

POLSKIE ARCHIWUM HYDROBIOLOGII (Pol. Arch. Hydrobiol.)	40	2	139-163	1993
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DISTRIBUTION OF TRICHOPTERA LARVAE IN VERTICAL PROFILE OF LAKES

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ABSTRACT

Studies of four lakes of the Olsztyn Lakeland pointed to the occurrence, in vertical profile, of two maxima of larvae numbers: in the most shallow littoral and in the zone of elodeids (submerged plants). The elodeid maximum was shifted towards smaller depths with a drop in water transparency. This was mainly due to a rise of the numbers of larvae preferring more shallow habitats, and to a decrease in the numbers of larvae preferring the deeper littoral. Moreover, in the winter-early spring season the numbers of larvae in the elodeid zone decreased because of higher lake trophy and reduced water transparency. It seems that the distribution of Trichoptera larvae in vertical profile is secondary to their habitat distribution.

Key words: vertical distribution, Trichoptera, lakes, trophy

1. INTRODUCTION

Vertical distribution of caddis larvae, being benthic organisms, has been investigated but seldom. Only the paper by Czachorowski (1989) has, as a whole, dealt with this problem. Many earlier papers have, however, mentioned the vertical occurrence of caddis larvae (Fehlmann 1912, Rzóska 1935, Moon 1936, Despax 1951, Romaniszyn 1954, Okland 1964, Nocentini 1966, Solem 1973, 1978). Many authors have in the first place considered the Trichoptera in the rank of order (Romaniszyn 1954, Kajak et al. 1968, Kajak, Dusoge 1971, 1976, June 1982, Resh et al. 1983, Barton 1986, Kornijów 1988).

In the main, all caddis larvae species inhabit the littoral and descend only to depths of 5-10 m (Nocentini 1966, Rzóska 1935, Solem 1973). Exceptionally, they may occur at a 40-m depth (Fehlmann 1912) or even at a 84-m depth (Despax 1951).

The zonation of the vertical distribution of caddis larvae in lakes has not so far been fully elucidated. The principles of this distribution and the causes of the relevant differences between lakes remain unclear. The range of the vertical occurrence is relatively well known for only few species.

The present studies were aimed at determining the vertical distribution of caddis larvae, with special consideration of lake trophy.

2. MATERIAL AND METHODS

Four lakes situated in the Olsztyn Lakeland were studied. For evaluation of the trophic state of these lakes, in the years 1988 and 1989 in the mid-lake the physico-chemical properties of water were determined (Tables I–III); moreover, use was made of the data of the Centre for Environmental Studies and Control in Olsztyn (Table IV), as well as of the morphometric characteristics (lake surface area and depth) made available by the Institute of Inland Fisheries in Olsztyn. The Narckie Lake was classified as mesotrophic, Warchaldzkie Lake – as eutrophic, Skanda Lake – as eutrophic-hypertrophic (on account of water transparency in 1989) and Brajnickie Lake – as hypertrophic.

Table I. Physicochemical properties of the Narckie Lake waters: mean values (or range) for the measurements taken on 21 April, 28 August and 8 November 1988

Depth (m):	0	1	15	30
water temperature (°C)	10.7	12.5	5.7	5.7
pH*	7.9	7.8–8.3	7.8	7.5–7.9
dissolved O ₂ (mg dm ⁻³)	11.5	11.7	10.1	9.8
oxidizability (mg dm ⁻³)	16.0	6.0	10.4	12.8
orthophosphate (mg P–PO ₄ dm ⁻³)	0.08	0.07	0.035	0.077
total phosphorus (mg P dm ⁻³)	0.09	0.165	0.215	0.15
nitrate (mg NO ₃ dm ⁻³)	0.08	0.03	0.0	0.03
ammonia (mg NH ₃ dm ⁻³)	0.015	0	0	0.015
total nitrogen (mg N dm ⁻³)	0.7	0.6	0.75	0.69
chlorophyll (µg dm ⁻³)	0.4	4.66	1.2	0.18
conductivity (µS cm ⁻¹)	103.4	162.7	174.2	154.7
BOD ₅ (mg O ₂ dm ⁻³)	9.8	1.66	2.56	4.93
suspended matter (mg dm ⁻³)	4.9	3.95	3.9	3.03
Secchi's depth (m)	6			

The Trichoptera larvae material was collected at 1-month intervals (except for winter months when the lake was ice-bound) between November 1987 – October 1990. Larvae were caught with a manual hydrobiological sampler and a dredge (B o w k i e w i c z 1956). A single sample corresponded to a bottom surface of ca. 0.3–0.5 m². In the studies 27 sampling stations and 129 types of habitats were taken into account. The following depth zones were singled out: 0–0.2, 0.2–0.4, 0.4–0.6, 0.6–0.8, 0.8–1.0, 1–2, 2–3, 3–4, 4–5, 5–10 m. Each time, in all habitats and at all sampling stations collection was made of one sample from every depth zone. On account of the greater habitat differentiation, more samples were collected in the zone of the most shallow littoral (up to a 0.8-m depth) than in the deeper littoral. There were no complete data for the deeper zones of the Skanda Lake, and thus with respect to phenology the material is less representative. For analysis of the caddis larvae distribution in vertical profile of different types of the littoral, 7 sampling stations situated in three lakes were considered. A total of more than 800 samples were collected, and Trichoptera larvae were present in 714 of them. Altogether, 15 856 larvae belonging in 55 taxa were caught.

Table II. Physicochemical properties of the Warchałdzkie Lake waters: mean values (or range) for the measurements taken on 21 April, 28 August and 8 November 1988

Depth (m):	0	1	6	12
water temperature (°C)	14.4	1	6	12
pH*	–	7.8–8.3	–	7.4–7.9
dissolved O ₂ (mg dm ⁻³)	12.4	11.67	8.00	7.27
oxidizability (mg dm ⁻³)	–	15.47	–	13.2
orthophosphate (mg P–PO ₄ dm ⁻³)	–	0.092	–	0.41
total phosphorus (mg P dm ⁻³)	–	0.267	–	0.62
nitrate (mg NO ₃ dm ⁻³)	–	0.65	–	0.042
ammonia (mg NH ₃ dm ⁻³)	–	0.03	–	0.74
total nitrogen (mg N dm ⁻³)	–	1.21	–	1.64
chlorophyll (µg dm ⁻³)	–	14.2	–	5.84
conductivity (µS cm ⁻¹)	–	238.4	–	257.4
BOD ₅ (mg O ₂ dm ⁻³)	–	5.84	–	7.46
suspended matter (mg dm ⁻³)	–	4.60	–	3.93
Secchi's depth (m)	3			

Table III. Physicochemical properties of the Brajnickskie Lake waters: mean values (or range) for the measurements taken on 21 April, 28 August and 8 November 1988

Depth (m):	0	1	2.5
water temperature (°C)	14.9	10.5	10.2
pH*	–	7.8–8.4	7.7–8.4
dissolved O ₂ (mg dm ⁻³)	10.85	11.03	10.37
oxidizability (mg dm ⁻³)	–	25.06	28.8
orthophosphate (mg P–PO ₄ dm ⁻³)	–	0.087	0.093
total phosphorus (mg P dm ⁻³)	–	0.413	0.410
nitrate (mg NO ₃ dm ⁻³)	–	0.125	0.095
ammonia (mg NH ₃ dm ⁻³)	–	0.225	0.110
total nitrogen (mg N dm ⁻³)	–	2.42	1.9
chlorophyll (µg dm ⁻³)	–	42.53	44.03
conductivity (µS cm ⁻¹)	–	254.9	208.47
BOD ₅ (mg O ₂ dm ⁻³)	–	4.93	6.15
suspended matter (mg dm ⁻³)	–	3.63	6.33
Secchi's depth (m)	0.3		

Table IV. Physicochemical properties of the Skanda Lake waters according to the measurement performed on 11 August 1982 (data of the Centre for Environmental Studies and Control in Olsztyn) and in June 1989 (Secchi's depth)

Depth (m):	1	5	10
pH*	7.92	7.59	7.43
total phosphorus (mg P dm ⁻³)	0.46	0.65	2.23
calcium (mg Ca dm ⁻³)	47.1	38.1	69.7
magnesium (mg Mg dm ⁻³)	6.2	16.7	5.1
CO ₂ (mg P dm ⁻³)	0.0	6.6	11.0
dissolved O ₂ (mg dm ⁻³)	9.2	1.8	0.0
saturation of oxygen (%)	105	19	0
sulphate (mg SO ₄ dm ⁻³)	12.7	13.6	7.8
total nitrogen (mg N dm ⁻³)	2.39	2.11	3.12
organic nitrogen (mg dm ⁻³)	1.68	1.40	0.28
Secchi's depth in 1989 (m)	0.7		

3. RESULTS

GENERAL CHARACTERIZATION OF THE ORDER

The numbers of Trichoptera larvae and the number of species dropped with an increase in depth (Fig. 1). Two maxima of the greater numbers of larvae stood apart: in the most shallow littoral and deeper – in the zone of elodeids (submerged plants). The latter maximum was shifted towards smaller depths with a rise of lake trophy and with a drop in water transparency. In the mesotrophic Narckie Lake the deeper zone of the greater numbers corresponded to a 2-m depth, in the eutrophic Warchałdzkie Lake – to a 0.8-m depth, in the eutrophic – hypertrophic Skanda Lake – to a depth of 0.8–2 m, and in the hypertrophic Brajnkie Lake – to a 0.6-m depth (Fig. 1).

In the mesotrophic Narckie Lake the drop in the mean density of larvae after winter was slight and concerned only the deeper littoral zones (Fig. 2). In the most shallow littoral the density of the larvae was greater in spring than in autumn. Moreover, at nearly all depths the density dropped in summer. The shift of the density maxima in July and August towards smaller depths may testify to migration of larvae towards the bank for pupation or to migration towards less deeply situated habitats. In the eutrophic Warchałdzkie Lake the drop in the density of larvae in winter (or rather in the winter–early spring season) was greater and more clear-cut (Fig. 3), and mainly concerned the deeper zones of the lake and the species associated with elodeids (underwater meadows). The substantial increase in the density in the deeper parts of the Narckie and Warchałdzkie Lakes in autumn (Figs. 2, 3) was doubtless due to egg laying and to the appearance of a new generation of the Trichoptera.

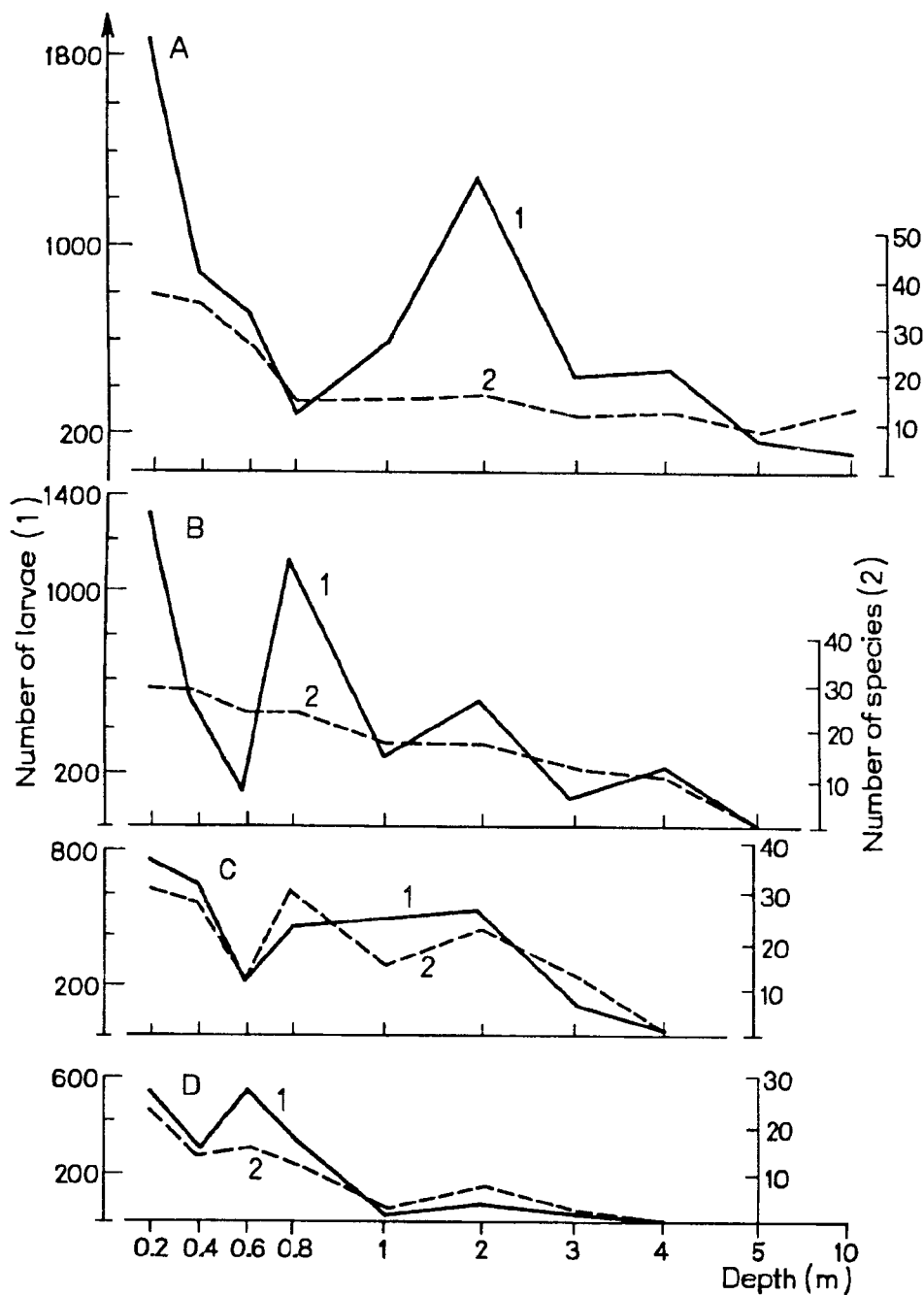


Fig. 1. Distribution of the number of Trichoptera larvae (1) and number of species (2) in vertical profile: A – Narckie Lake (water transparency 6 m), B – Warchaldzkie Lake (transparency 3 m), C – Skanda Lake (transparency 0.7 m), D – Brajnickie Lake (transparency 0.3 m)

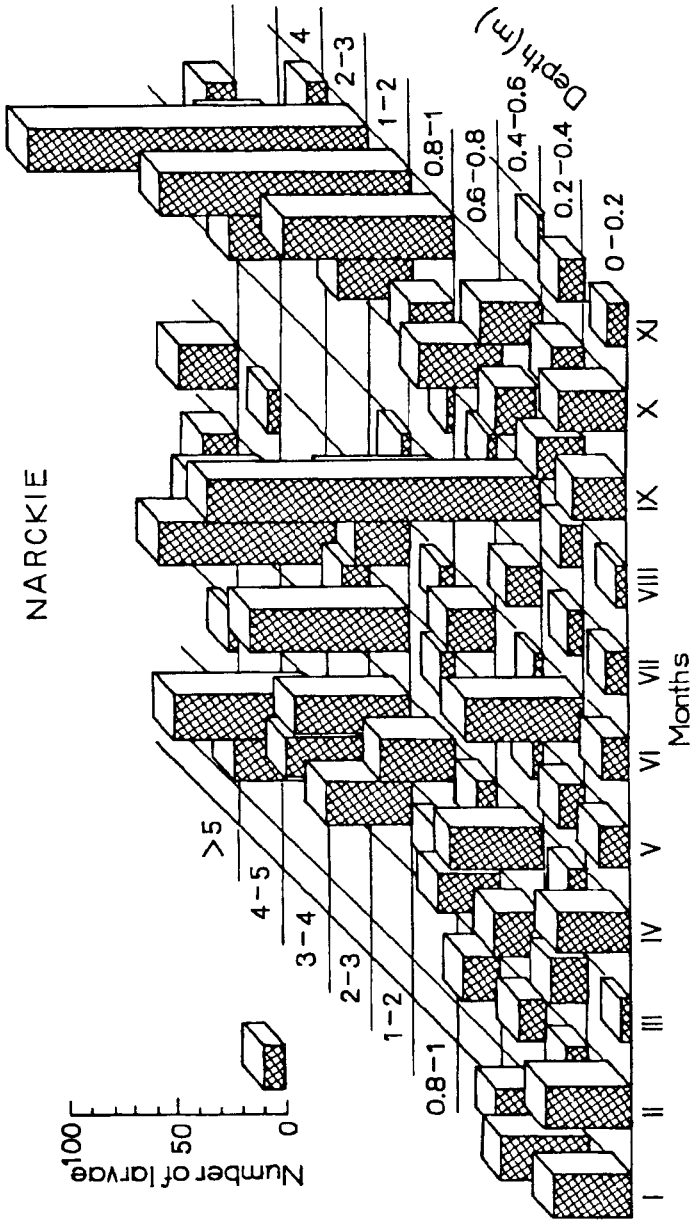


Fig. 2. Phenological changes in the estimated density of Trichoptera larvae (per 0.3-0.5 m² of bottom surface) in vertical profile of the Narckie Lake

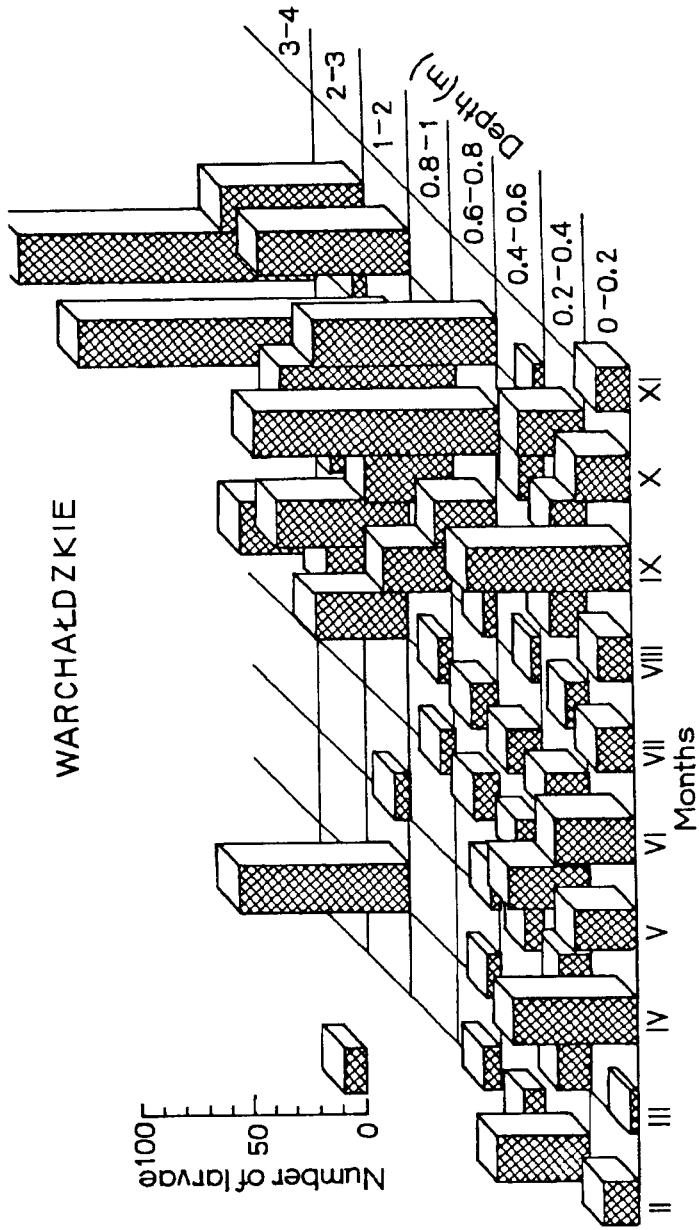


Fig. 3. Phenological changes in the estimated density of Trichoptera larvae (per 0.3-0.5 m² of bottom surface) in vertical profile of the Warchałdzkie Lake

In the most shallow littoral the dynamics of the density were different (Figs. 2, 3). The high density observed in spring was associated with the development of the Limnephidae larvae; these animals spend the major part of winter in the diapause of the first larval instars which have not yet left the egg cocoons. The drop in their density in summer resulted from pupation and occurrence of the imagines.

In the Skanda Lake, in the most shallow littoral the spring maximum of the density was evident (Fig. 4). It was due to the development of the Limnephilidae being dominant in the rushes and bulrush zones. In the case of the elodeid zone it is difficult to detect any regularity, on account of the incompleteness of the data. The high density of larvae in June was due to the considerable density of the Hydroptilidae known to produce two generations yearly. Thus it cannot be univocally stated whether and to what an extent the density of the larvae decreased in winter in the submerged vegetation zone.

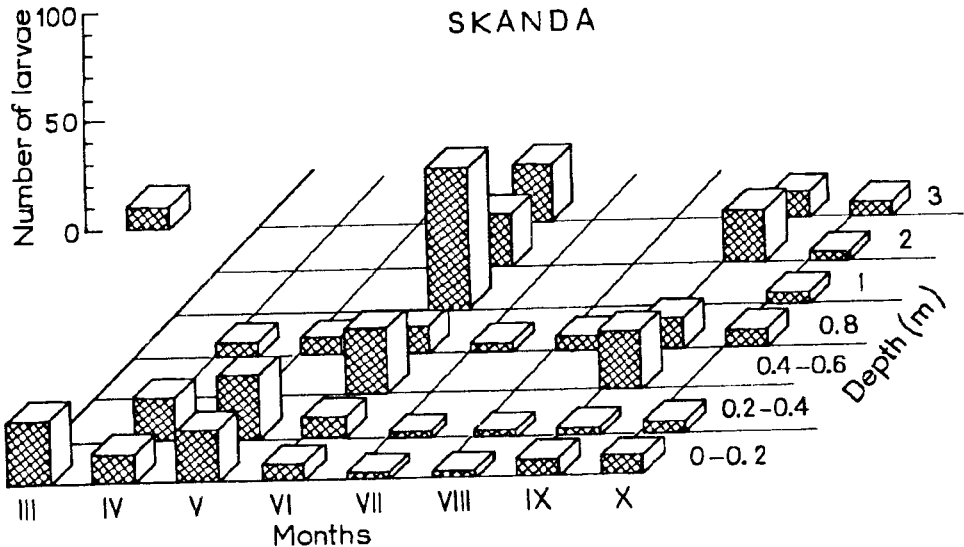


Fig. 4. Phenological changes in the estimated density of Trichoptera larvae (per 0.3-0.5 m² of bottom surface) in vertical profile of the Skanda Lake

In the hypertrophic Brajnkie Lake the phenological dynamics of the estimated density of larvae in the vertical profile (Fig. 5) were characterized by a drop in this density in the winter-early spring season; this drop was more evident than that found in the case of the Warchaldzkie Lake (Fig. 3) and – all the more so – than that observed in the first place all species occurring in the elodeid zone. Furthermore, in the case of the Brajnkie Lake there were no differences between the most shallow and deeper littoral. This resulted from the low density of the species characteristic of the zone of the helophytes (emerged plants).

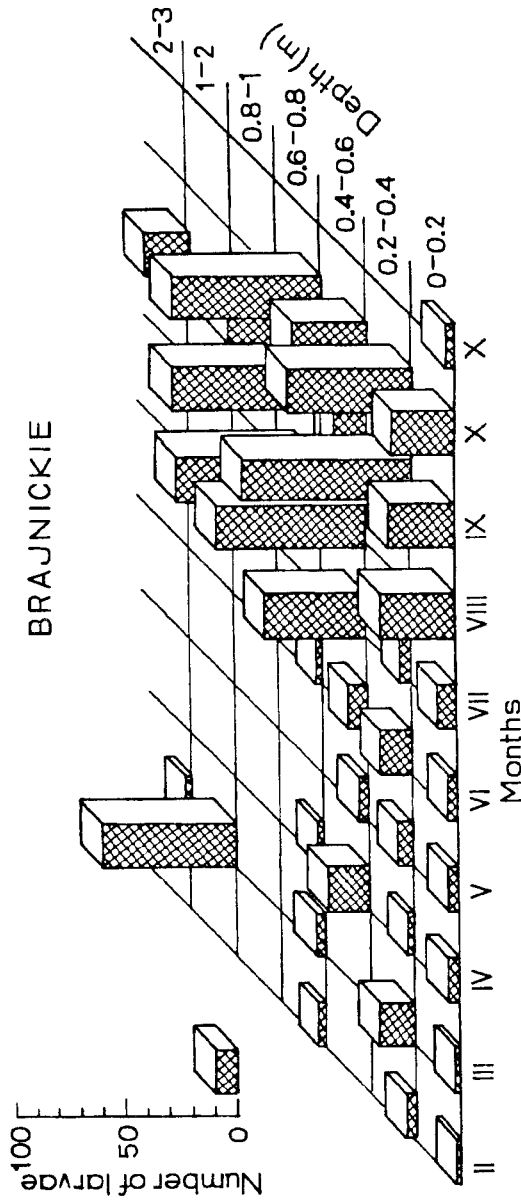


Fig. 5. Phenological changes in the estimated density of Trichoptera larvae (per 0.3-0.5 m² of bottom surface) in vertical profile of the Brajnackie Lake

VERTICAL DISTRIBUTION OF INDIVIDUAL TAXA

In the Narckie Lake almost all taxa occurred at the smallest depths (Tab. V). Individual taxa appeared in greater numbers in some definite depth zone. For example, *Oxyethira* sp. – though present within a very wide range of depths – was caught most abundantly at a depth of 1–2 m. On the other hand, *Cyrnus crenaticornis* was most numerous in the depth zones of 0.4–0.6 and 1–4 m.

Table V. Distribution of the Trichoptera larvae in vertical profile of the Narckie Lake (total number of the collected larvae)

Taxon*	Depth (m)									
	0.2	0.4	0.6	0.8	1	2	3	4	5	>5
La	79									
Lm	3									
Lt	3									
Lv	1									
Eb	1									
Lg	680	1								
Lp	8	1								
Ld	5	4								
Hp	2	3								
Ne	2	6								
Pg	1	8								
Ls	42	2	1							
Hd	32	25	9							
Lr	4	36	2							
Os	3	2	1						1	
Al	12	6	3							1
Lc	127	23	8	5						
Hy	2	2	5	2	4					
Lf	131	117		1		2				
Ci	17	12	7		3	1				
Pb	12	8	5		4	2				
Ps	7	12	2	4		1				
Oo	3	1	1	1		1	1			
Tb	125	50	26	3	1	29			1	
Ag	68	29	79		98			9	1	
Tw	3	6	5	5						3
Et	2	7	5		5					1
Mo	6	10	17		18					3
Cs	33	1			2	17				1

Taxon*	Depth (m)									
	0.2	0.4	0.6	0.8	1	2	3	4	5	>5
Cf	31	68	51	31	43	57	13	4		15
Or	2	8	1	1	3	14	8	5		2
Ac	216	111	191	134	92	37	4	21		17
Cc	24	72	102	8	20	94	89	192	65	7
Ox	5	5	15	3	7	354	31	26	21	1
Aa	79	32	46	45	67	78	44	25	13	19
Ml	39	127	44	35	129	157	14	50	15	18
Ms	28	25	14	11	87	329	116	30	15	10
Le	12	38	33			78	74	47	37	8
Mn	3						17	2		
Ca		3	1	2		2	5	1		
Of		2								
Ts		1								
Ly		2	1							
Gp			1							
Total	1852	866	676	291	583	1253	416	427	169	106

*Aa - *Athripsodes aterrimus* (Steph.), Ac - *A. cinereus* (Curt.), Ag - *Agraylea multipunctata* Curt., Al - *Anabolia laevis* (Zett.), Ao - *Agrypnia obsoleta* (Hag.), Ca - *Ceraclea annulicornis* (Steph.), Cc - *Cyrnus crenaticornis* (Kol.), Cf - *C. flavidus* McL., Ci - *C. insolutus* McL., Cs - *C. sp. juv.*, Eb - *Erotesis baltica* McL., Et - *Ecnomus tenellus* (Ramb.), Gi - *Grammotaulius signatipennis* McL., Gn - *G. nigropunctatus* (Retz.), Gp - *Glyptotaelius pellucidus* (Retz.), Gs - *Grammotaulius sp. juv.*, Ha - *Halesus sp.*, Hd - *Holocentropus dubius* (Ramb.), Hp - *H. picicornis* (Steph.), Hy - *Hydroptila sp.*, La - *Limnephilus auricula* Curt., Lb - *L. borealis* (Zett.), Lc - *L. fuscicornis* Ramb., Ld - *L. decipiens* (Kol.), Le - *Leptocerus tineiformis* (Curt.), Lf - *Limnephilus flavicornis* (Fabr.), Lg - *L. griseus* (L.), Ll - *L. lunatus* Curt., Lm - *L. marmoratus* Curt., Ln - *L. nigriceps* (Zett.), Lp - *L. politus* McL., Lr - *L. rhombicus*, Ls - *L. sp. juv.*, Lt - *L. stigma* Curt., Lu - *L. sparsus* (Curt.), Lv - *L. vittatus* (Fabr.), Ly - *Lype sp.*, Ma - *Mystacides azurea* (L.), Ml - *M. longicornis* (L.), Mn - *M. nigra* (L.), Mo - *Molanna angustata* Curt., Ms - *Mystacides sp. juv.*, Ne - *Nemotaulius punctatolineatus* (Retz.), Of - *Oecetis furva* (Ramb.), Ol - *O. lacustris* (Pict.), Oo - *O. ochracea* (Curt.), Or - *Orthotrichia sp.*, Os - *Oecetis sp. juv.*, Ox - *Oxyethira sp.*, Pb - *Phryganea bipunctata* Retz., Pg - *P. grandis* L., Ps - *P. sp. juv.*, Tb - *Triaenodes bicolor* (Curt.), Ts - *Tinodes sp.*, Tw - *T. waeneri* (L.)

With respect to the character of the vertical distribution of the Trichoptera, three groups of species may be singled out. The first group comprised caddis larvae which do not occur at depths exceeding 0.6 m, this being the depth reached by emerged vegetation. This group mostly included the taxa of the family Limnephilidae. Moreover, a single individual of *Erotesis baltica* occurred in this group. The presence of *Holocentropus picicornis* and *H. dubius* within this depth range was due to the fact that in the Narckie Lake, at the sampling station located in the atrophic littoral, the habitat preferred by these species (*Stratiotes aloides*) was situated close to the bank and at a small depth. At this sampling station *Stratiotes aloides* emerged to the water level.

The second group may include the taxa present abundantly at depths not exceeding 1 m, and sporadically occurring also at greater depths. They comprised the seasonally migrating species of the genus *Phryganea*, but in a great majority there belonged the taxa preferring the bulrush and rushes zones (a part of the Limnephilidae, *Agraylea multipunctata*, *Triaenodes bicolor*). The presence of larvae in some even deeper parts of the littoral was most likely due to migration.

The third group may include the species most often caught at depths of 0.8–5 m in the clodeid zone. Only *Athripsodes cinereus* displayed somewhat more shallow occurrence zones. This group comprised nearly all species being most abundant in the Narckie Lake. It contained species of the families Polycentropodidae, Hydroptilidae and Leptoceridae. The remaining five taxa did not occur at the smallest depths, but the numbers of these taxa were small.

The fact that the *Mystacies* sp. juv. larvae (larvae at younger instars) occurred in great numbers at depths of 1–3 m, and the older *Mystacides longicornis* larvae were present mainly at the depths of 0.2–0.4 and 0.6–2 m pointed to seasonal migrations of larvae during growth, from the deeper parts of the littoral towards the bank (Tab. V). The vertical distribution testified, in a lesser measure, to similar migrations of *Triaenodes bicolor* and *Agraylea multipunctata*. On the other hand, the fact that *Cyrnus crenaticornis* exhibited two maxima of the numbers at different depths was due to its abundant occurrence in *Stratiotes* situated at a small depth and to its being numerous in the clodeid zone.

In the Warchałdzkie Lake, the character of the vertical distribution of the individual taxa (Tab. VI) resembled that found for the Narckie Lake, with only few exceptions. *Leptocerus tineiformis* preferred somewhat smaller depths, whereas *Cyrnus flavidus* and *C. renaticornis* displayed more narrow zones of vertical occurrence.

Table VI. Distribution of the Trichoptera larvae in vertical profile of the Warchałdzkie Lake (total number of the collected larvae)

Taxon*	Depth (m)							
	0.2	0.4	0.6	0.8	1	2	3	4
La	15							
Ln	17	1						
Gp	1	2						
Lm	3	5						
Ls	537	39	6					
Al	121	11	2					
Lc	6	1	1					
Ag	3	9	8					
Cs	1		1					
Pg	1		2					
Ld	51	2		2				
Lr	16	2	3	5	1			
Lp	14	35	9	2	1			

Taxon*	Depth (m)							
	0.2	0.4	0.6	0.8	1	2	3	4
Tw	153	83	5	64	5			
Ps	3	1		7	2			
Lb	1		2		1			
Tb	29	5	4	9		1		
Lf	102	90	13	4		1		
Pb	3	2	1	4		1		
Hy	5	9	9	12	7	4	1	
Et	6	79	5	235	1	17	1	
Ml	31	25	16	46	31	89	1	
Ox	7	2		18	18	33	15	11
Mo	12	6	6	12	8	27		2
Or	15	16	8	38	4	15	19	83
Cf	31	27	22	339	136	72	6	12
Aa	131	42	20	65	13	110	16	4
Ms	2	5	6	34	8	29	7	1
Le	2	1		110	22	56	8	21
Ne		2						
Ly		3		2				
Cc		3	8	95	45	76	47	64
Mn			9			1		
Ci			3					1
Hp				1				
Oo				1	1	6	2	
Os				2		1	1	2
Ac				1				1
Total	1319	508	169	1108	304	539	124	202

*denotations of the taxa – as in Table V.

Some species typical of the zone of emerged vegetation likewise occurred at slightly smaller depths (e.g. *Agraylea multipunctata*, *Triaenodes bicolor*), while other ones were present deeper (e.g. *Limnephilus rhombicus*, *L. politus*, *L. decipiens*). *Athripsodes aterrimus* exhibited two clear-cut zones of greater numbers: at depths of 0–0.2 and 1–2 m.

In the Warchałdzkie Lake the zonation of the vertical distribution was relatively well visible, and in some cases was even more evident than in the Narekie Lake. This is doubtless due to the uniformness of the littoral of the Warchałdzkie Lake, as compared with the very greatly differentiated littoral of the Narekie Lake.

In the Skanda Lake as many as 12 species did not occur at the smallest depths (Table VII). Except for *Limnephilus nigriceps*, all these taxa belong in the families:

Polycentropodidae, Hydroptilidae, Leptoceridae, Phryganeidae, Molannidae and Psychomyiidae, and in most cases are characteristic of the elodeid zone. In this lake the zonation of the vertical distribution of larvae became more evident when consideration was given to the numbers of larvae. Many species with wide occurrence ranges were most abundant only at definite depths. For example, *Orthotrichia* sp. was most numerous at depths of 0.4–2 m, *Mystacides longicornis* – at depths of 0.8–2 m, *Anabolia laevis* – in the zone of 0–0.4 m, *Limnephilus flavicornis* – at depths of 0–0.4 and 0.6–0.8 m, and *Molanna angustata* – at a depth of 2–3 m (Tab. VII).

Table VII. Distribution of the Trichoptera larvae in vertical profile of the Skanda Lake (total number of the collected larvae)

Taxon*	Depth (m)						
	0.2	0.4	0.6	0.8	1	2	3
Lt	3						
Lg	1						
Ila	21	7					
Ly	2	1					
Gp	3	3					
La	2	2					
Gi	2	29					
Gn	25			1			
Gs	6			1			
Ll	1			1			
Lc	4	7		7			
Lb	2	14		6			
Ls	44	55		16			
Ao	2	1		3			
Ne	9	7		4			
Lr	138	56		17			
Lm	16	3		38			
Pb	8	2		6	1		
Et	1	2		1	3	3	
Tb	48	12		39	2	2	
Al	192	68		37	5	5	
Lp	3	17		4		1	
Lf	145	175		109	1	6	
Mn	2	8	17	1		1	
Ms	1		2	1		9	
Ma	5	7		2		3	1
Ld	42	56		15			1

Taxon*	Depth (m)						
	0.2	0.4	0.6	0.8	1	2	3
Or	1	58	156	77	307	185	38
MI	3	1	14	38	57	121	34
Hly	1		1	4	51	8	1
Ac	1			2		13	11
Ln		10		2			
Aa		5	3	2	2	41	
Cf		3	1	1	1	9	1
Ox		4	5	3	36	61	4
Mo		7		7		13	34
Ps			1	1		4	
Ag			1		3	9	1
Tw			1	2	1	1	2
Pg					1		
Lc					1	1	1
Hd						1	
Cs						1	1
Total	734	620	202	448	472	498	130

*denotations of the taxa – as in Table V.

In the Brajnickie Lake (Tab. VIII), below the depth of 0.8 m the larvae were scarce. Only a few taxa present in small numbers did not occur at the smallest depths: *Economus tenellus*, *Cyrnus* sp. juv., *C. flavidus*, *Leptocerus tineiformis* (species characteristic of the elodeid zone of the Narckie and Warchaldzkie Lakes), *Oecetis furva*, *Athripsodes cinereus* and *Tinodes* sp. Species of the family Limnephilidae occurred at the smallest depths, whereas *Orthotrichia* sp. and *Mystacides* sp. juv. were present at the greatest ones.

Analysis of the distribution of the individual taxa allowed for detection of the species whose numbers most influenced the observed maxima of the numbers, presented in Fig. 1. The great numbers of caddis larvae in the most shallow littoral of the Narckie Lake were due to abundant occurrence of *Limnephilus griseus*, *Athripsodes cinereus*, *Limnephilus fuscicornis*, *Triaenodes bicolor*, *Limnephilus flavicornis*, as well as of *Athripsodes aterrimus*, *Agraylea multipunctata* and *Limnephilus auricula*. On the other hand, the great numbers of larvae at a 2-m depth (elodeid maximum of great numbers) resulted from the high numbers of: *Oxyethira* sp., *Mystacides* sp. juv., *Mystacides longicornis*, as well as of *Cyrnus crenaticornis*, *Athripsodes aterrimus* and *Leptocerus tineiformis* (Tab. V). The great numbers of larvae in the most shallow littoral of the Warchaldzkie Lake were caused by the high numbers of: *Limnephilus* sp. juv., *Tinodes waeneri*, *Athripsodes aterrimus*, *Anabolia laevis* and *Limnephilus flavicornis*. Therefore, the numbers in the most shallow littoral of the Warchaldzkie Lake depended, apart from *Athripsodes*

Table VIII. Distribution of the Trichoptera larvae in vertical profile of the Brajnackie Lake (total number of the collected larvae)

Taxon*	Depth (m)						
	0.2	0.4	0.6	0.8	1	2	3
Lb	3						
Lu	2						
Pb	2						
Ol	1						
Ll	1						
Ag	1						
Lp	1						
Lm	1						
Ln	1						
Ls	8	1					
Pg	4	1					
Cc	1	1					
Lg	1	1					
Al	23		5				
Lf	11	1		1			
Ox	4		3	3			
Mn	15		95	3			
Mo	16	2	8	5		1	
Ml	202	66	213	40		30	
Oo	19	8	1	9		3	
Lc	39	2	2	1		1	
Ms	47	5	8	32	1		1
Or	141	213	197	255	21	22	10
Lr		2					
Aa		1					
Et		2	6			1	
Ts			1				
Ac			1				
Of			2				
Cf			1	3			
Le			1	1			
Cs				1		1	
Total	544	306	544	354	22	59	11

*denotations of the taxa – as in Table V.

aterrimus and *Limnephilus flavicornis*, on other taxa than in the case of the Narckie Lake. The great numbers of larvae in the 0.6–0.8 m zone of the Warchałdzkie Lake (elodeid maximum of the high numbers) were due to the high numbers of: *Cyrnus flavidus*, *Ecnomus tenellus* as well as *Leptocerus tineiformis*, *Cyrnus crenaticornis*, *Tinodes waeneri* and *Athripsodes aterrimus*. At a depth of 1–2 m in the Warchałdzkie and Narckie Lakes the same species were dominant (Tabs. V and VI). Therefore, the shift in the Warchałdzkie Lake, as compared with the Narckie Lake, of the zone of increased numbers of caddis larvae towards the shallow littoral was unrelated to translocation of the taxa dominating at a depth of 1–2 m in the Narckie Lake. The latter shift occurred in an only small measure. The great numbers of larvae in the deepest littoral of the Skanda Lake (0–0.2 m in depth) resulted from the abundant occurrence of: *Anabolia laevis*, *Limnephilus flavicornis*, *L. rhombicus* and, in a lesser measure, of *Triaenodes bicolor*, *Limnephilus decipiens* and *Limnephilus* sp. juv. Unlike the remaining lakes, in this zone the typically elodeid species did not occur abundantly. The great numbers of larvae in the depth zone of 0.6–2 m were due to mass occurrence of: *Orthotrichia* sp., *Mystacides longicornis*, *Limnephilus flavicornis*, *Oxyethira* sp. and *Athripsodes aterrimus*. At 0.6–0.8 m depths *Limnephilus flavicornis* was the most numerous species, and at 0.8–1 m depths *Orthotrichia* sp. was most abundant, whereas *Mystacides longicornis* and *Hydroptila* sp. occurred in smaller numbers. At depths of 1–2 m *Orthotrichia* sp. and *Mystacides longicornis*, as well as *Oxyethira* sp. and *Athripsodes aterrimus* were most numerous (Tab. VII). The great numbers of caddis larvae in the most shallow zone of the Brajnkie Lake were related to the occurrence of *Mystacides longicornis* and *Orthotrichia* sp. The abundance of the species typical of rushes was relatively low, this making a distinction between the Brajnkie Lake, on the one hand, and the other lakes: Narckie, Warchałdzkie and Skanda. The high numbers of larvae in the depth zone of 0.4–0.6 m (deeper maximum of the numbers in the Brajnkie Lake) were most related to the mass occurrence of *Mystacides longicornis* and *Orthotrichia* sp. In the Brajnkie Lake, as compared with the Narckie and Warchałdzkie Lakes, these two taxa displayed evidently more shallow occurrence ranges. The same concerns all species characteristic of the elodeid zone. All Limnephilidae (except for *Limnephilus fuscicornis*), Phryganeidae, as well as *Agraylea multipunctata* and *Cyrnus crenaticornis* occurred exclusively at the smallest depths (Tab. VIII).

Summing up it can be stated that the numbers of species preferring definite depth zones changed with an increase in trophy. Therefore, the shift of the elodeid maximum of great numbers was mainly related to changes in the numbers of species, but not to alterations of the preferences regarding the vertical occurrence.

VERTICAL DISTRIBUTION OF INDIVIDUAL TAXA IN DIFFERENT TYPES OF LITTORAL

The character of the vertical occurrence of different taxa at selected sampling stations corresponding to several types of the littoral generally resembled the distribution of taxa in the individual lakes. There was, however, a certain individualism related to the habitat structure of the sampling stations. At all sampling stations three groups of species were singled out: the species occurring

only in the most shallow zone of the littoral (A), species found in the whole vertical profile (B) and species present more abundantly in the elodeid zone (C). Results of this analysis are presented in detail for two selected sampling stations in the Narckie Lake (Figs. 6, 7).

At the sampling station situated in wide, shallow psammolittoral, where the helophyte and elodeid zones were spatially apart (Fig. 6), the species characteristic of the elodeid zone (e.g. *Cyrnus crenaticornis*, *C. flavidus*, *Oxyethira* sp.) occurred in small numbers, if any, in the most shallow zone of the littoral (e.g. *Leptocerus tineiformis*, *Athripsodes aterrimus*). At the sampling station where the elodeid zone immediately adjoined the helophyte zone (Fig. 7), the same species were caught in greater numbers in the most shallow littoral zone. Furthermore, some species characteristic of the emerged vegetation occurred deeper than at the sampling station located in wide psammolittoral (e.g. *Triaenodes bicolor*).

The described picture testifies to migrations between vicinal habitats. The intensity of these migrations is proportional to the distance between the habitats.

4. DISCUSSION

The bimodal character of the distribution of caddis larvae in the vertical profile of the investigated lakes (Fig. 1) is consistent with the earlier findings concerning the Charzykowo Lake (Romaniszyn 1954), Borrevann Lake (Okland 1964), Lille-Jonsvann Lake (Solem 1973) and Sharpe Lake (June 1982).

Comparison of the larval numbers distribution in the vertical profile of the investigated lakes of the Olsztyn Lakeland points to the following shifts of the elodeid (deeper) maximum of greater numbers towards the more shallow zones: beginning from the Narckie Lake (2 m), through the Warchałdzkie (0.8 m) and Skanda (0.8–2 m) lakes, to the Brajnickie Lake (0.6 m). This may be grounded on decreasing water transparency in these four lakes (6, 3, 0.7 and 0.3 m, respectively) and to rising trophy (mesotrophy, eutrophy, eutrophy-hypertrophy, respectively). The observed regularity may be related to shallowing of the elodeid zone with a drop in water transparency (Bernatowicz, Wolny 1969), and to floristic changes consisting in, among others, alterations of the plant species composition, disappearance of the *Characeae* and *Ceratophyllum*, and more abundant occurrence of *Potamogeton*, with a decrease in water transparency (Pieczyńska, Rybak 1986).

Detailed analysis of the vertical distribution of the individual taxa indicated that the shift of the zone of increased numbers of larvae resulted to a greater extent from changes in the numbers of the species preferring various depths than from a change in the vertical distribution ranges of the individual taxa (though the latter phenomenon occurred as well).

Analysis of the phenological changes in the estimated numbers of larvae in vertical profile testified to a drop in the numbers of larvae in winter and early spring (Figs. 2–4). This drop exclusively concerned the deeper parts of the lake, i.e. the zone of submerged vegetation, and depended on lake trophy and water transparency.

According to detailed analysis of the distribution of the individual taxa, the species with narrow preference ranges (slight ecological valence), characteristic of the elodeid zone (e.g. *Cyrnus crenaticornis*), were eliminated to the greatest extent. On the other hand, the more eurytopic species (e.g. *Cyrnus flavidus*, *Mystacides longicornis*) displayed a smaller decrease in the numbers in the elodeid zone, with a drop in water transparency. In connection with the above-mentioned process of elodeid plant shallowing and changes in the elodeid species composition with a drop in water transparency, the observed faunistic changes in the vertical profile may be related to an increase in the astacitism in the elodeid zone. In lakes of greater trophy (and lower water transparency), the occurrence of the *Ceratophyllum* and *Myriophyllum* communities is of a more seasonal nature, and in the case of the *Potamogeton* communities seasonality is a rule. In lakes of lower trophy the *Characea*, *Ceratophyllum* and *Myriophyllum* display greater stability; namely, vegetative shoots persist throughout the year, and seasonal variations of the biomass are smaller than in the case of *Potamogeton*.

Moreover, there is no winter reduction of the numbers of larvae in the helophyte zone (most shallow littoral). This fact may be related to distinct life cycles of the Trichoptera species characteristic of this zone, among others to those enabling them to live under conditions of greater astacitism (Cz a c h o r o w s k i 1989).

In different lakes the vertical occurrence ranges of the same taxa were, in the main, similar. In the lakes of higher trophy, the vertical occurrence ranges of some taxa were, however, slightly more narrow and were shifted to the more shallow zone. Only in the case of some taxa it was possible to compare their distribution in vertical profile with that in other European lakes. It seems, furthermore, that the character of the vertical distribution of various taxa depends on the habitat structure in different fragments of the littoral, either facilitating or hindering the migrations of larvae. This was distinctly proved by an analysis of the vertical distribution in different types of the littoral (Figs. 6, 7).

Vertical distribution of *Cyrnus flavidus* in the Borrevann Lake (O k l a n d 1964), Lille-Jonsvann Lake (S o l e m 1973) and Konnevesi Lake (S a r k k a 1983) resembled that found in the present studies. Also the occurrence ranges of *Agraylea* were similar to those found for the Charzykowo Lake (R o m a n i s z y n 1954).

In the Borrevann Lake *Ecnomus tenellus* has been observed to be most abundant at a depth of 3 m (O k l a n d 1964), and in the Warchałdzkie Lake – at that of 0.8 m. *Oxyethira flavicornis* has been found to occur in the oligotrophic Konnevesi Lake (Finland) exclusively at a 3–5 m depth (S a r k k a 1983). Larvae of the genus *Oxyethira* have most abundantly occurred in the Charzykowo Lake at depths of 0.5 and 1–4.5 m (R o m a n i s z y n 1954). Larvae of this genus were most numerous in the Narckie and Warchałdzkie lakes at a 1–2 m depth (Tabs. V and VI).

The question arises why these are differences between various lakes in the preferences concerning the vertical distribution of both above-mentioned species. Lake trophy may be one of the causal factors. It is difficult, however, to detect a direct effect of trophy. This may only be an indirect effect resulting from changes in habitat conditions, e.g. from alteration of the vertical distribution of vegetation or from changes in its species composition.

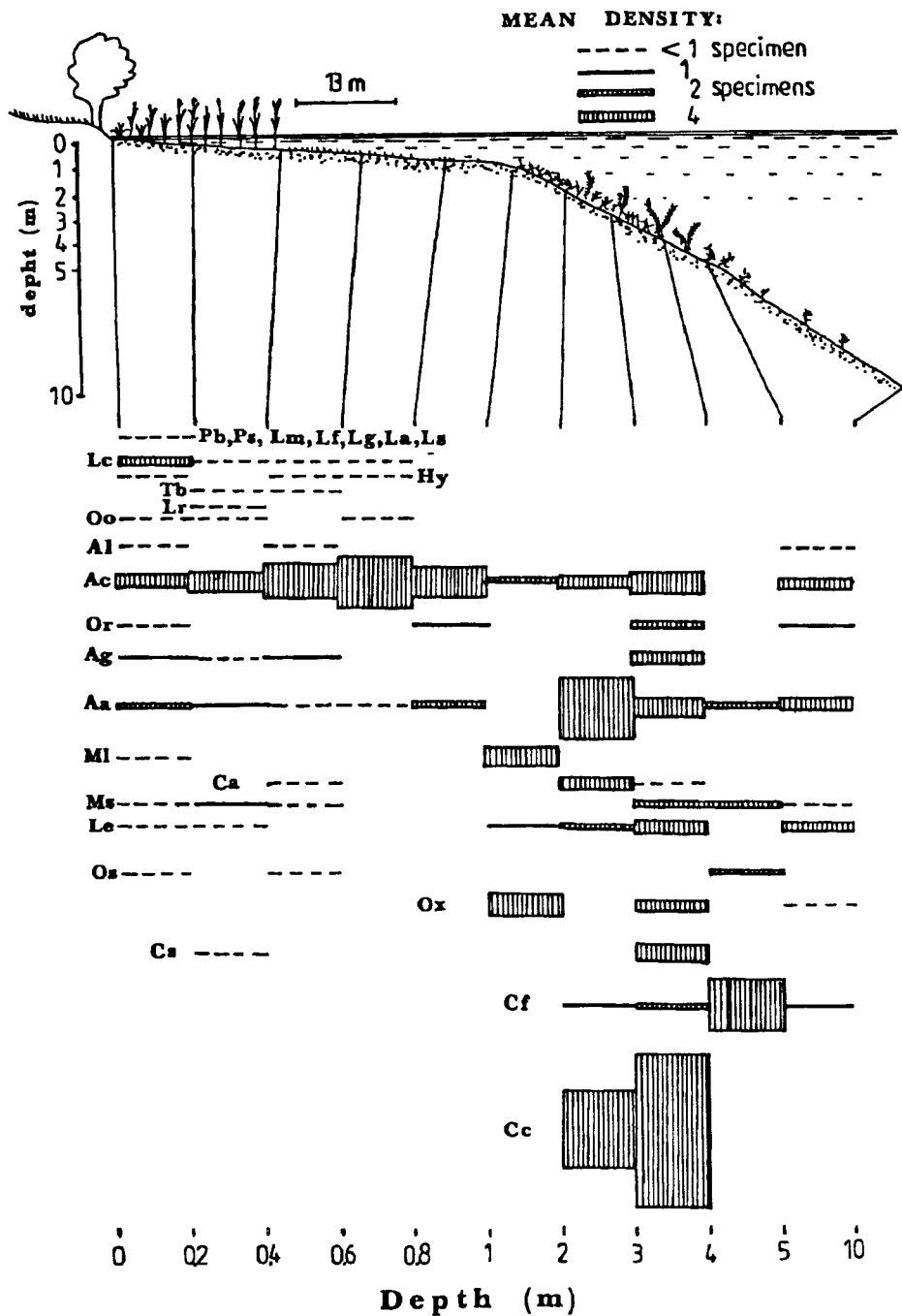


Fig. 6. Distribution of larvae of individual Trichoptera taxa (mean estimated density in one sample) in vertical profile; littoral with wide psammolittoral (Narckie Lake); denotation of the taxa – as in Table V

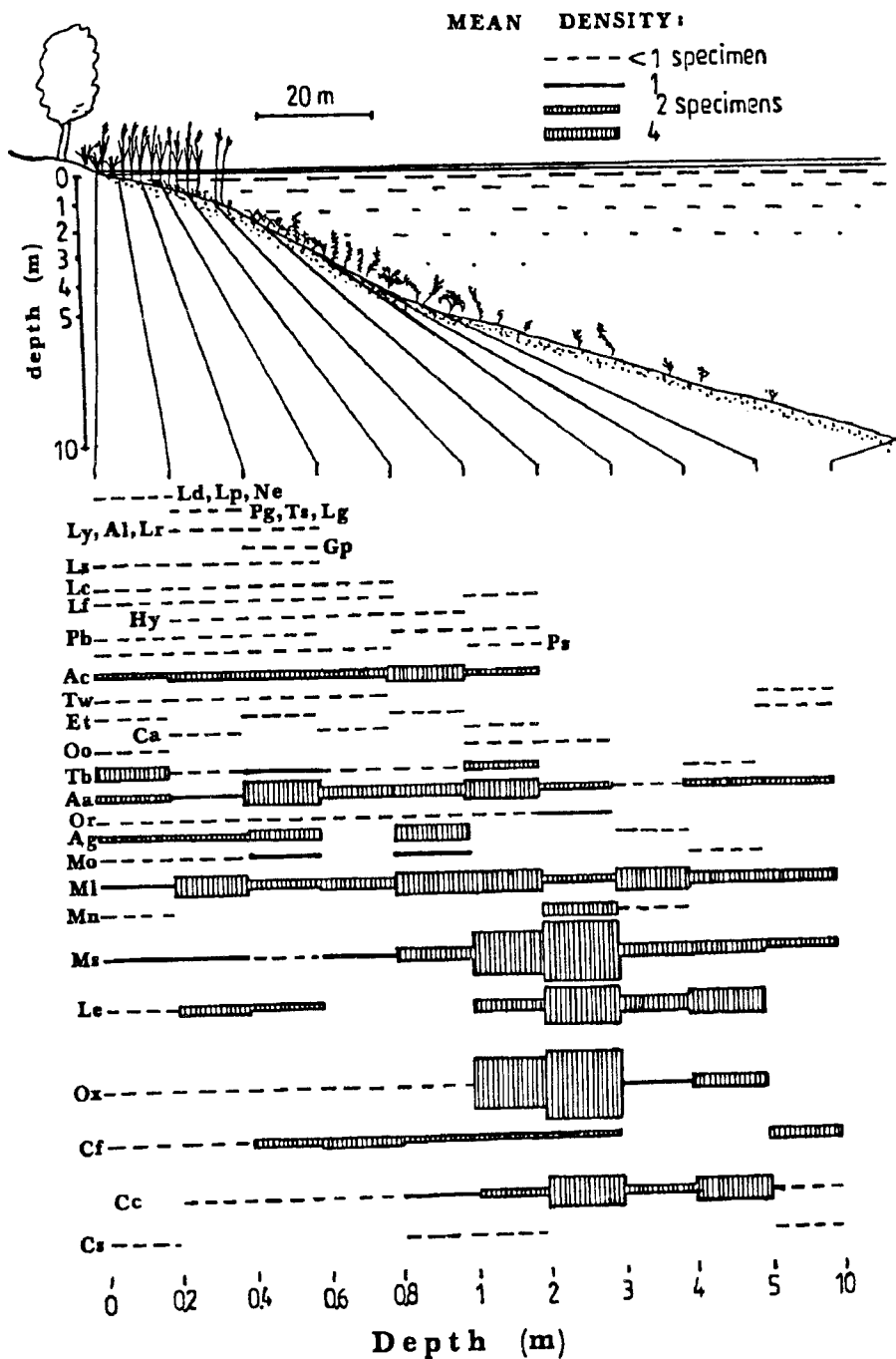


Fig. 7. Distribution of larvae of individual Trichoptera taxa (mean estimated density in one sample) in vertical profile; small-lake littoral (Narckie Lake); denotations of the taxa – as in Table V

It is well known that shallow littoral, as compared with the deeper parts of lakes, displays greater species diversity. For example, J a k h e r (1986) has found a high negative correlation between species differentiation in lake macrobenthos and depth. A similar relationship has been reported for the Chironomidae (B a n a s z a k 1984), Oligochaeta (P r e j s 1977) and macrobenthos (M i c h a ł k i e w i c z 1990). Likewise, also the present results point to the occurrence of many more species in the most shallow littoral, as compared with the elodeid zone. This character of species diversity in vertical profile may be due to the greater astacitism of the more shallow littoral, as compared with the deeper parts of lakes. Usually the less stable habitats are characterized by a greater number of species occurring in smaller numbers. Unstable habitats are to a greater extent colonized by species with wide ranges of ecological tolerance and low specialization, as well as with strong tendencies for migration and dispersitiveness (B r u t o n 1989, C o l l i e r et al. 1978, Czachorowski, in print).

It seems that the vertical distribution is secondary to the distribution and zonation of lake habitats (mainly vegetation) with which the Trichoptera larvae are associated. Therefore, the observed zonation and regularities in vertical distribution of the Trichoptera larvae would seem to result from zonation in the distribution of habitats in the elodeid zone. This suggestion is definitely confirmed by an analysis of the vertical distribution at individual sampling stations (Figs. 6, 7).

The present results testify to migrations of larvae between various habitats and depth zones. In the case of certain species, these are accidental migrations related to the distance between the habitats: the closer the habitats, the more abundant the migrations of larvae. This can be exemplified by the character of the occurrence of elodeid species (group C) at two different sampling stations in the Narckie Lake (Figs. 6, 7). Furthermore, a stronger tendency for such migrations was displayed by species with higher ecological valence. For example, *Cyrnus flavidus*, as compared with *C. crenaticornis*, was characterized by a stronger tendency for migration towards more shallow lake habitats (Figs. 6, 7).

In the case of other species, e.g. *Mystacides longicornis*, *Athripsodes cinereus* and *A. aterrimus*, it may be assumed that they undergo seasonal migrations between the elodeid zone and helophyte zone, irrespective of the distance between these habitats.

5. SUMMARY

In the years 1987–1990 studies were performed in four lakes of the Olsztyn Lakeland, differing in trophy: mesotrophic Narckie Lake, eutrophic Warchałdzkie Lake, eutrophic-hypertrophic Skanda Lake and hypertrophic Brajnkie Lake. In total, more than 800 samples containing over 15 000 Trichoptera larvae were collected.

There were two maxima of the greatest numbers of larvae in vertical profile of the lakes. One maximum occurred in the most shallow littoral (depths up to 0.2 m). The second maximum, referred to as the elodeid maximum of the numbers, appeared in the zone of submerged vegetation (depths of 0.6–2 m, in dependence on the lake) (Fig. 1). It was found that the lower the water transparency and the higher the lake trophy, the more shallow the occurrence of the elodeid maximum of the great numbers of larvae. Analysis of the distribution of the individual taxa (Tabs. V–VIII) showed that shallowing of the elodeid maximum of the numbers was mainly due to the greater numbers of species

preferring smaller depths, whereas it resulted to an only lesser extent from changes in the occurrence, in vertical profile, of the individual taxa in lakes of different trophy.

The drop in the density of larvae, observed in winter and early spring, was limited to only the deeper zone of the littoral (submerged vegetation) (Figs. 2–5). No such a regularity was found for the most shallow littoral, since there the larvae were most numerous in spring.

In the most shallow littoral, the larvae of the family Limnephilidae were most abundant. Species preferring the deeper and more stabile elodeid zone mainly belonged in the families Leptoceridae, Polysentropodidae and partly Hydroptilidae.

Vertical distribution of some species (e.g. of *Mystacides longicornis*, *Athripsodes aterrimus*) testified to migration of larvae from the deeper zones towards the bank during larval growth. Moreover, there was migration of the larvae between adjoining habitats, being dependent on the distance between these habitats (Figs. 6, 7).

The vertical occurrence ranges of the same species in the investigated lakes and in other European lakes were in the main similar. Most likely, the observed differences were to a great extent related to lake trophy. In lakes of higher trophy, the species typical of the more stabile elodeid zone, as compared with those characteristic of the less stabile bulrush-rushes zone, displayed more narrow and more shallow occurrence ranges.

6. STRESZCZENIE

Badania prowadzono w latach 1987–1990 w czterech jeziorach Pojezierza Olsztyńskiego o różnej trofii: mezotroficznym (J. Narckie), eutroficznym (J. Warchałdzkie), eutroficzno-hypertroficznym (J. Skanda) i hypertroficznym (J. Brajnickie). Pobrano łącznie ponad 800 prób, w których stwierdzono występowanie ponad 15 tys. larw Trichoptera.

Zauważono dwa szczyty największych liczebności larw w profilu pionowym jezior. Jeden występował w najpłytszym litoralu (głębokość do 0,2 m). Drugi natomiast – zwany dalej elodeidowym szczytem liczebności – występował w strefie roślinności zanurzonej (od 0,6 do 2 m w zależności od jeziora) (rys. 1). Zauważono, że im mniejsza przezroczystość wody i większa trofia jeziora tym płycej występował elodeidowy szczyt dużych liczebności larw. Analiza rozmieszczenia poszczególnych taksonów (tabele V–VIII) wykazała, że wypływanie się elodeidowego szczytu liczebności wynikało głównie z większych liczebności gatunków preferujących mniejsze głębokości. W mniejszym stopniu wynikało to ze zmiany występowania w profilu pionowym poszczególnych taksonów w jeziorach o różnej żyzności.

Obserwowany zimowy i wczesno-wiosenny spadek liczebności larw ograniczony był jedynie do głębszej strefy litoralu (roślinność zanurzona) (rys. 2–5). W najpłytszym litoralu nie obserwowano takiej prawidłowości, larwy najliczniejsze były w okresie wiosny.

W najpłytszym litoralu najliczniejsze były larwy należące do rodziny Limnephilidae. Gatunki preferujące głębszą i stabilniejszą strefę elodeidową należały głównie do rodziny Leptoceridae, Polycentropodidae i częściowo Hydroptilidae.

Rozmieszczenie pionowe niektórych gatunków (np. *Mystacides longicornis*, *Athripsodes aterrimus*) wskazuje na migrację larw ze stref głębszych ku brzegowi w trakcie wzrostu larw. Zaobserwowano także migrację larw pomiędzy sąsiadującymi siedliskami, zależną od odległości między tymi siedliskami (rys. 6, 7).

Pionowe zasięgi występowania tych samych gatunków w badanych jeziorach oraz innych jeziorach Europy były w zasadzie podobne. Zaobserwowane różnice wynikały najprawdopodobniej w dużym stopniu z wpływu trofii jezior. W jeziorach o większej trofii obserwowano węższe i płytsze zakresy występowania gatunków typowych dla stabilniejszej strefy elodeidowej, natomiast szersze i głębsze zakresy występowania gatunków charakterystycznych dla mniej stabilnej strefy szuwarowo-ooczeretowej.

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