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POPULATION DYNAMICS OF THREE GAMMARID SPECIES (CRUSTACEA, AMPHIPODA) IN A FRENCH CHALK STREAM

PART I. GENERAL ASPECTS AND ENVIRONMENTAL FACTORS

by

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ABSTRACT

This paper is the first of a series of four, it describes the general outline of a research project on the ecology of *Gammarus pulex pulex* (Linnaeus, 1758), *G. fossarum* Koch in Panzer, 1836, and *Echinogammarus berilloni* (Catta, 1878) in a small French chalk stream, the Slack. The entire study investigates the impact of (changes in) environmental factors on standing crop and migration of these three freshwater gammarids.

An account is given of biological and physicochemical research methods used. Special methods to capture both drifting and upstream migrating gammarids were developed.

In this first part, data on environmental factors are presented with an emphasis on the seasonal and microgeographic variation they show in this river. Detailed information about the diel variation of some environmental factors is given.

After mathematical treatment of the data on environmental factors the Slack is classified in four zones: an unstable headwater, a large stable upper/middle region, a rather polluted lower region and an estuarine part.

RÉSUMÉ

Cet article est le premier d'une série de quatre; il décrit le cadre d'un plan de recherches sur l'écologie de *Gammarus pulex pulex* (Linnaeus, 1758), *G. fossarum* Koch in Panzer, 1836, et *Echinogammarus berilloni* (Catta, 1878) dans un petit cours d'eau calcaire du Boulonnais, la Slack. L'étude entière recherche l'influence (du changement) des facteurs du milieu sur le «standing crop» et la migration de ces trois Gammares d'eau douce.

Les différentes méthodes de recherches biologiques et physico-chimiques utilisées ont été décrites. Des méthodes particulières pour capturer aussi bien les Gammares migrant en aval qu'en amont ont été développées.

Dans cette première partie, les données sur les facteurs du milieu sont présentées avec l'accent sur les variations saisonnières et microgéographiques qu'ils montrent dans cette rivière. Les fluctuations nycthémérales de certains facteurs abiotiques sont décrites en détail.

Après traitement mathématique des données sur les facteurs du milieu, la Slack a été classifiée en quatre zônes: une zône marécageuse instable près de la source, une large et stable partie supérieure et moyenne, une partie inférieure assez polluée et une zône estuarienne.

1. INTRODUCTION

The range of gammarid species in a given body of fresh or brackish water can vary considerably and sometimes shows vast changes. In estuaries, tide and season deeply affect the distribution and migratory pattern of gammarids (Dennert et al., 1969; Girisch et al., 1974). A newly introduced species may be very successful in its competition with indigenous animals and thus replace these in their original habitats (Pinkster et al., 1977). The marked environmental instability of a brackish lagoon brings about a dynamic balance between two coexisting species (Janssen et al., 1979). These phenomena, however, are all examples of distribution patterns influenced by one or two predominant ecological factors.

The longitudinal zonation of freshwater species in a stream is the result of a complex interaction between more than just one or two environmental factors. The distribution of gammarids over different stream habitats (Minckley & Cole, 1963; Roux, 1967; Meijering, 1971; Vincent, 1971) is relatively stable, which makes them good indicator species, e.g. for pollution. This stable type of distribution seems to be conflicting with rather high migration rates observed within gammarid populations (Waters, 1965; Lehmann, 1967; Elliot & Minshall, 1968; Hultin, 1971; Meijering, 1972).

This study sets out to analyse the variation in distribution area of certain freshwater gammarids throughout the year and the factors that cause, influence or regulate this variation. It tries to give a qualitative impression of biological processes encountered in a small river. Some details have to be investigated more thoroughly, while quantitative aspects have hardly been taken into account.

The research program served two purposes: firstly we came to know more about some poorly studied biological processes, secondly it offered a broad scala of topics useful in teaching ecology. At the same time some new ecological methods could be tested.

2. ACKNOWLEDGEMENTS

The present research project was subsidized by a grant of the Netherlands' Organization for Pure Scientific Research (ZWO) and the Foundation for Fundamental Biological Research (BION), but could only be carried out as it was, with the assistance of many people of the Institute of Taxonomic Zoology in Amsterdam, both in the laboratory and in the field.

Of all those people I especially would like to thank Mr. Herman Mittelberg, who made so many ideas work and Drs. Jan Dieleman for his technical help at the computer. Prof. Dr. Jan Stock did all he could to obtain the grant and never failed to back me up. Most grateful I am, however, to Dr. Sjouk Pinkster, because it is doubtful whether this work would have been done without his practical and moral support.

3. STUDY OUTLINE

A natural stream on the French Channel coast, the river Slack, was chosen as study area. We have set up a program combining the study of environmental factors, life histories and migration patterns of three gammarid species: *Gammarus pulex pulex* (Linnaeus, 1758), *G. fossarum* Koch in Panzer, 1836, and *Echinogammarus berilloni* (Catta, 1878), living in the limmic part of this river (Stock et al., 1966).

The field program started in September 1973 and lasted till July 1976. Fifteen sampling stations were chosen in the main stream with an emphasis on the less polluted stretches (fig. 1). During the first year we took samples of the standing crop, estimated the diel migration activity (both upstream migration and drift) and measured a number of environmental factors every two weeks at each station. The next year this sampling program was carried out once a month. Every three months a special set of chemical data was gathered.

Each sampling period the hourly variation in migration as well as the variation in environmental factors was measured during 24 hours at a single station. An eight week period in the summer of 1975 and a two week period in July 1976 of continuous mensuration completed this program. During these two periods migratory activity was measured every hour, while the changes in environmental factors were continuously registrated.

In this way we came to know the daily and annual variation in environmental factors, which could be correlated with the population dynamics (distribution, life history, migration patterns etc.) of the three gammarid species.

In order to extend our knowledge of certain aspects, we conducted some additional experiments (like marking and releasing of special groups of animals; counting numbers of eggs, carried by females of each of the three species in their marsupium; and testing reproduction under laboratory conditions) at various stages of the research project.

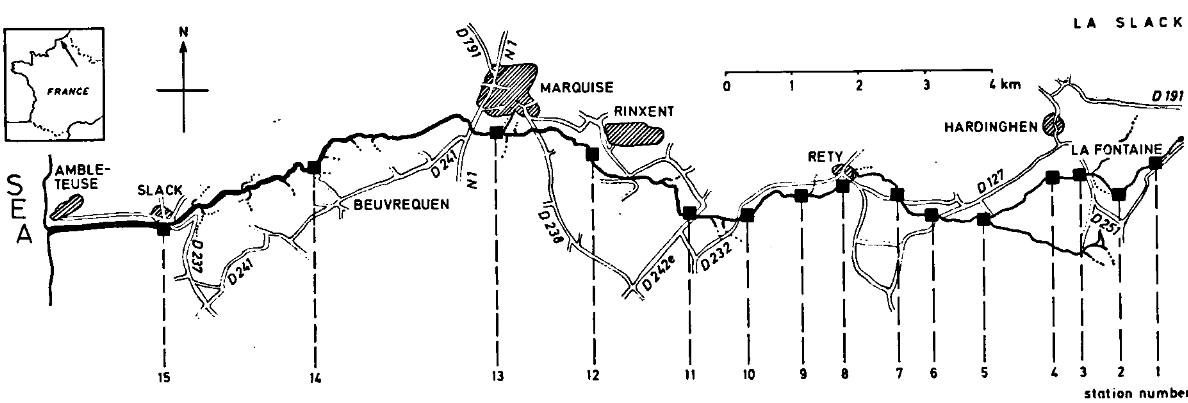

Fig. 1. Map of the river Slack with the fifteen sampling stations.

4. DESCRIPTION OF THE RIVER SLACK

The Slack is a stream of about 20 km long, which runs from east to west in the northwestern part of France (Pas-de-Calais), a calcareous region called the Boulonnais. It is partly fed by chalk springs, but mainly by seepage and surface run-off. It debouches into the Strait of Dover just south of the village of Ambleteuse. The upper reaches flow through low hills covered by farmland interspersed with hedgerows and small villages. It is polluted by human waste and bio-industries. From the twin-towns Rinxent and Marquise onwards, the Slack becomes a small lowland river, polluted by industrial effluent as well (Hoestlandt, 1971). Due to a sluice which is closed automatically by the incoming tide, the Slack has a semi-open estuary with tidal influences upstream of this sluice (Dennert et al., 1969). The fifteen sampling sites are shown in fig. 1.

Station 1. La Fontaine. — This sampling site is situated about 300 m downstream of the main spring. (Unfortunately we were not allowed to take samples from the main source itself, which is used for growing watercress commercially.) Most of the time the Slack here is merely a tiny trickling stream, flowing through open muddy grassland. In summer it is completely overgrown with *Berula erecta* (= *Sium erectum*), *Nasturtium officinale* and *Veronica beccabunga*. Cattle often use it as a watering place.

Details of this and other stations are given in figs. 2, 3 and 4 and tables I and II.

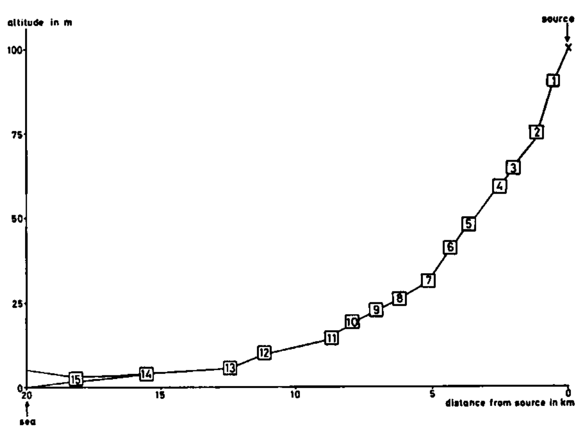

Fig. 2. Profile of the river Slack.

Station 2. Fouhen. — The Slack gets the character of a fast flowing streamlet. This station is heavily overshadowed by shrubs and trees. At this place, cattle often ford the river, so it is shallow and muddy.

Station 2a. Fouhen spring. — At station 2 a small chalk spring empties itself in the Slack. It is constantly covered with *Berula erecta* and *Nasturtium officinale*, a vegetation typical of spring regions in this part of France.

Station 3. Le Fart. — This station is named after a farm lying next to it, which houses a small bioindustry. The river flows fast between low grassy banks.

Station 4. Héronval. — Héronval is one of the farms around this station. The waste of its quite sizable bioindustry (pigs, poultry) is discharged directly into the Slack. Often large trucks drive through the river at this site. One riverside is grown by shrubs and trees.

Station 4a. Héronval tributary. — Station 4a is situated in a small brooklet, 40 m upstream of the spot where it flows into the Slack (fig. 4). On its way through flat meadows it is contaminated by muck water from many cattle-raising farmsteads to an even larger extent than the main stream at this point.

Station 4b. Héronval springbrook. — Station 4b is situated in a small unpolluted springbrook, which flows into the Slack 30 m downstream of station 4 (fig. 4). It is sometimes disturbed by grazing cattle. It is covered by the spring vegetation also found at station 2a.

Station 5. Les Moines. — Between stations 4 and 5 the Slack drops down three metres over a man-made waterfall, which causes an intensive aeration. Foam flocks are formed and often cover all of the river as the organic waste in the water is oxydated. When discharge is low, large beds of *Cladophora* sp. can develop. Beyond the farm "Les Moines" the Slack flows through a stretch of open grassland with a hedgebank at one side.

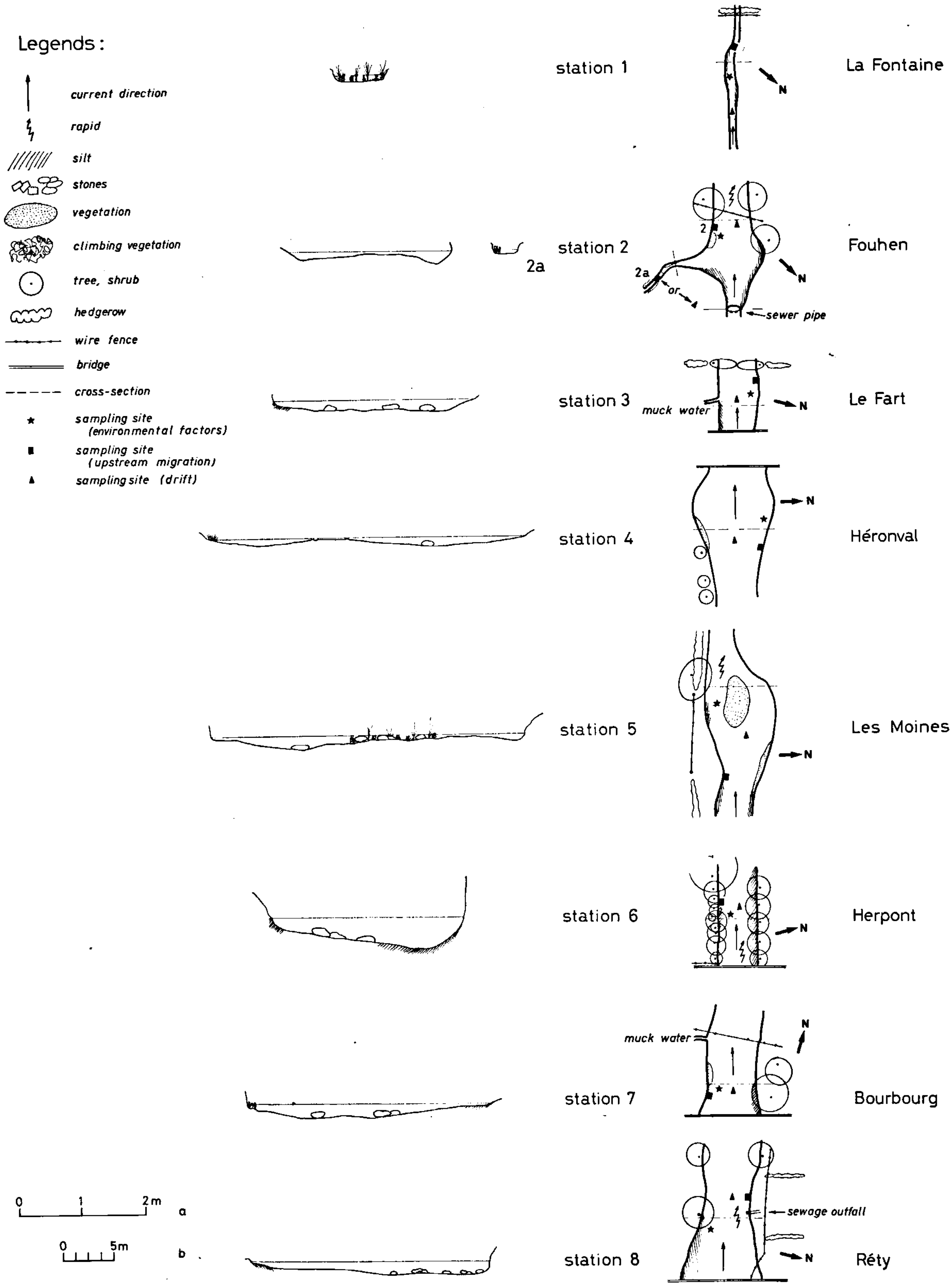

Fig. 3. Maps (scale b) and cross-sections (scale a) of the sampling stations (11-13 April 1975).

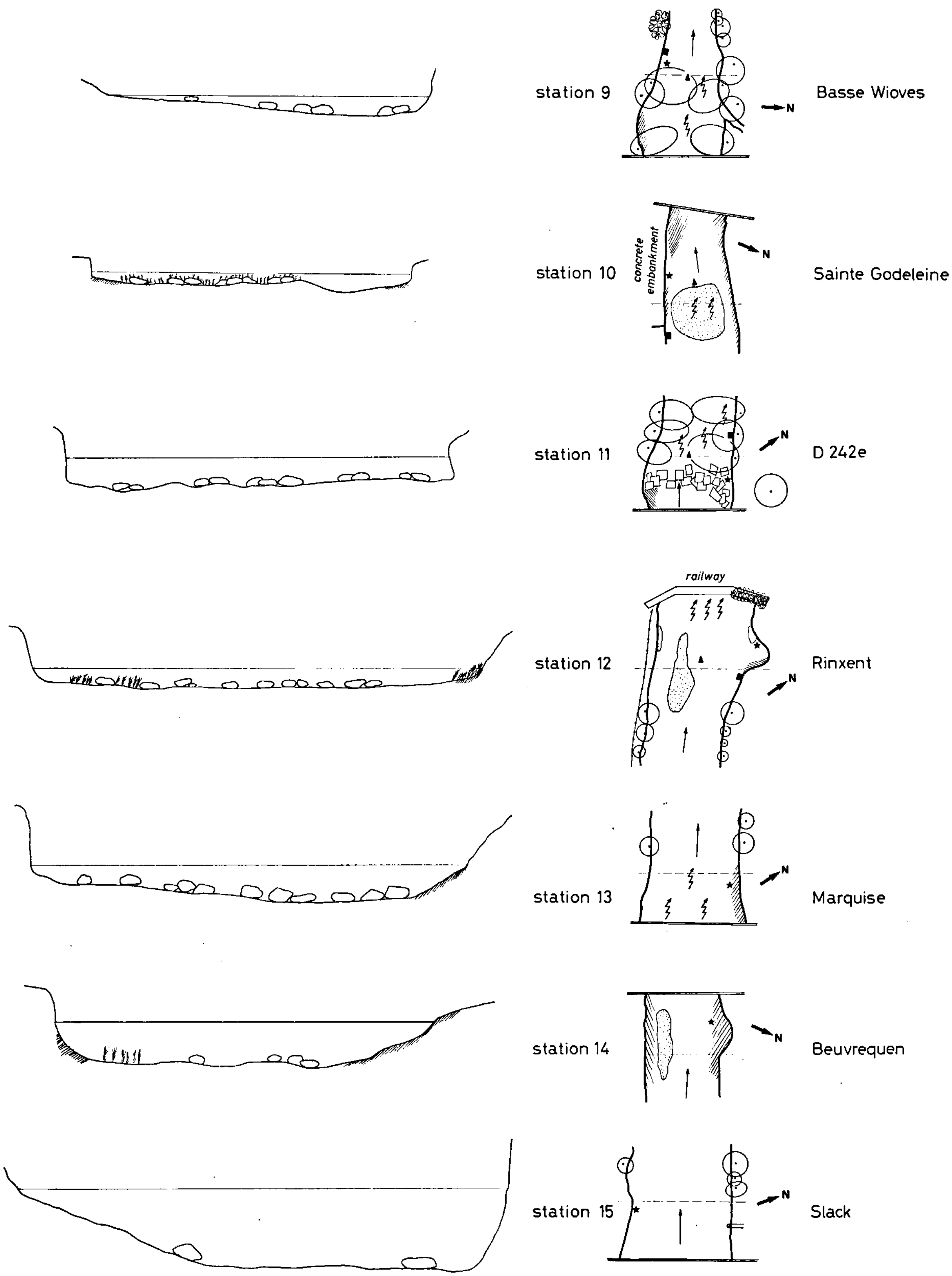

Fig. 3. Continuation of previous page.

TABLE I

Values of environmental factors measured each time the standing crop was sampled (for explanation see the main text, section 6.2).

		water temperature (°C)	air temperature (°C)	dissolved oxygen (ppm)	percentage oxygen saturation (%)	conductivity at 20 °C (μmho)		measured current velocity ($m \cdot s^{-1}$)	estimated current velocity (1-7)	depth (cm)	width (m)	silt (0-2)	sand (0-2)	gravel (0-2)	stones (0-2)	estimated pollution (1-7)	food (0-2)	*Asellus* (0-2)
Sept. 1973-Sept. 1975		t_w	t_a	O_2	% O_2	*C*	*pH*	v_m	v_e	*d*	*w*	*si*	*sa*	*gr*	*st*	*p*	*f*	*A*
Slack (Sta. 1-15)	*n*	587	460	485	478	580	511	505	515	541	248	577	577	577	577	577	600	594
	mean	**10.8**	**13.6**	**10.0**	**91.1**	**557**	**7.9**	**0.33**	**4.7**	**27.0**	**5.6**	**1.1**	**0.4**	**1.2**	**1.4**	**3.2**	**2.0**	**0.1**
	SD	4.0	9.3	1.8	14.7	69	0.5	0.18	1.2	61.5	9.0	0.9	0.8	0.9	0.9	1.3	0.0	0.3
	max.	25.6	35.2	18.4	192.7	1400	9.2	1.36	7	140	12.0	2	2	2	2			2
	min.	2.0	— 0.5	3.2	32.5	350	6.0	0.03	2	2	0.2	0	0	0	0			0
Sta. 1	*n*	36	30	30	29	38	33	27	36	35	15	38	38	38	38	38	38	38
	mean	**11.9**	**13.5**	**8.8**	**80.3**	**581**	**7.7**	**0.32**	**4.3**	**11.8**	**0.9**	**1.9**	**0.0**	**0.5**	**0.0**	**1.2**	**2.0**	**0.3**
	SD	5.7	6.6	2.4	15.3	43	0.5	0.13	1.1	7.9	1.6	0.3	0.0	0.7	0.2	0.5	0.0	0.6
	max.	25.6	30.2	13.4	101.6	685	8.3	0.62	6	31	6.5	2	0	2	1	3		2
	min.	3.8	0.0	3.2	32.5	435	6.6	0.11	3	4	0.2	0	0	0	0	1		0
Sta. 2	*n*	36	29	30	29	35	32	33	34	36	15	35	35	35	35	36	37	37
	mean	**10.3**	**11.1**	**10.1**	**91.4**	**515**	**7.6**	**0.38**	**4.8**	**12.3**	**2.6**	**1.1**	**0.8**	**1.6**	**1.0**	**1.3**	**2.0**	**0.0**
	SD	1.7	5.6	0.9	6.5	29	0.5	0.14	0.9	3.4	0.7	1.0	1.0	0.8	0.9	0.7	0.0	0.0
	max.	14.8	21.5	12.0	101.3	590	8.7	0.74	6	20	4.0	2	2	2	2	4		
	min.	7.8	— 0.5	8.6	76.1	440	6.4	0.12	3	5	1.5	0	0	0	0	1		
Sta. 2a	*n*	30	27	25	24	19	26	12	20	24	6	21	21	21	21	21	34	29
	mean	**10.2**	**11.1**	**9.3**	**83.1**	**557**	**7.5**	**0.23**	**4.2**	**6.0**	**0.5**	**1.3**	**0.4**	**1.6**	**0.5**	**1.0**	**2.0**	**0.0**
	SD	1.0	5.6	0.6	5.1	47	0.5	0.10	0.9	3.2	0.1	1.0	0.8	0.7	0.8	0.0	0.0	0.0
	max.	12.8	21.5	10.6	92.2	640	8.3	0.52	5	13	0.7	2	2	2	2	1		
	min.	8.4	— 0.5	8.0	70.5	490	6.0	0.13	3	2	0.3	0	0	0	0	1		
Sta. 3	*n*	38	31	32	30	39	34	37	33	38	17	39	39	39	39	39	39	39
	mean	**10.9**	**13.6**	**10.5**	**95.5**	**514**	**7.8**	**0.26**	**4.2**	**14.2**	**3.4**	**0.9**	**0.8**	**1.0**	**1.7**	**3.4**	**2.0**	**0.0**
	SD	2.5	6.8	0.9	7.0	33	0.6	0.11	0.8	4.6	0.6	0.9	1.0	0.9	0.7	0.6	0.0	0.0
	max.	17.1	33.0	11.9	107.0	595	8.6	0.53	6	27	5.0	2	2	2	2	5		
	min.	7.2	— 0.3	8.4	78.2	460	6.4	0.11	3	10	2.6	0	0	0	0	2		
Sta. 4	*n*	38	29	31	31	38	33	33	34	36	16	38	38	38	38	37	38	38
	mean	**11.1**	**13.1**	**10.3**	**94.4**	**528**	**7.9**	**0.38**	**4.6**	**13.7**	**5.1**	**0.8**	**0.1**	**1.9**	**1.4**	**3.9**	**2.0**	**0.0**
	SD	3.1	5.9	1.0	8.0	38	0.4	0.12	0.9	5.8	0.5	0.9	0.5	0.5	0.8	0.9	0.0	0.0
	max.	16.8	24.7	11.4	109.7	645	8.3	0.65	6	30	6.0	2	2	2	2	6		
	min.	6.2	0.7	8.2	78.8	470	6.8	0.17	2	7	4.0	0	0	0	0	3		

TABLE I, continued

Sept. 1973-Sept. 1975		t_w	t_a	O_2	% O_2	*C*	*pH*	v_m	v_e	*d*	*w*	*si*	*sa*	*gr*	*st*	*p*	*f*	*A*
Sta. 4a	*n*	7	7	6	6	7	7	4	8	7	1	8	8	8	8	8	9	9
	mean	**15.0**	**17.3**	**10.8**	**106.9**	**597**	**8.2**	**0.26**	**4.4**	**5.3**	**1.4**	**2.0**	**0.8**	**1.9**	**0.6**	**3.2**	**2.0**	**0.0**
	SD	5.9	6.1	1.1	13.1	22	0.1	0.19	0.5	2.6		0.0	1.0	0.4	0.7	1.4	0.0	0.0
	max.	22.7	23.9	12.4	128.7	625	8.4	0.44	5	9		2	2	2	2	6		
	min.	8.4	8.5	9.3	95.6	570	8.0	0.26	4	2		2	0	1	0	1		
Sta. 4b	*n*	3	3	2	2	3	3	2	3	3	1	3	3	3	3	3	3	3
	mean	**13.8**	**19.5**	**9.2**	**90.3**	**692**	**8.1**	**0.20**	**3.7**	**5.3**	**0.3**	**1.3**	**1.3**	**1.3**	**0.0**	**1.0**	**2.0**	**0.0**
	SD	2.5	3.0	1.6	11.0	24	0.0	0.05	0.6	1.5		1.2	1.2	0.6	0.0	0.0	0.0	0.0
	max.	16.4	22.5	10.3	98.1	710	8.1	0.23	4	7		2	2	2	0	1		
	min.	11.4	17.5	8.1	82.4	665	8.0	0.16	3	4		0	0	1	0	1		
Sta. 5	*n*	38	32	31	31	39	34	37	33	36	17	38	38	38	38	39	39	39
	mean	**10.6**	**12.0**	**10.4**	**94.7**	**533**	**8.0**	**0.39**	**5.1**	**14.3**	**5.0**	**1.1**	**0.0**	**1.6**	**1.6**	**3.7**	**2.0**	**0.0**
	SD	3.3	5.5	1.3	8.3	36	0.4	0.22	0.9	6.2	0.7	0.9	0.2	0.8	0.8	0.7	0.0	0.2
	max.	16.2	26.8	12.3	110.7	638	8.5	1.36	7	30	6.0	2	1	2	2	5		1
	min.	4.0	3.0	7.3	71.9	435	6.8	0.17	4	5	3.5	0	0	0	0	3		0
Sta. 6	*n*	39	30	32	32	39	32	36	33	37	17	39	39	39	39	38	39	39
	mean	**11.0**	**12.8**	**9.9**	**89.6**	**527**	**8.0**	**0.21**	**4.1**	**27.7**	**3.1**	**1.8**	**0.4**	**0.8**	**1.4**	**3.5**	**2.0**	**0.0**
	SD	4.2	5.9	1.5	8.7	36	0.5	0.08	0.7	12.8	0.5	0.6	0.8	1.0	0.8	0.8	0.0	0.0
	max.	17.9	26.7	12.6	99.5	660	8.5	0.39	5	65	4.0	2	2	2	2	5		
	min.	3.0	2.0	6.7	69.7	475	6.8	0.05	3	13	2.0	0	0	0	0	1		
Sta. 7	*n*	38	31	32	31	39	33	37	34	36	16	39	39	39	39	38	39	39
	mean	**10.6**	**16.2**	**10.1**	**91.3**	**526**	**8.0**	**0.33**	**4.7**	**24.5**	**3.9**	**0.9**	**0.2**	**1.5**	**1.8**	**3.2**	**2.0**	**0.0**
	SD	4.3	17.1	1.5	8.0	38	0.7	0.13	0.8	8.5	0.9	0.9	0.5	0.8	0.6	0.8	0.0	0.2
	max.	18.9	35.2	12.4	104.9	645	9.2	0.67	7	45	6.0	2	2	2	2	5		1
	min.	2.5	4.3	7.4	76.7	470	6.2	0.11	3	10	3.1	0	0	0	0	1		0
Sta. 8	*n*	39	29	32	32	39	34	36	34	37	17	39	39	39	39	38	39	39
	mean	**10.5**	**14.4**	**10.4**	**92.9**	**529**	**8.0**	**0.35**	**5.1**	**23.7**	**3.8**	**0.9**	**0.1**	**1.6**	**1.4**	**4.0**	**2.0**	**0.0**
	SD	4.1	6.8	1.6	9.5	80	0.6	0.17	1.2	12.4	0.5	0.9	0.4	0.8	0.9	0.7	0.0	0.2
	max.	18.6	29.8	12.6	107.9	645	8.5	0.76	7	55	5.5	2	2	2	2	5		1
	min.	2.0	1.2	7.2	74.2	475	6.5	0.09	3	10	3.0	0	0	0	0	3		0
Sta. 9	*n*	39	27	33	33	39	32	37	34	36	15	38	38	38	38	38	39	39
	mean	**10.6**	**13.4**	**10.4**	**93.9**	**548**	**8.0**	**0.41**	**5.3**	**28.1**	**5.2**	**0.8**	**0.3**	**1.6**	**1.5**	**3.2**	**2.0**	**0.3**
	SD	4.0	5.5	1.5	8.9	59	0.5	0.21	1.0	16.8	1.6	0.9	0.6	0.8	0.9	0.9	0.0	0.6
	max.	17.6	24.2	12.7	111.4	690	8.6	0.93	7	60	8.0	2	2	2	2	5		2
	min.	3.5	4.4	7.8	77.0	350	6.6	0.13	3	8	3.2	0	0	0	0	1		0

TABLE I, continued

		water temperature (°C)	air temperature (°C)	dissolved oxygen (ppm)	percentage oxygen saturation (%)	conductivity at 20 °C (µmho)		measured current velocity ($m.s^{-1}$)	estimated current velocity (1-7)	depth (cm)	width (m)	silt (0-2)	sand (0-2)	gravel (0-2)	stones (0-2)	estimated pollution (1-7)	food (0-2)	*Asellus* (0-2)
Sept. 1973-Sept. 1975		t_w	t_a	O_2	% O_2	*C*	*pH*	v_m	v_e	*d*	*w*	*si*	*sa*	*gr*	*st*	*p*	*f*	*A*
Sta. 10	*n*	39	32	33	33	39	34	37	35	38	17	39	39	39	39	39	39	39
	mean	**10.3**	**13.1**	**9.8**	**88.1**	**545**	**7.9**	**0.47**	**6.3**	**24.4**	**5.1**	**1.1**	**0.2**	**1.3**	**1.7**	**2.8**	**2.0**	**0.0**
	SD	3.9	6.9	1.8	11.7	73	0.6	0.23	0.8	11.7	0.9	0.9	0.5	0.9	0.7	1.1	0.0	0.0
	max.	18.1	31.0	13.4	117.0	670	8.5	1.00	7	60	7.5	2	2	2	2	5		
	min.	2.8	1.7	6.8	66.9	495	6.0	0.10	5	9	3.7	0	0	0	0	1		
Sta. 11	*n*	38	29	33	32	39	34	36	33	35	14	39	39	39	39	39	39	39
	mean	**10.3**	**12.8**	**9.9**	**88.5**	**579**	**8.0**	**0.32**	**5.5**	**33.7**	**6.2**	**0.6**	**0.4**	**1.1**	**2.0**	**3.3**	**2.0**	**0.0**
	SD	4.2	6.3	2.1	14.1	45	0.5	0.15	1.2	9.2	1.2	0.8	0.8	0.9	0.3	0.6	0.0	0.2
	max.	18.4	29.8	12.4	109.6	735	8.6	0.69	7	60	8.0	2	2	2	2	5		1
	min.	2.8	2.8	5.7	60.2	520	6.6	0.06	3	15	4.2	0	0	0	0	2		0
Sta. 12	*n*	39	33	33	33	39	33	34	34	38	16	37	37	37	37	39	39	39
	mean	**10.3**	**12.6**	**9.7**	**86.7**	**583**	**7.9**	**0.24**	**4.2**	**24.4**	**7.3**	**0.8**	**0.6**	**0.9**	**2.0**	**3.9**	**2.0**	**0.1**
	SD	4.0	6.5	2.2	15.6	49	0.6	0.15	1.1	7.5	0.7	0.9	0.9	1.0	0.0	1.2	0.0	0.3
	max.	17.5	28.0	13.0	115.4	730	8.4	0.61	6	50	9.0	2	2	2		7		1
	min.	3.5	0.0	6.5	54.5	415	6.4	0.07	3	15	6.3	0	0	0		1		0
Sta. 13	*n*	30	21	23	23	30	26	26	27	28	16	29	29	29	29	29	30	29
	mean	**10.6**	**13.0**	**9.5**	**87.3**	**632**	**7.9**	**0.38**	**6.0**	**37.3**	**7.0**	**1.0**	**0.1**	**0.7**	**2.0**	**4.6**	**2.0**	**0.3**
	SD	4.1	6.2	2.0	17.5	47	0.6	0.16	0.8	17.4	1.7	1.0	0.5	0.9	0.0	1.3	0.0	0.5
	max.	18.1	24.8	13.2	124.3	765	9.3	0.75	7	85	10.0	2	2	2		7		2
	min.	4.3	3.8	6.4	59.7	555	6.6	0.10	4	15	4.0	0	0	0		3		0
Sta. 14	*n*	30	20	24	24	30	26	21	25	24	19	29	29	29	29	30	30	30
	mean	**11.2**	**12.9**	**11.2**	**104.8**	**629**	**7.9**	**0.24**	**3.3**	**44.0**	**6.0**	**1.8**	**0.5**	**0.6**	**1.5**	**3.8**	**2.0**	**0.3**
	SD	4.7	6.0	3.2	35.0	47	0.6	0.11	0.8	18.2	1.9	0.6	0.9	0.9	0.8	1.2	0.0	0.5
	max.	18.8	24.3	18.4	192.7	710	8.7	0.51	4	100	10.4	2	2	2	2	7		2
	min.	4.5	0.4	5.2	49.1	460	6.6	0.06	2	15	4.0	0	0	0	0	1		0
Sta. 15	*n*	30	20	23	23	29	25	20	25	15	13	29	29	29	29	28	30	30
	mean	**11.3**	**12.6**	**9.8**	**92.4**	**672**	**7.9**	**0.17**	**3.1**	**73.3**	**8.0**	**0.1**	**2.0**	**0.0**	**1.0**	**4.8**	**2.0**	**0.2**
	SD	5.5	6.3	2.2	22.8	181	0.5	0.06	0.7	23.5	2.6	0.4	0.0	0.0	0.9	0.8	0.0	0.6
	max.	21.4	21.8	14.4	128.7	1400	8.7	0.30	5	140	12.0	2			2	6		2
	min.	4.0	0.8	5.4	53.6	470	6.6	0.03	2	35	4.0	0			0	3		0

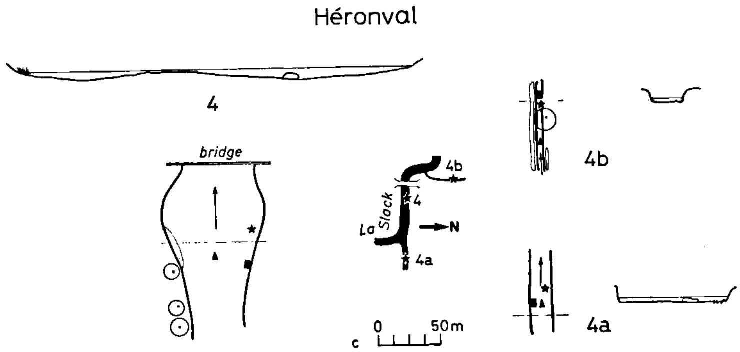

Fig. 4. Relative position of stations 4, 4a and 4b (scale c) with maps and cross-sections. Legends as in fig. 3.

Station 6. Herpont. — At this station, which is situated downstream of the farm "Herpont", the Slack is relatively deep and slowly flowing. Trees hide it from sight.

Station 7. Bourbourg. — At about 100 m east of the now deserted farm Bourbourg, the Slack is a rather fast flowing little stream, meandering through open grassland flanked by shrubs and trees.

Station 8. Réty. — This sampling site is situated just a couple of metres downstream of the bridge across the Slack in the village of Réty. It is bordered by gardens and grassland. The sewers of Réty discharge directly into the Slack.

Station 9. Basse Wioves. — This spot is situated near the small farm of the same name. The heavily overshadowed river has fast flowing and stagnant patches. The sampling site is chosen in the fast flowing part of the river. At this station a small tributary flows into the main stream.

Station 10. Sainte Godeleine. — At this station, which is named after a small chapel containing a spring, the river comes into the open after having flowed through a heavily overshadowed area for about 500 m. To one side there is a concrete embankment. In the summer of 1973 the bottom was wholly covered with mosses, which disappeared after the winter of 1973/1974. Figs. 5A and B show the normal situation and the flooding at this station after one night of heavy rainfall.

Station 11. D242e. — At this station, named after the road that crosses the river at this spot, the Slack is partly dammed by large boulders. It is fully overshadowed by dense shrubs and trees, which separate it from the bordering grassland.

Station 12. Rinxent. — This sampling site is situated just upstream of a railroad crossing and a large open rubbish dump of the village Rinxent. The water flows evenly over a gravel bed with scattered boulders. Dense bed of *Cladophora* sp. cover the substrate most of the time.

Station 13. Marquise. — This station lies just outside the town of Marquise next to a refuse dump. It is polluted by human waste and industrial sewage. In spring 1974 some barrels of waste motor oil, thrown into the Slack at this place, destroyed for some time all invertebrate life at this site and further downstream.

Station 14. Beuvrequen. — The Slack flows at this point, situated 500 m northwest of the village of Beuvrequen, through a wide treeless valley, which is often flooded. As the sluice near Ambleteuse blocks the stream at every high tide, a freshwater tidal regime is found at this station, causing the deposition of fine silt along the banks. The chlorinity of the interstitial water in the bottom sediment is higher than that of the overflowing river water (Nooter & Liebregts, 1971). Seasonally a dense vegetation of waterweeds (*Elodea canadensis* and *Potamogeton pectinatus*) is present.

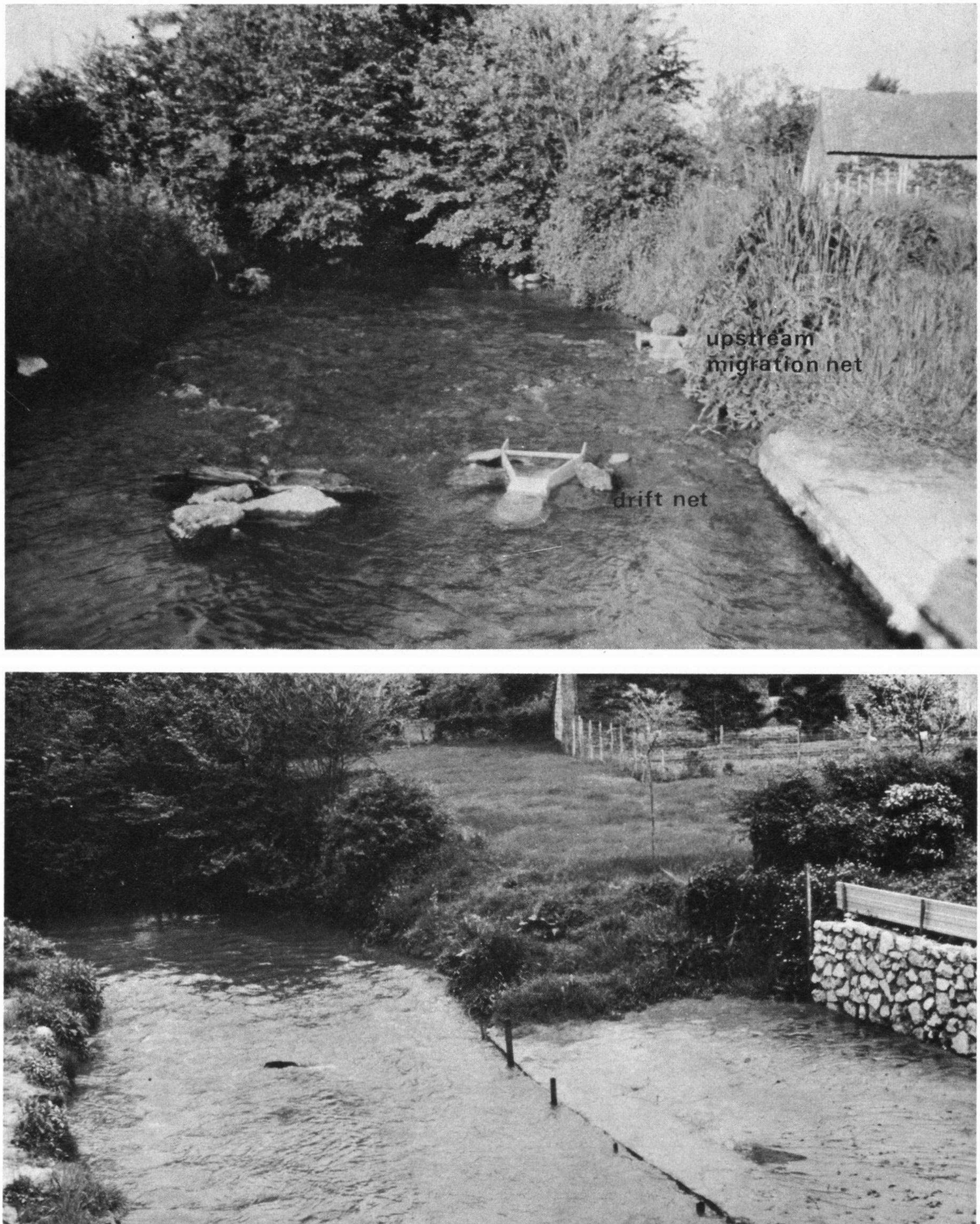

Fig. 5. (A, top): station 10, normal situation; (B, bottom): station 10 after one night of heavy rainfall.

Station 15. Slack. — This station is situated downstream of the bridge in the hamlet Slack. Due to tidal influences both water level and chlorine content of the water change vastly every day, although the sluice near Ambleteuse reduces the tidal variation. This station has been sampled at low tides only.

TABLE II

Vegetation at the different sampling stations (after Tels, unpubl.). In the upper section the trees, shrubs and plants of which the leaves are found in the stream, in the middle section the dominant terrestrial vegetation at a certain site, and in the bottom section the aquatic vegetation are given.

FLORA	STATION NUMBER														
	1	2	2a	3	4	5	6	7	8	9	10	11	12	13	14
Fraxinus excelsior L.			×		×		×					×			
Tilia platyphyllos Scop.			×												
Salix alba L.												×			
Salix cinerea L.								×							
Ulmus sp.		×		×			×			×		×	×		
Alnus glutinosa (L.)			×						×			×	×		
Acer campestre L.			×									×			
Corylus avellana L.							×					×			
Sambucus nigra L.			×		×										
Crataegus monogyna Jacq.					×	×	×		×	×			×		
Rubus sp.	×	×		×		×		×		×		×	×		
Clematis vitalba L.				×				×		×		×	×		
Hedera helix L.				×			×					×			
Epilobium hirsutum L.								×		×			×	×	
Solanum dulcamara L.				×	×			×							
Cirsium arvense L.		×								×	×				
Trifolium repens & pratense L.	×														
Allium ursinum L.							×								
Lamium album L.								×							
Equisetum cf. *arvense*	×														
Arum maculatum L.		×													
Urtica dioica & urens L.			×	×	×		×		×	×			×		
Chrysosplenium sp.			×												
Aethusa cynapium L.										×					
Ranunculus repens L.			×												
Euphorbia helioscopia L.									×						
Myosotis scorpioides L.					×	×							×	×	
Mentha aquatica L.					×	×									
Veronica beccabunga L.	×		×			×		×		×			×		
Berula (= Sium) erecta (Huds.) Coville	×	×	×			×			×	×					
Juncus effusus L.	×				×	×				×					
Juncus articulatus L.	×														
Nasturtium officinale R. Br.	×		×			×					×	×			
Potamogeton crispus L.													×		
Potamogeton pectinatus L.															×
Elodea canadensis Michx.													×	×	×
Callitriche sp.												×	×	×	
Lemma minor L.												×			×
Hepaticae div. sp.							×					×			
Enteromorpha intestinalis Link															×
Cladophora sp.						×					×	×	×		
Musci											×		×		

5. METEOROLOGY

Most data on air temperature and precipitation were obtained from the meteorological service at Boulogne-sur-Mer. Data from the weather station at Boulogne-sur-Mer, situated on the semaphore at the entrance of the harbour (alt. 73 m) and from the station at Licques, some 30 km inland (alt. 50 m) are given here, representing the weather during the research period (figs. 6 and 7, respectively).

The data from the coastal and the inland station show that the influence of the sea rapidly decreases up-country. Temperatures reach more extreme values and precipitation is higher at Licques.

The temperature cycles during the three years show the relatively warm summers of 1975 and 1976 and the rather long but mild cold period during the winter of 1974-1975, which started early in the year.

In the Boulonnais, periods of heavy rainfall as a rule commence in September. The autumn of 1974 and spring of 1975 were very wet, whereas the autumn of 1973 was comparatively dry. The summer of 1976 was an exceptionally dry one.

Detailed information on weather conditions at a certain station was obtained with a Lambrecht meteorograph, which registrates air temperature, relative humidity and air pressure continuously.

6. METHODS

During the first year (September 1973—September 1974) of this research project each station was visited every two weeks. The second year (September 1974—September 1975) we sampled once a month. At each sampling site the standing crop and the migratory activity (both upstream migration and drift) over 24 hours was sampled, while a number of physicochemical and biotic data were measured or noted.

Every sampling period one station was selected, where migratory activity and certain environmental factors were measured every hour for 24 hours on end.

A 16 mm film (Goedmakers & Pinkster, 1977) shows our methods for the sampling of standing crop and migration in detail.

6.1. Biological methods

6.1.1. *Sampling of the standing crop*

The standing crop (viz. the population of gammarids living at a certain station) was sampled in two ways: by electrofishing and with a hand net.

6.1.1.1. *Electrofishing*

A 250 V DC, 0.6 kW Sachs aggregate with two electrodes was used to fish an area of 1 m in front of a drift net (see section 6.2.2.1). We held the kathode fixed in the opening of the drift net and ferreted the riverbed by moving the anode slowly through the substrate towards the kathode (fig. 8A). The animals were temporarily paralysed by the electric shock so that the current could take them into the drift net. At both sides of the drift net an additional net was placed to collect the animals swept sideways (fig. 8B). We took care to sample always at least at two different places at each station.

Thus the absolute density or biomass of the population could be determined in numbers or ml of animals per m^2 (Meyering, 1972). Since this is a very time-consuming method, it was done only a few times at some stations but at least once at every station during the period of investigation.

6.1.1.2. *Hand-net fishing*

We moved a hand net (18 $\times$ 12 cm, mesh size 1.0 $\times$ 1.5 mm) with a metal scraper during 10 seconds slowly over the bottom of the stream. We disturbed the area just upstream of it by kicking the substrate in order to rouse the gammarids from it. Once disturbed, the current sweeps the animals into the net. This procedure was repeated until at least a hundred gammarids were collected. Each time all different microhabitats at the various stations were examined.

Comparison of the electrofishing and hand-net catches learned that the size distribution in the two methods of sampling standing crop was roughly the same (table III). The Mann-Whitney test gave only in the case of station 4a a significant difference between the two ways of sampling standing crop. The samples obtained by electrofishing tend to contain more small animals. We concluded that hand-net samples not only can be

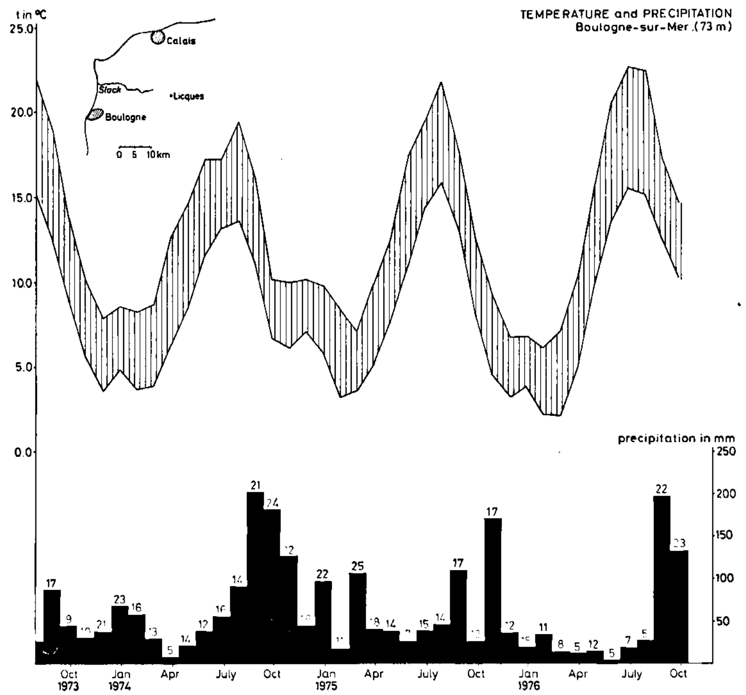

Fig. 6. Seasonal variation of air temperature and rainfall at the weather station at Boulogne-sur-Mer. Mean minimum and mean maximum day temperatures during each month and total amount of rainfall in each month are given together with the number of rainy days.

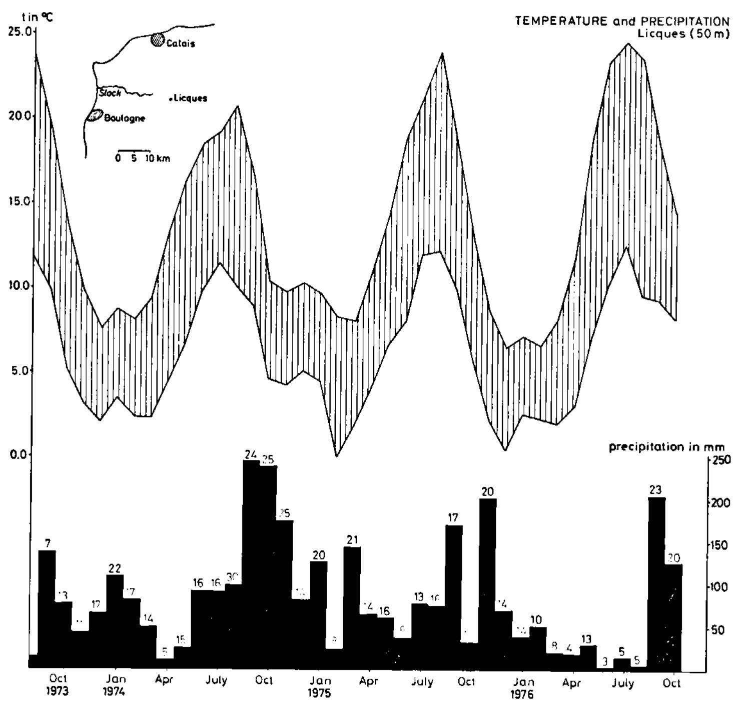

Fig. 7. Seasonal variation of air temperature and rainfall at the weather station at Licques. Mean minimum and mean maximum day temperatures during each month and total amount of rainfall in each month are given together with the number of rainy days.

Fig. 8. (A, top): position of kathode (—) and anode (+) with respect to the drift net during electrofishing at station 2a; (B, bottom): position of the drift net with side nets during electrofishing at station 10.

compared with each other, but also give a reliable picture of the composition of the standing crop. The number of scoops one has to take for a total catch of one hundred animals reflects in our opinion rather accurately the (relative) density of the population.

TABLE III

Mean cephalic length of gammarid samples collected by electrofishing and hand-net fishing.

		Mean cephalic length in mm	
		electrofishing	hand-net fishing
Sta. 1	13 Febr.1974	0.78	0.84
Sta. 4	3-5 July 1974	0.67	0.67
Sta. 4a	3-5 July 1974	0.80	1.05
Sta. 4b	3-5 July 1974	0.93	1.01

To measure sexual activity in the field, we counted the number of animals in precopulation every time; likewise counted were the animals infested with Acanthocephala larvae.

Each sample of animals was killed immediately with 4% formaldehyde and afterwards stored in 70% ethanol.

6.1.2. *Sampling of the migrating animals*

Both up- and downstream migrating animals were collected with specially designed traps. These traps were placed in the stream and emptied after 24 hours or every hour (during continuous mensuration). Except in periods of extreme flooding, migrating animals in the whole water column were caught.

6.1.2.1. *Drift net*

The drift net (figs. 9A, B) consists of a simple plastic tray, which is shoved with its open end into the substrate. The drifting animals are swept by the stream over the smooth hard plastic tray and trapped in an exchangeable net. This net can be removed very easily and exchanged for a new one.

Although fishing in the middle of the river or near its banks did not make much difference to the number of drifting animals caught (table IV),

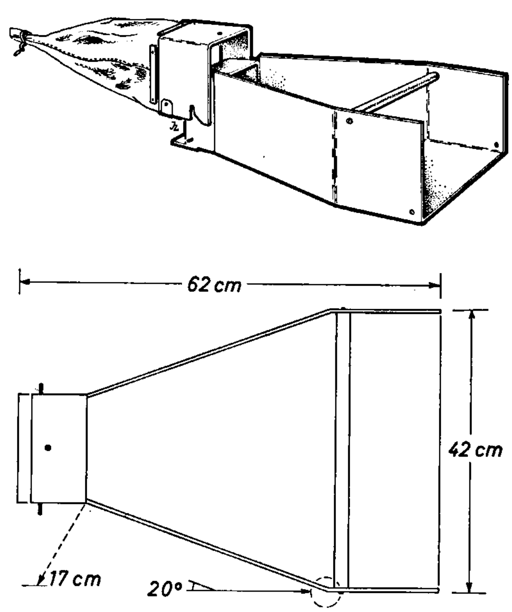

Fig. 9. (A, top): drift net with exchangeable net; (B, bottom): diagram of a drift net.

we have always put drift nets in the middle of the river (fig. 5A).

6.1.2.2. *Upstream migration net*

The upstream migration nets (figs. 10A, B) are made of the same smooth hard plastic. They consist of a closed square tunnel in the middle and an open channel on each side. The bottom of these channels can be covered with the type of substrate found at a given station. Gauze flaps attached to the open end of the channels are buried in the substrate and serve to prevent the animals from creeping under the apparatus. The upstream end of the net is V-shaped, protected by a coarse metal wiring to prevent the net from clogging and provided with a fine gauze to keep the drifting animals out.

When animals migrating upstream through the channels reach this gauze they can no longer continue moving in the same direction and after a while they are swept away by the stream through the smooth tunnel in the middle. They are trapped in an exchangeable net, similar to that attached to the drift nets (fig. 11).

A comparison of upstream migration catches from different places over a cross-section of the river showed that most animals move upstream

TABLE IV

Drifting and upstream migrating gammarids captured along the banks or in the middle of the stream at stations 4 and 5.

		drift		upstream migration	
		bank	middle	bank	middle
Sta. 4	3-4 June 1974	26	15	500	2
	17-18 June 1974	38	19	305	10
	1-2 July 1974	542	177	4600	3
Sta. 5	2-3 July 1974	133	511	739	20
	29-30 July 1974	108	331	263	65
	11-12 August 1974	75	368	95	18

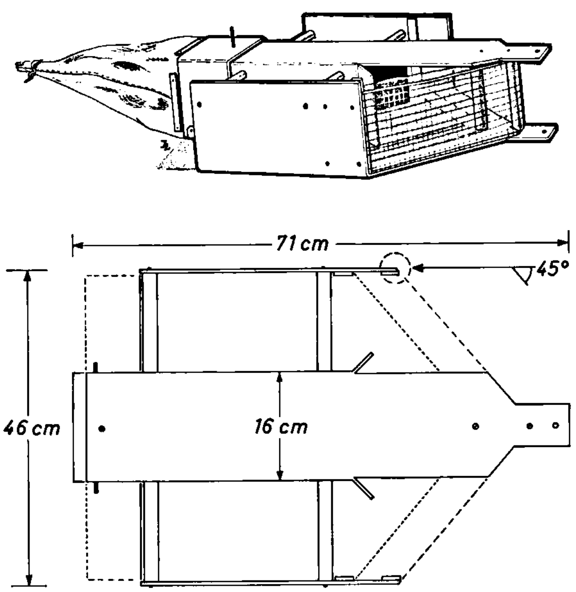

Fig. 10. (A, top): upstream migration net; (B, bottom): diagram of an upstream migration net.

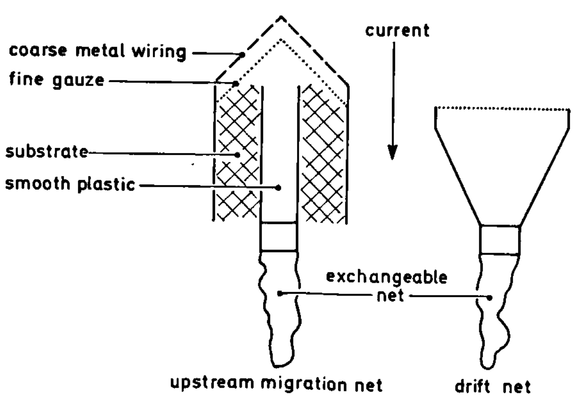

Fig. 11. Diagrammatic top view of drift net and upstream migration net.

along the banks (table IV). Consequently, the upstream migration nets were always dug into the substrate, but in contrast to the drift nets, along the banks of the river (fig. 5A).

The animals caught in the exchangeable nets were either killed and stored like the standing crop samples or released at the place they were heading for, behind the net in which they were captured. During continuous mensuration both number and ml of animals found in the migration nets was counted and measured.

It must be emphasized that the sampling methods (except the scarcely done electrofishing) used for both standing crop and migration research mainly have a qualitative character. Some conclusions on quantitative aspects can be derived from a comparison of qualitative results. Real quantitative sampling would require a quite different research program, which was not our goal.

6.2. Determining of environmental factors

Details on the chemical analysis of the water of the Slack will not be given here. We used Standard Methods (Taras et al., 1975) and Golterman (1971) as handbooks.

6.2.1. *Temperature*

Both water and air temperature were measured in °C with a Yellow Springs telethermometer model 46 TUC.

6.2.2. *Oxygen*

The oxygen content of the water was measured in ppm with a Yellow Springs oxygen meter model 54 (A)RC. Combining this content with the values for water temperature and air pressure, the percentage of saturation with oxygen could be computed.

6.2.3. *Conductivity*

A water sample was taken and conductivity was measured in μmho with a WTW conductivity meter model LF 39 in our field laboratory at Ambleteuse. This instrument compensates for temperature with a temperature coefficient of 2.0% ± 0.1% per °C and reads conductivity values corrected to the conductivity at 20°C.

6.2.4. *pH*

A portable Metrohm pH meter E 488 was used to measure the pH in the field.

6.2.5. *Current velocity*

Current velocity was measured in m/sec. with an Ott current meter type 10.152 and simultaneously estimated with the naked eye, expressed in a scale from 1 to 7 (1 = stagnant, 3 = slowly running, 5 = moderately running, 7 = fast running).

Although measuring with a device is useful to quantify the results, estimations proved to be more

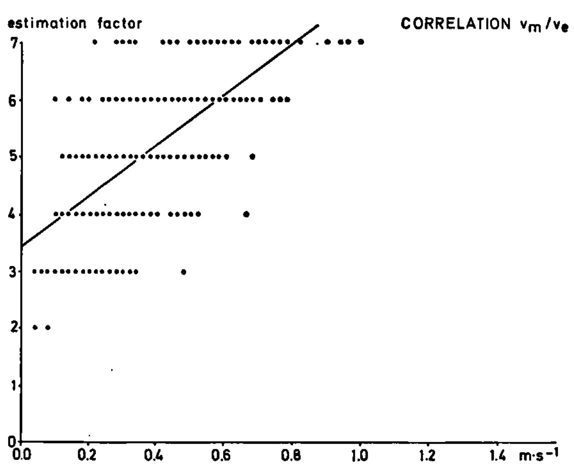

Fig. 12. Correlation between measured (v_m) and estimated (v_e) current velocity. Each dot may represent several data (1 = stagnant, 3 = slowly running, 5 = moderately running, 7 = fast running).

reliable for the comparison of all data. Measuring gave too high mean values, because often low current velocities could not be measured. The correlation between measured and estimated values is given in fig. 12.

6.2.6. *Depth*

Depth was measured in cm at all stations at a fixed spot. It is also used as a relative measure for river discharge.

6.2.7. *Substrate*

The composition of the bottom substrate (silt, sand, gravel and presence of boulders; 0 = absent, 1 = present, 2 = abundant) was noted.

6.2.8. *Pollution*

Pollution was estimated and expressed in a scale from 1 to 7 (1 = unpolluted, 3 = slightly polluted, 5 = moderately polluted, 7 = heavily polluted).

Once during the research period the biological quality of the water was determined after the method of Tuffery & Verneaux (1968) and with the saprobic index of Pantle & Buck (Revier, unpubl.).

6.2.9. *Biotic aspects*

Macrofauna other than gammarids, waterplants, algae, overgrowth and food availability (presence of leaves, twigs or roots, detritus and bioindustrial waste; 0 = absent, 1 = present, 2 = abundant) were noted as well.

6.2.10. *Chemical composition*

Every three months water samples of every station were analysed in the field laboratory with a Hach DC/DR colorimeter and Hach titrametric tests. Thus alkalinity, total hardness, calcium hardness, COD, chlorine, sulfate, phosphate, total nitrogen (nitrate and nitrite), nitrite nitrogen, ammonium nitrogen and detergent content were measured.

6.2.11. *Light*

During the periods of continuous mensuration, light was measured either every hour in lux with a Gossen lux meter (type 8.72 119) or continuously with a Grubb Parsons photo electron multiplier measuring device in units shown on a Goerz miniscript recorder. The relation between the two ways of measuring light is given in fig. 31 (1 lux means about 100 recorder units during dusk and dawn; this relation changes with changing light intensity).

The lux meter is reliable at values of more than 1 lux, while the Grubb Parsons is trustworthy from 1 to 50,000 recorder units. This means that the lux meter must be used during daytime and the Grubb Parsons at night. The Grubb Parsons has a range from 0-5,000 recorder units, when the lux meter does not indicate any light anymore. (The Grubb Parsons photo electron multiplier measuring device consists of the Photopak with an E.H.T. power supply and an amplifier, a variable frequency chopping unit VFC2 and a photomultiplier tube 1 P 28, chosen to resemble the sensitiveness of the lux meter.)

7. ENVIRONMENTAL FACTORS

Differences in environmental factors have both a spatial and a temporal aspect. Environmental factors can differ largely from one station to another, resulting in a microgeographic variation. But environmental factors vary often also considerably throughout the day and the year. This diel and seasonal variation with its special amplitude and level is typical of each station. Microgeographic and seasonal variation will be discussed first, while diel variation showing details of these phenomena is dealt with later.

7.1. Microgeographic and seasonal variation

In our normal sampling routine, all stations were visited successively and thus at different times of the day. Therefore, strictly speaking, the values of the environmental factors of the various stations can not be compared offhand. However, we did not use a correction factor (derived from weather conditions and local daily variation as measured during 24 hour cycles) as the conversions involved most likely would introduce more errors than a comparison (after statistical treatment) of the data found over a two year period

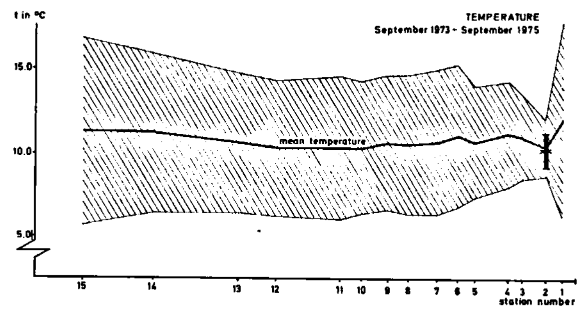

Fig. 13. Microgeographic variation in mean water temperature (entire sampling period averaged) and its standard deviation. Station 2a is indicated separately.

at any time of the day. We put more trust in the sheer mass of our data than in the construction of intricate correction factors (cf. table I).

7.1.1. *Temperature* (figs. 13, 14 and table I)

The annual mean water temperature at each station does not show large differences throughout the river, fluctuating between 10.3 and 11.9°C. The standard deviation of the water temperatures however, shows striking distinctions between the stations. For instance, the mean water temperatures and their standard deviations of the adjacent stations 1 and 2 are 11.9 ± 5.7 and 10.3 ± 1.7°C, respectively. This difference can be easily explained by comparing the situation at the two stations. At station 1 a small amount of water is flowing through a very shallow riverbed in a completely open countryside, while at station 2 a far larger amount of water, predominantly originating from nearby springs, is flowing through a fully overshadowed riverbed.

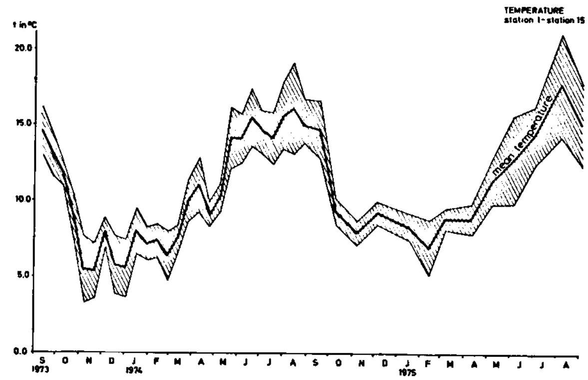

Fig. 14. Seasonal variation in mean water temperature (stations 1-15 averaged) and its standard deviation.

The overall picture of the river shows a short spring region (station 1) with a largely fluctuating temperature regime, an upper region (stations 2-5) with little variation in water temperature and a lower region with larger seasonal (and daily) changes, slowly increasing as the river flows seawards.

The seasonal variation in water temperatures is clearly much larger than the microgeographic variation (cf. figs. 14 and 13). A comparison of water temperatures (fig. 14) with those of the air (figs. 6 and 7) makes it clear that the river Slack has a temperature regime closely following that of the surroundings.

7.1.2. *Oxygen* (figs. 15, 16, 17, 18 and table I)

The mean oxygen content of the water at each station varied between 8.8 and 11.2 ppm (fig. 15), but since this value is dependent on the water temperature, the mean percentage of saturation of dissolved oxygen is used to describe the condition at the different stations (fig. 16).

In spring regions the mean oxygen content of the water is relatively low (80.3 and 83.1% for station 1 and 2a, respectively). Through aeration oxygen content of the water increases rapidly, but the oxydation of organic matter lowers the oxygen content again. This phenomenon is clearly seen downstream of polluted areas (stations 6 and 10-13).

On the whole, a picture similar to that of water temperatures emerges: station 1 has a relatively low percentage of oxygen saturation showing large fluctuations, there is an upper region (stations 2-9) with rather constant and relatively high percentages of oxygen saturation and a lower region (stations 10-15) with comparatively large fluctuations and low percentages of oxygen saturation.

The differences in mean percentage of oxygen

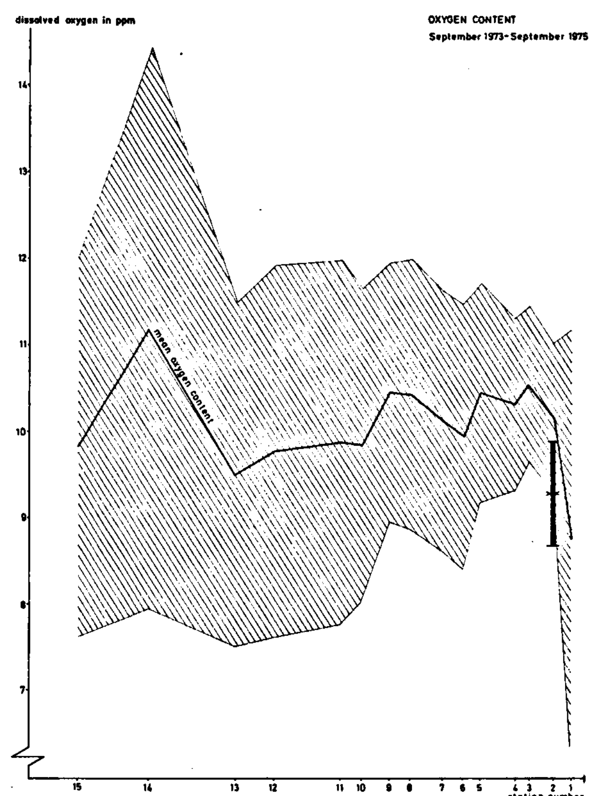

Fig. 15. Microgeographic variation in mean oxygen content of the water (entire sampling period averaged) and its standard deviation. Station 2a is indicated separately.

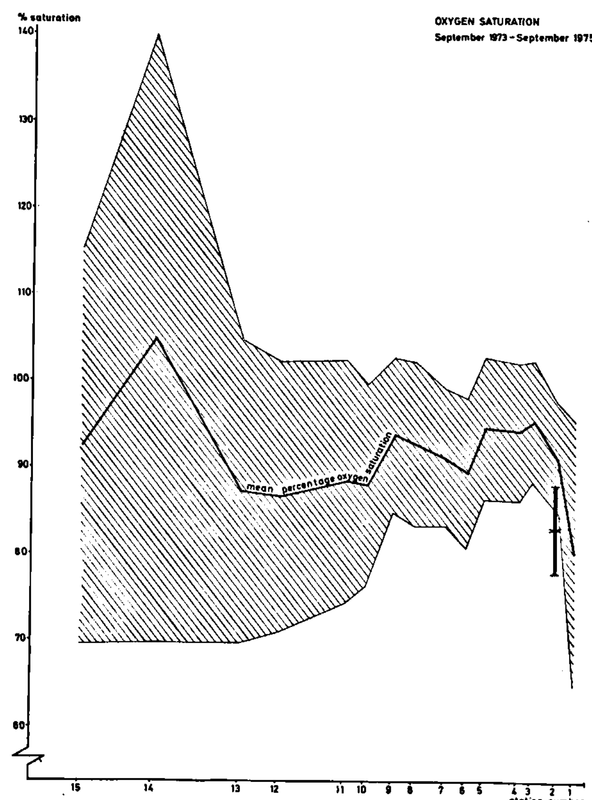

Fig. 16. Microgeographic variation in mean percentage of oxygen saturation of the water (entire sampling period averaged) and its standard deviation. Station 2a is indicated separately.

saturation between the various stations in the upper region can be explained by the local circumstances. At station 2 the greater part of the water originates from nearby springs and consequently does not contain much oxygen. Between stations 2 and 3 this water is aerated and since pollution is almost absent the mean percentage of oxygen saturation at station 3 is higher than that at station 2. The organic pollution at station 4 and the almost stagnant character of station 6 cause the drop in mean oxygen content between stations 5 and 6. The heavy organic pollution by the village of Réty brings on another decline in the oxygen content between stations 9 and 10.

As in the water temperature curves, the seasonal variation in both mean oxygen content (fig. 17) and mean percentage of oxygen saturation (fig. 18) is much larger than their microgeographic variation.

The mean oxygen content of the water (figs. 15 and 17) shows larger fluctuations than the mean percentage of saturation with oxygen (figs. 16 and 18), but follows the same pattern. Since only the actual oxygen content of the water is important for gammarids, this value will be used to correlate behaviour with environmental factors.

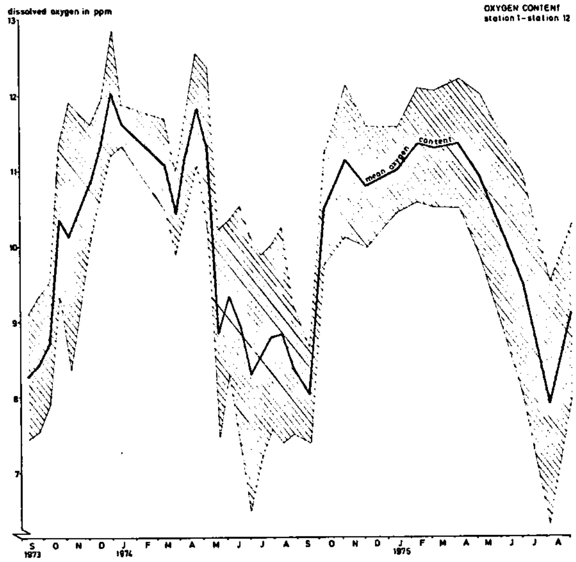

Fig. 17. Seasonal variation in mean oxygen content of the water (stations 1-12 averaged) and its standard deviation.

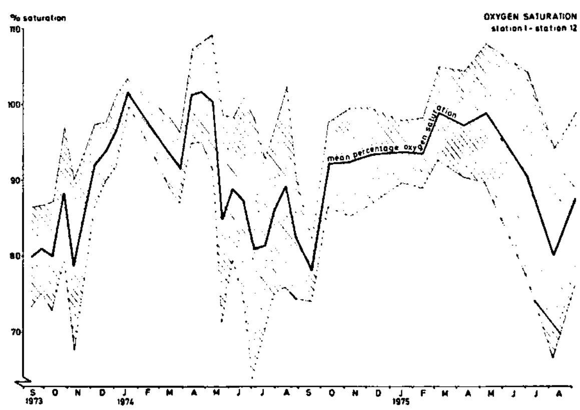

Fig. 18. Seasonal variation in mean percentage of oxygen saturation of the water (stations 1-12 averaged) and its standard deviation.

7.1.3. *Conductivity* (figs. 19, 20 and table I)

The conductivity is a measure for the total amount of dissolved salts. In the part of France studied, water coming from sources has a high chalk (calcium carbonate) content. When the water comes into the open air this chalk precipitates and conductivity decreases. Surface run-off, seepage and pollution cause an accumulation of ions and therefore an increase in conductivity towards the sea.

Stations influenced by springs show a somewhat higher variability in conductivity than the other parts of the upper region (stations 1 and 2a versus stations 2-7, fig. 19). Likewise the pollution at Réty (station 8) has a fluctuating character (due to variation in discharge) which shows its effects in an increased variability of the conductivity as far as station 10.

The seasonal variation in conductivity reflects the weather conditions in this period. The relatively dry winter of 1973/1974 caused an increase in conductivity, since the load of organic material is the highest in winter, while dilution with rainwater occurred only to a small extent in that particular season. In summer the conductivity increases somewhat, while periods of heavy rainfall make conductivity decline (fig. 20).

7.1.4. *pH* (figs. 21, 22 and table I)

The only conclusions the measured pH values allow, are that the pH of water originating from sources is considerably lower than that of the other stations, and that pollution causes a decrease of pH (compare stations 9 and 10 in fig. 21).

The large fluctuations in pH are most likely due to technical problems encountered when measuring pH in a field situation, for instance the minima of fig. 22 are probably too low. Nevertheless pH shows a seasonal variation, with minima in autumn due to the presence of decaying leaves in the water and occurrence of heavy rainfall.

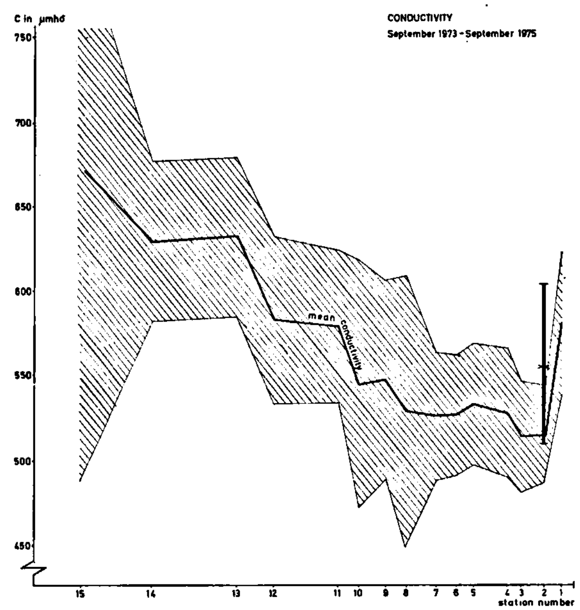

Fig. 19. Microgeographic variation in mean conductivity of the water (entire sampling period averaged) and its standard deviation. Station 2a is indicated separately.

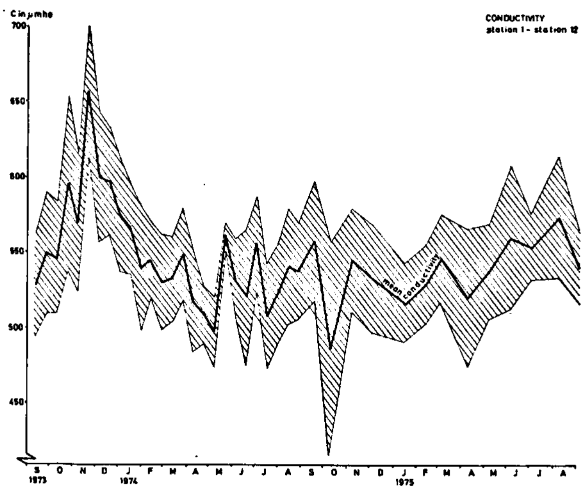

Fig. 20. Seasonal variation in mean conductivity of the water (stations 1-12 averaged) and its standard deviation.

7.1.5. *Current velocity* (figs. 23-25 and table I)

As discussed in section 6.2.5 the mean estimated current velocity is a better criterion to characterize a station than measured current velocity (compare figs. 23 and 24). Although it shows a certain variation during the year (fig. 25) (due to variation in discharge) the differences observed between the various stations (fig. 23) remain more or less constant.

The tendency throughout the river is that the current velocity is rather low in the spring region; it gradually increases in the upper and middle region (stations 2-10), where it sometimes can attain rather high values; in the lower region the Slack grows wider and deeper, it becomes a more

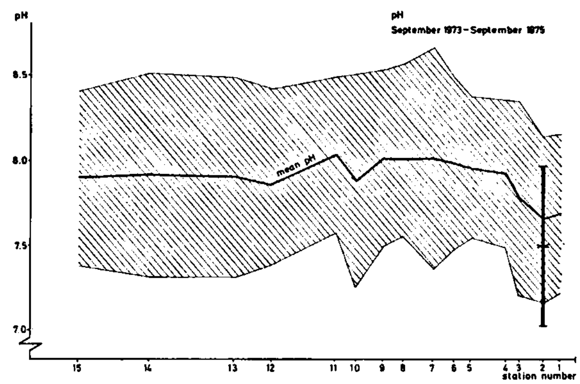

Fig. 21. Microgeographic variation in mean pH of the water (entire sampling period averaged) and its standard deviation. Station 2a is indicated separately.

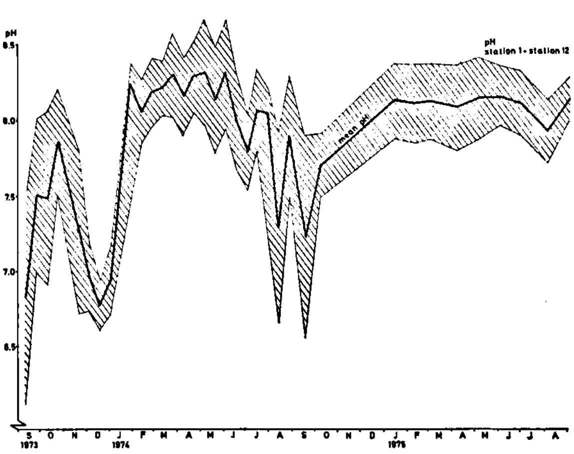

Fig. 22. Seasonal variation in mean pH of the water (stations 1-12 averaged) and its standard deviation.

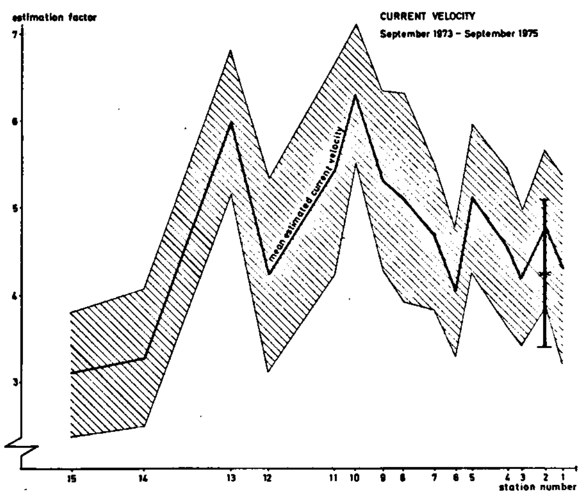

Fig. 23. Microgeographic variation in mean estimated current velocity (entire sampling period averaged) and its standard deviation (1 = stagnant, 3 = slowly running, 5 = moderately running, 7 = fast running). Station 2a is indicated separately.

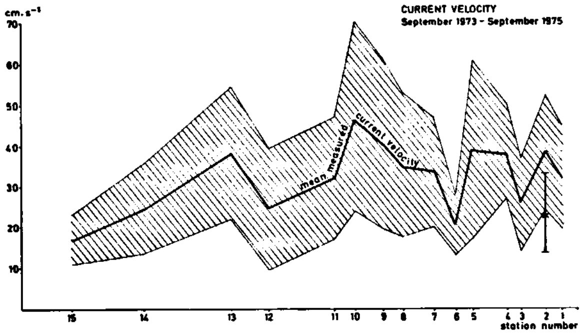

Fig. 24. Microgeographic variation in mean measured current velocity (entire sampling period averaged) and its standard deviation (scale of measured current velocity is the same as that of estimated current velocity in fig. 23 after computation with the correlation in fig. 12). Station 2a is indicated separately.

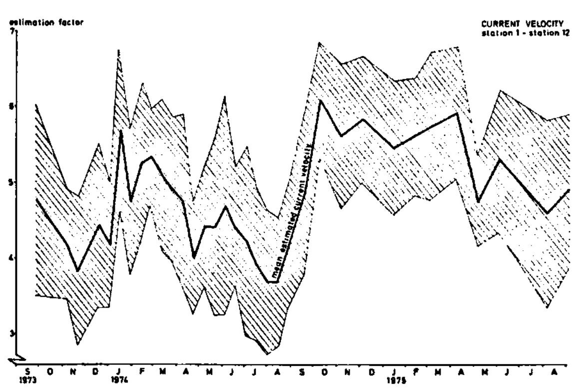

Fig. 25. Seasonal variation in mean estimated current velocity (stations 1-12 averaged) and its standard deviation (1 = stagnant, 3 = slowly running, 5 = moderately running, 7 = fast running).

steadily flowing river and current velocities decrease again.

7.1.6. *Depth* (fig. 26 and table I)

Like current velocity and substrate structure (see section 7.7.7) depth is a good feature to characterize a station. The seasonal variation in depth (fig. 26) is correlated with rainfall and follows the same pattern as the seasonal variation in current velocity.

In a small river like the Slack, heavy rainfall may cause floodings (fig. 5B), which can sometimes (especially in fall and winter) last for a month or longer, inundating large plains in the lower region.

7.1.7. *Substrate* (fig. 27 and table I)

The structure of the substrate is very important for the gammarids living at a given place, but it

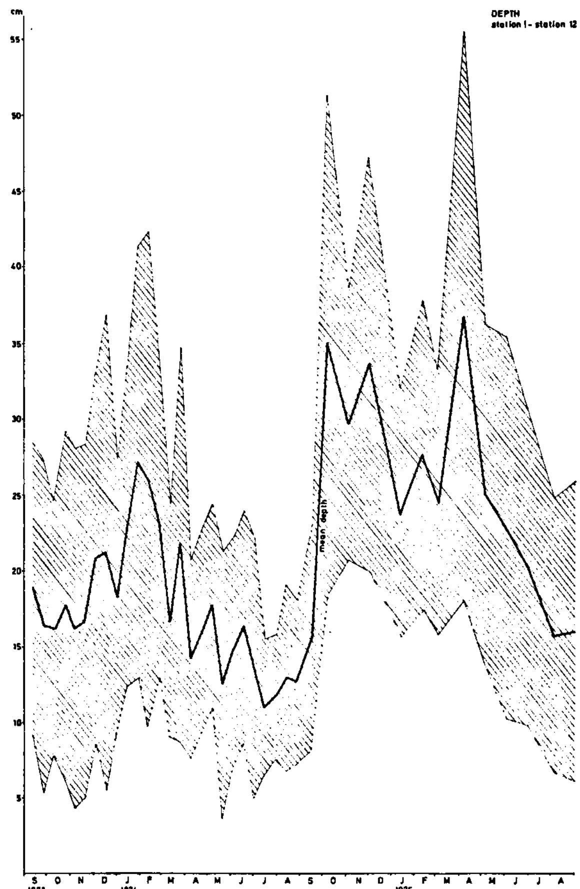

Fig. 26. Seasonal variation in mean water depth (stations 1-12 averaged) and its standard deviation.

is a difficult factor to quantify. Since it is directly correlated with depth and current velocity, these factors can serve as indirect measures for the size of the particles in the substrate (Hynes, 1972). Fig. 27 visualizes the mean composition of the substrate at each station.

7.1.8. *Pollution* (figs. 28, 29 and table I)

An estimation of a value for pollution may seem precarious from a scientific point of view. A trained field worker, however, observes many phenomena during her sampling. These can be used in determining the degree of pollution at a given spot. Therefore such an estimated value may be used as a rapid way to get a rough idea about the grade of pollution at a certain station. In our case such estimated values agree fairly well with the values for the water quality (fig. 29) determined once according to the method of Tuffery & Verneaux (1968) and that of Pantle & Buck (cf. Revier, unpubl.).

Stations 3, 4 and 8 stand out clearly as heavily polluted with organic waste. Although the water quality gradually recovers from these pollutions within a certain distance, the overall effect is still a slow but clear increase of pollution towards the sea.

7.1.9. *Biotic aspects* (tables I, II and V)

Gammarids are the dominant animals in the river Slack. Invertebrates other than gammarids never form more than 50% of the total biomass. In this particular river, the presence of *Asellus* sp. proved to be a good indication for instability

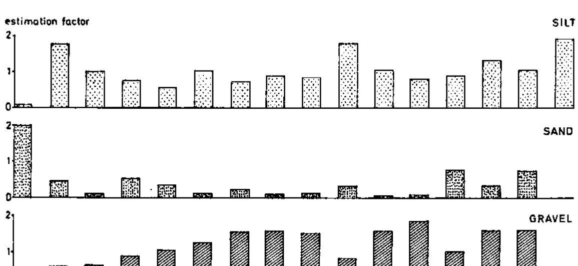

Fig. 27. Mean abundance of silt, sand, gravel and stones at the sampling stations (entire sampling period averaged; 0 = absent, 1 = present, 2 = abundant).

(either caused by pollution or largely fluctuating salt or temperature conditions) of the environment at a given station (table I: stations 1, 9, 12-15).

Hoestlandt (1971) mentions *Cottus gobio* L., *Lampetra planeri* (Bloch), *Salmo trutta* L., *Phoxinus phoxinus* (L.), *Anguilla anguilla* (L.) and *Platichthys flesus* L. as fishes living in the Slack. From our own observations we can add *Gobio gobio* (L.) to this list. Table V gives an impression of the invertebrate macrofauna, other than gammarids, found in this river at the different stations.

The floral aspects of the different sampling sites, as regards both vegetation in the water and of the surrounding area, are shown in table II. Food was never a limiting factor (table I).

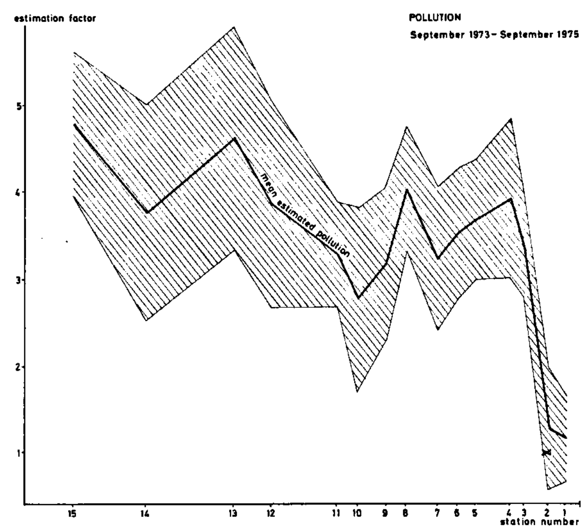

Fig. 28. Microgeographic variation in mean estimated pollution of the water (entire sampling period averaged) and its standard deviation (1 = unpolluted, 3 = slightly polluted, 5 = moderately polluted, 7 = heavily polluted). Station 2a is indicated separately (cross).

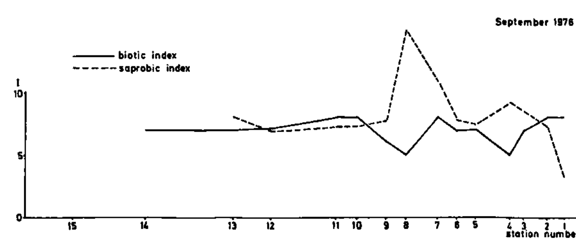

Fig. 29. Microgeographic variation in pollution of the water, measured in September 1976, according to Tuffery and Verneaux (1968) expressed as *I*, and using the saprobic index of Pantle & Buck (Revier, unpubl.) expressed as *S*.

TABLE V

Macrobenthic fauna sampled quantitatively (after Revier, unpubl.) from September 1976 to June 1977.
• = rare (1-2 specimens); o = unfrequent (3-10 specimens); ⊙ = extant (11-20 specimens); ● = common (21-50 specimens); ⬤ = abundant (more than 51 specimens).

MACROBENTHIC FAUNA	STATION NUMBER													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
TURBELLARIA — TRICLADIDA														
Dugesia gonocephala (Dugès)			o			⊙	●	⊙			•	•	o	
Dugesia polychroa (Schmidt)							•						•	
Crenobia alpina (Dana)		•												
Polycelis felina (Dalyell)	o	⬤	⊙					•						
Dendrocoelum lacteum (O. F. Müller)		•	o		•	•		•						
OLIGOCHAETA														
Tubificidae/Lumbriculidae indet.	⊙	o	●	●	⬤	⊙	●	⬤	⊙	⬤	●	●	⬤	⊙
Eiseniella tetraedra (Savigny)	•		•	o	o	•			o				o	
HIRUDINEA														
Erpobdella octoculata (Linnaeus)	⊙	•	o	⊙	●	⊙	⊙	⊙	⊙	⊙	⊙	o	⬤	⊙
Glossiphonia complanata (Linnaeus)		⊙	o		⊙	⊙	o	o	⊙	o	•	●	⬤	o
Helobdella stagnalis (Linnaeus)					⊙	⊙	o	•	•	•	•		o	
Piscicola geometra (Linnaeus)											•	o	o	•
Haementeria costata (Fr. Müller)												o		o
CRUSTACEA														
Gammarus pulex pulex (Linnaeus)	⬤	⊙	o	⊙	o		•							
Gammarus fossarum Koch	●	⬤	⬤	⬤	⬤	⊙	●	⊙	⊙	o	o			
Echinogammarus berilloni (Catta)				•	⬤	●	⬤	⬤	●	⬤	⬤	⬤	⬤	⊙
Asellus aquaticus (Linnaeus)	o				⊙	o	•	•	•	o	•	•	●	
Asellus meridianus Racovitza												⊙	⊙	o
INSECTA — PLECOPTERA														
Perlodes microcephala (Pictet)	•			o										
Taeniopterix nebulosa (Linnaeus)												⊙	•	
Nemoura avicularis Morton												•		
Brachyptera risi (Morton)					•									
INSECTA — TRICHOPTERA														
Rhyacophila dorsalis (Curtis)		●	•	o	⬤	•	●	●	⊙	⊙	⊙	o		
Hydropsyche instabilis (Curtis)				•	⊙	⊙	⊙	o	●	●	⬤	⬤	⊙	o
Plectrocnemia conspersa (Curtis)		o	•	o										
Limnephilus extricatus McLachlan					•									
Limnephilus lunatus Curtis	•				•									
Stenophylax lateralis (Stephens)	•						•							
Drusus trifidus McLachlan		⬤	⊙		o		⬤	⊙	•	o				
Halesus div. sp.	•	o			⊙	o	⊙	o		⊙	o	⬤	⬤	o
Potamophylax stellatus (Curtis)		o			o			•		o		⊙	•	
Sericostoma personatum (Spence)		o					o	o	•	⊙		o	o	
Notidobia ciliaris (Linnaeus)		o	•		•	•	⊙	⊙		⊙	⊙	●	⊙	
Silo pallipes (Fabricius)		●	o			o	●	⊙		o	•	•		
Athripsodes cf. *annulicornis* (Stephens)			o											

TABLE V, continued

MACROBENTHIC FAUNA	STATION NUMBER 1	2	3	4	5	6	7	8	9	10	11	12	13	14
INSECTA — TRICHOPTERA, continued														
Agapetus fuscipes Curtis		⊙												
Lepidostoma hirtum (Fabricius)						•				•			•	
Tinodes assimilis McLachlan		○												
Odontocerum albicorne (Scopoli)		○						○			•			
Mystacides nigra (Linnaeus)												•		
Mystacides longicornis (Linnaeus)										•				
Cyrnus trimaculatus (Curtis)										○				
INSECTA — EPHEMEROPTERA														
Baetis div. sp.	●	●	●	●	●	●	●	●	●	●	●	●	●	⊙
Ephemera danica O. F. Müller										○		○		
Ephemerella ignita (Poda)					•		⊙	○	⊙	●	⊙	⊙	⊙	•
Paraleptophlebia submarginata (Stephens)							•							
Centroptilum luteolum (O. F. Müller)							•							
Habrophlebia fusca (Curtis)								•		•			•	
Heptagenia fuscogrisea (Retzius)								•						
INSECTA — ODONATA														
Coenagrionidae indet.														○
INSECTA — MEGALOPTERA														
Sialis fuliginosa Pictet		•	•		○	•	•	○	•	○	•		•	
Sialis lutaria (Linnaeus)		•			○	•	•	○		⊙		○		
INSECTA — PLANIPENNIA (NEUROPTERA s.s.)														
Sisyra sp.									•					
INSECTA — COLEOPTERA adults														
Elmis aenea (Ph. Müller)	•	•		⊙	●	●	●	⊙	•	⊙	●	•	•	⊙
Limnius volckmari (Panzer)		○			○	•	○	•	○	⊙	•	⊙	○	•
Riolus div. sp.					•	○			○	•	⊙		•	
Oulimnius tuberculatus (Ph. Müller)												•		○
Agabus didymus (Olivier)					•									
Scarodytes halensis (Fabricius)								•						
Potamonectes depressus (Fabricius)					•				•	•		○	⊙	
Oreodytes rivalis (Gyllenhal)		•			○	○	○	•	○	○			○	
Platambus maculatus (Linnaeus)					•		•							
Porhydrus lineatus (Fabricius)								•						•
Laccophilus hyalinus (Degeer)														○
Hyphydrus ovatus (Linnaeus)														•
Haliplus lineatocollis Marsham								•		○	•	•		⊙
Brychius elevatus (Panzer)					○	•	⊙	•		⊙	•	●	●	○
Helophorus griseus Herbst					•					•				
Laccobius alutaceus Thomson											•			
Helophorus arvernicus Mulsant		•												
Haliplus sp.														○

TABLE V, continued

	STATION NUMBER													
MACROBENTHIC FAUNA	1	2	3	4	5	6	7	8	9	10	11	12	13	14
INSECTA — COLEOPTERA larvae														
Helodes minuta Linnaeus	●		•	•	○		⊙		•			•		
Elmis sp.		○			⊙	⊙	•	○		○	⊙	•		
Limnius sp.							⊙		○	○	○		•	
Brychius elevatus (Panzer)					•					•		•	•	•
Gyrinus sp.					•		○			○	○	○	○	○
Agabus/Platambus sp.					⊙		•		•	○				
Hyphydrus ovatus (Linnaeus)					⊙									○
INSECTA — HETEROPTERA														
Sigara semistriata (Fieber)					○				⊙	•		○	•	
Sigara distincta (Fieber)					○									
Sigara striata (Fieber)					○									
Sigara limitata (Fieber)					•					•				
Sigara falleni (Fieber)												○		
Naucoris maculatus Fabricius					•									
Notonecta glauca Linnaeus										•				
Velia cf. *saulii* Tamanini							•							
Nepa cinerea Linnaeus	○						•	•						
larvae *Velia* sp.								○	○					
INSECTA — DIPTERA Chironomidae														
Prodiamesa olivacea (Meigen)		•	●	•	●	•	•	•	⊙	○				
Odontomesa fulva (Kieffer)	○	○	•	○										
Eukiefferiella gr. *discoloripes* Goetghebuer	○			○	●	○	○	○	○	●	●	•	○	•
Eukiefferiella cf. *hospita* Edwards				○	○		•		•		•	○	⊙	
Eukiefferiella cf. *brevicalcar* (Kieffer)	•			○	○			•		○	○	○	○	
cf. *Rheocricotopus* sp.		•		•	•	•	○	○		⊙	⊙	•	○	
Brillia modesta (Meigen)	•	•	○	○	⊙	•	•	•		○	○	○	•	
Cricotopus cf. *bicinctus* (Meigen)			•	•	○		○		○	○	○	•		
Brillia longifurca Kieffer								•		•				
Thienemanniella sp.					•		•							
Micropsectra gr.*praecox* Meigen		○	•	⊙	●	○	○	○	•	•	○	⊙	⊙	○
Paratanytarsus sp.														⊙
Cladotanytarsus sp.														⊙
Chironomus sp.		•	•	•	○	○			○	•		○		○
Cryptochironomus sp.										•				•
Polypedilum gr. *laetum* (Meigen)				⊙	•	○	○	•	○	⊙	⊙	•		
Microtendipes gr. *chloris* Kieffer				•						●	○	○	○	
Paratendipes sp.			○	•	⊙	⊙		○	○	•	○	○		
Pseudochironomus sp.													•	•
Potthastia longimana Kieffer					○					•				
Polypedilum gr. *convictum* (Walker)														⊙
Macropelopia sp.	•	•	○	○	●	⊙	•	⊙	○	•	○	⊙	•	
Apsectrotanypus trifascipennis (Zetterstedt)		○	•		○	○	•	○	○	⊙		•	•	
Procladius sp.						•	•			•				•
Clinotanypus sp.					•						•			
cf. *Conchapelopia* sp.				•	•		•							
Orthocladiinae indet.				●	•	○	⊙	○	○	⊙	•	•	○	•

TABLE V, continued

MACROBENTHIC FAUNA	STATION NUMBER 1	2	3	4	5	6	7	8	9	10	11	12	13	14
INSECTA — DIPTERA other families														
Tipula (Yamatotipula) sp.		○		•	○		•	○	•		•			
Tipula gr. *lunata* Linnaeus							•				•			
Tipula oleracea Linnaeus					•					•				
Tipula varipennis Meigen									•					
Nephrotoma div. sp.								•	•	•	•	•		
Clogmia sp.							•					•		
Bezzia/Probezzia/Johansenomya sp.				○	⊙	•			•	•				
Bezzia sp.			•					•						
Palpomyia tibialis Meigen/ *Sphaeromias pictus* Meigen				•	○			•	•	•				
Oxycera trilineata (Linnaeus)				•										
Dicranota bimaculata Schummel		•	⊙	⊙	●	⊙	●	⊙	⊙	⊙	⊙	⊙		
Limnophora riparia (Fallén)										○				
Tabanus sp.	•	○			○	○	○	•	○	⊙		○	•	
Atherix sp.								○		•	•			
Simulium sp.	●	⊙	○	⊙	●	○	○	•	⊙	○	⊙	○		
Ptychoptera paludosa Meigen	○	•		○	•	○	○	○	○	○	○	•	○	
Solva sp.				•										
Hemerodromia sp.										•				
Beris sp.					•									
Dolichopodidae indet.					•									
Scatophagidae indet.					•									
Hexatominae indet.		•	•		○		•		○	•	○	•		
Antocha sp.							•							
Diptera indet.										○		○		
ARACHNIDA — HYDRACARINA														
Sperchon clupeifer Piersig			○	⊙	⊙									
Hygrobates sp.					⊙							•		○
Lebertia sp.												○		⊙
GASTROPODA														
Potamopyrgus jenkinsi (Smith)		•		⊙	⊙	⊙	●	•	⊙	•	⊙	⊙	•	•
Lymnaea glabra (O. F. Müller)					•									
Lymnaea palustris (O.F. Müller)		○	•								•			
Lymnaea peregra (O. F. Müller)	○	○	○		⊙	⊙	○	•	○	•	⊙	•	●	⊙
Valvata piscinalis (O. F. Müller)											•	⊙	•	⊙
Valvata macrostoma Mörch											•	•	○	○
Planorbis planorbis (Linnaeus)											•	○	○	•
Planorbis leucostoma Millet											•	•		
Planorbis contortus (Linnaeus)											•	•		•
Ancylus fluviatilis (O. F. Müller)										○	•	⊙	•	
Physa fontinalis (Linnaeus)													•	○
Aplexa hypnorum (Linnaeus)													•	
LAMELLIBRANCHIATA														
Sphaerium div. sp.					○	○	○	○	○	•	⊙	⊙	⊙	•
Pisidium div. sp.										•	○	⊙	•	⊙

TABLE VI

Chemical composition of the water (mean values of water samples taken every three months).

	number of water samples taken	total hardness	calcium hardness	alkalinity	chloride	sulfate	total nitrogen	nitrite nitrogen	ammonium nitrogen	total inorganic phosphate (ortho plus meta)	anionic detergent	chemical oxygen demand
Sept. 1973 - Sept. 1975	*n*	ppm $CaCO_3$	ppm $CaCO_3$	ppm $CaCO_3$	ppm Cl	ppm SO_4	ppm (NO_2+NO_3)-N	ppm NO_2-N	ppm NH_4-N	ppm PO_4-P	ppm ABS/LAS	ppm COD
Sta. 1	8	313	303	308	23.4	33.4	7.0	0.09	0.77	7.7	0.031	155
Sta. 2	8	293	273	280	19.8	15.4	10.6	0.04	0.46	9.2	0.039	149
Sta. 2a	6	328	301	287	21.5	13.8	9.0	0.01	0.46	9.4	0.053	166
Sta. 3	8	292	276	270	18.9	35.7	12.1	0.03	0.31	7.4	0.148	153
Sta. 4	8	296	278	263	20.6	25.4	16.3	0.07	0.56	11.3	0.523	163
Sta. 4a	2	332	286	268	27.5	38.5	3.0	0.05	0.54	14.6	0.001	85
Sta. 4b	1	362	332	302	28.0	44.0	6.0	0.02	0.35	9.0	0.005	800
Sta. 5	8	298	269	265	20.8	32.6	6.5	0.13	0.73	8.9	0.051	242
Sta. 6	8	307	267	262	21.2	27.1	6.2	0.13	0.59	8.0	0.372	123
Sta. 7	8	298	272	259	21.7	40.8	7.9	0.09	0.45	6.4	0.042	182
Sta. 8	8	304	273	259	23.4	30.6	7.0	0.08	0.54	8.8	0.188	134
Sta. 9	8	304	263	248	24.1	56.5	8.3	0.06	0.53	6.6	0.052	189
Sta. 10	8	318	278	263	26.0	37.9	8.9	0.08	0.43	7.3	0.061	145
Sta. 11	8	323	287	263	28.6	45.1	6.8	0.14	0.49	4.8	0.203	148
Sta. 12	8	317	274	249	29.2	46.8	11.0	0.10	0.50	10.4	0.402	172
Sta. 13	8	334	286	261	33.0	68.6	9.6	0.14	0.68	11.3	0.326	185
Sta. 14	7	326	283	254	32.1	84.9	9.6	0.13	0.61	9.6	0.087	150
Sta. 15	7	335	277	250	70.4	75.5	7.6	0.18	0.65	11.8	0.087	156

7.1.10. *Chemical composition* (table VI)

Values for alkalinity, total hardness and calcium hardness are clearly those of a chalk stream (Nisbet & Verneaux, 1970; Casey & Newton, 1973). According to the data of Nisbet & Verneaux (1970) for the whole of France, all data on chemical composition are an indication of the rather high organic pollution rates of the Slack.

7.2. Diel variation (figs. 30 and 31)

The variation in environmental factors during the day is sometimes very large depending on what factor is investigated and the nature of the sampling station. The kind of fluctuations found is illustrated by data on mean values of water temperature, conductivity, oxygen content, pH and light at a certain time during ten days of continous mensuration in 1976 (figs. 30 and 31). Stations 4, 4a and 4b (fig. 4) with normal, very unstable and very stable temperature regimes respectively, are compared. The proximity of these stations ensures similar weather conditions for all three.

7.2.1. *Temperature*

The amplitude of the variation in water temperature at a given station during 24 hours shows the same tendency as the seasonal variation in water temperature. Some stations have a large range between minimum and maximum water temperatures, others only a small one. Of course this diel variation is influenced by the weather: on sunny days the variation is much larger than on cloudy days.

7.2.2. *Oxygen*

Daily variations in photosynthesis, respiration, oxydation of organic waste and water temperatures make oxygen content vary during 24 hours. The respectively stable and very unstable environmental conditions of station 4b (springbrook) and station 4a (small tributary highly influenced by organic pollution) are reflected in the diel variation in oxygen content (fig. 30): a comparatively high oxygen content at night for station 4b, while the oxygen content of station 4a is relatively high during the day (fig. 30).

7.2.3. *Conductivity*

Conductivity does not fluctuate in a regular way throughout night and day. The diel variation observed for instance at station 4a is caused by pollution, which is brought about mainly during daytime.

Heavy rainfall also influences conductivity. Especially where the amount of water in the stream is comparatively small, rain may cause a clear decrease of conductivity.

7.2.4. *pH*

Especially in the springbrook (station 4b) the effect of respiration and photosynthesis becomes clear in pH changes. At night pH is higher than during daytime due to the high amount of calcium carbonate in the water of the springbrook, which precipitates when photosynthesis removes carbon dioxide, thereby lowering pH during the day.

Heavy rainfall makes pH drop considerably.

7.2.5. *Light*

Light conditions show vast changes during 24 hours (fig. 31). For gammarids, with their noc-

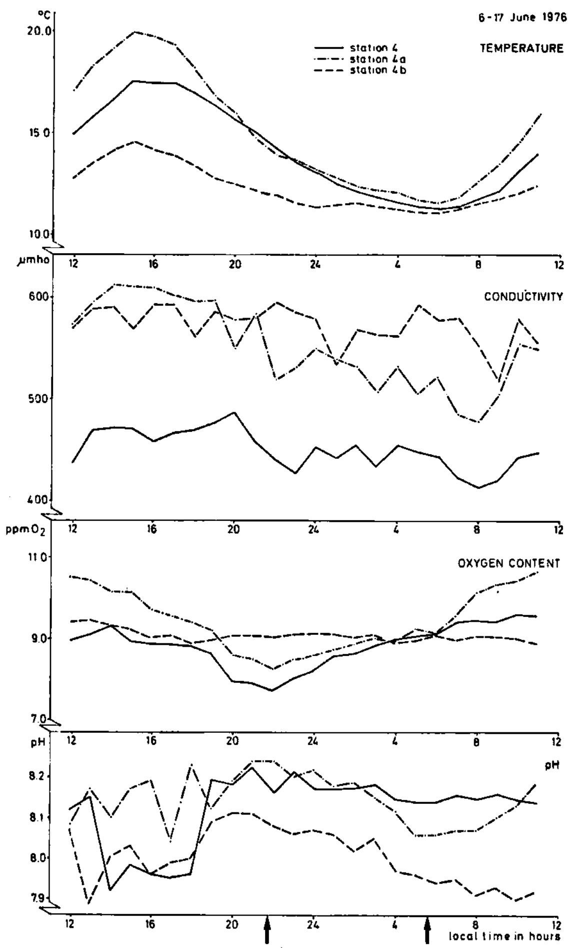

Fig. 30. Diel variation in mean water temperature, conductivity, oxygen content, and pH during 10 days at stations 4, 4a and 4b.

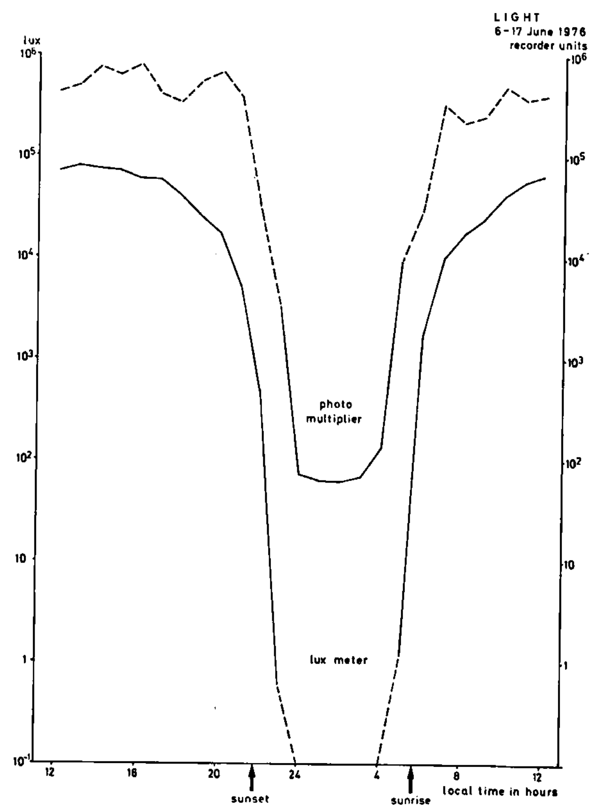

Fig. 31. Diel variation of mean light conditions measured continuously with a photo electron multiplier (in recorder units) and a lux meter (in lux) during 10 days at station 4.

TABLE VII
Discriminant analyses (cf. Nie et al., 1975-1979).

	Station numbers entered [1])	Variables entered [2])	Solution method	Prior probabilities	Cases with missing data during classification	Percentage of known cases correctly classified
DA 1	1—14	13	direct	equal	deleted	5.2
DA 2	2—14	8	direct	equal	deleted	47.1
DA 3	1—14	8	direct	equal	deleted	52.5
DA 4	6—12	9	direct	equal	deleted	58.2
DA 5	1—14	8′	direct	equal	deleted	51.1
DA 6	1—14	8′	direct	size	deleted	50.8
DA 7	2—12	8	direct	equal	included	44.6
DA 8	1—14	8′	direct	size	included	43.7
DA 9	1—14	8′	direct	equal	included	43.2
DA 10	1—14	8	direct	equal	included	45.3
DA 11	1—14	8	stepwise	equal	included	45.3
DA 12	1—14	7	stepwise	equal	included	38.0
DA 13	1—14	13	stepwise	equal	included	6.5
DA 14	1—14	13	stepwise	equal	deleted	7.0
DA 15	1—15	13′	stepwise	size	deleted	8.7
DA 16	1—15	7′	stepwise	size	deleted	54.2
DA 17	1—15	6	stepwise	size	deleted	45.1
DA 18	1—15	5	stepwise	size	deleted	49.1
DA 19	1—15	8″	stepwise	size	deleted	54.2

1) Except in DA 2, 4 and 7, station 2a was always included in the analyses.
2) Variables: 13 = p, C, d, v_e, gr, si, st, % O_2, t_w, A, pH, v_m, sa
13′ = d, C, v_e, p, si, gr, pH, % O_2, st, t_w, sa, t_w - mean t_w, SD t_w
9 = p, C, d, v_e, % O_2, A, t_w, v_m, pH
8 = p, C, d, v_e, % O_2, A, t_w, v_m
8′ = p, C, d, v_e, % O_2, A, range t_w, pH
8″ = d, C, v_e, p, pH, % O_2, t_w - mean t_w, A
7 = p, v_e, C, % O_2, A, t_w, v_m
7′ = d, C, v_e, p, pH, % O_2, t_w - mean t_w
6 = p, C, v_e, % O_2, pH, t_w - mean t_w
5 = d, C, v_e, p, % O_2

Except in the cases with 9 and 8′ variables, variables are placed in the order in which they were entered in the classification. For explanation of the symbols used, see the boxhead of table I.

turnal activity pattern, the amount of light during the night may be very important. Measurements with the Grubb Parsons enabled us to compare light conditions at night.

But also the manner in which light increases or decreases at sunrise or sunset (fig. 31) may have a large influence on the behaviour of gammarids.

7.3. Mathematical analysis of data on environmental factors

All data on environmental factors, measured each time the standing crop was sampled, were used to establish the distinction between or similarity of the fifteen sampling stations. The mathematical treatment of our material necessary for this analysis was done with the CDC computer of SARA (Stichting Academisch Rekencentrum Amsterdam). We applied discriminant analyses (Nie et al., 1975-1979) and cluster analyses (Wishart, 1975) to our data. Both methods give essentially the same outcome, only arrive at it in a different manner.

The outcome can differ largely when different sets of data are used as input, since each environmental factor is of a different nature. For instance

TABLE VIII

Cluster analyses (cf. Wishart, 1975).

	Station numbers entered	Variables entered [3]	Method	Clustered stations [4]
CLUSTAN 1	1—14	13 mean + SD	single linkage	A = 1 B = 14 C = 13 D = 2-12
CLUSTAN 2	1—14	8 min. + max. + SD or mean + SD (v_e, v_m, d, A)	single linkage	A = 14 B = 1 C = 13 D = 2-12
CLUSTAN 3	1—14	13 min. + max. + SD	single linkage	A = 1 B = 14 C = 4 and 5 D = 2 and 3, 6-13
CLUSTAN 4	1—14	13 mean + SD + min. + max.	single linkage	A = 1 B = 14 C = 4 and 5 D = 2 and 3, 6-13
CLUSTAN 5	1—14	8 min. + max. + SD	single linkage	A = 14 B = 1 C = 5 D = 2-4, 6-13
CLUSTAN 6	1—14	8 mean + SD	single linkage	A = 1 B = 14 C = 2a D = 2-13
CLUSTAN 7	1—14	8 mean + SD + min. + max.	single linkage	A = 1 B = 14 C = 13 D = 2-12
CLUSTAN 8	1—15	6 mean + SD + min. + max.	single linkage	A = 1 B = 13 C = 14 and 15 D = 2-12
CLUSTAN 9	1—15	6 mean + SD + min. + max.	Ward's method	A = 2 and 3 B = 1 C = 14 and 15 D = 4-13
CLUSTAN 10	1—15	6 mean + SD or min. + max. + SD (t_w)	single linkage	A = 1 B = 14 and 15 C = 2a D = 2-13
CLUSTAN 11	1—15	6 mean + SD or min. + max. + SD (t_w)	Ward's method	A = 2-5 B = 14 and 15 C = 1 D = 6-13

[3]) Variables: 13 = p, C, d, v_e, gr, si, st, % O_2, t_w, A, pH, v_m, sa
8 = p, C, d, v_e, % O_2, A, t_w, v_m
6 = p, C, v_e, % O_2, t_w, pH
For explanation of the symbols used, see the boxhead of table I.

[4]) Except in CLUSTAN 6 and 10, station 2a is always classified in the same group as station 2.

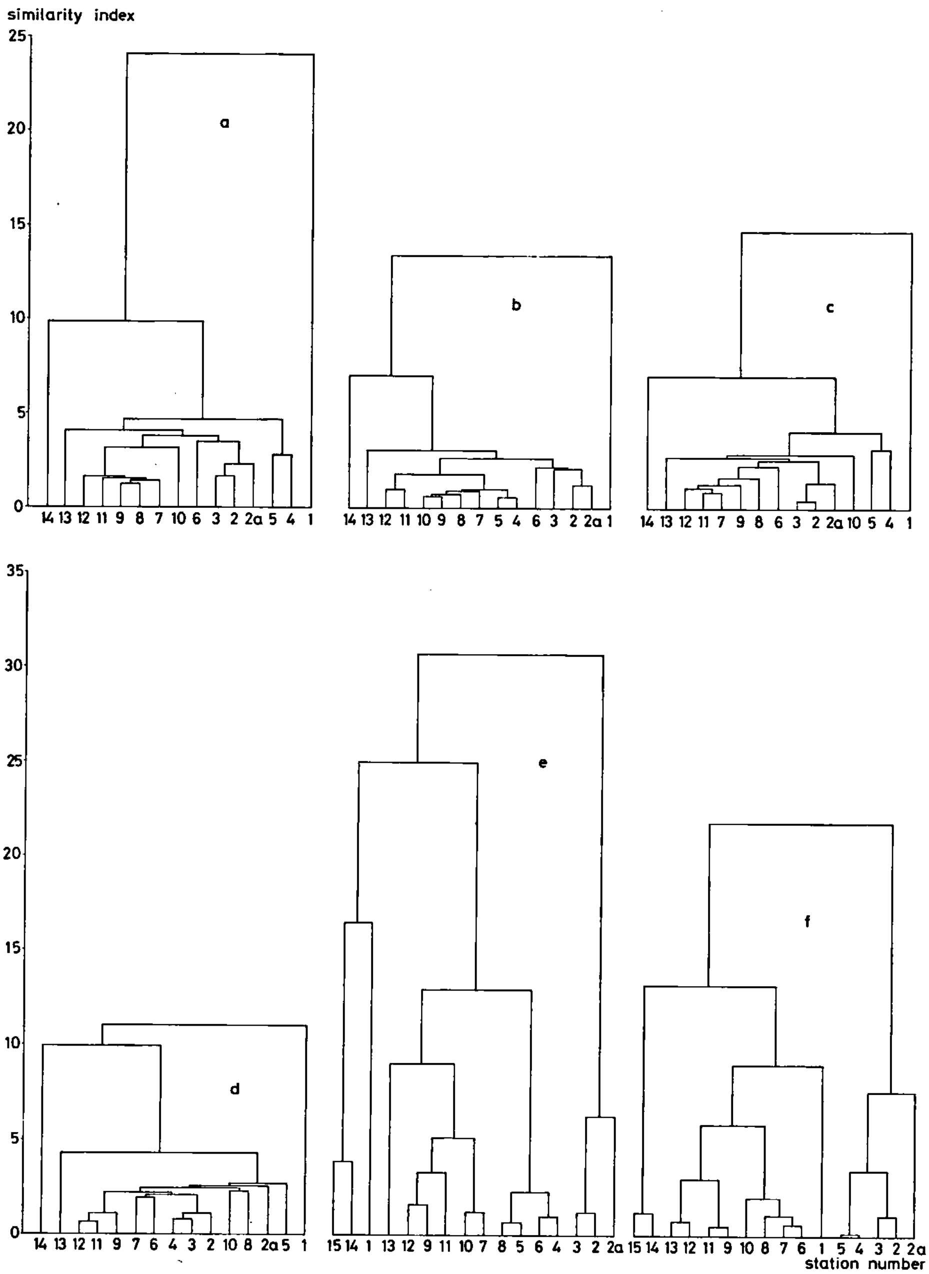

Fig. 32. Cladograms resulting from cluster analyses (cf. table VIII): a = CLUSTAN 4, b = CLUSTAN 1, c = CLUSTAN 3, d = CLUSTAN 7, e = CLUSTAN 9, f = CLUSTAN 11. Only those cluster analyses with a similarity index exceeding 10 at least once are drawn in this figure.

water temperature has almost the same mean value for every station in our research period, but its standard deviation differs largely between all stations. This makes water temperature very important to gammarids. Depth, however, is a factor with an obviously distinct mean value for each station, but with a low meaning to explain gammarid behaviour, since it has no direct impact on gammarid life.

7.3.1. *Discriminant analysis* (table VII)

Discriminant analysis compares every single observation with a characteristic of each station, derived from all data on environmental factors. It then attributes it to the station where it seems to fit best. With discriminant analysis we tried to determine to what extent the environmental conditions found at each station were specific features of that station. It enabled us also to distinguish between environmental factors that influence this specific distinction to a large extent and those that are not very important.

Discriminant analyses were carried out in several ways and with different sets of data (table VII): sometimes using data of all stations (DA 15-19), other times using data of only some of the stations (DA 1-14); sometimes with the data for all environmental factors (DA 1, 13 and 14), at other times using only some of them (DA 2-12 and 15-19).

Thus we could determine that pollution, depth, estimated current velocity and conductivity were the environmental factors responsible for most of the distinction between the various stations. Of all discriminant analyses we did including all stations, those with the best results were those in which slightly more than half of the data was attributed to the station from which they originated (DA 16 and 19). (If there would have been a large difference between all stations, 100% of the data would have been correctly classified; if all stations would have been identical, a very low percentage of the data would have been imputed to the right station.) This means that most stations were very much alike.

7.3.2. *Cluster analysis* (table VIII and fig. 32)

To know whether stations can be grouped together on basis of their environmental conditions, we used cluster analyses. As in discriminant analyses we applied different methods of cluster analysis and used different sets of data (table VIII). Sometimes all (CLUSTAN 1, 3 and 4), other times only some (CLUSTAN 2 and 5-11) of the measured environmental factors were taken into account.

Mean, standard deviation and/or minimum and maximum of these environmental factors were used as data input. Station 15 was only four times included in the analyses (CLUSTAN 8-11) because of its rather distinct, brackish character.

The following conclusions can be drawn (fig. 32 and table VIII):

— stations 14 and 15 form a distinct group;
— station 1 is clearly different from all other stations, but frequently shows more resemblance to stations 5-15 than to stations 2 and 3;
— in almost half of the analyses station 13 is segregated as a distinct group;
— in the majority of the analyses stations 2-12 are grouped together, but sometimes this group is divided in two or three subgroups (stations 4 and 5 sometimes fall in a separate group, other times in one of the two other groups),
— station 2a is twice considered a separate group.

7.4. Conclusions

Environmental factors are largely alike from stations 2-12. Station 13 is a little different, due to its heavily polluted character. Stations 14 and 15 form the estuarine part of the river (fresh and brackish tidal area, respectively). Station 1 has special environmental conditions: very unstable, in character more like the middle or lower reaches of the river than like the upper region.

There is no sharp distinction and certainly no boundary between the upper and middle region. Stations 4 and 5 form a kind of transitional zone between what could be called the upper (stations 2 and 3) and the middle (stations 6-12) region of the Slack.

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