the summer occurred (Kajak 1997). As far as they are mostly occasional and short lasting (at nights), they should not increase seriously the time of the *Chironomus* development.

From other causes, which could influence the time of *Chironomus* development during summer, the activity of fish and near-bottom movements of water should be considered. The fish, apart from feeding on the benthos, can ”frighten” the larvae. This effect can be caused directly by penetration of the surface mud layer by fish, and indirectly – by physical and chemical information about the presence of fish, annoying the larvae and thus decreasing its time of feeding. This time is also decreased by bestrewing the tubes holes with mud and destroying the tubes, so the larvae must spend time and energy to rebuild them. Also the near-bottom flows of water can bestrew the tubes with the mud. The flows of water act all the season, but in the spring, when *Chironomus* larvae are very abundant (e.g. 30–40 thousands indiv. m^{-2} in the spring of 1997 and 2001 – see Figs 2, 5), their tubes often touch each other, forming the uniform, compact, tight ”carpet” (4–5 cm thick). Such ”carpet” undoubtedly reinforces the mud surface on the huge areas of the reservoir against resuspension.

So both the fish activity and movements of water (disturbing the mud surface) could prolong the time of the development of the larvae. This effect is probably stronger in the summer, when *Chironomus* population is less abundant, and is not able to modify the environment to such extent, as it is observed during the spring peaks of abundance. The main causes of the lower population abundance in the summer are probably: increased fish predation on *Chironomus* larvae and pupae after the spawning period and increased intra-specific competition between larvae of different size (Kajak and Prus 2003). Also abundant newly hatched fish population starts to feed on *Chironomus* larvae in the late summer (Terlecki *et al.* 1990) as well as new generation of birds (mainly swallows) starts to feed on imagos (Kajak, unpublished).

The time of development of the larvae from summer generations was estimated to be about 5 weeks, that is 2 weeks more than for the spring generation. This supports the above hypothesis about the prolonged *Chironomus* development in summer, however such estimation could be done only for the year 2001, when the recruitment of young larvae was not continuous (Fig. 5).

5. CONCLUSIONS

1. The most favourite period of *Chironomus* larvae development in the study site (considering the temperature, moderate water flow, and low disturbance of the mud surface) lasts from the middle of May till the middle of September, that is four months (about 120–130 days).

2. The time of the full development of larvae from the spring generation was estimated to be about 3 to 3.5 weeks (21–25 days). Such estimate has been possible due to simultaneous mass appearance of young larvae (the new generation) and the lack of older larvae at this time.
3. Under favourable conditions (like during the spring *Chironomus* peak) there could be theoretically up to five generations (compare points 1 and 2). It is rather high number if compared with the literature data (see Sokolova 1983, Armitage *et al.* 1995), but quite realistic one.
4. Some limiting mechanisms, like: oxygen deficits, various fish and birds pressure, mixing and resedimenting of bottom deposits, can slow down the rate of larval development in the summer, and then decrease the generation number.
5. In the reservoir studied there are probably four *Chironomus* generations during a year, out of five theoretically possible (in the favourable conditions). These are: the well pronounced and abundant spring generation (forming a uniform cohort), usually two less abundant summer generations (usually not clearly visible in population demographic structure), and the autumn generation (sometimes forming the second peak of abundance) which over-winters and emerges in the next spring.
6. The above estimation of *Chironomus* generation time and the number of generations during a year is a good basis for further studies of the production of this very important component of the benthos and fish diet in the studied reservoir.

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6. SUMMARY

The time of *Chironomus plumosus* (Diptera: Chironomidae) generation was investigated in natural, field conditions, in the shallow, eutrophic, lowland Zegrzyński dam reservoir (Central Poland), during five (1993–2001; Figs 1–5) vegetation seasons (April–October). Two steps were taken to estimate the time of the generation: frequent sampling (every one-two weeks) and precise (every mm) measurements of the length of larvae.

The time of *Chironomus plumosus* generation was estimated to be about 3 to 3.5 weeks in the spring (Figs 1–5). This estimate has been possible due to simultaneous mass appearance of young larvae (the new generation) and the lack of older larvae at this time. Later in the season there usually was some amount of the youngest larvae, indicating the permanent emergence of imagos and the egg-laying, but without clear peaks of numbers and boundaries between successive generations (Figs 1–4). Only in the year 2001 two summer generations could be distinguished, due to discontinuous recruitment of young larvae (Fig. 5). The relatively low total numbers of larvae during the summer indicate the heavy fish pressure on the benthos, not allowing for the mass appearance of young larvae and usually also for the estimate of the generation time. During the spring peak of Chironomus abundance the fish pressure is probably reduced, due to the spawning period.

The generation number could be theoretically as high as five during the vegetation season, due to good oxygen and feeding conditions in the reservoir. However the annoyance by fish and bestrewing of larval tubes with the mud transported by the water flow, which slows down larval development, results in lower generation number. In the reservoir studied there are probably four generations of *Chironomus* during a year (out of five theoretically possible): the spring generation, two summer ones and the autumn generation, which over-winters.

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