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RESPONSE OF CHIRONOMIDS (CHIRONOMIDAE, DIPTERA) TO DAMMING. PRODUCTION

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Summary: Chironomid production was estimated at two sites of the 7th order lowland Warta River: upstream (WAA) and downstream (WAB) of the Jeziorsko Reservoir over two annual periods. The first of them was chosen soon after the reservoir was filled in with water (1988/89) and the other one several years later, when the hydropower station was put into operation (1995/96). At the beginning of the dam's functioning the pattern of chironomid spatial distribution and production was similar at both sites reaching 2.295 g m^{-2} y^{-1} at WAA and 2.957 g m^{-2} y^{-1} at WAB. Later on periodical discharge manipulation resulted in its summer mean being reduced below the median level downstream of the dam. One of the results of this manipulation was alternate reduction and enlargement (by exposing of bottom to air) of the shoreline region at WAB. Thus, many chironomid species were eliminated and only two large sized Chironomini species were able to exist at this habitat (*G. gripekoveni* and *C. riparius*) – chironomid production decreased. The other result was development of macrophytes (Potamogeton) in the habitat located several meters from the banks; they appeared to be responsible for substantial increase in abundance of periphyton scrapes (Cricotopus) and their predators (*P. arcuatus*). Due to Potamogeton the retention of FPOM also increased and consequently the production of two pelophilous Chironomini forms *G. gripekoveni* and *C. riparius*. Finally the outcomes of these mechanisms, which operate in opposite directions, equalled – chironomids again reached similar productions at both sites, but at higher levels than during the first period (at WAA – 6.460 g m^{-2} y^{-1} and at WAB 7.508 g m^{-2} y^{-1}).

Key words: dam reservoir, river, Chironomidae, production

INTRODUCTION

The damming belongs to this kind of river regulations which has great effect on river biota [Ward and Stanford 1980, Armitage 1987, Troelstrup and Hergenrader 1990, Blinn and Cole 1991, Moog 1993, Brusven *et al.* 1995, Nyman 1995, Stevens 1997]. Two primarily physical effects of dams on downstream waters are: alternations of natural temperature and flow regimes [Robinson *et al.* 2003]. These and other effects of this kind of impoundments are rather well known, but better understanding of cause-and-effect relationships is needed [Allan 1995]. In particular, paucity of knowledge both in abiotic and biotic mechanisms controlling riverine macroinvertebrate productivity in large rivers is stressed. According to Benke *et al.* [1988], Benke [1993] and Shieh *et al.* [2003] macroinvertebrate production may be a useful means to estimate changes in benthic assemblages in response to the environmental stresses.

Huryn and Wallace [2000] stated that annual production of macroinvertebrate communities in streams world-wide ranges from approximately 10^0 to 10^3 g dry mass m^{-2} y^{-1}. Diptera, especially Chironomidae, usually contribute most to total macroinvertebrate production in lotic habitats [Lindegaard 1989, Morin 1997, Meyer and Poepperl 2003, Shieh *et al.* 2003]. Midges have two peaks in frequency distribution: one representing less than 2 g dry weight m^{-2} y^{-1}, and the other between 8-32 g dry weight m^{-2} y^{-1} [Tokeshi 1995]. Values exceeding the upper limit of this range are rare in river; Benke [1998] estimated dipteran production at 65 g m^{-2} y^{-1} at snag surface in a six-order stream of the subtropical Ogeechee River. Undoubtedly, however, the highest production value for one species of Chironomidae, *Orthocladius (E.) calvus* Pinder, 34.2 g dry weight m^{-2} was recorded over only 37 days at a temperature of 10.5°C; however, this occurred in an artificial recirculating channels, soon after filling it in with water [Ladle *et al.* 1985]. In terms of productivity the natural reach of the alluvial Warta River, backwater of the dam, belonged to the first group sensu Tokeshi [1995], Grzybkowska *et al.* [1990].

The main purpose of this paper is to show the influences of the lowland Warta River damming on riverine chironomid secondary production after over 8 years, but only several months soon after the hydropower station started functioning (1995/1996) and a comparison of this parameter with that estimated soon after damming the river (1988/89, [Grzybkowska *et al.* 1990]). The response of all macroinvertebrates, including the chironomids, to more constant environments downstream of the dam, was presented earlier [Grzybkowska and Dukowska 2001, 2002, Grzybkowska *et al.* 2003].

STUDY AREA

The Jeziorsko Reservoir, one of the largest reservoirs in Poland as regards its area (42.3 km^2 [Andrzejewski 1987]), impounds the 7th order lowland Warta River. This man-made reservoir began operating in 1986, but the hydroelectric plant „Jeziorsko" was completed later (September 1994). The present study was conducted in 1988/89 and 1995/96, which is 1.5 and 8.5 years after the reservoir had started functioning and, respectively, 6.5 before, and 0.5 years after hydroelectric plant was constructed.

The Warta River is 50-56 m wide at WAA (upstream of the Jeziorsko Reservoir's backwater), and 60-70 m at WAB (downstream of the Jeziorsko Reservoir's dam). Based on previous studies [Grzybkowska *et al.* 1990], we selected three habitats at each site: H_1 (WAA) and H_{11} (WAB) in the depositional area close to the bank, H_2 (from 1.5 to 7.0 m towards the mid-zone) and H_{12} (respectively 2.5 to 9.5 m) and H_3 and H_{13} in the mid-channel (Fig. 1). Habitat H_{11} may be called the „varial" zone because it enlarged and contracted in response to the dam operations. The inorganic substratum was mainly sand, except that at H_{12}, where gravel and pebbles were scattered. During the summer of the second period, small patches of *Potamogeton lucens* L. and large patches of *Potamogeton pectinatus* L. covered the riverbed at H_{12}; these plants used to appear in the river downstream of the dam only after the hydropower station started functioning. Further details of the habitats are given by Grzybkowska *et al.* [1990, 2003].

MATERIALS AND METHODS

Benthic samples from the five sampling habitats were collected in the Warta River monthly, in the morning, from April 1988 to March 1989 (I – the first period) and from April 1995 to March 1996 (II – the second one). Ten samples were collected with a 10 cm^2 (100 cm^2 of stream-bed area) tubular sampler at each habitat (H_n). The sampler was pushed into sediment to a depth of 15 cm and also through vegetation if it was present.

In each habitat (Hn) temperature, depth, current speed and area of the habitat were measured. Additional samples were taken to analyse the composition of particulate inorganic matter according to Cummins [1962] and amounts of benthic organic matter [Petersen et al. 1989]; these data are presented in earlier papers [Grzybkowska and Dukowska 2001, 2002].

The macroinvertebrates were hand-sorted in the laboratory, counted and preserved in 10% formaldehyde. Invertebrates were sorted from the detritus by hand and preserved in 10% formalin prepared with river water. Chironomids were identified to species on the basis of larvae (if possible) or imagines obtained from laboratory rearings. All animals were weighed using a Sartorius R 160 P. These data were then used to estimate biomass for given sampling habitats (H_n) and then recalculated for 1 m^2 of the total riverbed area, taking into account the proportion of given habitats.

The size frequency method of Hynes and Coleman [1968] as modified by Hamilton [1969] and Benke [1979] was applied; further details of the methods are given by Grzybkowska *et al.* [1990].

RESULTS

Abiotic parameters

During the first period (1988/89) the realised hydrological regime of the river downstream of the dam (WAB) was similar to the natural river section due to discharge manipulations occurring as the result of closing the dam's sluice for renovating the dam. In turn, during the second studied cycle (1995/96) flow regimes deviated from natural conditions – low discharge in the whole summer while high in September was observed. These changes in the flow regime downstream caused two processes. Firstly, the shoreline region of the Warta River enlarged and contracted in response to dam operations; the bottom was sometimes stranded (exposure to air). Secondly, low flow in summer made the riverbed at H_{12} covered by patches of macrophytes (*Potamogeton*) and *Cladophora glomerata* (L.) Kutz from end of May until August or September. The extensive surface area of the branched filaments of *C. glomerata* and macrophytes provided an excellent substratum for epiphytes and macroinvertebrates.

In the autumn rapid changes in flow associated with repeatedly released large volumes of water usually uprooted aquatic plants. The disturbance of sediment and subsequent washing out of particulate organic matter affected the distribution, composition and abundance of the zoobenthos; the larvae as well as their food were flushed downstream.

Benthic community

Biotic assemblages downstream changed in response to alterations in habitats resulting from changes in environmental conditions. During the second period many of ma-

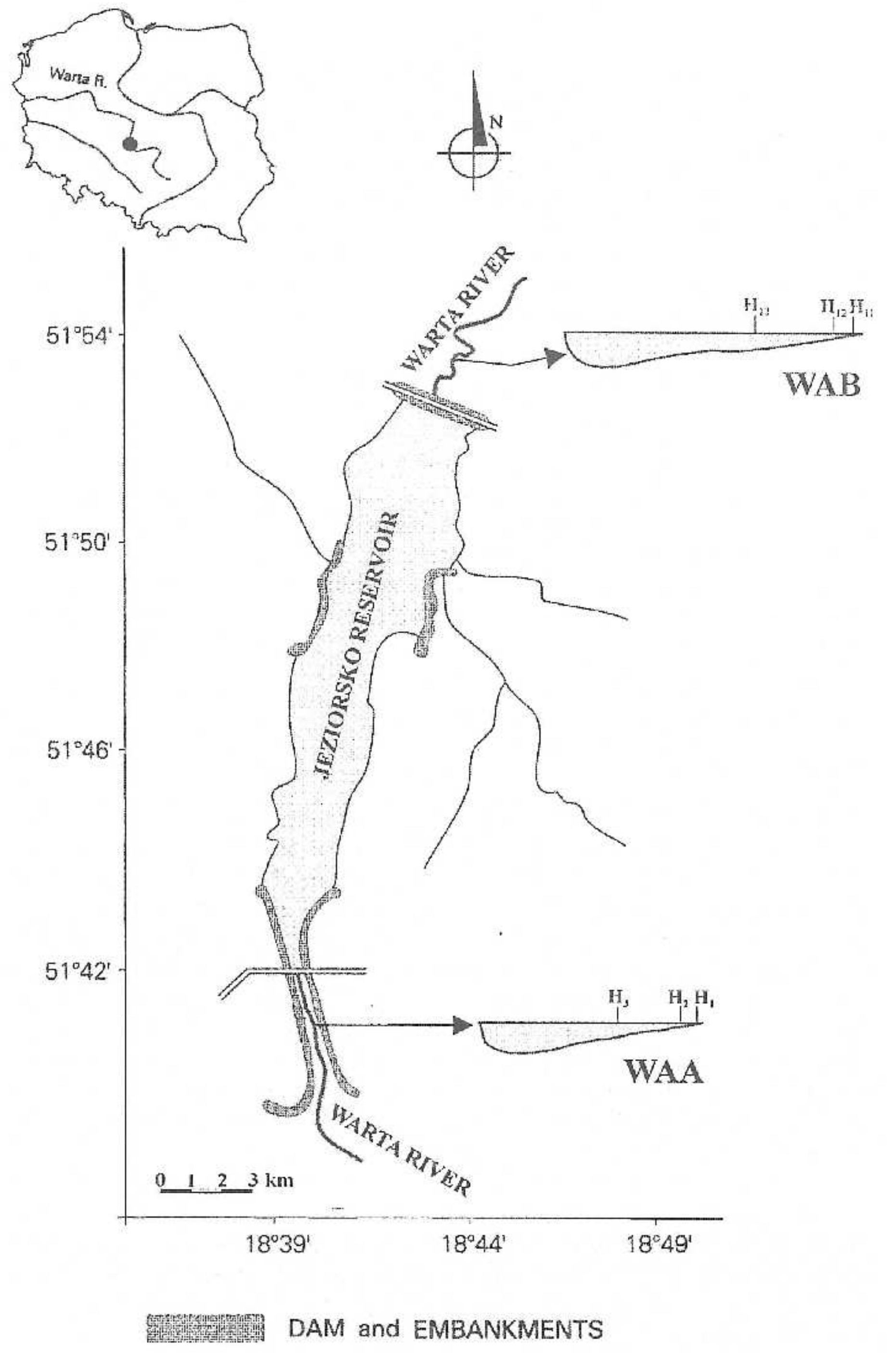

Fig. 1. Study area with the marked sampling sites
Rys. 1. Teren badań z zaznaczonymi stanowiskami badawczymi

croinvertebrates were gradually eliminated from the shoreline zone of the Warta River as the effect of regular exposure of the riverbed to the atmosphere (H_{11}, Fig. 2). In these conditions, with low oxygen and a large amount of fine particulate organic matter, only large size species of Chironomini (*Glyptotendipes gripekoveni* Mg. and *Chironomus riparius* Mg.) and Oligochaeta were able to exist.

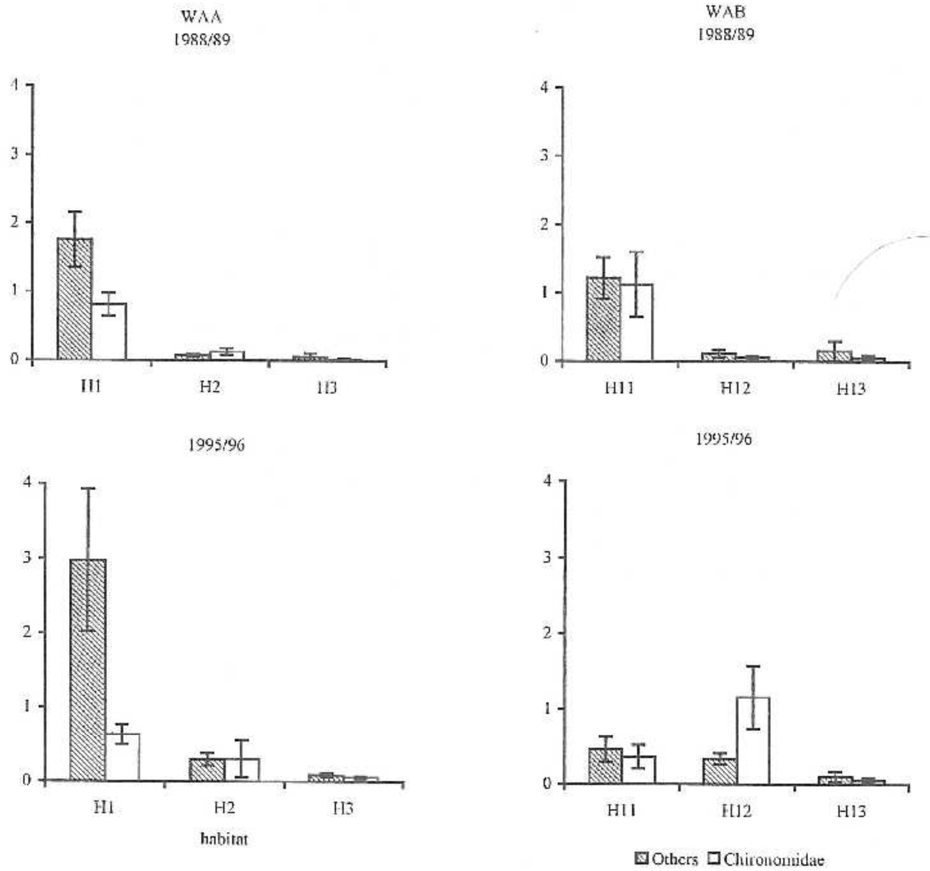

Fig. 2. Mean annual and standard errors of chironomid biomass and other macroinvertebrate biomass at the studied habitats of the two sites of the Warta River: upstream (WAA) and downstream (WAB) in the two sampling periods. Bars – the means with whiskers of standard errors

Rys. 2. Średnia roczna biomasa i błąd standardowy Chironomidae i innych makrobezkręgowców w badanych siedliskach na dwu stanowiskach Warty: powyżej cofki (WAA) i poniżej tamy (WAB) Zbiornika Jeziorsko. Słupki – średnie, wąsy – błędy standardowe

At the other habitat (H_{12}), with two species of Potamogeton, which appeared as the consequence of water management, macroinvertebrates were observed in high abundance. Firstly, as epiphytic fauna colonizing the macrophytes such as simuliids, caddisflies and mainly chironomids (small-size orthoclad larvae such as Cricotopus – scrapers and *Parachironomus arcuatus* Goetgh. Chironomini – predators), and secondly, thanks to the retention of FPOM due to filtration by a dense bed of macrophytes. This kind of habitat created favourable conditions for pelophilous, large sized taxa of *Chironomini* (*G. gripekoveni* and *C. riparius*). Thus in summer the macrobenthic abundance reached very high values (Fig. 2), but in September this community was destroyed – the aquatic macrophytes were washed away by the large releases of water from the reservoir.

Chironomidae also belong to the key groups of macroinvertebrates in the other habitats of the Warta River (Fig. 2). The pattern of their distribution was similar at anthropogenically disturbed site (WAB) in the first period and at nearby undisturbed section (WAA) in both periods – the absolute highest abundance of these midges were noted close to the river banks and decreased towards the mid-river (Fig. 2). However, the relative chironomid biomass in the total macrobenthos reached the highest values at H_2 (62.3%) and at H_{12} (77.4%); both findings were obtained during the second period.

Chironomid production

During the first investigated period the chironomid production at both sites, upstream and downstream of the dam reservoir, was similar both in terms of values reached at given habitats' sampling locations and recalculated for the total riverbed (Tab. 1, 2). However, during the second period the production increased: at WAA the production was higher in all habitats while at WAB the pattern of production distribution in the Warta River was not unequivocal (Tab. 1, 2).

Table 1. Biomass (B – g of dry weight) and production (P – g of dry weight m^{-2} y^{-1}) of the dominant Chironomidae species in three habitats (L_n) and recalculated for the site in the Warta River upstream of the backwater (WAA) in the two annual cycles
Tabela 1. Biomasa (B – g suchej masy) oraz produkcja (P – g suchej masy m^{-2} rok^{-1}) dominujących gatunków Chironomidae w trzech siedliskach (L_n) oraz przeliczona na stanowisko w odcinku rzeki Warty powyżej cofki (WAA) w dwóch cyklach rocznych

Habitat / Taxa	Year	H_1		H_2		H_3		WAA	
		B	P	B	P	B	P	B	P
C. riparius	1988	0.483	6.096	0.035	0.714			0.040	0.568
	1995	0.015	0.154					0.001	0.010
G. gripekoveni	1988	0.016	0.321	0.033	0.557	0.012	0.195	0.017	0.290
	1995	0.276	4.355					0.018	0.284
M. chloris	1988								
	1995	0.181	3.430					0.012	0.224
P. albimanus	1988	0.0003	0.018	0.012	0.384	0.006	0.185	0.007	0.222
	1995								
R. demeijerei	1988	0.0001	0.006	0.004	0.145	0.003	0.116	0.003	0.116
	1995			0.060	2.456	0.085	3.452	0.073	2.989
P. arcuatus	1988								
	1995								
P. confusus	1988	0.006	0.433	0.005	0.326			0.002	0.106
	1995	0.081	3.921	0.045	1.950	0.0001	0.019	0.016	0.735
C. bicinctus	1988	0.023	0.751	0.004	0.139			0.002	0.082
	1995	0.008	0.217	0.019	0.536	0.002	0.046	0.006	0.174
Others	1988	0.284	9.382	0.036	1.238	0.001	0.004	0.028	0.911
	1995	0.247	11.574	0.081	1.545	0.057	1.322	0.075	2.044
Total	1988	0.812	17.007	0.129	3.503	0.022	0.500	0.099	2.295
Total	1995	0.808	23.651	0.205	6.487	0.144	4.839	0.202	6.460

Table 2. Biomass (B – g of dry weight) and production (P – g of dry weight m^{-2} y^{-1}) of the dominant Chironomidae species in three habitats (L_n) and recalculated for the site in the Warta River below the dam (WAB) in the two annual cycles

Tabela 2. Biomasa (B - g suchej masy) oraz produkcja (P – g suchej masy m^{-2} rok^{-1}) dominujących gatunków Chironomidae w trzech siedliskach (L_n) oraz przeliczona na stanowisko w odcinku rzeki Warty poniżej tamy (WAB) w dwóch cyklach rocznych

Habitat / Taxa	Year	H_{11}		H_{12}		H_{13}		WAB	
		B	P	B	P	B	P	B	P
C. riparius	1988	0.154	1.815	0.014	0.163			0.016	0.189
	1995	0.263	2.706	0.232	2.374	0.005	0.054	0.079	0.816
G. gripekoveni	1988	0.913	11.339	0.005	0.145	0.0002	0.004	0.077	0.981
	1995	0.319	5.117	0.919	14.733	0.040	0.653	0.268	4.310
M. chloris	1988	0.024	0.443	0.001	0.022			0.002	0.042
	1995			0.002	0.038			0.0005	0.009
P. albimanus	1988	0.0005	0.023	0.013	0.453	0.012	0.480	0.011	0.436
	1995								
R. demeijerei	1988	0.0005	0.024	0.013	0.451	0.007	0.250	0.008	0.278
	1995					0.005	0.230	0.003	0.157
P. arcuatus	1988								
	1995			0.041	0.551			0.010	0.129
P. confusus	1988	0.006	0.323	0.0004	0.022			0.0006	0.032
	1995	0.001	0.050	0.020	0.991	0.003	0.140	0.007	0.331
Tanytarsus sp.	1988								
	1995			0.002	0.099			0.0005	0.023
C. bicinctus	1988	0.001	0.361	0.0001	0.004	0.0001	0.004	0.0002	0.034
	1995	0.001	0.036	0.005	0.148	0.004	0.117	0.004	0.117
C. sylvestris	1988								
	1995			0.062	1.810			0.014	0.422
Others	1988	0.023	0.700	0.014	0.450	0.037	1.172	0.030	0.964
	1995	0.062	1.036	0.167	3.615	0.039	0.385	0.071	1.193
Total	1988	1.122	15.028	0.060	1.710	0.056	1.910	0.146	2.957
Total	1995	0.646	8.945	1.450	24.359	0.096	1.579	0.458	7.508

At the bank zone of the upstream site the large size species of Chironomini (*C. riparius*, mainly in the first period and *G. gripekoveni* and *Microtendipes chloris* (Mg.) in the second one), small larvae of Tanytarsini (*Paratanytarsus confusus* Palmen mainly in the first period) and Orthocladiinae (*Cricotopus bicinctus* (Mg.)) contributed most to the production, i.e. between 44.6% of total chironomid production in the first period and 51.1% in the second one. The same chironomid species and additionally small size larvae of *Paratendipes albimanus* (Mg.) and the psammophilous form of *Robackia demeijerei* Krus. dominated at H_2. A relatively high contribution was made by *R. demeijerei*, as much as 23.2% of total production in the first period and 71.3% in the other one.

Absolute high value of chironomid production were noted at H_{12} (WAB) during the second period due to a numerous increase of two ecological chironomid groups: pelophilous and epiphytic ones (Tab. 2). The appearance of submersed macrophytes, in spite of their seasonal existence, caused the sixteen-fold increase in chironomid production over the whole period. In turn, elimination of many chironomid species from the bank zone of WAB (H_{11}) as a consequence of regular exposure of the riverbed to the atmosphere was the effect of the high relative contribution (over 87%) of two Chironomini species to the midge production. It is worth to note that the secondary production at the mid river bed at WAB was at the same level during the two studied cycles (Tab. 2). In spite of these two opposite tendencies at H_{11} and H_{12} the chironomid production recalculated for the whole examined riverbed of WAB at the second cycle was over three times higher than at the first one. The same growing trend with respect to the chironomid secondary production after years as at the „disturbed" site was observed at the natural one of the Warta River.

DISCUSSION

In river ecosystems, various bottom habitats (stony, muddy, sandy-gravely as well as those covered by macrophytes may be very productive [Mackey 1977, Waters 1977, Benke *et al.* 1984, Lindegaard *et al.* 1988, Lindegaard 1989, Lugthart *et al.* 1990, Berg and Helllental 1991, Tokeshi 1995, Benke 1998]. In the Warta River, the most productive were narrow bands along each bank; production decreases towards the mid-river zone. This trend was observed both in the upstream section, as well as downstream site in the initial period of the reservoir functioning [Grzybkowska *et al.* 1990]. The high diversity, abundance and production of zoobenthos close to the banks may be the effect of riparian vegetation, including a large amount of leaf litter [Brady and Cowell 2003], typical for large rivers [Cogerino *et al.* 1995]. And it was only the value of Chironomidae production close to the banks of the Warta that equaled the amount of energy produced in its tributaries, the Widawka and Grabia, in sections of more mosaic bottom and more covered by macrophytes [Grzybkowska 1989, Grzybkowska and Witczak 1990]. This pattern of chironomid distribution and production changed when the Jeziorsko Reservoir started functioning according to its purpose: water temperature became more constant while flow regimes deviated from the natural conditions. One consequence of water management were macrophytes that appeared in the Warta River. They provided more diverse habitats for macroinvertebrates (substrates for epiphytic food, refuges from predation and heterogeneous substrate for co-existence) and then supported higher secondary production in 1995-1996. Another consequence was simultaneously highly frequent exposition of the „varial" zone to the atmosphere, eliminated oxybiontic and rheophilous taxa from this area. These two processes counterbalanced each other and production calculated per entire river bottom while taking the proportions of given habitats into account reached values similar at both analysed river sites.

Taking into account given taxa the highest production was realised by Chironominae – Chironomini, large size species, such as *G. gripekoveni* and *C. riparius*; this was typical of lakes, particularly polluted, more rarely of rivers [Tokeshi 1995]. This rule was also confirmed in the Warta River where the highest productivity, exceeding even 50% of all Chironomidae, was estimated for *G. gripekoveni* and both in the initial period of the reservoir functioning [Grzybkowska *et al.* 1990] as well as later. Note that these high values were recorded mostly in the „littoral" zone. Other Chironomini may also make a high contribution to production despite considerably smaller sizes. These included a tiny psammophilous form *R. demeijerei*; as the sandy benthic habitat covered a large area of the Warta River this species may play a keystone role in energy or organic matter flow. It should be noted that one more Chironomini taxon, predatory *P. arcuatus*, was a species regulating density in this seasonal epiphyte community [Grzybkowska *et al.* 2003]. But all predators, including Tanypodinae, did not reach as high production as those in other anthropogenically disturbed stream sections [Whiles and Wallace 1995].

Chironominae – Tanytarsini were also small size species, but sometimes may have considerable importance for the over–all organic energy budget of the river. Very high production was estimated for *Micropsectra* (Tanytarsini) in a small lowland disturbed river, Bzura, over 5 g m^{-2} y^{-1} [Grzybkowska 1989]). In the Warta *P. confusus* was one of the dominant species, which reached the similar production in both river sites. Much higher values were obtained for the Tanytarsini from the stagnant waters [Tokeshi 1995].

Temperature may be a key factor for distribution of cold-stenothermic Orthocladiinae (algal grazers [Lindegaard and Brodersen 1995]); hence their low density in the Warta was understandable. One exception was an epiphytic form, associated with submersed macrophytes (*Potamogeton*), *Cricotopus sylvestris* (F.), which in a short period of this biocoenosis' occurrence was the major consumer (periphyton grazers [Grzybkowska *et al.* 2003]). But the respective values were not as high as they were in the sixth order stream river section, where small size orthoclad psammophilous taxa produced even up to 26 g m^{-2} y^{-1} [Benke *et al.* 1984].

The remaining subfamilies, Prodiamesinae and Diamesinae similarly as predatory Tanypodinae, were infrequent in the Warta River, and thus were not included in the tables. These taxa may sometimes contribute to high production in rivers. For one of the most common species, *Prodiamesa olivacea* Mg. (Prodiamesinae), connected with coarse organic detritus content in the sediments (frequently leaf packs of allochthonous origin), production estimated at favorable conditions was over 12 g m^{-2} y^{-1} (the Bzura River [Grzybkowska 1995]), although in smaller temperate streams the respective values were much lower, about 2 g m^{-2} y^{-1} [Lindegaard and Mortensen 1988, Bisthoven *et al.* 1992]. Results obtained in the Warta and its tributaries, the Grabia and Widawka [Grzybkowska and Witczak 1990, Grzybkowska 1995] and in other rivers [Smock *et al.* 1985, Petersen *et al.* 1989], prove that this kind of habitat was more stable in small than in large rivers. The dislodgement of leaf packs during high discharge periods does not favor its colonization inhabited even by slowly growing populations of large size shredders and collectors [Reice 1977].

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REAKCJA OCHOTKOWATYCH (CHIRONOMIDAE, DIPTERA) NA PIĘTRZENIE. PRODUKCJA

Streszczenie. Celem badań było oszacowanie struktury zgrupowania ochotkowatych i ich wtórnej produkcji ekologicznej na dwóch stanowiskach siedmiorzędowego odcinka rzeki Warty: 1,5 km poniżej tamy zbiornika retencyjnego Jeziorsko (WAB) oraz kontrolnego, 2 km powyżej cofki tego zbiornika (WAA). Badania przeprowadzono w dwóch cyklach rocznych: pierwszy w kilka miesięcy po napełnieniu zbiornika wodą (w cyklu rocznym 1988/89), a drugi kilka lat później, po uruchomieniu hydroelektrowni (1995/96). W początkowym okresie funkcjonowania zbiornika rozmieszczenie i produkcja ochotek były zbliżone na obu stanowiskach, osiągając 2,295 g m^{-2} r^{-1} na WAA i 2,957 g m^{-2} r^{-1} na WAB. W drugim okresie badań rytm uwalniania wody ze zbiornika różnił się od naturalnego, przede wszystkim latem; w okresie piętrzenia wody w zbiorniku (czerwiec–sierpień, początek września) upust wody z tamy był minimalny. Konsekwencją niskiego przepływu było: po pierwsze, odsłanianie dna strefy przybrzeżnej Warty z wysoką częstotliwością, a po drugie, rozwój zanurzonych makrofitów (od maja do września) kilka metrów od brzegu. Częściowe, ale intensywne opróżnianie zbiornika we wrześniu powodowało destabilizację tej biocenozy – następowało wymywanie lub zasypywanie roślin naczyniowych oraz zmywanie mułu wraz z żyjącymi tam makrobezkręgowcami.

Strefa przybrzeżna Warty poniżej tamy, ze względu na wahania poziomu wody, stanowiła bardzo specyficzne siedlisko; w takich warunkach były w stanie egzystować dwa pelofilne gatunki: *Glyptotendipes gripekoveni* i *Chironomus riparius*, reprezentujące grupę zbieraczy; produkcja ochotek w tej strefie wyraźnie spadła. Z kolei na dnie z rozwiniętą roślinnością zanurzoną (*Potamogeton*) produkcja była bardzo wysoka, a dominujące w faunie ochotki reprezentowały formy zeskrobujące naroślinny peryfiton (Cricotopus) i drapieżniki (*Parachironomus arcuatus*). Rozwój makrofitów spowodował również kumulację bentonicznej drobnocząsteczkowej materii organicznej (BFPOM) i w konsekwencji wzrosła produkcja dwóch pelofilnych ochotek, *G. gripekoveni* i *C. riparius*. W końcowym efekcie, mimo działania tych dwóch mechanizmów w dwóch przeciwstawnych kierunkach, produkcja ochotek po przeliczeniu na powierzchnię dna rzeki poniżej tamy osiągnęła podobną wartość (7,508 g m^{-2} r^{-1}) jak powyżej cofki (6,460 g m^{-2} r^{-1}).

Słowa kluczowe: zbiornik zaporowy, rzeka, Chironomidae, produkcja