Trichoptera from River Vindelälven in Swedish Lapland

A four-year study based mainly on the use of light-traps

By Staffan Ulfstrand

Department of Animal Ecology, University of Lund

1. Introduction

Long since national organisations for nature conservancy and scientific research have been aware of the need for, and more recently also been able to raise the means for ecological documentation of those Swedish rivers that are facing large-scale exploitation for hydroelectric purposes. One of the few major river systems still practically unaffected by regulations is River Vindelälven, the eighth in size of Swedish rivers, where I have had the opportunity of carrying out ecological and faunistical research during a number of years.

The present report deals with a collection of adult caddisflies (Trichoptera) assembled in the Ammarnäs area at the upper parts of River Vindelälven. The material comprises about 100,000 specimens.

Probably few caddisfly species new to the Swedish fauna remain to be discovered, so that the general qualitative composition of this group may be regarded as fairly wellknown (Forsslund & Tjeder 1942, Forsslund 1955). But the distribution patterns of the species, not to speak of their bionomics, are only known in very broad terms, although Tobias' (1969 a and other papers) recent work has added considerably to our knowledge. Most valuable for comparative purposes is a report by Forsslund (1954) on a large collection of caddisflies from the lower part of River Vindelälven. Nybom's (1960) comprehensive survey of Finnish caddisflies might also be mentioned here.

The main purpose of my mission to River Vindelälven was to analyze the benthic communities of some lotic biotopes (Ulfstrand 1968 a). Alongside this work I attempted a qualitative survey of the aquatic fauna; this has produced a previous report on the mayflies (Ephemeroptera) and stoneflies (Plecoptera) from the same area (Ulfstrand 1969 a).

2. Study area

Since detailed information about the environmental conditions in the study area has been published elsewhere (Ulfstrand 1968 a, 1969 a), only some essential features need be repeated here.

The work was centred around the small village of Ammarnäs (lat. 65°58′N, long. 16°12′E) in the province of Lycksele Lappmark, Lapland. The present material exclusively derives from within 20 km distance of Ammarnäs. Within this restricted area a wide variety of aquatic biotopes occur, ranging from large rivers to small streams and from deep lakes to small pools and temporary inundations. All the biotopes are practically unaffected by direct pollution and similar influences of civilization.

The Ammarnäs area is situated partly within the high-boreal coniferous forest zone (the taiga), partly in the subalpine birch forest region. Altitudes vary from about 380 m in the east to 550 m in the west; these figures refer to the valley bottom. Mountains with perennial snow fields and a few small glaciers rise to 1200 to 1600 m everywhere around the valley.

Environmental factors of special significance in this region are the long period of ice and snow cover, usually from November to late May or June, and the extraordinarily large seasonal and daily fluctuations of water flow, the average annual maximum being as much as 100 times as large as the average annual minimum.

3. Methods

Adult caddisflies were collected manually and with the use of light-traps. Sweep-nets were used to collect caddisflies resting in vegetation, and stones and debris along lake shores and river banks were searched for insects. Comparatively much less time was spent at lenitic than at lotic localities, with obvious consequences for the composition of the catch. The field work periods are shown in Tab. 1.

In 1962 to 1965, inclusively, light-traps with UV-lamps (Philips HPW 125 W, maximal emission at 3655 Å, mainly "black light") were operated for long periods (Tab. 2). The traps were looked after by local people who were instructed to change the jars as soon as these were half-filled with insects but at least, irrespectively of the catch, every seventh day. For certain periods in 1964 and 1965, the jars were changed daily. All the light-traps were placed close to lotic localities.

Light-trap I (LT I) was placed at River Vindelälven, about 18 km SE of Ammarnäs. At this site the river comes out from a long lake-like extension and is broad, rapid and shallow. The trap was on the top of a steep river bank with the lamp about 5 above normal summer water level. Both lotic and lenitic biotopes were close to the trap site. The immediate surroundings were hay-fields, with coniferous and mixed forest at further distance.

LT II was at River Tjulån, a large tributary of River Vindelälven, about 3 km W of Ammarnäs. This river has a relatively steep and even gradient so that there were no lenitic localities worth mentioning near the trap site. The surroundings were similar to those at LT I. The lamp was about 2 m above normal summer water level.

LT III was also at River Tjulån, within the village of Ammarnäs. At this site the river flows rapidly over stony bottom, but about 200 m further downstream the current slackens and the bottom is soft. Shortly thereafter River Tjulån and River Vindelälven unite and build up a large delta with still-water biotopes of many kinds. The lamp was about 2 m above normal summer water level. The surroundings were similar to those at LT I and II.

In all three cases, the nearest artificial light-sources were about 100 m from the traps. The traps were placed openly, so that no vegetation was to screen the light.

Tab. 1. *Field work periods in the Ammarnäs area.*

1961	16—31/7
1962	14—28/7, 1—22/8, 3—8/10
1963	7/6—13/8, 12—17/11
1964	4/5—18/9
1965	13/7—23/8
1966	8—10/6, 29/9—2/10

The flight periods of most of the important species were covered in all years, but the differences in trapping periods should be kept in mind when evaluating the data. The most serious gap was in 1963, when LT III was out of function from 11 September to 4 October.

4. *Taxonomical remarks*

The nomenclature of Botosaneanu (1967) is followed except in the genus *Potamophylax,* in which recent work by Neboiss (1963) and Tobias (1969 b) seems to call for a change affecting the wellknown "species" *Potamophylax stellatus* Curt. According to the authorities quoted, this in fact consists of two species, *P. latipennis* Curt. and *P. cingulatus* Steph. Although with some hesitation I have adopted their conclusion. Most males are easily referable to either of the two forms, using the characters discussed by Tobias, viz. the shape of the apex of the phallus and the curvature of the parameres. But I have seen a few males which seem to be intermediate between *latipennis* and *cingulatus*: the apical cusps of the phallus being much shorter and blunter than in *latipennis,* but not absent as in *cingulatus.* The upper and middle appendages seem to be useless as species criteria. I wish to emphasize that only a small minority of males are thus doubtful. Judging from the shape of the parameres I have usually grouped them with *cingulatus.* Moreover, in spite of Décamps' (1966) work I am unable to distinguish between the females of the two forms. Therefore, in Tab. 3, a small number of *P. latipennis* females may have been included among *P. cingulatus.*

5. *General survey of the collection*

The total collection of adult caddisflies from the Ammarnäs area amounts to 99,939 specimens belonging to 82 species (Tab. 3). Much the most species-rich family is Limnephilidae with 47 species. Two species are very dominant in the material, viz. *Rhyacophila nubila* with 63,401 specimens (63.4 %) and *Apatania stigmatella* with 25,973 specimens (26.0 %). The remaining 80 species make up only 10.6 % of the total material (cf. Tobias 1968).

The light-traps yielded 96,416 specimens (96.5 %), while 3523 specimens (3.5 %) were hand-collected.[1]

6. *Faunistically notable records*

Rhyacophila obliterata McL. Only recorded from a very few places in Lapland, but possibly overlooked because of its late flight period.

[1] The following abbreviations are used heretoafter: LTC=light-trap collection(s), HC=hand-collection(s).

Tab. 2. *Periods of light-trap operation.*

Year	Light-trap: I	II	III
1962	13/7— 4/10	16/7—7/10	14/7—30/9
1963	10/6—15/11	—	12/6—11/9, 4/10—16/11
1964	2/5—15/9	—	20/4—15/9
1965	1/7— 1/10	—	1/7— 1/10

Synafophora intermedia Klap. The same comment, but in this case the reason for its rarity in collections rather may be its early flight period. Its limited local distribution in the Ammarnäs area indicates that it also has relatively restricted habitat requirements (Ulfstrand 1968 a).

Oxyethira frici Klap. New to Lycksele Lappmark. The distribution of hydroptilids in Sweden is poorly known.

Hydroptila forcipata Etn. New to Lycksele Lappmark.

Chimarra marginata L. New to Lapland; the most northerly previous record was from the province of Jämtland.

Holocentropus insignis Mart. New to Lycksele Lappmark. Probably widely distributed in northern Sweden.

Holocentropus picicornis Steph. New to Lycksele Lappmark. Same comment.

Limnephilus extricatus McL. New to Lycksele Lappmark. Used to be regarded as a very rare species in the north but recently recorded from several places by Tobias (1969 a).

Limnephilus flavicornis F. New to Lycksele Lappmark. A distinctly southerly species although known also from Lule Lappmark to the north of Lycksele Lappmark.

Limnephilus lunatus Curt. New to Lapland, apart from an old doubtful record from Lule Lappmark.

Limnephilus sparsus Curt. According to Tobias (op. cit.) "presumably" known from Lycksele Lappmark. The present records would thus be the first definite ones.

Colpotaulius incisus Curt. New to Lycksele Lappmark. Widespread.

Grammotaulius atomarius F. New to Lapland. The previous most northerly record is from the province of Uppland.

Glyphotaelius pellucidus Retz. Apart from an unsubstantiated record from Lule Lappmark this is the first from Lapland. Previously reported from the provinces along the Bothnian Gulf; in the interior not known farther north than Jämtland.

Asynarchus impar McL. A very rare species in Sweden.

Lenarchus bicornis McL. The type specimen with unknown locality somewhere in Swedish Lapland and a female collected in Lycksele Lappmark in 1967 by Tobias (in litt.) are the only other records from the Scandinavian peninsula.

Lenarchus productus Mort. New to Lycksele Lappmark. A very rare species in Sweden although Tobias (op. cit.) cites a number of recent records from Lule Lappmark.

Potamophylax cingulatus Steph. and *P. latipennis* Curt. Both are to be registered for Lycksele Lappmark.

Micropterna sequax McL. New to Lycksele Lappmark.

Hydatophylax infumatus McL. New to Lycksele Lappmark.

Goera pilosa F. Previously known from Lycksele Lappmark, but a scarce species in the north.

Athripsodes dissimilis Steph. New to Lycksele Lappmark.

7. *The caddisfly fauna at the upper and lower parts of River Vindelälven*

Over a number of years Forsslund (1954) using sweep-nets collected caddisflies at the lower parts of River Vindelälven, particularly around the village of Vindeln (approx. 64°15′N, 19°45′E), about 60 km from the coast of the Bothnian Gulf.

Entomol. Ts. Årg. 91. H. 1–4, 1970

Tab. 3. *The total collection of caddisflies (Trichoptera) from the Ammarnäs area at upper Vindelälven, Swedish Lapland. LTC=light-trap collection, HC=hand-collection. Months are divided in ten-day periods (I, II, III).*

	LTC		HC		6	6	6	7	7	7	8	8	8	9	9	9	10	Total	To-	Grand
	♂♂	♀♀	♂♂	♀♀	I	II	III	I	II	III	I	II	III	I	II	III	I—III	LTC	tal HC	total
Rhyacophila nubila Zett.	9038	53711	373	279	—	—	—	—	5	1360	2231	8014	22956	24154	3197	1262	222	62749	652	63401
Rh. obliterata McL.	13	—	6	—	—	—	—	—	—	—	—	—	—	4	8	6	1	13	6	19
Synafophora intermedia Klap.	218	186	136	146	—	15	61	208	368	29	4	1	—	—	—	—	—	404	282	686
Oxyethira frici Klap.	1	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	—	1
Hydroptila forcipata Etn.	94	136	—	—	—	—	—	—	3	65	46	116	—	—	—	—	—	230	—	230
Agraylea cognatella McL.	1	—	1	—	—	—	—	—	—	2	—	—	—	—	—	—	—	1	1	2
Philopotamus montanus Don.	—	—	51	43	—	23	—	19	16	36	—	—	—	—	—	—	—	—	94	94
Chimarra marginata L.	1	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1	—	1
Arctopsyche ladogensis Kol.	20	12	64	34	—	—	—	17	71	41	—	1	—	—	—	—	—	32	98	130
Hydropsyche nevae Kol.	1	5	—	—	—	—	—	1	—	—	1	3	1	—	—	—	—	6	—	6
Plectrocnemia conspersa Curt.	—	—	2	8	—	—	—	—	4	2	4	—	—	—	—	—	—	—	10	10
Polycentropus flavomaculatus Pict.	15	28	194	89	—	—	—	—	59	169	89	9	—	—	—	—	—	43	285	328
Holocentropus insignis Mart.	—	—	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1	1
H. picicornis Steph.	—	—	2	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	2	2
Cyrnus flavidus McL.	—	—	2	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	2	2
C. trimaculatus Curt.	—	—	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1	1
Agrypnia obsoleta McL.	1	2	97	61	—	—	—	32	51	67	9	1	1	—	—	—	—	3	158	161
Phryganea bipunctata Retz. (=*striata* L. auctt.)	—	—	4	2	—	—	—	—	1	5	—	—	—	—	—	—	—	—	6	6
Oligotricha lapponica Hag.	1	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	—	1
Micrasema naevum Hag. (=*gelidum* McL. auctt.)	1	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	—	1
Apatania stigmatella Zett.	6049	19484	168	272	—	—	—	1	39	248	962	3065	17699	2616	1324	16	3	25533	440	25973
A. wallengreni McL.	221	240	105	180	62	352	144	130	57	1	—	—	—	—	—	—	—	461	285	746
A. zonella Zett.	—	—	—	27	—	—	—	15	12	—	—	—	—	—	—	—	—	—	27	27
Limnephilus algosus McL.	—	—	—	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	1
L. borealis Zett.	273	118	6	16	—	—	—	—	—	3	28	114	150	92	23	2	1	391	22	413
L. coenosus Curt.	87	2	10	5	—	—	—	—	6	15	9	7	12	37	8	7	3	89	15	104
L. elegans Curt.	2	1	1	—	—	—	—	—	—	2	—	—	2	—	—	—	—	3	1	4
L. externus Hag.	3	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	3	—	3
L. extricatus McL.	15	—	—	—	—	—	—	—	1	5	5	3	1	—	—	—	—	15	—	15
L. femoratus Zett.	1	—	46	45	—	—	—	—	49	40	2	1	—	—	—	—	—	1	91	92
L. fenestratus Zett.	11	—	1	—	—	—	—	—	—	—	—	1	3	8	—	—	—	11	1	12
L. flavicornis Fbr.	—	—	—	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	1
L. fuscicornis Ramb.	7	—	1	4	—	—	—	—	1	11	—	—	—	—	—	—	—	7	5	12
L. lunatus Curt.	2	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	2	—	2
L. nigriceps Zett.	2	—	11	4	—	—	—	—	—	—	—	—	1	4	12	—	—	2	15	17
L. pantodapus McL.	11	—	—	9	—	—	—	—	8	11	1	—	—	—	—	—	—	11	9	20

L. picturatus McL.	—	—	3	—	—	—	—	—	2	—	1	—	—	—	—	—	—	—	3	3
L. rhombicus L.	30	1	—	—	—	—	—	—	—	5	4	3	18	—	—	1	—	31	—	31
L. scalenus Wall.	6	—	—	—	—	—	—	—	—	—	1	—	2	2	1	—	—	6	—	6
L. sericeus Say	17	3	4	—	—	—	—	1	—	1	—	4	9	8	1	—	—	20	4	24
L. sparsus Curt.	39	—	—	—	—	—	—	—	—	—	—	—	17	13	7	2	—	39	—	39
L. stigma Curt.	86	6	2	7	—	—	—	1	1	8	4	22	32	28	3	2	—	92	9	101
L. vittatus Fbr.	39	—	1	1	—	—	—	—	—	—	4	5	5	19	3	5	—	39	2	41
Colpotaulius incisus Curt.	—	—	1	1	—	—	—	—	—	1	1	—	—	—	—	—	—	—	2	2
Grammotaulius atomarius Fbr.	1	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	—	1
G. signatipennis McL.	5	2	—	1	—	—	—	—	—	2	3	3	—	—	—	—	—	7	1	8
Glyphotaelius pellucidus Retz.	2	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	2	—	2
Anabolia concentrica Zett.	1042	12	3	—	—	—	—	—	—	14	39	264	624	108	8	—	—	1054	3	1057
Phacopteryx brevipennis Curt.	2	—	2	3	—	—	—	—	1	5	1	—	—	—	—	—	—	2	5	7
Asynarchus contumax McL.	4	—	—	—	—	—	—	—	1	3	—	—	—	—	—	—	—	4	—	4
A. impar McL.	—	—	2	2	—	—	—	—	4	—	—	—	—	—	—	—	—	—	4	4
A. lapponicus Zett.	16	—	7	5	—	—	—	—	—	7	5	1	9	5	1	—	—	16	12	28
A. thedenii Wall.	69	—	4	3	—	—	—	—	—	1	3	6	56	10	—	—	—	69	7	76
Lenarchulus trimaculatus Zett.	3	—	18	32	—	—	—	3	16	31	1	—	1	1	—	—	—	3	50	53
Lenarchus bicornis McL.	3	—	—	—	—	—	—	—	—	1	1	1	—	—	—	—	—	3	—	3
L. productus Mort.	3	—	—	—	—	—	—	—	—	1	1	—	1	—	—	—	—	3	—	3
Rhadicoleptus alpestris Kol.	44	—	6	1	—	—	—	—	6	8	6	3	7	6	2	5	8	44	7	51
Potamophylax cingulatus Curt.	1030	118	59	77	—	—	—	38	290	573	253	70	32	23	2	2	1	1148	147	1295
P. latipennis Curt.	6	—	6	—	—	—	—	—	—	6	6	—	—	—	—	—	—	6	6	12
P. nigricornis Pict.	5	1	2	—	—	—	—	—	1	1	2	—	1	3	—	—	—	6	2	8
Halesus digitatus Schrk.	453	521	14	18	—	—	—	—	—	2	19	70	373	303	89	100	50	974	32	1006
H. radiatus Curt.	400	57	17	6	—	—	—	—	—	15	150	104	146	51	5	7	2	457	23	480
H. tesselatus Ramb.	750	741	26	21	—	—	—	—	—	59	6	125	937	348	45	11	7	1491	47	1538
Micropterna sequax McL.	27	3	1	—	—	—	—	—	—	—	—	2	3	24	2	—	—	30	1	31
Hydatophylax infumatus McL.	1	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	—	1
Chaetopteryx villosa Fbr.	95	10	29	28	—	—	—	—	—	1	—	5	1	26	32	55	42	105	57	162
Annitella obscurata McL.	135	57	55	30	—	—	—	—	—	—	—	7	8	34	87	132	9	192	85	277
Goera pilosa Fbr.	—	—	1	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	1
Silo pallipes Fbr.	17	1	1	4	—	—	—	—	2	21	—	—	—	—	—	—	—	18	5	23
Lepidostoma hirtum Fbr.	36	408	22	69	—	—	—	—	72	14	412	30	6	1	—	—	—	444	91	535
Athripsodes annulicornis Steph.	20	49	20	11	—	—	—	—	2	8	63	25	1	1	—	—	—	69	31	100
A. cinereus Curt.	—	—	3	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—	3	3
A. dissimilis Steph.	2	1	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	3	—	3
A. fulvus Ramb.	—	—	1	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	1
A. nigronervosus Retz.	13	3	73	12	—	—	—	2	6	90	3	—	—	—	—	—	—	16	85	101
A. perplexus McL.	—	1	1	—	—	—	—	—	1	—	—	—	1	—	—	—	—	1	1	2
Mystacides azurea L.	—	—	15	4	—	—	—	—	10	—	9	—	—	—	—	—	—	—	19	19
M. longicornis L.	—	—	65	21	—	—	—	—	—	86	—	—	—	—	—	—	—	—	86	86
Oecetis ochracea Curt.	—	—	2	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	2	2
Molanna albicans Zett.	—	—	58	47	—	—	—	—	50	53	—	2	—	—	—	—	—	—	105	105
M. angustata Curt.	—	—	49	15	—	—	—	23	29	12	—	—	—	—	—	—	—	—	64	64
Molannodes tincta Zett.	—	—	11	4	—	—	—	—	—	14	1	—	—	—	—	—	—	—	15	15
																		96416	3523	99939

Forsslund's list from the Vindeln area includes 40 species absent from the Ammarnäs list, on which there are 30 species absent from the Vindeln list. No less than 32 of the 40 species exclusively found by Forsslund were non-limnephilids, while of the 30 species only found by myself 11 were non-limnephilids. These large discrepancies between the caddisfly lists from the two areas provide a good illustration of the faunistical and ecological transition along the river (cf. p. 53).

8. Flight periods

In comparison with mayflies and, still more, stoneflies, the caddisflies in North Sweden have very late flight periods. In the Ammarnäs area only three species were taken in June, viz. *Synafophora intermedia, Philopotamus montanus* and *Apatania wallengreni*. It is worth noting that all three belong to the small group of exclusively lotic caddisflies.

Twelve species were taken in October, and some were abundant as late as this, viz. *Rhyacophila nubila, Rhadicoleptus alpestris, Halesus digitatus, Chaetopteryx villosa* and *Annitella obscurata*. All these are limnephilids.

As a rough estimate of the peak of the flight period of a given species, the decade during which the median specimen was taken may be used. Adopting this method and including every species obtained in the LTC and/or HC, one finds that, generally speaking, limnephilids have much later flight periods than non-limnephilids (Fig. 1) (cf. Crichton 1960, Tobias 1968, 1969 a). The most species-rich decade is the last third of July with 58 species; but this comparison is not correct because of the different periods of field work in the different years.

The bimodality in the histogram for the limnephilids does not seem to be explicable in terms of irregularities in the functioning of the traps, and the relative importance of the hand-collection is too small to affect the pattern like this. However, since many species are present in the material in very low numbers, there is plenty of room for random deviation from the normal curve.

The life cycles of many lotic species were found to be correlated with changes in the food abundance in the larval habitats (Ulfstrand 1968 a, b, 1969 a). As we do not know the habitat and food requirements of the lenitic caddisfly species which make up the great majority of species in the present material, it is not yet possible to look for similar relationships among them. It seems very likely that the basic cause will often be found to be connected with larval ecology. In the adult stage caddisflies seem to make very modest demands on their environments, particularly in terms of nutrition (e.g. Crichton 1957, 1960). The fact that the flight periods of many species extend until well after severe autumnal frosts are regular, indicates that caddisfly imagines are not particularly sensitive to this kind of vicissitudes. Presumably the flight periods are often consequential to selective pressures operating in the aquatic larval stages. This would be in agreement with the findings by Novak & Sehnal (1963) who established that in several *Limnephilus* spp. adults have a long period of quiescence after their emergence from the water and before the time of copulation and egg laying.

Since artificial light sources are more attractive when contrasted with a dark background than when background illumination is strong, light-traps

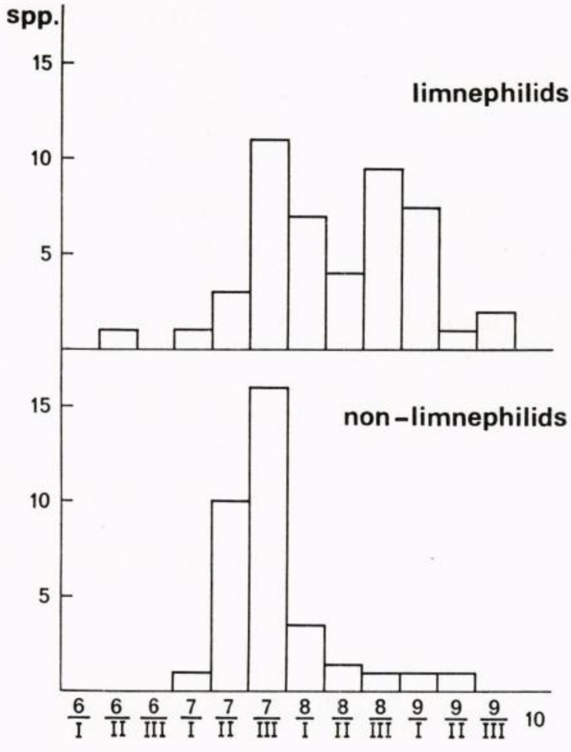

Fig. 1. Time distribution of peaks of flight periods: a comparison between limnephilids and non-limnephilids.

must be expected to be more efficient towards autumn when nights are relatively dark even at high latitudes than in the middle of summer (cf. Verheijen 1958, Southwood 1966). Because the average limnephilid has a later flight period than the average non-limnephilid, light-traps are *ipso facto* likely to be more effective for the former than for the latter group. This circumstance may enhance the difference in composition between Forsslund's and my own collections from different parts of River Vindelälven (cf. above). An examination in zoogeographical terms, however, supports the contention that the difference was chiefly due to the environmental conditions (geographical positions) of the two study areas.

9. Comparison between the hand-collection (HC) and the light-trap collection (LTC)

9.1. Quantitative differences

As already mentioned, no less than 96.5 % of the caddisflies were obtained in the LTC. This is in contrast to the mayflies and stoneflies (Ulfstrand 1969 a). Mayflies usually were totally unattracted by the light-sources used, and of the stoneflies only one species, viz. *Leuctra fusca* L., was obtained in large numbers. It may be worth noting that the flight period of *L. fusca* is much later than in any other Scandinavian stonefly species.

Again it seems possible that part of the explanation is the later flight periods of caddisflies, as a group, compared with the mayflies and stoneflies. In addition most caddisflies are active only during rather low illumination (cf. Brindle 1958, Crichton 1960); there are exceptions though. On the other hand mayflies and stoneflies are often fully active in bright sunshine, although certain activities, such as egg laying, are chiefly carried out in late afternoon or evening.[2]

The large numbers of caddisflies obtained in the LTC suggest that this group is very suitable for long-term quantitative studies using automatic trapping devices.

9.2. Qualitative differences

Of the 22 species not obtained in the LTC but in the HC, six were limnephilids and 16 were non-limnephilids (Tab. 3). The reverse proportion was found among the 19 species absent from the HC, viz. 12 limnephilids and 7 non-limnephilids.

It is rather interesting that almost the same number of species was obtained in the HC and the LTC, although the species composition was different in important respects. If one wants to make an inventory of the caddisfly fauna of an area, then obviously light-traps and manual collecting activities produce supplementary collections, and neither method could be neglected.

9.3. The dominant species

As shown in Fig. 2 the degree of dominance of the two most abundant species in the total material, viz. *Rhyacophila nubila* and *Apatania stigmatella,* was very different in the LTC and HC.

In the LTC, *Rh. nubila* and *A. stigmatella* in combination made up 92.1 % of the total. The six most abundant species made up 96.4 % leaving only 3.6 % for the other 54 species.

In the HC, *Rh. nubila* and *A. stigmatella* were again the most numerous species but between themselves only made up 31 % of the total. The six most abundant species made up 59.4 % and the remaining 57 species 40.6 %.

A human collector deliberately spreads his efforts over a variety of biotopes and discontinues his activity having procured what he regards an adequate sample from a locality. It is not surprising that abundant species become "over-represented" in the LTC in comparison with the HC; rather it is remarkable that the LTC included so large a proportion of the total number of species recorded from the study area.

9.4. Some factors affecting the trappability of the species

For reasons given previously the traps were located at sites near lotic biotopes, and a large proportion of the HC also derives from such places. Therefore it is not unexpected that all the six most numerous species in the HC derive from lotic biotopes. It is more surprising that three of these species do not at all occupy so prominent positions in the LTC, where their dominance might be expected to be greater still, if distance to reproduction

[2] This difference between caddisflies on the one hand and mayflies on the other breaks down under different climatical conditions where both groups may be more or less nocturnal (Corbet & Tjönneland 1955, Tjönneland 1960).

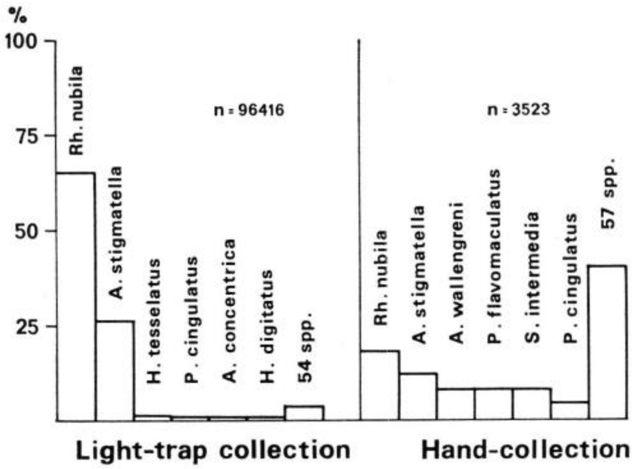

Fig. 2. Showing the proportion of the six most numerous species in the total light-trap and hand-collections.

localities was a decisive factor for the probability of a given species being obtained in a trap (the trappability of the species). It would seem that, in these three species, although they occur abundantly near the traps, some factor prevents them from being trapped in quantities. It is then noteworthy that two of them are among the very early species, viz. *Synafophora intermedia* and *Apatania wallengreni* (cf. Tab. 3). The light conditions during their flight periods probably render the traps comparatively ineffective.

The third species, *Polycentropus flavomaculatus,* is not so early. Although rich larval populations occurred close to the trap sites, the species was taken in very low numbers indeed. This remains unexplicable for the moment.

Lotic biotopes in the Ammarnäs area were found to harbour only a small number of caddisfly species, several of which, moreover, were restricted to a few of the localities investigated (Ulfstrand 1968 a). This means that the majority of the 60 species obtained in the LTC emanated from other biotopes than the strictly lotic ones. Their habitat requirements are known only in very general terms (e.g. Brindle 1956, Nybom 1960). Some probably live in slow-flowing streams, others in truly lenitic biotopes.

At least for Lepidoptera the general opinion seems to be that light-traps do not exert a far-reaching attractive force (Robinson & Robinson 1950, Robinson 1952, Hollingsworth et al. 1968). An insect has to approach a light-source closely before getting under its influence. The fact that a light-trap usually produces a great many species that have no reproduction localities near the trap site (cf. Crichton 1960, Nimmo 1966, Ulfstrand 1969 b) proves that caddisfly imagines spontaneously must range over wide areas away from the localities where they have spent their larval life. One may get a different impression when collecting only manually (Meshkova 1967), but in my opinion light-trapping results are quite conclusive in this respect. Obviously if a species within a given area is limited to one locality, the probability of its being obtained in a light-trap must be greater near this locality than far from it. Distance to reproduction localities, thus, is one of the factors influencing the number trapped.

Many other factors also affect the trappability of a given species. Judging from field experience a good many lenitic caddisfly species were numerous relatively close to the trap sites, for example *Athripsodes* spp., *Molanna* spp. and *Mystacides* spp., and yet they were obtained in very small numbers in the LTC (if at all). Partly this was probably due to their early flight periods. In addition they seem to be relatively stationary (Mori & Matutani 1953, Brindle 1957) and spend both day and night close to the water (Crichton 1965). If a trap is placed very close to swarming areas of such species, many individuals may get trapped (Tobias 1968). Some of them are, moreover, day-active (Weerekoom 1956, Lewis & Taylor 1964), which presumably reduces their trappability still further. It might be mentioned that many statements in the literature to the effect that caddisflies are nocturnal or crepuscular animals are based solely on LTC experiences which may be totally misleading as far as diel periodicities are concerned and therefore must be taken *cum grano salis*.

In comparison with the non-limnephilids mentioned above, limnephilids tend to have later flight periods, do not seem ever to be active in day-light and are known to travel extensively from the water (Crichton 1961, 1965, Novak & Sehnal 1963). All these circumstances increase the trappability of limnephilids.

Interestingly, one limnephilid species was taken in larger numbers in the HC than in the LTC, thereby recalling the pattern usual among the non-limnephilids. This species, viz. *Limnephilus femoratus,* spends the day in sedge over shallow water, where it may easily be netted, in contrast to most other limnephilids which are found in tall trees during the day.

Collecting caddisflies with sweep-nets, one is likely to miss such species that rest in inaccessible sites. Apart from those spending the day in trees, species inhabiting bogs and boulder areas would be difficult to collect.

It is conceivable that specific differences in, for example, spectral sensitivity or other physiological properties may lead to different trappability at light sources of the type used in this study (Williams, French & Hosni 1955).

Many factors, thus, influence the trappability of a given species. Distance between reproduction localities and traps is one of them; seasonal and diel flight activity periodicities, general habits and habitat preferences are other factors of obvious importance. The dispersal of caddisfly imagines from their breeding localities and the movements back to these places for mating and/or egg laying present an involved but most interesting problem.

10. Differences between LT I and LT III

Both these traps were placed at lotic localities at a distance of about 18 km from each other. The general surroundings were rather similar: hay-fields and, at further distance, coniferous and mixed forest. It may be worth while examining the differences between the two LTC obtained.

Over the years, LT I yielded 60,879 and LT III 33,180 caddisflies (Fig. 3). This considerable difference is chiefly due to differences in the two dominant species, *Rh. nubila* and *A. stigmatella.* Not only was the former much more numerous in absolute figures in LT I than in LT III (52,900 and 8961 specimens, respectively), but its relative dominance was also much greater in LT I (86.9 % and 27.0 %, respectively). *A. stigmatella,* on the other hand,

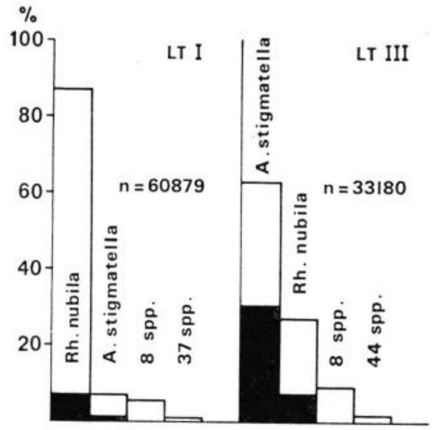

Fig. 3. Comparison of the collections obtained in light-trap I and III, respectively. The black parts of the columns of *Rhyacophila nubila* and *Apatania stigmatella* indicate the proportion of males.

was five times more numerous in LT III than in LT I and made up almost two thirds of the LTC in the former trap.

A partial explanation may presumably be found in the behaviour of the species. Roos (1957) demonstrated that *Rh. nubila* belongs to those lotic species whose females fly upstream before egg laying. At the site of LT I, upstream moving females encounter a totally different biotope, a wide lake-like extension of the river, uninhabitable to *Rh. nubila*. It seems reasonable that this change arrests many of the females, leading to an accumulation of individuals near the trap site and thereby to increased trappability. This would explain not only the the large number obtained but also the high percent of females in this LTC (92 %).

At LT III there is no corresponding break in the environmental conditions for an upstream moving insect. A short distance downstream of this site, however, the river changes its character, so that the recruiting area for *Rh. nubila* moving past the trapping site is very limited. This would explain both the lower number and the less unequal sex ratio in this LTC.

In *A. stigmatella*, the more unequal sex ratio in LT I than in LT III might indicate that a similar pattern prevails in this species which is not mentioned by Roos (op. cit.). The larger number taken in LT III fits with results obtained in the benthic sampling, for *A. stigmatella* was frequently a dominant species in the community in River Tjulån but found only in comparatively small numbers in River Vindelälven (Ulfstrand 1968 a, localities N+B and H, respectively).

Large differences between the two LTC were found also in many other species. Thus, for example, of 404 *Synafophora intermedia* all were taken in LT III, of 371 *Limnephilus borealis* 304 were taken in LT III, of 69 *Asynarchus thedenii* 65 were taken in LT I, of 442 *Lepidostoma hirtum* 430 were taken in LT I and of 69 *Athripsodes annulicornis* 68 were taken in LT I.

In spite of the fact that caddisflies, at least many species, seem to travel over considerable distances, the two light-traps, although placed in similar general surroundings within a rather homogeneous region, yielded collections that differed in many important respects, both qualitatively and quantitatively (cf. Williams 1951, Williams, French & Hosni 1955). This is interesting from the view-point of monitoring environmental changes using automatic population sampling devices, a project of current interest. It seems clear that findings at one site must not be extrapolated to other thus, for example, a light-trap only reflects strictly local changes. The study of regional fluctuations and trends would therefore require the use of very many sampling points.

11. Sex ratios

For *Rh. nubila* and *A. stigmatella,* see above.

Taking into account species found in at least 20 individuals in LTC and HC, respectively, it emerges from Tab. 3 that, in the LTC, sex ratios vary from 8 % males in *Lepidostoma hirtum* and 14 % males in *Rh. nubila* to 100 % males in several limnephilids, viz. *Limnephilus sparsus, L. vittatus, Asynarchus thedenii* and *Rhadicoleptus alpestris.* Ratios closely approach 100 % males also in several other limnephilids, such as *Limnephilus stigma, Anabolia concentrica* and *Potamophylax cingulatus.* In *Halesus digitatus* and *H. tesselatus* ratios are about 50 %, while *H. radiatus* conforms with what seems to be the general rule among limnephilids, that is, has a large surplus of males.

In the HC, sex ratios vary from 24 % males in *Lepidostoma hirtum* to 77 % males in *Molanna angustata.* The samples are smaller than in the LTC, but still it is obvious that ratios tend to be less unequal than in the HC.

In the small material of *Apatania zonella,* in which the males are known to make up less than 1 % of the population (Schmid 1954, p. 32), no males were found.

Thus the general pattern seems to be that almost all scarce and many abundant limnephilids have a large majority in the LTC (as found also by Crichton 1960 and Ulfstrand 1969 b), that this is not so in most non-limnephilids (cf. Nimmo 1966) and that the ratios are less unequal in the HC than in the LTC.

There seem to be several possible interpretations of this pattern. In the first place, limnephilid males may be more strongly attracted to light than females. This, in turn, may be due to different reasons. Females may be physiologically differently equipped in terms of light perception or have different phototactic response mechanisms. Or they may be active at those times of the day when the light-sources are ineffective. In the second place, males may range over wider distances than females. Of course, one interpretation does not exclude the other.

The fact that the male surplus is less marked in the HC, which has been brought together mainly close to the reproduction localities seems to favour the hypothesis that males travel more widely than females. The almost complete absence of females among the scarce limnephilids which presumably derive from distant localities seems to speak in the same direction. On the other hand, *Potamophylax cingulatus* was the only big limnephilid frequently occurring around the trap sites in considerable numbers, apparently emerging from nearby river parts, and although this species had no great distance to cover from the reproduction area to the trap, the male

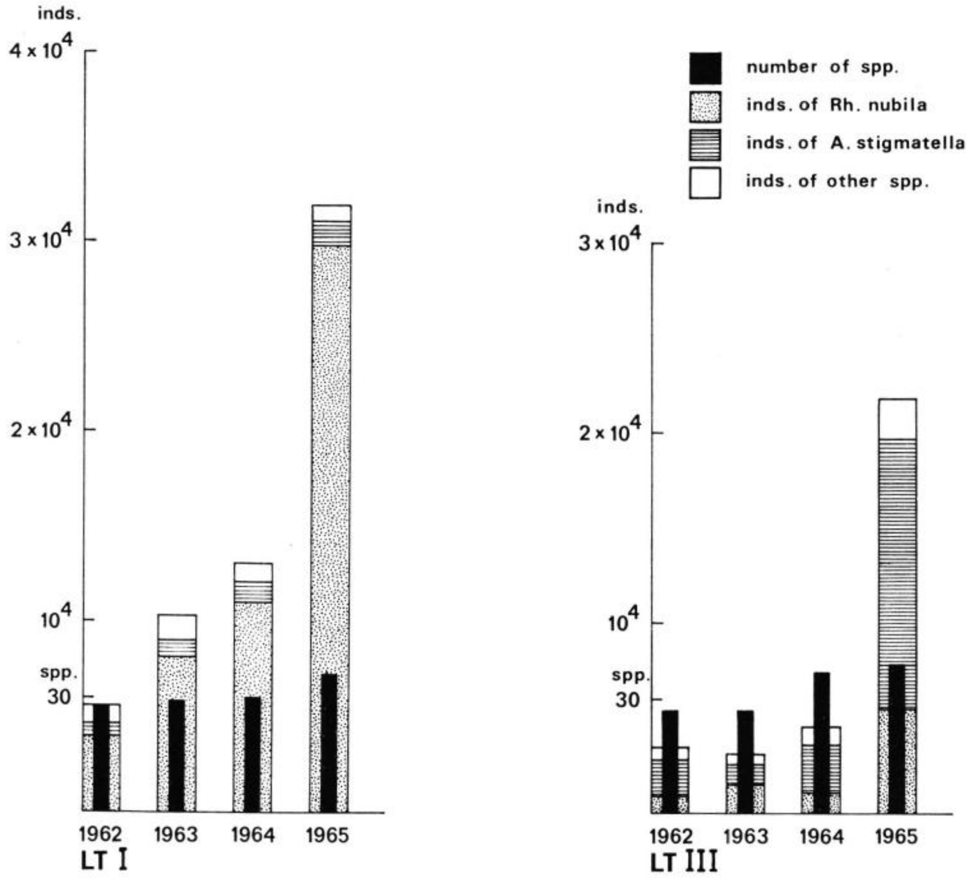

Fig. 4. Annual fluctuations of the collections obtained in light-trap I and III.

excess was very large indeed. This might favour the hypothesis of different phototactic reactions between the sexes.[3]

The present material does not allow the conclusion that there was a genetically unequal sex ratio in any species, except *Apatania zonella* (cf. Morgan 1956).

The discussion of the ecological significance of population movements in caddisflies would gain in clarity, if the basically different concepts of migration and dispersal were kept rigidly separate. The issue is of great current interest (cf. e.g. Novak & Sehnal 1963, Johnson 1963, 1969, Crichton 1965, Haskell 1966).

12. Annual fluctuations

The light-traps were in exactly the same positions every year. No changes in their surroundings could be seen. Thus it may be taken for granted that

[3] In a light-trap placed at a small stream in South Sweden in which larvae of *P. cingulatus* were abundant, a moderate excess of females was obtained (Ulfstrand 1969 b) thus making the situation still more puzzling.

annual fluctuations of the LTC were due to "natural" factors, namely 1) population fluctuations, 2) changes in trappability, for example for meteorological reasons.

The gap in the functioning of LT III in 1963 seems to have left very little trace in the material.

In Fig. 4 the annual fluctuations have been summarized with particular reference to the dominant species, *Rh. nubila* and *A. stigmatella*. There is good agreement between the two LTC compared. In both, 1965 was an outstanding year in terms of number of individuals caught. This was due to both *Rh. nubila* and *A. stigmatella* being trapped in exceptional quantities.

As may be seen from Fig. 5, the abundance of *Rh. nubila* in LT I in 1965 was combined with an extraordinarily low proportion of males. No similar relationship was seen in *A. stigmatella*. This supports the contention that upstream moving females are a key component of the *Rh. nubila* catch in this trap.

In many other species large annual fluctuations may also be seen. Taking into account all species obtained in at least 30 specimens in LT I+LT III, it is found that two species were taken in largest numbers in 1962, one in 1963, six in 1964 and ten in 1965. In this connection the following species have been omitted because their flight periods were only incompletely covered by the trapping periods: *Synafophora intermedia, Arctopsyche ladogensis, Apatania wallengreni, Chaetopteryx villosa* and *Annitella obscurata*.

It is of course tempting to look for possible relationships between the benthic populations and the LTC. According to sampling results, benthic populations were particularly high in 1964 in practically all taxa studied (Ulfstrand 1968 a, pp. 72 et seq.). In *A. stigmatella* this might directly affect the same year's catch, but perhaps also that of the following year, viz. if many imagines were produced in 1964 and they met with very favourable meteorological conditions granting successful mating and egg laying. In *Rh. nubila* the larval population studied in the summer will influence the number of imagines in both the same and in the following year, because of the particular life cycle of this species (Ulfstrand 1968 b). However, a much longer series of benthic sampling results and of light-trap collections are required, before a proper analysis of this problem can be attempted.

13. Some conclusions

A collection of about 100,000 adult caddisflies was assembled from within a narrowly restricted area at River Vindelälven in Swedish Lapland. Eighty-two species were recorded, that is about one third of the entire Swedish fauna. Several records were of faunistical interest.

The largest part of this collection was obtained in light-traps equipped with long-wave UV lamps which were obviously highly effective for this purpose. Caddisflies seem to be suitable for long-term population studies, since they are easily collected in automatic traps.

Very large differences were found between the present collection and one brought together by Forsslund (1954) at the lower parts of River Vindelälven. This illustrates the amplitude of ecological change from the lower to the upper parts of this river. In this particular instance the differences

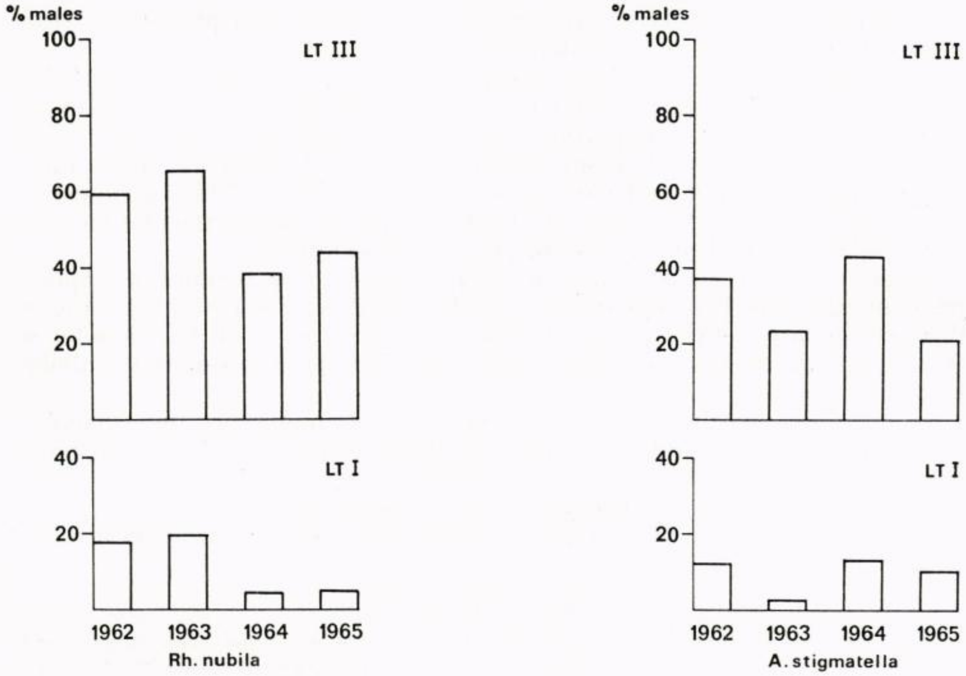

Fig. 5. The annual fluctuations of male proportion in *Rhyacophila nubila* and *Apatania stigmatella* in light-trap I and III.

were, however, somewhat exaggerated because of the collecting methods employed.

The flight periods of caddisflies are later than those of most other aquatic (or more correctly, amphibiotic) insects in Lapland (cf. Ulfstrand 1969 a). Limnephilids on average are later than non-limnephilids. The significance of the seasonally shifting attraction force of any artificial light source in the far north is pointed out.

Two species grossly dominated in the light-trap collection, viz. *Rhyacophila nubila* and *Apatania stigmatella*. They were also the most abundant species in the hand-collection, although their dominance was much less pronounced there. Important differences were found in the quantitative and qualitative composition of the light-trap and hand-collections, respectively, showing that the two methods are equally necessary in order to obtain a reasonably adequate species list from a given area.

Many factors affect the trappability of a given species. As far as caddisflies are concerned, a light-trap placed close to a given locality only very imperfectly reflects the species composition of its benthic community. Scattered specimens of many species presumably recruited from distant localities were obtained, but on the other hand several species known to have dense larval populations on the river bottom close to the trap site were taken in very small numbers only. Apart from sheer distance, differences in behaviour, motility and diel and seasonal periodicity obviously influence the trappability. If specific or sex differences in phototactic reactions occur in any species is unknown.

The two light-traps providing most of the material were placed 18 km from each other in comparatively uniform surroundings. Still the collections obtained differ in many important respects. Although adult caddisflies seem to travel extensively away from their reproduction localities, a single light-trap supplies a sample reflecting purely local conditions. This fact must be taken into account when plans are made to monitor environmental changes using light-traps as instruments for population sampling.

Large-scale movements along the river in egg-bearing females of *Rhyacophila nubila* probably explain the great numbers and unequal sex ratio of this species in a light-trap, placed where the river changed its character so that upstream moving individuals were suddenly facing a totally unsuitable biotope.

In most limnephilids males were much more numerous than females. Although there seems to be indications that this is due to a higher frequency of distanct travels in the males, the possibility of a sex difference in phototactic response cannot be excluded for the present time.

Annual fluctuations were largely parallel in the two traps and in a majority of species.

Acknowledgements

I am much indebted to Professor Per Brinck for constant support and many stimulating discussions and to Dr. Bo Tjeder for much good advice, particularly in the beginning of my trichopterological studies. The research at River Vindelälven was financed through grants from the Swedish Natural Science Research Council, the Swedish National Board for Nature Conservancy (and its predecessors) and from funds at Lund and Uppsala Universities. For all this I am deeply grateful.

References

BOTOSANEANU, L. 1967. Trichoptera. — In: ILLIES, J. Limnofauna Europaea, pp. 285—309. Stuttgart.

BRINDLE, A. 1956. The ecology of north-east Lancashire Trichoptera. With special reference to the use of light as a collecting method. — Entom. Gaz. 7: 179—184.

— 1957. The effect of temperature and humidity on the flight of Trichoptera. — Entom. Mon. Mag. 93: 63—66.

— 1958. Night activity of Trichoptera. — Entom. Mon. Mag. 94: 38—42.

CORBET, P. S. & TJÖNNELAND, A. 1956. The flight of twelve species of East African Trichoptera. — Univ. Bergen Årb. Naturv. Rekke 1955 (9): 1—49.

CRICHTON, M. I. 1957. The structure and function of the mouth parts of adult caddisflies (Trichoptera). — Phil. Trans. Roy. Soc. London (B) 241: 45—91.

— 1960. A study of captures of Trichoptera in a light trap near Reading, Berkshire. — Trans. Roy. Entom. Soc. London 112: 319—344.

— 1961. Observations on the longevity and dispersal of adult Limnephilidae. — Proc. XI Int. Entom. Congr. Vienna 1960 (1): 366—371.

— 1965. Observations on captures of Trichoptera in suction- and light-traps near Reading, Berkshire. — Proc. Roy. Entom. Soc. London (A) 40: 101—108.

DÉCAMPS, H. 1966. Sur la détermination des femelles de *Potamophylax latipennis* (Curt.) Neboiss et *Potamophylax cingulatus* (Stephens) (Trichoptera). — Annal. Limnol. 2: 537—541.

FORSSLUND, K.-H. 1953. Catalogus insectorum Sueciae. Additamenta ad partes I—X. Trichoptera. — Opusc. Entom. 18: 72—74.

— 1954. Über die Trichopterenfauna eines nordschwedischen Flusses. — Opusc. Entom. 19: 173—189.

— & TJEDER, B. 1942. Catalogus insectorum Sueciae. II. Trichoptera. — Opusc. Entom. 7: 92—107.

HASKELL, P. T. 1966. Flight behaviour. — In: HASKELL, P. T. (Ed.). Insect behaviour. Symp. Roy. Entom. Soc. London 3: 29—45.

HOLLINGSWORTH, J. P., HARTSTACK, A. W. & LINDQUIST, D. A. 1968. Influence of near-ultraviolet output of attractant lamps on catches of insects by light traps. — J. Econ. Entom. 61: 515—521.

JOHNSON, C. G. 1963. Physiological factors in insect migration by flight. — Nature (London) 198: 423—427.

— 1969. Migration and dispersal of insects by flight. — London. 763 pp.

LEWIS, T. & TAYLOR, L. R. 1965. Diurnal periodicity of flight by insects. — Trans. Roy. Entom. Soc. London 116: 393—479.

MESHKOVA, A. M. 1967. The behaviour of adults of abundant species of caddisflies (Trichoptera) in the tributaries of Lake Sevan. — Entom. Rev. 46: 59—60.

MORGAN, N. C. 1956. The biology of *Leptocerus aterrimus* (Steph.) with reference to its availability as a food for trout. — J. Anim. Ecol. 25: 349—365.

MORI, S. & MATUTANI, K. 1953. Daily swarmings of some caddis fly adults and their habitat segregations. (Engl. summ.). — Zool. Mag. Tokyo 62: 191—198.

NEBOISS, A. 1963. The Trichoptera types of species described by J. Curtis. — Beitr. z. Entom. 13: 582—635.

NIMMO, A. P. 1966. The arrival pattern of Trichoptera at artificial light near Montreal, Quebec. — Quaest. Entom. 2: 217—242.

NOVAK, K. & SEHNAL, F. 1963. The development cycle of some species of the genus *Limnephilus* (Trichoptera). — Cas. Ceskosl. Spol. Entom. 60: 68—80.

NYBOM, O. 1960. List of Finnish Trichoptera. — Fauna Fenn. 6: 1—56.

ROBINSON, H. S. 1952. On the behaviour of night-flying insects in the neighbourhood of a bright source of light. — Proc. R. Entom. Soc. London (A) 27: 13—21.

— & ROBINSON, P. J. M. 1950. Some notes on the observed behaviour of Lepidoptera in flight in the vicinity of light-sources etc. — Entom. Gaz. 1: 3—20.

ROOS, T. 1957. Studies on upstream migration in adult stream-dwelling insects. I. — Inst. Freshw. Res. Drottningholm Ann. Rep. 38: 167—193.

SCHMID, F. 1954. Contribution à l'étude de la sous-famille des Apataniinae (Trichoptera, Limnophilidae). II. — Tijdschr. Entom. 97: 1—74.

SOUTHWOOD, T. R. E. 1966. Ecological methods. — London. 391 pp.

TJÖNNELAND, A. 1960. The flight activity of mayflies as expressed in some East African species. — Univ. Bergen Årb. Naturv. Rekke 1960 (1): 1—88.

TOBIAS, W. 1968. Die Trichopteren der Lule Lappmark. UV-Lichtfänge am Stora Lulevatten. — Entom. Z. 78: 12—16.

— 1969 a. Die Trichopteren der Lule Lappmark (Schweden), II. Verzeichnis der Arten, Fundorte und Flugzeiten. — Entom. Z. 79: 77—96.

— 1969 b. Die Trichopteren der Lule Lappmark (Schweden), III. Zur Differenzierung der Arten *Potamophylax cingulatus* (Stephens 1837) und *P. latipennis* (Curtis 1834) (Limnephilidae). — Entom. Z. 79: 96—100.

ULFSTRAND, S. 1968 a. Benthic animal communities in Lapland streams. — Oikos Suppl. 10: 1—120.

— 1968 b. Life cycles of benthic insects in Lapland streams (Ephemeroptera, Plecoptera, Trichoptera, Diptera Simuliidae). — Oikos 19: 167—190.

— 1969 a. Ephemeroptera and Plecoptera from River Vindelälven in Swedish Lapland. — Entom. Tidskr. 90: 145—165.

— 1969 b. Nattsländorna (Trichoptera) vid en skånsk bäck. — Fauna o. Flora (Stockholm) 64: 122—130.

VERHEIJEN, F. J. 1958. The mechanisms of the trapping effect of artificial light sources upon animals. — Arch. Néerl. Zool. 13: 1—107.

WEEREKOON, A. C. J. 1956. Studies on the biology of Loch Lomond. 2. The repopulation of McDougall Bank. — Ceylon J. Sci. Sect. C 7 (=N. S. 1) (2): 95—133.

WILLIAMS, C. B. 1951. Comparing the efficiency of insect traps. — Bull. Entom. Res. 42: 513—517.

— FRENCH, R. R. & HOSNI, M. M. 1955. A second experiment on testing the relative efficiency of insect traps. — Bull. Entom. Res. 46: 193—204.