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SMALL ASTATIC POOLS IN THE VICINITY OF MIKOŁAJKI AND THEIR CADDIS FLY (TRICHOPTERA) FAUNA

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ABSTRACT

Studies comprised 25 astatic pools in which 17 caddis fly species occurred. A single astatic pool should not be regarded as a uniform unit, but as a mosaic, a system of various habitats differing in the astacism and environmental conditions, characterised by zonation. The higher the astacism, the greater the individualism, and the more unique the faunistic character of these pools. This individualism results from fauna migration from the vicinal water bodies (permanent and temporary) via water or air, as well as from dying out of the fauna under adverse conditions due to yearly and many-years' astacism. It seems that the unstability, i.e. the astacism of the enviromental conditions in the many-years' cycle depends, among others, on the effect of cyclic and noncyclic climatic changes.

1. INTRODUCTION

Small astatic pools are a convenient subject of ecological studies owing to their small size and relatively great internal homogeneity (as compared with other water bodies with clear-cut zonation, e.g. lakes), with simultaneous richness of various types. The literature presents many papers dealing with different types of astatic water bodies, which take into account the period of water occurrence (Chodorowska, Chodorowski 1958, Paschalski 1959, Wiggins et al. 1980), trophy (Klimowicz 1959) and succession changes (Solińska 1963); moreover, the life strategies of organisms inhabiting these ponds (Chodorowski 1969, Klekowski 1959, Wiggins et al. 1980), and the biocenotic mechanisms (Chodorowski 1958, 1968) have been studied. So far, however, common nomenclature and a general theoretical model are lacking.

In years 1956–1958 complex studies of small astatic pools in the vicinity of Mikołajki (north-eastern Poland) were performed. These pools were investigated in the phytosociological aspect; (Solińska 1963), rotifers (Klimowicz 1967, 1970), dragonflies (Fischer 1959), molluscs (Klimowicz 1959) and Culicinae (Wojnarowicz 1960) were studied. Investigations were performed from the angle of typology of these pools, with stress laid on the yearly astacism. In the case of plants, the many-years' astacism was considered to an only small extent (Solińska 1963).

These studies were aimed at the determination of the species composition of caddis larvae of these water bodies, statistical verification of the significance of the differences between the pond types singled out, and verification of the applied terminology and typology of astatic (temporary) water bodies. Moreover, the goal of the studies was to construct a general theoretical model of astatic pool functioning.

2. MATERIAL AND METHODS

Caddis larvae were collected at more or less 2-week intervals between April–December 1956 and occasionally in 1957. Larvae were caught with a manual hydrobiological sampler with a triangular ring and tweezers, directly from the pool. Studies comprised 17 pools from which 1342 larvae were collected.

For statistical analysis, we also applied the data concerning rotifers (Klimowicz 1970), molluscs (Klimowicz 1959), dragonflies (Fischer 1959) and Culicinae (Wojnarowicz 1960). In total 25 pools were investigated. The faunistic similarity was calculated according to Jaccard's equation:

$$P_{xy} = \frac{c}{a+b-c} 100\%$$

where: p_{xy} – faunistic similarity between pools x and y,
c – number of species common to these pools,
a – number of species found in pool x,
b – number of species found in pool y.

Co-occurrence of species was calculated for 10 pools, in which all invertebrate groups were studied, also according to Jaccard's equation:

$$W_{xy} = \frac{c}{a+b-c} 100\%$$

where: W_{xy} – co-occurrence of species x and y,
c – number of pools in which species x and y occurred simultaneously,
a – number of pools containing species x,
b – number of pools containing species y.

DESCRIPTION OF POOLS (SAMPLING SITES)

Pool 1. „Huczkowy", field pool surrounded by fallow ground, on one shore – a poplar and willows. Substantial water level fluctuations; water completely disappears once per several years in summer, muddy bottom with detritus, completely overgrown with: *Sparganium ramosum, Carex stricta, Comarum palustre* and *Lysimachia thyrsiflora*. In 1956 the maximal length of the pool was 52 m, width 48 m, depth 1 m, area 700 m^2, volume 53.4 m^3. No complete drying out.

Pool 2. „Don Quichote's" – no data.

Pool 3. „Krzaczkowy", pool situated on a meadow; one part with a shore overgrown with alders and brush is a post-peat excavation. The second part is not shaded and is drying out. Disappears completely once per several years, bottom very muddy overgrown with: *Carex vesicaria, Glyceria fluitans, Lytherum salicaria, Alisma plantago aquatica, Polygonum amphibium* and *Lysimachia thyrsiflora*. In 1956 without complete drying out, maximal length 14 m, width 6 m, depth 0.78 m, area 29.4 m^2, volume 8.19 m^3.

Pool 4. „Gospodarski", outflow pool (to pool 8), situated between cultivated field and meadow. Small water level fluctuations, disappears once per several years. Bottom muddy, densely overgrown with: *Carex rudsoni, Comarum palustre, Polygonum amphibium* and *Typha latifolia*. In another part of the pool the bottom is overgrown with: *Equisetum limosum, Galium palustre* and *Iris pseudoacorus*. In 1956 without complete drying out, maximal length 110 m, width 50 m, depth 0.7 m, area 600 m^2, and volume 18.2 m^3.

Pool 5. „Szczawiowy", field pool, shaded, completely disappears in summer. On the bottom a thin mud layer, as well as branches and leaves. Poor vegetation, in the middle of the pool *Carex vesicaria* and *Carex alongata* tufts. In 1956 the pool once dried out in June for 17 days, maximal length 13.5 m, width 4 m, depth 0.6 m, area 22 m^2, volume 1.5 m^3.

Pool 6. „Rzęsisty", one of the larger pools is a woodland water body, does not disappear. Bottom without vegetation. In the middle — flowing islands and *Lemma minor, Bidens cernuus* and *Juncus* sp. In 1956 maximal area 1208 m^2, volume 106.8 m^3.

Pool 7. „Efemeryczny", field pool, bottom overgrown with grasses. In 1956 it dried out three times for a total period of 90 days, maximal area 51 m^2, volume 4.16 m^3.

Pool 8. „Trójkątny", flow-through field pool, pronouncedly astatic, sandy-muddy bottom, overgrown with: *Carex vesicaria, Equisetum limosum, Comarum palustre*. In 1956 it once dried out completely in June for 10 days. Maximal length 30 m, width 14 m, depth 0.6 m, area 216 m^2, volume 17 m^3.

Pool 9. „Chirocephallusowy" — flat depression among cultivated fields, in the middle part artificially deepened. Water disapears in the beginning of May and appears in autumn; in the deepened part it persists longer. The bottom is not muddy, overgrown with: *Polygonum hydropipe, Glyceria fluitans, Carex stricta, Agromyza reptans* and *Cirsium palustre*. In 1956 it dried out three times for a total of 99 days, maximal length 20 m, width 15 m, depth 1.25 m, area 217 m^2, volume 19 m^3.

Pool 10. „Zosinek" — no data.

Pool 11. „Stały", natural eutrophic field pool never disappearing, overgrown with tufts of: *Phragmites communis, Equisetum limosum, Elodea canadensis, Alisma plantago aquatica* and *Polygonum amphibium*. In 1956 the maximal length was 55 m, width 28 m, depth 2 m (minimal 1.7 m), area 1101 m^2, volume 97 m^3.

Pool 12. „Serdelkowy" — no data.

Pool 13. „Świerkowy", pool situated at a slope distant by 300 m from the Mikołajskie Lake. In 1956 it dit not disappear, whereas in 1957 it disappeared completely. Muddy bottom overgrown with: *Carex stricta, Carex vesicaria, Glyceria fluitans, Polygonum amphibium, Comarum palustre, Alisma plantago* and *Lemna minor*. In 1956 maximal length 22.5 m, width 7.5 m, depth 1 m, area 97 m^2, volume 7.8 m^3.

Pool 14. „Cyrkowy", woodland pool with daylong shadowing, small water level fluctuations, disappears once per several years. In 1956 it did not disappear. On the bottom abundant mud, leaves and branches. In the middle a small island with *Calla palustris*. In 1956 the maximal length was 29.5 m, width 16.5 m, depth 0.85 m, area 308 m^2, volume 30 m^3.

Pool 15. „Ósemkowy", flow-through pool situated on fallow ground, on the shore — alders and brush. Small water level fluctuations, bottom slightly muddy with *Carex vesicaria* and *Alisma plantago aquatica*. Brown colour of water. In 1956 the pond dried out in July for 3 days, maximal length 38 m, width 11 m, depth 0.7 m, area 242 m^2, volume 19 m^3.

Pool 16. „Olszynkowy", shallow pool often disappearing. On one shore — alders and brush. Bottom with a thick layer of leaves and branches, in some places overgrown with: *Carex vesicaria, Comarum palustre, Glyceria fluitans*. Sometimes freezes to the bottom. In 1956 it dried out for 50 days (June and July), maximal length 24 m, width 9 m, depth 0.27 m, area 138 m^2, volume 8 m^3.

Pool 17. „Sfagnusik" — no data.

Pool 18. „Turzycowy", field pool disappearing once per several years. Bottom with a thick layer of mud and detritus, overgrown with: *Carex stricta*. In summer the pool is almost completely shadowed by trees on the shore. In 1956 it did not disappear, maximal length 45 m, width 28 m, depth 1.45 m, area 965 m^2, volume 60 m^3.

Pool 19. „Osi", pool of the character of a natural dystrophic water body, situated on a forest clearing, never disappears. There occurs *Lemna minor*, on the bottom many rotting leaves and branches, poor vegetation in the shore zone. In 1956 maximal length 56 m, width 26 m, depth 1.8 m, area 1208 m^2, volume 147 m^3.

Pool 20. „Leśny", frequently disappearing water body in a forest. On the bottom – mud an rotting leaves, vegetation poorly developed, comprising: *Glyceria fluitans, Lysimacha thyrsiflora, Juncus conglomerans, Alnus glutinosa, Salix aurita*. In 1956 it dried out completely in June for 3 days, maximal length 28.5 m, width 12 m, depth 0.6 m, area 184 m^2, volume 15 m^3.

Pool 21. „Romantyczny", field pool disappearing once per several years, with shores overgrown with alder, completely shaded. It disappears several times per year, in 1956 for a total of 50 days. Water is brown, bottom covered with a big amount of mud and rotting leaves. Scarce plants: *Carex hudsoni, Carex elongata, Iris pseudoacorus*. In 1956 maximal length 34 m, width 11 m, depth 0.6 m, area 176 m^2, volume 13 m^3.

Pool 22. „Komarowy", steadily shaded woodland pool. On the bottom – mud, leaves and branches. Poor vegetation occurs on the shore: *Juncus conglomeratus, Lysimachia vulgaris, Lemna minor, Bidens cernuus, Salix cynerea, Epilobium montanum*. In 1956 the pond dried out three times for a total of 70 days, maximal length 44 m, width 9 m, depth 1.2 m, area 217 m^2, volume 18 m^3.

Pool 23. „Wulgarny", pool overgrown with grasses. In 1956 maximal area 100 m^2, depth 0.3 m, disappeared from June until November.

Pool 24. „Sarnie dołki", field pool overgrown with grasses. In 1956 maximal area 4 m^2, depth 0.2 m. Disappeared from June until November.

Pool 25. „Polny", eutrophic field pool.

3. RESULTS

A. CHARACTERIZATION OF THE DISTRIBUTION OF CADDIS LARVAE

In a material of 1342 larvae, 17 species were singled out (Table I). The eudominants comprised: *Limnephilus griseus* (27.4%), *L. rhombicus* (20.1%), *L. auricula* (19.4%) and *Holocentropus stagnalis* (14.8%). There was no class of dominants. Among subdominants, 4 taxa were observed: *Limnephilus sparsus* (?) (4.7%), *L. vittatus* (4.3%), *L. flavicornis* (3.4%) and *L.* sp. juv. (3.1%). The remaining 11 taxa belonged in recedents.

Most larvae were caught in spring, in April and May (Fig. 1). From June until October the numbers of Trichoptera larvae were very low. In November these numbers again increased. The number of species was greatest in November, April and May. The drop in the numbers and in the number of species in winter suggests dying out of Trichoptera fauna in this period (Fig. 1).

Pools 7 and 9 can be classed as belonging in the type of vernal pools; pool 9 contained, however, an artificially deepened part being of the nature of a permanent pool. This was probably the reason of the presence of *Hylocentropus stagnalis* and *Agrypnia picta* in this water body. When these corrections were taken into account, *Limnephilus griseus, L. auricula* and *L. rhombicus* could be assumed to be species characteristic of astatic pools of this type.

Pool 16 can be regarded as a vernal-autumnal water body. Apart from the species characteristic of the vernal type, there occurred: *Limnephilus flavicornis* and *L. marmoratus*.

Pools 5, 8 and 15 may be assumed to be intermittent water bodies (several

Table I. Caddis larvae of the astatic pools. *N* – number of specimens, *D* – dominance (%), *F* – frequency (%)

Taxon	*N*	*D*	*F*	Pools																
				1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Holocentropus stagnalis (Alb.)	199	14.83	8	28	36	11	73	1		1	48					1				
Agrypnia picta Kol.	2	0.15	1									2								
Limnephilus flavicornis (Fabr.)	45	3.35	8	3	1		7				5			3		12		8	6	
Limnephilus rhombicus (L.)	270	20.12	14	49	26	34	10	11	30	13	11		7		4	1	44	32		8
Limnephilus marmoratus Curt.	1	0.07	1																1	
Limnephilus decipiens (Kol.)	1	0.07	1	1																
Limnephilus griseus (L.)	367	27.35	12	2	7	5	60	24	5	61	101	49	15		3			35		
Limnephilus vittatus (Fabr.)	58	4.32	4				2				23		29					4		
Limnephilus sparsus (?) Curt.	63	4.69	2				56								7					
Limnephilus auricula Curt.	260	19.37	8	3		22	44	10		3	7	41						130		
Limnephilus borealis (Zett.)	4	0.3	2	1													3			
Nemotaulius punctatolineatus (Retz.)	4	0.3	1											4						
Glyphotaelius pellucidus (Retz.)	3	0.22	2					1							2					
Grammotaulius signatipennis McLach.	6	0.45	4		1		2				1							2		
Halesus sp.	8	0.6	2				1							7						
Limnephilus sp. juv.	41	3.06	3	7	30													4		
Limnephilidae indet.	6	0.45	2	5												1				
Oecetis furva (Ramb.)	1	0.07	1											1						
Triaenodes bicolor (Curt.)	3	0.22	1											3						

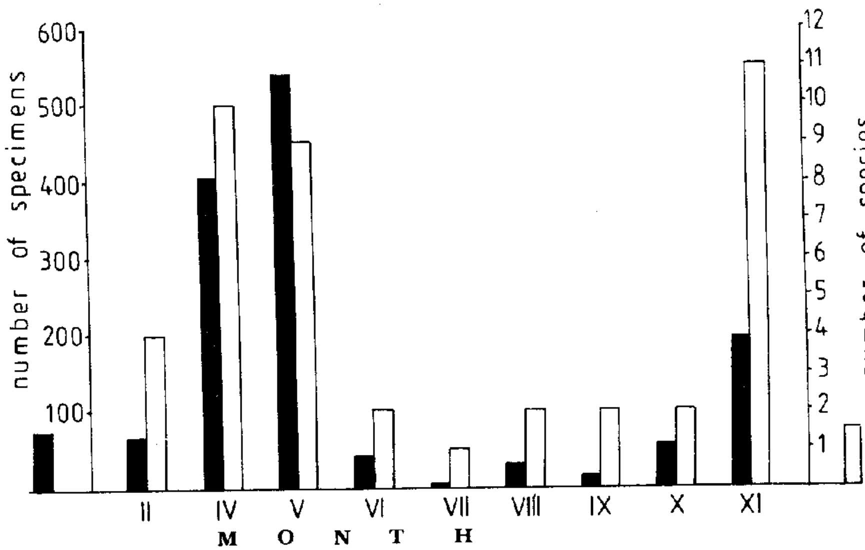

Fig. 1. Changes in the numbers and number of species of caddis larvae in the yearly cycle

days without water). Apart from the above-mentioned species from the more astatic pools: *Limnephilus griseus*, *L. auricula*, *L. rhombicus* and *L. flavicornis*, there occurred: *Limnephilus vittatus*, *L. sparsus* (?), *L. borealis*, *Holocentropus stagnalis* and *Glyphotaelius pellucidus*, which are doubtless elements of more static and stable habitats.

In the permanent pool 11 and pool 4 with stability properties, apart from the species found in astatic waters, there occurred: *Nemotaulius punctato-lineatus*, *Halesus* sp., *Oecetis furva* and *Triaenodes bicolor*, and frequently *Holocentropus stagnalis*.

Moreover, we analysed the species composition of caddis larvae in pools of two succession series: long succession series typical of deep water bodies, characterized by the succesion of *Caricetum elatae* after communities from the *Eu-Potamion* and *Phragmition alliance*, as well as a short succession series typical of shallow water bodies, which leads to *Caricetum vesicariae*, with omission of the *Caricetum elatae* stage; both series have three developmental phases: early, transitional and late (Solińska 1963). The early phase of overgrowth is characrerized by a lack of vegetation in the middle part of the water body and by occurrence of fragments of communities from the *Eu-Potamion* and *Phragmition alliance*. Pools in the transitional phase of overgrowth displayed the most developed zonation. Pools in the late phase of overgrowth were most often completely dominated by communities of big sedges (*Caricetum elatae* and *C. vesicariae*).

Limnephilus griseus and *L. auricula* occurred in both series and in all phases. *Limnephilus flavi-cornis* and *L. rhombicus* did not occur in water bodies in the early phase of the succession series. *Holocentropus stagnalis* did not occur in water bodies in the late phase of the short succession series. *Limnephilus* *vittatus* and *Grammotaulius signatipennis* appeared in the late phase of the long series and in the transitional and late phase of the short series.

Limnephilus sparsus occurred in the late phase of the long succession series. *Nemotaulius punctatolineatus*, *Oecetis furva* and *Triaenodes bicolor* appeared in the permanent water bodies in the early phase of the long series.

It was found that the more permanent the water body, the richer the caddis larvae fauna; furthermore, the more the water body is differentiated in habitats (in time and space), the greater the number of species. Species of pronouncedly astatic waters (vernal water bodies) occurred also in the more permanent pools. Prolongation of the waterless period gradually eliminated the occurrence of some species.

B. ANALYSIS OF THE FAUNISTIC SIMILARITY OF POOLS

Faunistic similarities of all pools were analysed for each animal group separately.

Rotatoria

Pools 11 (permanent), 14 and 15 (dystrophic) distinctly departed from the

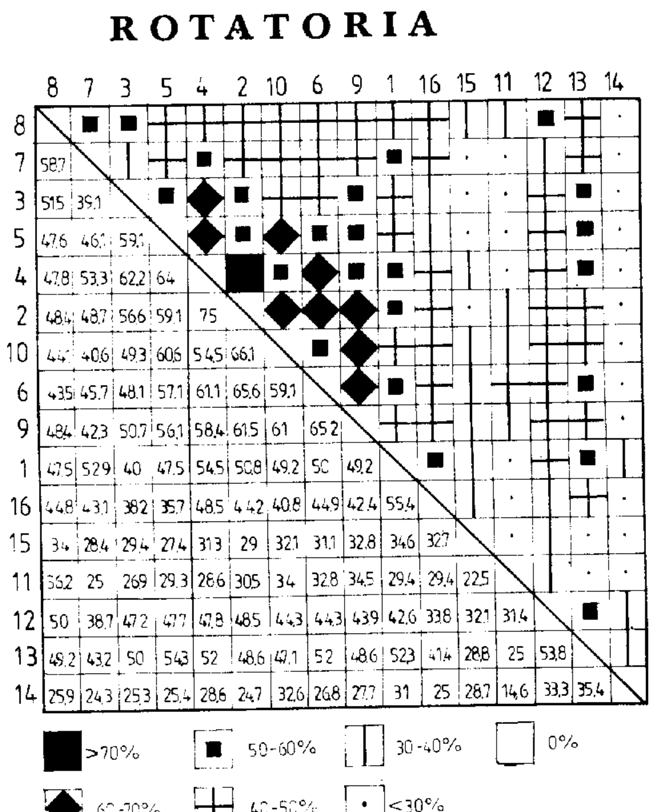

Fig. 2. Diagram of the similarities between astatic pools, calculated on the basis of rotifers

other ones. The remaining pools were similar in the similarity class above 40%. In the similarity class above 60 % there occurred many pools: 3, 5, 4, 2, 10, 6 and 9, and in the similarity class above 50 % also pools 1 and 13 (Fig. 2). We found no consistence between so distinguished the groups and the general limnological properties of these water bodies.

Mollusca

Three groups of pools were singled out. The first comprised: field pools 1 and 18, woodland pool 15, and field pools 8 and 4 (Fig. 3). The second group included the woodland pools 25, 5 and 3. Both these groups of pools link because of the similarities between pools 15, 8 and 4, on one hand, and pools 5 and 3, on the other. The third group comprised pools: 13, 5, 21, 14; it linked with the second group because of the similarity to pool 5.

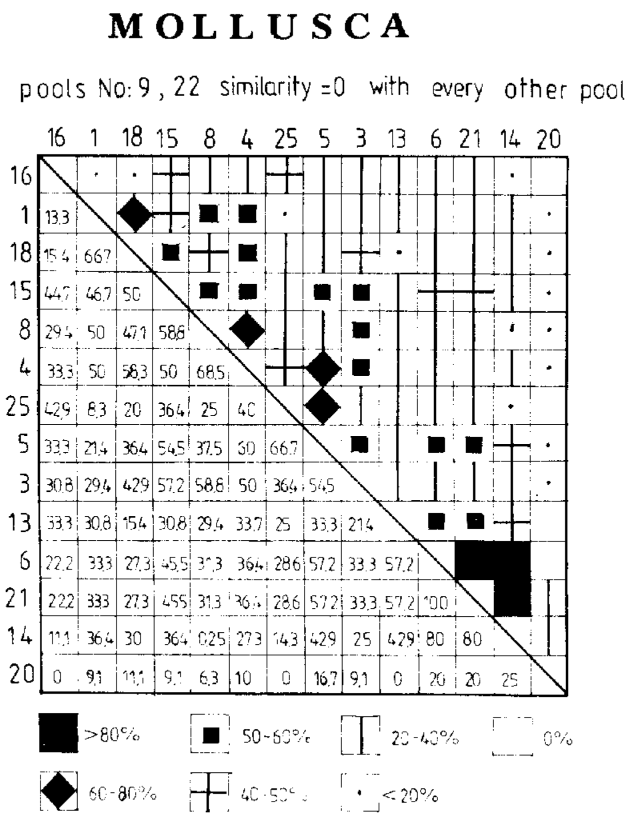

Fig. 3. Diagram of the similarities between astatic pools, calculated on the basis of molluscs

Culicinae

A group including field pools: 1, 18, 3, 16, 4 and 9 (Fig. 4) stood out very distinctly. This group of pools linked with the group arranged in a continuum of similarities: 11, 13, 6, 21, 5, 8, 18, 1, in which the water bodies changed from woodland pools through pool 5 (field pool with shore overgrown with trees) to field pools. This transitional character of changes in Culicinae fauna suggests the occurrence of gradual, gradient changes in the environment (e.g. illumination, pH, temperature etc.).

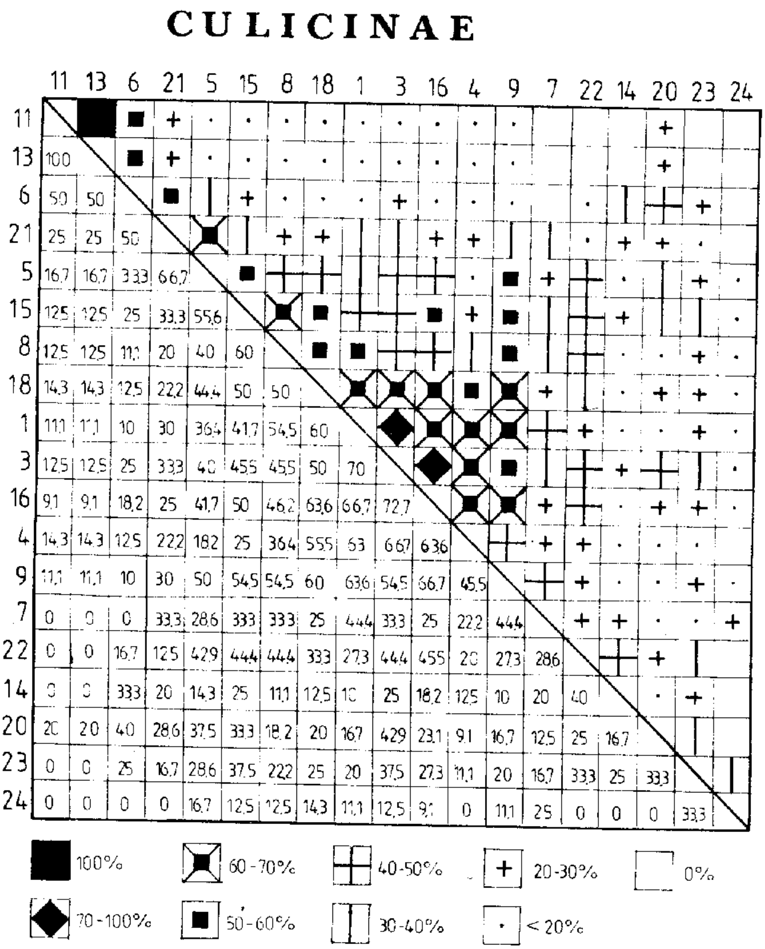

Fig. 4. Diagram of the similarities between astatic pools, calculated on the basis of Culicinae

Odonata

We observed relatively low faunistic similarities among pools, and high specificity of the species composition of dragonflies (Fig. 5). Pools 7 and 22 formed a distinct group of vernal, pronouncedly astatic pools. Pools 8, 9 and 3 made up a group comprising field pools overgrown with sedges. The third group of pools was of the character of a continuum with decreasing similarities: pools 1, 4, 18, 15, 11, 6 (this group somewhat resembles the first group singled out on the basis of similarities in the mollusc fauna). These water bodies varied from eutrophic and flow-through pools to dystrophic and permanent ones.

Trichoptera

Also on the basis of this group of animals we found relatively low faunistic similarities among the investigated pools (Fig. 6). There stood apart a group of dystrophic woodland pools (13, 17, 6) and two groups: 3, 7, 5, 12 and 8, 4, 2, 25, which comprised pools of different types.

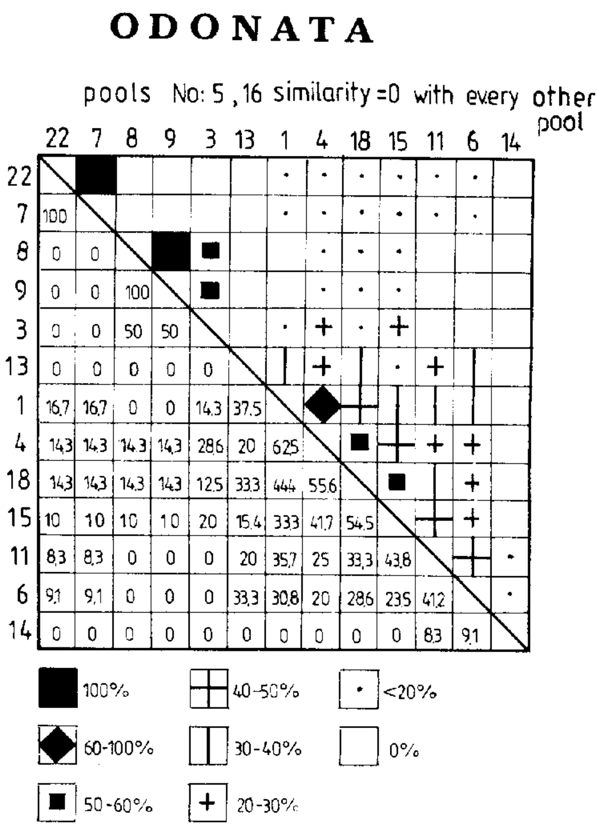

Fig. 5. Diagram of the similarities between astatic pools, calculated on the basis of dragonflies

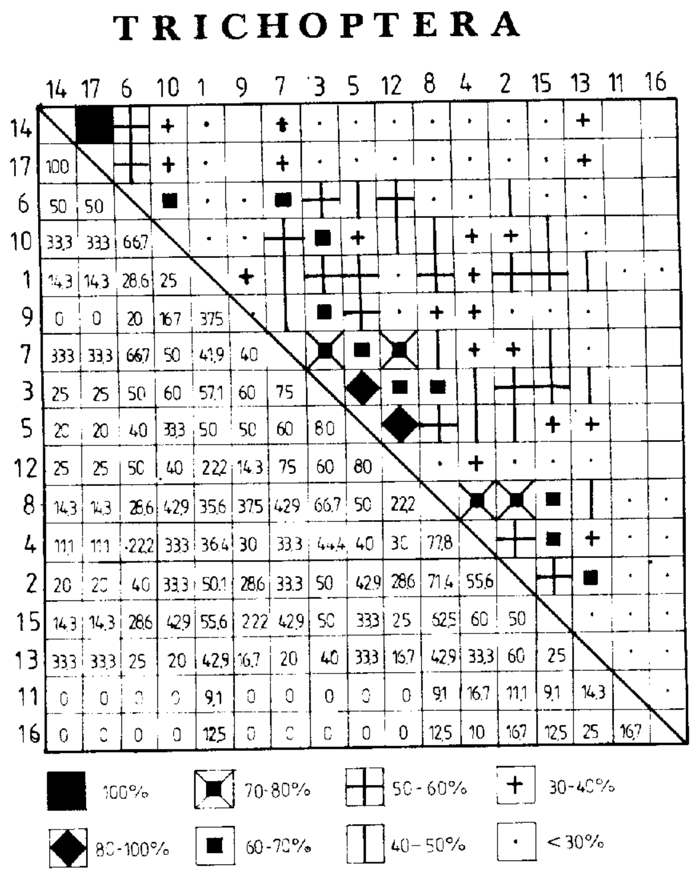

Fig. 6. Diagram of the similarities between astatic pools, calculated on the basis of caddis larvae

General similarities

We selected 10 astatic pools in which molluscs, dragonflies, Culicinae and caddis larvae occurred simultaneously. Subsequently we calculated the faunistic similarities among these pools, considering all groups of animals simultaneously. From the faunistic stanpoint, pool 9 (lowest similarities to the remaining ones) distinctly deviated; it was a vernal pool (Fig. 7). Moreover, there stood out two groups of pools which – owing to the similarities to pool 16 – were interrelated: 13, 14, 15, 16 and 4, 8, 5, 1, and 3.

We found a high individualism and uniqueness of the species composition of these pools, with a simultaneous lack of clear-cut faunistic boundaries (species composition) between single pools and types of astatic pools. The investigated water bodies assumed a different grouping in the analysis of faunistic similarities calculated for each group of invertebrates separately.

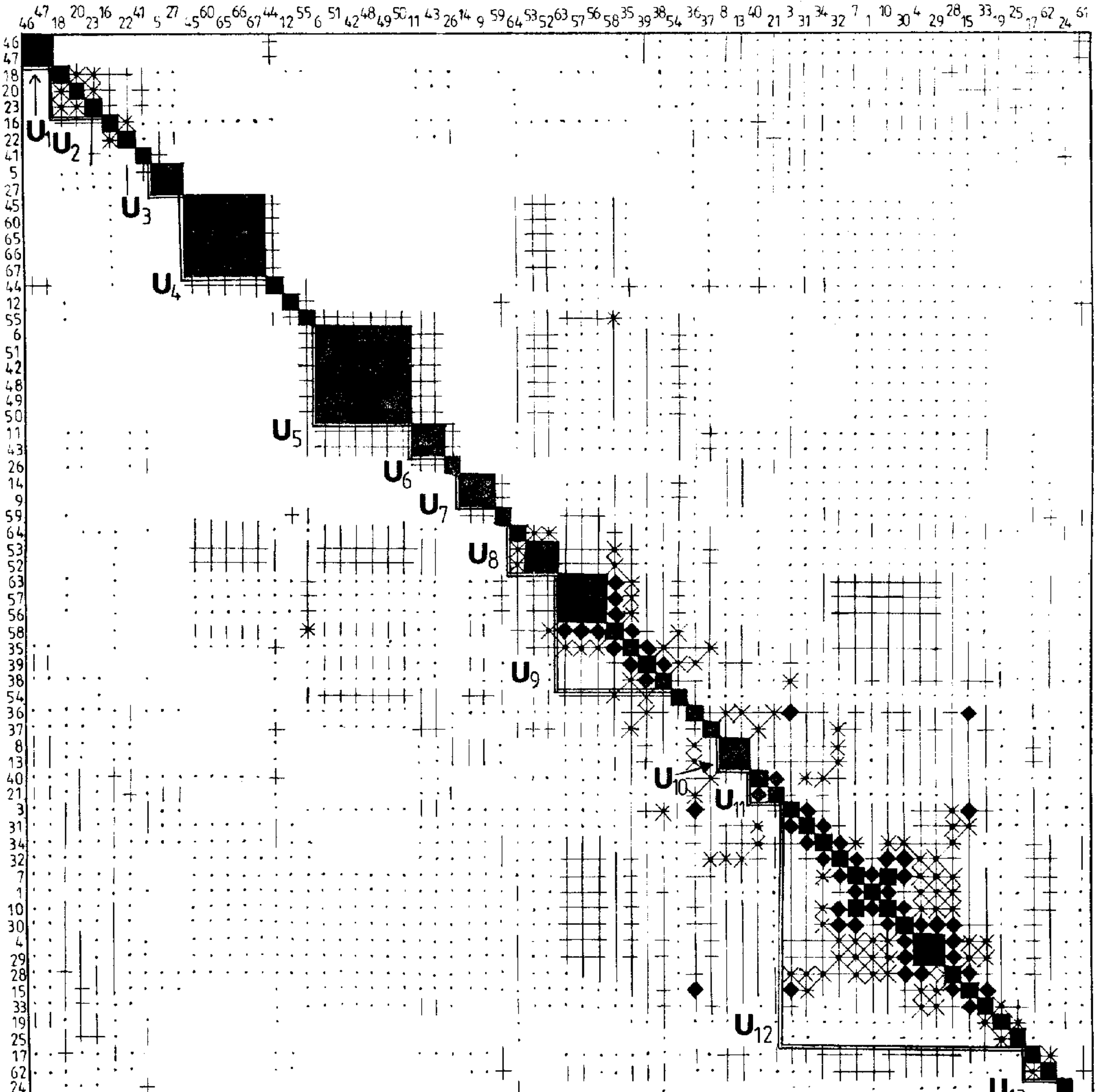

Fig. 8. Diagram of co-occurrence between species of molluscs, dragonflies, caddis larvae and Culicinae. U_1-U_{13} — groupings singled out. **Trichoptera**: 1. *Holocentropus stagnalis*, 2. *Agrypnia picta*, 3. *Limnephilus flavicornis*, 4. *L. rhombicus*, 5. *L. marmoratus*, 6. *L. decipiens*, 7. *L. griseus*, 8. *L. vittatus*, 9. *L. sparsus?*, 10. *L. auricula*, 11. *L. borealis*, 12. *Glyphotaelius pellucidus*, 13. *Grammotaulius signatipennis*, 14. *Halesus* sp. **Culicinae**: 15. *Anopheles maculipennis* Meig., 16. *Aedes cinereus* Meign., 17. *A. maculatus* Meig., 18. *A. excrucians* Was., 19. *A. cataphyla* Dy., 20. *A. nigrinus* Eck., 21. *A. vexans* Meig., 22. *Culex pipiens* L., 23. *Aedes flavescens* M l., 24. *Theobaldia ochroptera* Peus., 25. *Aedes caspius dorsalis* Meig., 26. *Culex apicalis* Ad., 27. *Anopheles bifurcatus* L. **Mollusca**: 28. *Segmentina nitida* (M l.), 29. *Galba palustris* (M l.), 30. *Pisidium obtusale* Jen., 31. *Anisus septemgyratus* (rys.), 32. *Valvata pulchella* Stud., 33. *Sphaerium lacustre* (M l.), 34. *Planorbis planorbis* (L.), 35. *Sphaerium corneum* (L.), 36. *Pisidum casertanum* (Pol.), 37. *Anisus contortus* (L.), 38. *Valvata cristala* M l., 39. *Hippeutis riparius* (West.), 40. *Aplexa hypnorum* (L.), 41. *Galba trunculata* (M l.), 42. *Acroloscus lacustris* (L.), 43. *Armiger crista* (L.), 44. *Coretus corneus* (L.), 45. *Limnea stagnalis* (L.), 46. *Bithynia tentaculata* (L.), 47. *Viviparus contectus* (Mil.). **Odonata**: 48. *Leucorrhinia caudalis* (Char.), 49. *Somatochlora matalica* (Vand.), 50. *Erythroma najas* (Hans.), 51. *Enallagma cyathigerum* (Char.), 52. *Ischnura elegans* (Vand.), 53. *I. pumilio* (char.), 54. *Lestes barbarus* (Fabr.), 55. *Sympetrum sanguineum* (M l.), 56. *Coenagrion armatum* (Char.), 57. *C. pulchellum* (Vand.), 58. *C. hastulatum* (Char.), 59. *Sympetrum flaveolum* (L.), 60. *Coenagrion puella* (L.), 61. *Leucorrihinia pectoralis* (Char.), 62. *Lestes nympha* (Sel.), 63. *L. sponsa* (Nahs.), 64. *Aeschna grandis* (L.), 65. *Sympetrum striolatum* (Char.), 66. *Pyrrhosoma nymphula* (Sul.), 67. *Sympetrum danae* (Sul.)

ski diagram (Fig. 8). We distinguished 13 groupings. Some groupings are coherent and distinct from the remaining species, whereas other groupings are of the character of a continuum, suggesting a gradual (gradient) replacement of species (U_9 and U_{12}).

U_1 – grouping comprising two mollusc species: *Bithynia tentaculata* and *Viviparus contectus*.

U_2 – grouping including three Culicinae species: *Aedes excrucians*, *A. nigrinus* and *A. flavescens*.

U_3 – grouping containing caddis fly *Limnephilus marmoratus* and mosquito *Anopheles bifurcatus*.

U_4 – grouping comprising mollusc *Limnea stagnalis* and four dragonfly species: *Coenagrion puella*, *Sympetrum striolatum*, *Pyrrhosoma nymphula* and *Sympetrum danae*. When co-occurrence of a lower value is considered, the mollusc *Coretus corneus* is also included in this grouping.

U_5 – relatively numerous grouping containing caddis fly *Limnephilus decipiens*, mollusc *Acroloscus lacustris*, and dragonflies: *Enallagma cyathigerum*, *Leucorrhinia caudalis*, *Somatochlora metalica* and *Erythroma*. When considering co-occurrence of lower value, *Sympetrum sanguneum* and grouping U_6 are linked to grouping U_5.

U_6 – small grouping containing caddis fly *Limnephilus borealis* and mollusc *Armiger crista*. When considering co-occurrence of a lower value, *Culex apicalis* adds to these species.

U_7 – grouping comprising two molluscs: *Limnephilus sparsus* and *Halesus* sp. When considering co-occurrence of a lower value, *Sympetrum falveolum* adds to them.

U_8 – grouping including three dragonfly species: *Isnura elegans*, *Ischnura pumilio* and *Aeschna grandis*.

U_9 – grouping containing four dragonfly species of a coherent character of co-occurrence: *Lestes sponsa*, *Coengarion pulchellum*, *C. arnatum*, *C. hastulatum*. The second part of this grouping comprises species whose co-occurrences are arranged in a continuum: *Coenagrion hastulatum*, *Spaherium corneaum*, *Hippeutis riparius* and *Valvata cristata*.

U_{10} – comprised two caddis fly species: *Limnephilus vittatus* and *Grammotaulius signatipennis*.

U_{11} – grouping containing mollusc *Aplexa hypnorum* and mosquito *Aedes vexans*.

U_{12} – greatest grouping including 15 species whose co-occurrences were arranged in a continuum in which molluscs and caddis flies were replaced by Culicinae: *Limnephilus flavicornis* – *Anisus septemgyratus* – *Planorbis planorbis* – *Valvata pulschella* – *Limnephilus griseus* – *Holocentropus stagnalis* – *Limnephilus auricula* – *Pisidium obtusale* – *Limnephilus rhombicus* – *Galba palustris* – *Segmentina nitida* – *Anopheles maculipennis* – *Sphaerium lacustre* – *Aedes cataphyla* and *Aedes caspius dorsalis*. This continuum contained a group of species somewhat more distinctly standing apart: *Holocentropus stagnalis*, *Limnephilus griseus*, *L. auricula*, as well as a group of species *Limnephilus rhombicus*, *Segmentina nitida* and *Galba palustris*.

U_{13} – grouping of a low degree of co-occurrence, comprising two species: *Lestes nympha* and *Aedes maculatus*.

Upon consideration of lower values of co-occurrence, grouping U_4 displayed a link with grouping U_8, grouping 5 – with grouping U_8, grouping U_9 – with grouping U_{12} and U_{10} – with U_{12}.

4. DISCUSSION

The 25 investigated pools were characterized by relatively high invidividualism. This is testified to by both – their morphological data (size of pool, depth, number of days without water, trophy, character of watershed) and their individual species composition, with a simultaneous lack of clear-cut an stepwise faunistic changes (in species composition). An analysis of the faunistic similarities (Figs. 1–7) did not allow for distinct and univocal singling out of the different types of pools; rather there were faunistic changes of a gradual (gradient) character (Figs. 4, 5, 6). Moreover, for each invertebrate group distinct groups of pools stood apart. This is doubtless due to the differences in ecological requirements between these invertebrate groups and to their dissimilar sensitivity to environmental factors, such as: pH, temperature, insolation, trophy etc. This was clearly illustrated by correlation analysis of the number of species (Tab. II). High negative correlation between the number of Culicinae and Odonata species was undoubtedly related to the size and stability of pools. Culicinae occurred in greater numbers in small and very short-lasting pools, whereas dragonflies, owing to their mainly predatory mode of life and long developmental period (lasting even several years) were more numerous in the more stable and larger pools. In this respect Trichoptera and Mollusca have medium requirements (or in this respect they display a greater differentiation of species), although they also preferred the more stable and larger pools.

The lack of consistence in the similarity analysis (Figs. 1–7) suggests that the fauna is simultaneously and independently influenced by many factors (stability and size of astatic pool, trophy, water chemistry, pH, insolation, surroundings of the pool, biotic effects). Different invertebrate groups react dissimilarly to those factors, this leading to individual distribution of the faunistic similarities calculated for each invertebrate group separately. Thus, a single astatic pool should not be regarded as a homogenous unit; it would be more appropriate to analyse the individual habitats, and a single pool – as a mosaic, a system of habitats linked spatially and temporally.

The division of astatic pools earlier proposed by Klimowicz (1959, 1967), taking into account: pool stability, hydrological contact with other waters and trophy (eutrophy and dystrophy), is only partly suitable. The temporal types of pools (Chodorowska, Chodorowski 1958, Paschalski 1959, Wiggins et al. 1980) only allowed for singling out animal associations: the higher the astacism, the smaller the number of species, the longer the development in aquatic environment, the more stable the pool must be for inhabitation. Wiggins et al. (1980) have singled out four groups of animal species according to their adaptations to astatic conditions in the developmental cycle: group I – wintering permanent inhabitants, II – wintering spring recruits, III – wintering summer recruits, IV – nonwintering spring migrants. From the most astatic and short-lasting pools, species of groups II, III, IV are eliminated. From the somewhat more stable pools, species of groups III and IV are eliminated. In the most stable pools, all above-mentioned groups are present. Thus the species adapted to the most astatic conditions occur also in the permanent pools (Tab. I, Wiggins et al. 1980). This suggests that the small astatic pools are not internally homogenous and that they contain zones of a different degree of stability and static equilibrium (susceptibility to drying out and disappearing). This is also testified to by the development of zonation in these pools (Solińska 1963).

Small astatic pools also fail to be homogenous over time. During the vegetation year, four periods can be distinguished (Maganza et al. 1985, Paschalski 1959):

– early vernal period when the pool is filled with water of low temperature, well oxygenated, with a low CO_2 content and slight tendency for partial rotting. With a lapse of time the temperature rises, the content of organic matter increases (washing out from the water-logged bottom, plant remnants deposited in the pool), and the tendency for partial rotting is intensified.

– vernal (spring-summer) period characterized by cyclic processes of decomposition, which become attenuated and stabilized over time; the primary production increases.

– summer period when the primary production increases, the tendency for partial rotting is intensified and the temperature rises.

– autumnal period (disappearance of long-lasting pools) when the decomposition processes are again very distinctly intensified, oxygenation decreases, CO_2 concentration increases and the tendency for partial rotting is intensified.

In certain cases the above-mentioned periods may correspond with the types of pools, e.g. in vernal pools there occurs only the vernal period (owing to drying out, the remaining periods are not observed). Spring ice thawing and precipitation may influence pH and some other trophic factors; consequently the vernal conditions prevailing in pools of different trophy are similar and approach oligotrophy. Even in peatlands the conditions approaching those on flooded field meadows may prevail (Chodorowska, Chodorowski 1958).

Transformations of water relationships result, among others, from long-term climatic changes (Dynowska 1988). Thus, astatic water bodies are also variable in the many-years' period. The aquatic period (size, depth, duration) of the same pool may be completely dissimilar in various years (e.g. pool 13, see also Wiggins et al. 1980). As a result of such changes in the many-years' cycle there may occur reversible alterations in plant communities, unrelated to the succession series (Solińska 1963). Water abundance of astatic pools greatly depends on the amount of precipitation and evaporation, which are related to climatic conditions.

Over Poland the effects of oceanic and continental climate clash, and therefore in Poland the properties of the climate are of a transitional nature. It is characteristic of this climate that the amplitudes of precipitation on a multi-years' scale are considerable (more than twice wider than those found under the conditions of marine and continental climate) (Bac, Rojek 1979). Therefore, there happen years with low sums of yearly precipitation, similarly as in the continental climate, and years with high sums of yearly precipitation, alike as in the marine climate (Bac, Rojek 1979). Under conditions of Poland, such fluctuations of the amounts of precipitation are usually found in a several-years' period (Maruszczak 1988).

At the same time, the most distinct changes in the natural environment are observed during more than ten years' periods (excessively moist and excessively dry periods). These changes are most clear-cut on the boundary of forestrial and wetland-meadow-water formations (Maruszczak 1988). Cyclic and noncyclic fluctuations in the several-years', many-years', several hundred-years' and longer periods are common to not only the transitional climate (Lockwood 1984, Maruszczak 1988, Stankowski 1981).

After consideration of all the above-mentioned phenomena, a general model of an astatic pool can be proposed (Fig. 9). Hydrological contact with other waters (particularly with permanent ones) exerts a significant effect on the

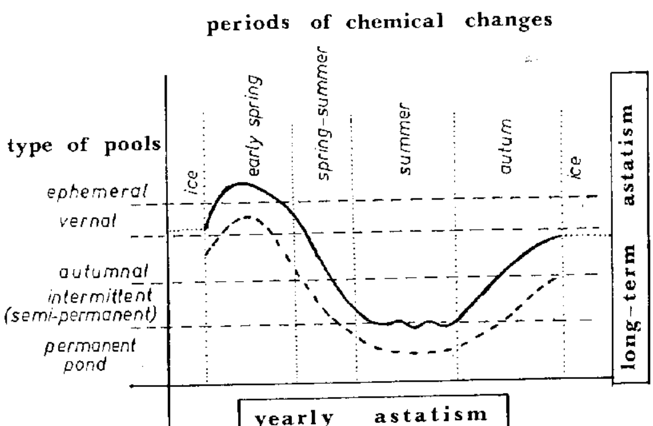

Fig. 9. Model of astatic water body typology. Vertical scale illustrates water depth in the pool. Heavy continuous line – water level in the pool, heavy broken line – water level in the pool in dry year

fauna of astatic water bodies. Therefore, a dissimilarity of the fauna of astatic waters of river valleys may be expected; namely, owing to spring floods these waters remain in systematic contact with the river fauna. Thus, *Lepidurus apus* L. occurs mainly in astatic pools of river valleys, and *Siphonophanes grubii* (Dyb.) – in non-valley pools of northern Poland (Czachorowski, unpubl.). Studies on caddis flies of small water bodies of northern Poland also confirm the differences between valley and non-valley pools (Czachorowski, in print).

In contrast to valley water bodies, pools of the lake landscape (young-glacial) are in hydrological contact with other permanent and astatic water bodies only via small, periodically disappearing watercourses or land reclamation ditches. Their contact with lakes by way of spring flood waters is very unferquent. As regards organisms such as rotifers and molluscs, a richer fauna occurs in flow-through water bodies or in those periodically connected with other permanent waters (Klimowicz 1959, 1967). For these animals, such contact allows for migration and recolonization of water bodies, after earlier perishing of the fauna (its part or all species) as a result of many-years' astacism.

For insects actively migrating at the imago stage (e.g. Trichoptera, Odonata, Culicinae) a lack of hydrological contact is not an obstacle. There is no significant relationship between the number of species of these insects and the degree of hydrological isolation of water bodies (see also Fischer 1959, Wojnarowicz 1960). At the same time, dying out of dragonfly larvae and a lack of completion of their ontogenetic development have been observed (Fischer 1959). This may testify to ineffective migration. It seems that high migration ability is one of the more important adaptation traits of species living in astatic waters. This particularly concerns many-years' astacism.

It seems that faunistic individualism of the investigated pools and their great variability (diversity) may be regarded as a resultant of fauna perishing under adverse environmental conditions of yearly and many-years' astacism, on one hand, and fauna migration from the vicinal permanent and astatic water bodies (Fig. 10). This is also testified to by the fact that the higher the

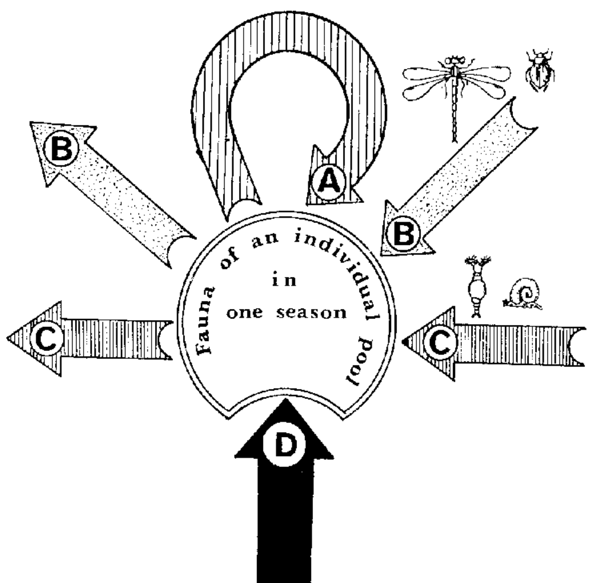

Fig. 10. A — fauna persisting from the previous season, B — migrations of insect imagines via air route, C — migrations via water route, D — perishing of fauna owing to adverse conditions (yearly and many-years' astacism)

astacism of the water body, the greater the variation of its species composition (Klimowicz 1967, Wojnarowicz 1960). It can thus be assumed that by studying one astatic water body during many years we may obtain a list of species approaching that found upon studies of many vicinal astatic water bodies during one season.

5. SUMMARY

Caddis larvae were collected at more or less 2-week intervals in 1956 and sporadically in 1957 in 17 astatic pools in the vicinity of Mikołajki. A total of 1342 larvae belonging in 17 species were collected (Tab. I). Moreover, for statistical analyses we used the data concerning rotifers (Klimowicz 1970), molluscs (Klimowicz 1959), dragonflies (Fischer 1959) and Culicinae (Wojnarowicz 1960). In total. 25 pools were studied.

The dynamics of the numbers and of the number of Trichoptera species during the year (Fig. 1) and the distribution of caddis larvae in dependence on the permanence of the pool and on its succession phase were investigated.

We studied the faunistic similarities between the pools on the basis of the fauna of rotifers (Fig. 2), molluscs (Fig. 3), Culicinae (Fig. 4), dragonflies (Fig. 5), caddis larvae (Fig. 6), as well as of jointly: dragonflies, Culicinae, caddis larvae and molluscs (Fig. 7). High faunistic individualism of the astatic pools and a lack of clear-cut boundaries between the species composition of single pools and species composition of different types of pools were observed. A significant negative correlation between the number of Culicinae species and that of dragonfly species was found (Tab. II). The co-occurrence of species of caddis flies, dragonflies, Culicinae and molluscs was calculated (Fig. 8), and 13 groupings of a coherent character of a continuum nature were singled out.

Taking into account the yearly astacism (changes in water chemistry and water level) and the many-years' astacism related to cyclic and noncyclic climatic changes, we proposed a model of typology of astatic water bodies (Fig. 9). This model takes into consideration the zonation and mosaicism of water bodies, and the lack of discrete boundaries between their different types.

It seems that the species composition of a single pool depends on dying out of the fauna under adverse conditions (yearly and many-years' astacism), on one hand, and on migration of the fauna by an aquatic route (e.g. rotifers and molluscs) and by an air route (winged insects) (Fig. 10). This model is consistent with the island theory of MacArtur and Wilson (1957).

6. STRESZCZENIE

Larwy chruścików zbierano w odstępach mniej więcej dwutygodniowych w 1956 roku oraz sporadycznie w 1957 w 17 zbiornikach okresowych okolic Mikołajek. Zebrano 1342 larwy, które zaliczono do 17 gatunków (Tab. I). Do analiz statystycznych wykorzystano ponadto dane odnoszące się do wrotków (Klimowicz 1970), mięczaków (Klimowicz 1959), ważek (Fischer 1959) i Culicinae (Wojnarowicz 1960). Łącznie badaniami objęto 25 zbiorników.

Zbadano dynamikę liczebności i liczby gatunków Trichoptera w ciągu roku (rys. 1) oraz rozmieszczenie larw chruścików w zależności od trwałości zbiornika i jego fazy sukcesywnej.

Zbadano podobieństwa faunistyczne pomiędzy badanymi zbiornikami w oparciu o faunę wrotków (rys. 2), mięczaków (rys. 3), Culicinae (rys. 4), ważek (rys. 5), chruścików (rys. 6) oraz łącznie ważek, Culicinae, chruścików i mięczaków (rys. 7). Zauważono dużą faunistyczną indywidualność zbiorników astatycznych (okresowych) oraz brak wyraźnych granic pomiędzy składem gatunkowym pojedynczych zbiorników oraz składem gatunkowym różnych typów zbiorników. Stwierdzono istotną korelację ujemną pomiędzy liczbą gatunków Culicinae a liczbą

gatunków ważek (tab. II). Wyliczono współwystępowanie pomiędzy gatunkami chruścików, ważek, Culicinae i mięczaków (rys. 8) i wyróżniono 13 zgrupowań o charakterze zwartym lub kontinuum.

Uwzględniając astatyzm roczny (zmiany chemizmu i poziomu wody) oraz astatyzm wieloletni uzależniony od cyklicznych i acyklicznych zmian klimatycznych zaproponowano model typologii zbiorników okresowych (rys. 9). Model ten uwzględnia strefowość i mozaikowość zbiorników oraz brak dyskretnych granic pomiędzy różnymi typami zbiorników.

Wydaje się, że skład gatunkowy w jednym zbiorniku uzależniony jest od ginięcia fauny w niesprzyjających warunkach (astatyzm roczny i wieloletni) oraz migracji fauny drogą wodną (np. wrotki i mięczaki) i powietrzną (owady uskrzydlone) (rys. 10). Model ten zgodny jest z teorią wysp MacArtura i Wilsona (1967).

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