Bijdragen tot de Dierkunde, 51 (2): 145-180 — 1981

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

PART III. MIGRATION

by

ANNEMARIE GOEDMAKERS & SJOUK PINKSTER
Institute of Taxonomic Zoology, University of Amsterdam, The Netherlands

ABSTRACT

Migration of *Gammarus pulex pulex* (Linnaeus, 1758), *G. fossarum* Koch in Panzer, 1836, and *Echinogammarus berilloni* (Catta, 1878) has been studied in a small French chalk stream, the Slack. Three different approaches to investigate both up- and downstream migration were used: (1) migration survey, with a sampling program of migration at intervals of two weeks or a month at twelve localities in the river Slack; (2) continuous measurement of migration at three habitats with very stable, normal and very unstable environmental conditions, respectively, lying within 100 m of one another and populated by the same species, *G. fossarum*; (3) finally, marking experiments in order to identify and trace animals with a given behaviour.

Both drift and upstream migration show a considerable microgeographic variation, which is larger for *Gammarus* than for *E. berilloni*. During the relatively warm year of 1975, the migration activity of *E. berilloni* was stronger than in 1974. Upstream migration was concentrated in early summer, while drift fluctuated during the year. Most animals migrated during the night, although the diel variation in drift was quite different from that in upstream migration. Water temperature and its diel fluctuations have a large effect on non-accidental migration. Changes in chemical composition of the water seem to be important as well. Light conditions have only a slight influence on migration patterns. Physical disturbance of the riverbed (for instance by wading cows or the scouring effect of spates) influences migration rather negatively.

The mean size of migrating animals was larger than the average size of the standing crop. Upstream migrants were larger during hours of high upstream migration activity, while the animals that drifted in peak hours were usually smaller than those drifting in hours of low activity. Both up- and downstream migration proved to be a constant behaviour; most drifters of a particular night drifted again the following night and most upstream migrants moved again upstream after they had been marked.

In particular our results on microgeographic and seasonal variation show clearly that a quantitative approach to migration would have been premature. Secondly, they make a direct correlation between production and drift unrewarding. The continuous measurement of migration showed that for this type of investigation field work is preferable to laboratory experimentation, since it gives more reliable results than those achieved under laboratory conditions.

RÉSUMÉ

La migration de *Gammarus pulex pulex* (Linnaeus, 1758), *G. fossarum* Koch in Panzer, 1836, et *Echinogammarus berilloni* (Catta, 1878) a été étudiée dans la Slack, une petite rivière côtière calcaire du Boulonnais. Trois méthodes distinctes furent utilisées pour étudier les migrations vers l'amont et l'aval: (1) un inventaire périodique de la migration fut effectué toutes les deux semaines ou tous les mois dans douze localités de la Slack; (2) des échantillonnages continus de la migration effectués dans trois habitats caractérisés par des paramètres du milieu stables, moyens et instables, respectivement, se trouvant à moins de 100 m l'un de l'autre et habités par la même espèce, *G. fossarum*; (3) enfin, des expériences de marquage permettant d'identifier et de suivre des animaux ayant un comportement défini.

A la fois la dérive et la migration vers l'amont sont sujettes à une variation microgéographique considérable, qui est plus importante pour *Gammarus* que pour *E. berilloni*. Pendant l'année 1975, relativement chaude, l'activité migratoire d'*E. berilloni* était plus intense qu'en 1974. La migration vers l'amont a surtout lieu au début de l'été, tandis que la dérive varie pendant l'année. La plupart des animaux migre pendant la nuit, bien que les fluctuations nycthémérales de la dérive diffèrent considérablement de celles de la migration vers l'amont. La température de l'eau et ses fluctuations diurnes ont un effet important sur la migration non-accidentelle. Les changements de composition chimique de l'eau semblent également avoir une grande influence. Les conditions de l'éclairage influent peu sur la migration. Des perturbations du substrat (par exemple par des vaches traversant la rivière, ou l'effet abrasif de crues soudaines) ont un effet plutôt négatif sur la migration.

La taille moyenne des animaux migrateurs était supérieure à celle du «standing crop». Les migrateurs vers l'amont étaient plus grands pendant les heures de migration dense, alors que les animaux dérivant pendant les heures de dérive maximale étaient en général plus petits que ceux rencontrés pendant les heures d'activité réduite. A la fois la migration vers l'amont et la dérive se sont avérées des comportements constants; la plupart des dériveurs d'une nuit donnée dérivait de nouveau la nuit suivante et la plupart des migrateurs vers l'amont migrait de nouveau vers l'amont après marquage.

Nos résultats sur les variations microgéographiques et saisonnières démontrent nettement qu'une approche quantitative de la migration aurait été prématurée. De plus, la possibilité d'établir une corrélation directe entre la production et la dérive semble petite. Les mesures continues de la migration ont démontré que pour ce genre de recherche le travail sur le terrain est préférable aux expériences de laboratoire, où les résultats sont moins sûrs que ceux obtenus sur le terrain.

CONTENTS

1. INTRODUCTION

Stream invertebrates migrate over much smaller distances than birds or fish. Nevertheless, migration may have a large impact on the life of such animals. So, insects with stream-dwelling larvae manage to find suitable habitats during their whole life cycle by drifting in the larval period and flying in the upstream direction as adults. Animals like gammarids, spending their whole lifetime under water, necessarily exhibit a more complex behaviour in their aquatic surroundings.

Migration is an ecological process, which is thought to serve many purposes. According to different authors gammarid migration regulates population density (Waters, 1965; Waters & Hokenstrom, 1980), facilitates mating and reproduction (Lehmann, 1967), enables (re)colonization (Hynes, 1972; Williams & Hynes, 1976), and helps to meet the specific needs during various stages of the life cycle (Dennert et al., 1969).

Furthermore, migration is a phenomenon with many aspects. Gammarids migrate both up- and downstream. Downstream migration (drift) is a movement in the same direction as the current flow. Waters (1972) makes a distinction between constant, behavioural and catastrophic drift. Since this distinction is not always very clear, Baker (1978) opted for two categories: accidental and non-accidental migration. In his opinion the use of the term "accidental migration" should be restricted to those situations in which both the initiation and the continuation of migration are beyond the control of the animal concerned, and are due to a failure in the normal station-keeping mechanisms of the animal. (A foraging gammarid that is swept away by the current, and the scouring action accompanying floodings which cause a large downstream migration, are examples of accidental migration: the first being constant or behavioural and the second catastrophic drift.) All other kinds of migration he calls non-accidental (migration induced by drought, high temperature, or pollution are examples of catastrophic, but non-accidental drift). Where migration is accidental it is obviously unnecessary to look for a function of migration, while in non-accidental migration there might be a certain advantage in this behaviour. Upstream migration is a movement against the current direction, which is necessarily always non-accidental. (The upstream migration observed in estuaries is of a special type, since animals moving in upstream direction make use of the tidal current reversal; they move along with the current in upstream direction. This, however, is evidently also non-accidental migration.)

Migration shows a geographic, seasonal and diel variation, which makes the interpretation of results very difficult. Diel variation of gammarid migration is relatively well investigated (Bournaud & Thibault, 1973; Müller, 1974). Data on seasonal variation are rather scarce (Lehmann, 1967; Meijering, 1977). Geographic variation is still rather unexplored. A comparison between different gammarid species or populations of gammarids has attracted even less interest. Data on these subjects are very rare (Bournaud & Thibault, 1973).

Light intensity is considered to be responsible for the diel periodicity in migration (Waters, 1972; Bournaud & Thibault, 1973; Müller, 1974). But also environmental factors like temperature, current velocity and water quality seem to influence phase and fluctuations of migration (Meijering, 1972; Waters, 1972).

As we stated in part I of this series of papers (Goedmakers, 1980), we aimed to acquire qualitative knowledge about the population dynamics of gammarids in a small stream. Our migration research therefore focused in the first place on the general pattern of migration throughout the year in different parts of the stream. Later on, with a continuous measurement of migration, we tried to learn more about the way in which migration fluctuates and is influenced by environmental factors. Marking experiments were used to differentiate between groups of animals and enabled us to identify them afterwards.

2. ACKNOWLEDGEMENTS

Migration research means a lot of tedious effort, especially due to continuous measurement in day and night shifts. Of all the people who participated in this part of the program, we are particularly grateful to Drs. Nico Broodbakker, not least for his moral support during long nocturnal hours.

The often very large numbers or enormous volumes of animals collected in the field meant that much work had to be done afterwards in the laboratory by inter alios Mr. Bert Meijering, Mr. Peter Finger and Mr. Bart van den Hoek. The students Mrs. Marie José Goedmakers and Mr. Wim Bosch worked on part of the material to measure differences in composition and size between migrating animals and standing crop.

The mathematical help of Drs. Jan Dieleman and Mr. Henk Olofsen enabled us to correlate environmental data to migration results.

This work has been done with financial support of the Netherlands Organization for the Advancement of Pure Research (ZWO), the Foundation for Fundamental Biological Research (BION), and the University of Amsterdam.

3. METHODS

The methods used to study migration activity are described in detail in part I of this study (Goedmakers, 1980). Specially designed nets (Goedmakers, 1980: section 6.1.2) trapped the animals moving either up- or downstream. The nets were emptied after a certain period of time (1-24 hours) and the number or volume of the thus collected animals was counted or measured.

As a rule all animals captured during the continuous measurement of migration were released in the stream behind the net in which they were caught (drifters downstream of the drift net; upstream migrants upstream of the upstream migration net), after they had been counted. Eventually the catches were preserved for further treatment in the laboratory (identification, sexing and measuring, see Goedmakers, 1981). A varying number of environmental factors was measured at the same time (Goedmakers, 1980).

Two problems arise with our method of trapping migrating animals. Firstly, part of the migrating population might be able to steer clear of the nets: e.g. small animals might crawl underneath them. Secondly, the nets may clog with silt and drifting material after some time. This last problem diminishes especially the catching capacity of our upstream migration nets after a certain time. The efficacy of these nets depends on the action of the current flow driving animals, that become too tired to grip the upstream end of these nets, into the exchangeable nets. Siltation of the square tunnel or clogging of the upstream gauze lowers the stream velocity and thereby the action of the current flow.

Therefore the number of animals gathered in 24 hours in the upstream migration nets can be up to seven times as large when the nets are emptied every hour instead of only once after 24 hours (table I). For the drift nets such difference is nonexisting or very small. Even if a clogging of the exchangeable net diminishes the current velocity in the drift net, this does not seriously affect the efficacy of this net since it is not directly dependent on the action of the current flow.

Both problems might be overlooked when comparing data collected in a qualitative way, although they would mean serious difficulties for a quantitative interpretation of the results.

At station 1 we separated *Gammarus pulex pulex* (Linnaeus, 1758) from *G. fossarum* Koch in Panzer, 1836, in our catches. At all other stations *G. p. pulex* was only sporadically found and therefore we subdivided the total catch there in *Gammarus* and *Echinogammarus berilloni* (Catta, 1878) only (Goedmakers, 1981).

The mathematical treatment of our material was done with the CDC computer of SARA (Stichting Academisch Rekencentrum Amsterdam).

TABLE I

Comparison of total daily migration catches after hourly (continuous measurement in 1 hour samples) or daily (24 hour sample) sampling. An hourly continuous measurement of migration over 24 hours was preceded and/or followed by a daily sampling of migration.

		drift			upstream migration		
		continuous measurement in 1 hour samples	24 hour sample		continuous measurement in 1 hour samples	24 hour sample	
			previous 24 hours	following 24 hours		previous 24 hours	following 24 hours
Sta. 4	17-20 June 1974	238	46	271	8922		1200
Sta. 5	8-10 April 1974	215	346		14	4	
	29 July – 1 August 1974	331	243	206	752	168	163
	11-13 August 1974	368		344	95		16
Sta. 7	8-10 April 1974	172	92		6	4	
Sta. 8	1-4 July 1974	646	234	408	13	4	2
Sta. 10	4-7 December 1973	43	82	34	1	1	2
	19-21 December 1973	15	22		0	1	

4. RESULTS

In the present migration research emphasis is laid on qualitative results, just as in our previous research into standing crop (Goedmakers, 1981). We tried to collect migrating animals in a constant and identical manner throughout our program, to be able to compare different catches. We felt, on the other hand, that an attempt to a more quantitative approach was not feasible at the present stage of knowledge (see section 1).

In drift nets we catch both animals swept into the net passively by the water current and animals either swimming actively downstream or carried away downstream after purposely leaving the substrate (accidental and non-accidental migration, respectively). Upstream migration is necessarily always active behaviour and consequently non-accidental. This is an important difference to be borne in mind at any time when comparing data on upstream migration with those on drift.

4.1. Migration survey

The 24-hour catches of both drifting and upstream migrating animals collected at 12 stations [1]) along the river Slack every two weeks (1973-1974) or every month (1974-1975) enabled us to get a rough insight into the migration patterns of gammarids in this small river. Each sampling period we selected a different station at which the hourly migration activity was measured during a period of 24 hours, together with some environmental factors. Some of the results obtained in the years 1974-1975 are discussed by M. J. Goedmakers (unpubl.).

[1]) For a description of all sampling stations see Goedmakers (1980).

4.1.1. *Transversal and vertical variation*

Since the drift rate is known to vary across a river (Waters, 1962; Besch, 1966), we compared migration along the banks to that in the middle of the stream (table II).

During times of low activity equally low numbers of animals were involved in both drift and upstream migration at different spots of the river. In times of high migration activity however, we caught most of the upstream migrants along the banks, whereas the highest drift rates occurred in places varying per station. For instance at station 4 the highest drift rates occurred along the banks and at station 5 in the middle of the stream (table II).

An explanation that is sometimes given for the high number of upstreamers along the banks, is that they make use of whirls along the banks and are thus in fact also drifters. This seems an unlikely hypothesis. We observed in periods of high

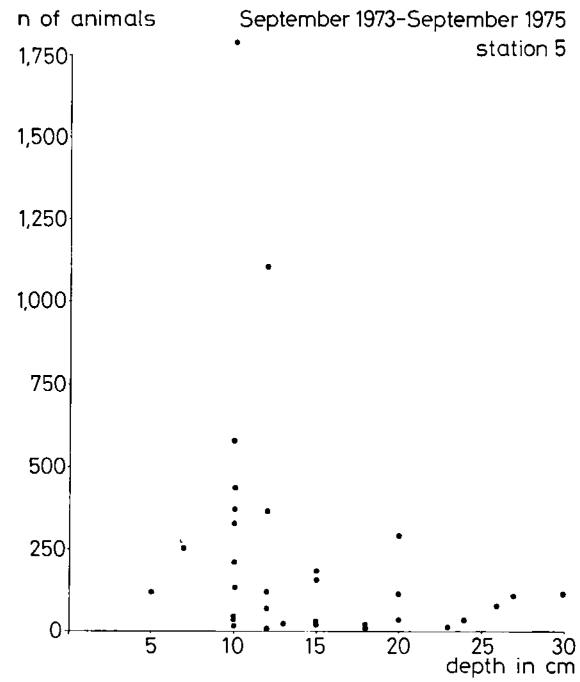

Fig. 1. Relation between the number of drifting animals and depth of the river at station 5.

upstream migration activity large numbers of gammarids leaving the substrate and swimming actively against the current for distances of tens of centimetres at a stretch. The relatively low current velocities mostly found along the banks of a stream provide a more convincing explanation for this behaviour.

Drifters were collected in the middle of the stream, where stream velocities were often highest, although this did not coincide always with the spot showing the highest drift rate at each station. A relation between the distribution of the standing crop at a certain station and the amount of drifting animals at a certain spot seems very likely, but this can be demonstrated only by a more quantitative sampling method.

As a general rule the entire water column was filtered through our nets. Only in times of heavy flooding part of the water rushed over the nets in the deeper middle and lower reaches of the Slack. We then placed a small-mesh netting on top of the upstream migration nets to prevent the trapping of drifting animals in these nets. We did not expect that a sampling of the bottom layer of the stream only would influence our results in these exceptional cases, since most bottom-dwelling animals (Besch, 1966) and certainly gammarids (Hughes, 1970) are known to drift in the lower part of the water column, directly above the substrate. This was further corroborated by our results at stations 1 to 5 where always, even in times of spates, the total water column could be sampled. When the water level was high, drift rates were always low (fig. 1) even though the

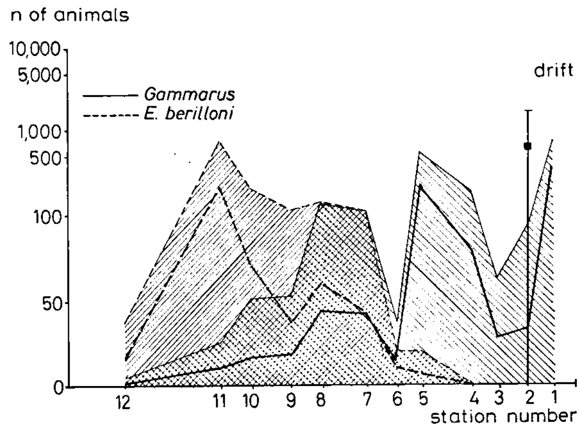

Fig. 2. Microgeographic variation of drift expressed in mean number of animals (bold line) and its standard deviation (thin line) (entire sampling period averaged) for *Gammarus* and *E. berilloni* separately. (The scale of the number of animals is logarithmic above 100.) Station 2a (*Gammarus*) is indicated separately.

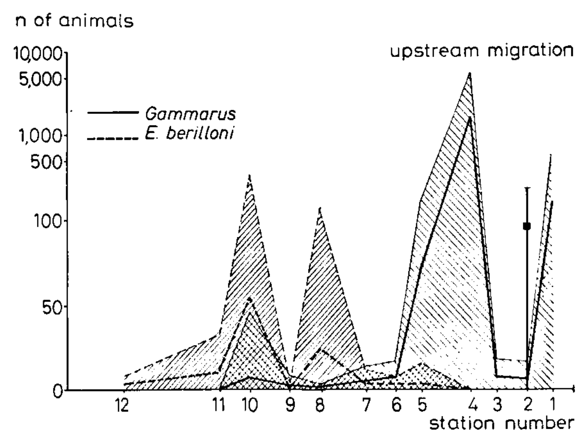

Fig. 3. Microgeographic variation of upstream migration expressed in mean number of animals and its standard deviation (entire sampling period averaged) for *Gammarus* and *E. berilloni* separately. (The scale of the number of animals is logarithmic above 100.) Station 2a (*Gammarus*) is indicated separately.

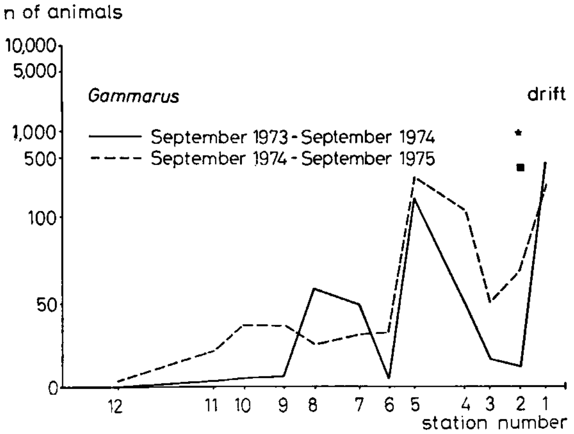

Fig. 4. Microgeographic variation of drift expressed in mean number of *Gammarus* for the first and the second sampling year. (The scale of the number of animals is logarithmic above 100.) Station 2a is indicated separately (* = 1973-1974; ■ = 1974-1975).

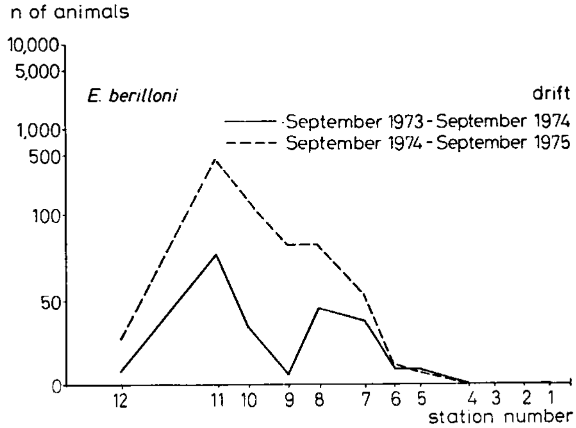

Fig. 6. Microgeographic variation of drift expressed in mean number of *E. berilloni* for the first and the second sampling year. (The scale of the number of animals is logarithmic above 100.)

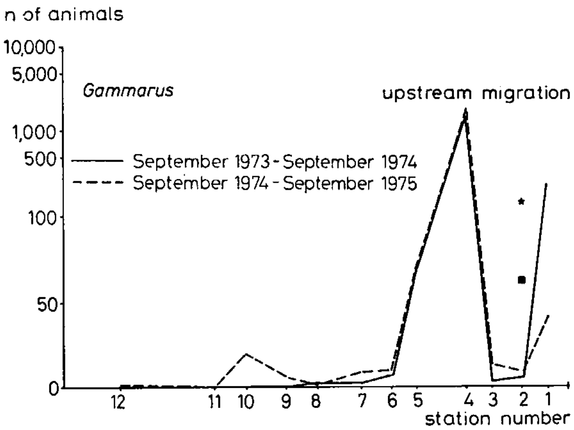

Fig. 5. Microgeographic variation of upstream migration expressed in mean number of *Gammarus* for the first and the second sampling year. (The scale of the number of animals is logarithmic above 100.) Station 2a is indicated separately (* = 1973-1974; ■ = 1974-1975).

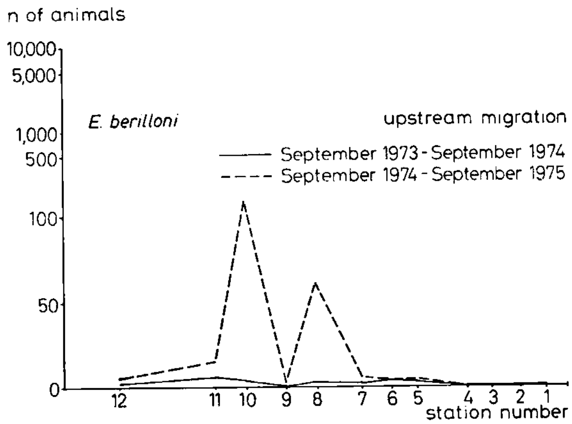

Fig. 7. Microgeographic variation of upstream migration expressed in mean number of *E. berilloni* for the first and the second sampling year. (The scale of the number of animals is logarithmic above 100.)

amount of water passing the nets could be twenty times the normal amount. So spates are probably only a small cause of gammarid migration, and may even have a resultant negative effect on drift (high drift rates occurred only at times of low water level).

4.1.2. *Microgeographic variation*

The migratory activity of *Gammarus* or *E. berilloni* is quite different at the various stations (tables III and IV, figs. 2 and 3). Some stations show always a rather low level of migratory activity (at stations 3, 6 and 12 daily migrational activity never exceeds 200), while other stations are characterized by periodically high migration rates (stations 1, 2a, 4 and 5; here the number of migrating animals is several times higher than 1000).

It does not seem very likely that these differences are caused by mere variations in population structure, i.e. species composition of the standing crop and/or presence of only young, adult or sexually active animals. Stations 2, 2a, 3 and 4, for instance, are all almost exclusively inhabited by *G. fossarum* (see Goedmakers, 1981), but show considerable differences in migration patterns. This holds also true for stations 10, 11 and 12 populated for almost 100% by *E. berilloni.* Furthermore, this comparison of adjoining stations makes clear that environmental factors provide no simple explanation for the microgeographic differences observed, as these stations have very much the same environmental characteristics (Goedmakers, 1980).

During the second year the percentage of ovigerous females in the standing crop was larger than during the first year of investigation (Goedmakers, 1981). Since probably ovigerous females constitute a larger part of the migrating populations than of the standing crop (see section 4.1.7), the high percentage of ovigerous females during the second sampling year may explain the higher migration rates in that year (figs. 4, 5, 6 and 7). A comparison of these same figures with results of our standing crop research (Goedmakers, 1981), however, clearly suggests that mere differences in age structure do not account for variations in migratory behaviour. For instance at station 11, drift of *E. berilloni* was considerably larger during the second year, while upstream migration remained almost the same, but at station 10 both drift and upstream migration were greater the second year. At both stations the mean size of the standing crop was larger during the second year (Goedmakers, 1981: table V).

Mean population densities (estimated by counting the number of ten second scoops necessary to catch a standing crop sample of one hundred animals) at different stations and mean migration rates over the second sampling year

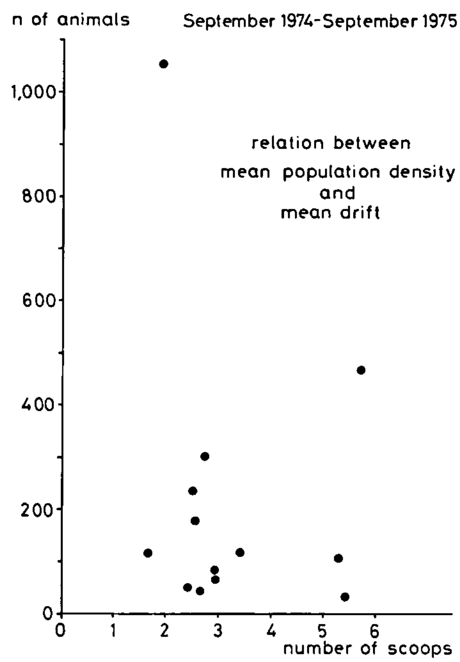

Fig. 8. Relation between the mean number of ten second scoops necessary to catch a standing crop sample of one hundred animals at a certain station and the mean number of animals drifting at that station (data of second sampling year averaged).

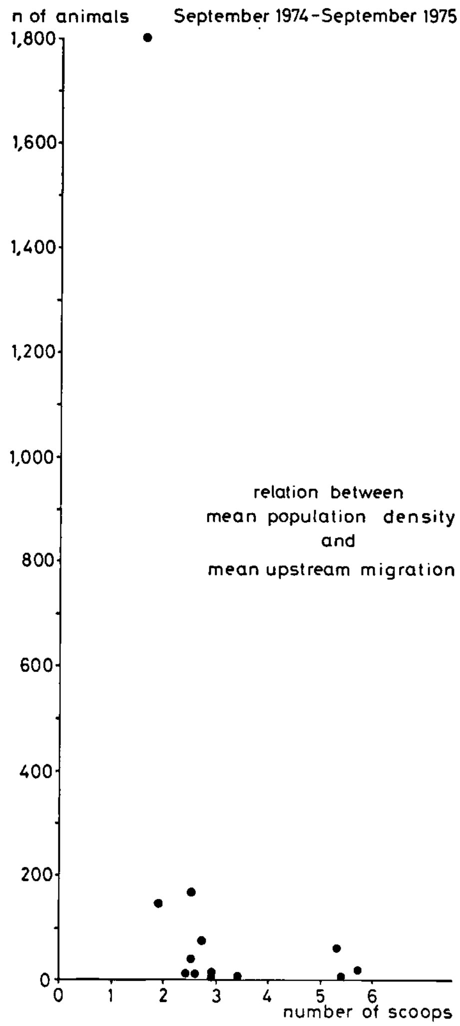

Fig. 9. Relation between the mean number of ten second scoops necessary to catch a standing crop sample of one hundred animals at a certain station and the mean number of animals migrating upstream at that station (data of second sampling year averaged).

TABLE II

Transversal variation in migration catches.

		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
	16-18 July 1974	21	14	1249	0
	31 July - 2 August 1974	682	55	65	7
	13-15 August 1974	349	203	62	17
Sta. 5	3-6 June 1974	4	24	0	1
	17-19 June 1974	39	40	2	7
	2-3 July 1974	133	511	739	20
	15-17 July 1974	159	585	17	44
	29-30 July 1974	108	331	263	65
	11-12 August 1974	75	368	95	18

* These sampling sites are not included in fig. 3 of Goedmakers, 1980, and are only occasionally used for additional experiments.

could not be correlated (figs. 8 and 9, with an insignificant r of -0.15 and -0.39, respectively): a none too surprising fact after perusal of figs. 2 and 3. For example at station 4 mean upstream migration is larger than mean drift, but at station 5 it is the other way round.

The data on mean population densities over a whole period and over all stations might be too gross to draw conclusions on a correlation of population density and migration rate. However, a correlation of population densities (Goedmakers, 1981: table II) and numbers of drifting or upstream migrating animals (tables III and IV) at station 8 during the second sampling year yielded in both cases insignificant correlation coefficients of 0.54 and -0.25, respectively. Also a correlation of the more reliable data on population densities measured by electrofishing (Goedmakers, 1981: table I) and numbers of drifting or upstream migrating animals (tables III and IV) collected in the period from 29 June to 6 July 1975 at the various stations in the Slack could not be found (insignificant r of 0.43 and 0.35, respectively).

The results obtained from our fortnightly or monthly sampling program did not enable us to gain an insight into the determinants of microgeographic differences in migration. We needed more detailed information about migration patterns at different stations (section 4.2) to work out a theory of possible causes of migration.

4.1.3. *Seasonal variation*

Apart from those stations that have a constantly low level of migratory activity, most stations show a large variation in numbers of migrants throughout the year (tables III and IV). Stations 1 and 2a (springbrook type) have migration rates fluctuating around a certain rather high level all year round, but at all other stations migratory activity is concentrated in certain periods of the year. The maximum number of migrants differs widely for the various stations.

At station 2a drift activity is highest in late winter to early spring; for most of the other stations drift reaches a peak in summer, while a secondary peak is sometimes found in autumn. Upstream migration activity shows very high peaks in the beginning of summer, e.g. station 4.

The results for separate stations are difficult to interpret. Nevertheless, the general picture of migration in the Slack (figs. 10 and 11) illustrates the distinctions between the seasonal variation in drift and that in upstream migration. Drift is a phenomenon fluctuating around a certain level with two minima a year, while upstream migration shows one very high peak a year.

During the second year migration peaks occurred somewhat earlier than during the first year (figs. 10 and 11). This may be the effect of the faster maturation of the gammarid populations during the second year (Goedmakers, 1981).

Seasonal variation in migratory activity of *Gammarus* and *E. berilloni* was not clearly different. At most stations both showed peaks in activity at about the same time (tables III and IV).

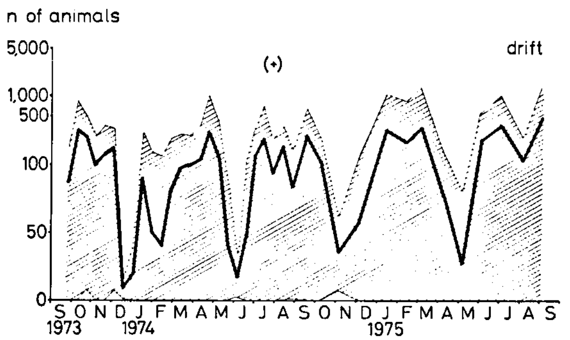

Fig. 10. Seasonal variation of drift expressed in mean number of gammarids and its standard deviation (stations 1-12 averaged). (The scale of the number of animals is logarithmic above 100.) The exceptional drift catch caused by pollution at station 8 end of July 1974 is not included.

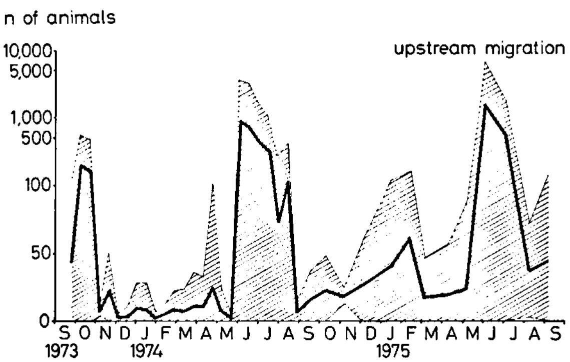

Fig. 11. Seasonal variation of upstream migration expressed in number of gammarids and its standard deviation (stations 1-12 averaged). (The scale of the number of animals is logarithmic above 100.)

4.1.4. *Diel variation*

Diel variation in migratory activity was measured by emptying migration nets each hour for 24 hours (fig. 12). The only conclusion that can be drawn from data on diel variation at different stations and particular times of the year is that gammarids are mostly migrating during the night. Generally, peaks in drift occur soon after sunset, whereas upstream migration is concentrated before sunrise, for those days during which migration rates were relatively high.

We did not observe clear differences in diel behaviour between *G. p. pulex, G. fossarum* and *E. berilloni* (figs. 13 and 14).

Furthermore, we found no evidence of differences in diel behaviour between males, females, and juveniles (fig. 15), although the drift rates of juveniles compared with those of adults might be somewhat higher during the day than during the night. The very complex migration patterns, however, make it difficult to draw definite conclusions. To investigate the behaviour of different species or developmental stages, quite another type of research would have been necessary.

4.1.5. *Interspecific differences*

The numbers of *E. berilloni* taking part in migration are definitely smaller than those of *Gammarus* (tables III and IV). This difference was more conspicuous in the first than in the second year, when *E. berilloni* was sometimes found in large numbers in both drift and upstream migration. An explanation might be that *E. berilloni*, being a warm eurythermous species (Goedmakers, 1981), benefitted from the higher water temperatures during the second sampling year (Goedmakers, 1980).

The percentage of *Gammarus* (out of the total gammarid population consisting of *Gammarus* and *E. berilloni*) in either drift or upstream migration shows remarkable differences between both sampling years along the river (figs. 16 and 17).

The percentage of *Gammarus* in the drift catches decreases steadily in downstream direction. Only station 6 shows a strikingly low percentage of drifting *Gammarus* in the first year, which could not be explained by a low percentage of *Gammarus* in the standing crop during that year (Goedmakers, 1981: fig. 15). The center of *Gammarus* drift activity shifted slightly in upstream direction during the second year, which could have been partly the effect of a change in population structure during this year (Goedmakers, 1981: fig. 15).

TABLE III

Results of daily drift expressed in number of animals of either *Gammarus* (*G*) or *E. berilloni* (*E*). Results of hourly sampling over 24 hours are printed in bold type.

YEAR 1

		24-29 September 1973	9-13 October 1973	22-26 October 1973	6-10 November 1973	20-24 November 1973	4-8 December 1973	18-21 December 1973	31 December 1973 – 5 January 1974	14-18 January 1974	28 January – 1 February 1974	11-15 February 1974	25 February – 1 March 1974	11-15 March 1974	25-29 March 1974	8-13 April 1974	21-26 April 1974	6-9 May 1974	20-23 May 1974	3-6 June 1974
Sta. 1	*G*		**1077**	**496**	342	505	378		63	5	300	23	**441**	**275**	528	889	751	1071	110	26
	E		**0**	**0**	0	0	0		0	0	0	0	**1**	**0**	0	0	0	0	0	0
Sta. 2	*G*					16		2	7	2		15	5	5	6	11	11	3	8	12
	E					0		0	0	0		0	0	0	0	0	0	0	0	0
Sta. 2a	*G*								51	645	175	287	355	569	204	12	2808	329	21	
	E								0	0	0	0	0	0	0	0	0	0	0	
Sta. 3	*G*	16			5	42	3		14	10	24	10	13	1		8	94	5	3	5
	E	0			1	0	0		1	0	1	0	0	0		0	0	0	0	0
Sta. 4	*G*					13		1	1		0		3			37	5	11	95	15
	E					0		0	0		0		0			0	0	0	0	0
Sta. 5	*G*	192	142	410	**47**	365	327		38	43	12	18	36	139	122	**211**	29	20	80	22
	E	29	17	31	**2**	11	6		0	0	0	0	0	0	1	**4**	0	0	0	2
Sta. 6	*G*					8		4	2	4	13	5	3	2	4	1	1	2	0	3
	E					6		0	0	1	17	0	2	1	4	9	0	3	5	11
Sta. 7	*G*					354	102		10	**125**	5	0	3	3	19	**76**	31	6	8	24
	E					273	133		5	**43**	1	1	2	0	15	**96**	44	3	4	37
Sta. 8	*G*					11		4	2	8	3		1		18	10	27	42	73	12
	E					9		6	7	1	4		2		8	4	15	27	50	2
Sta. 9	*G*					2		4	1		2			0		7	10	2	2	3
	E					3		1	0		1			0		5	1	0	3	4
Sta. 10	*G*	4	0	1	0	4	**1**	**2**	2	0	1	1	1	2	4	8	4	16	22	15
	E	73	36	77	77	165	**42**	**13**	27	8	1	3	5	3	18	13	3	23	33	18
Sta. 11	*G*					0		1	0					3	12	5	7	13	0	0
	E					3		22	3					52	30	31	24	53	4	6
Sta. 12	*G*	0	1	1		1	0		0	0	1	0	0	0	2		0	0	0	0
	E	33	6	7		1	38		9	0	0	0	3	14	3		1	5	8	4

TABLE III

Continuation of previous page.

	YEAR 2																	
17-20 June 1974	1-4 July 1974	15-18 July 1974	29 July – 2 August 1974	11-15 August 1974	26-29 August 1974	15-18 September 1974	8-10 October 1974	7-8 November 1974	30 November – 3 December 1974	11-14 January 1975	7-11 February 1975	6-9 March 1975	10-14 April 1975	7-10 May 1975	31 May – 7 June 1975	29 June – 5 July 1975	6-10 August 1975	5-8 September 1975
176	75	**1731**	123	534	131	382	272	73	72	100	99	174	150	6	1403	260	65	37
0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	4	15	1	58	41	74	33		6	305	55	119	150	13	33	21	1	16
0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
10	324	145	87	565	147	131	354		199	2826	2436	3632	265	181	112	2426	77	17
0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
2	39	13	6	21	2	62	9		96	162	30	58	47	9	67	1	35	26
0	0	0	0	0	0	0	0		0	0	0	0	0	0	3	0	0	0
19	177	14	55	202	139	129	11	21	125	114	15	17	16	8	**200**	**411**	18	428
0	0	0	0	1	1	0	0	0	0	0	0	0	0	0			1	0
40		552	**308**	**361**	247	1099	107	34	76	293	12	115	118	7	23	172	71	1738
0		33	**23**	**7**	9	16	1	0	1	0	0	0	0	0	0	14	1	61
7	9	13	7	10	10	11			115	54	21	39	38	4	9	23	9	24
5	27	26	22	17	21	17			29	8	1	5	3	2	2	11	11	38
21	7	62	0	107	3	146	19		5	75	2	17	4	1	26	0	35	37
16	12	21	8	38	8	261	14		0	11	0	1	2	0	76	0	180	86
139	**475**	56	20750*	54	35	31			4	76	21	24	33	0	25	21	35	5
51	**171**	71	17150*	189	159	75			2	87	13	11	28	1	112	135	404	44
5	14	21	1	23	7	4			5	14	0	32	5	2	50	166	30	85
22	8	30	2	9	1	7			0	1	2	5	0	3	197	249	268	182
2	7	5	3	18	2	21	3	1	4	49	22	2	24	11	56	207	35	38
24	88	24	45	73	26	153	18	11	3	58	19	2	4	7	165	531	165	705
0	2	0	0	3	3	9			0	11	11		51	13	38	24	6	49
50	126	169	441	114	100	585			0	23	62		62	88	308	382	88	2848
0	0	0	0	0	0	3			0	1	0	0	0	1	14	11	1	2
14	10	6	3	10	4	59			2	13	4	0	1	4	108	36	39	36

* The sample contained many dead animals.

TABLE IV

Results of daily upstream migration expressed in number of animals of either *Gammarus* (*G*) or *E. berilloni* (*E*). Results of hourly sampling over 24 hours are printed in bold type.

YEAR 1

		24-29 September 1973	9-13 October 1973	22-26 October 1973	6-10 November 1973	20-24 November 1973	4-8 December 1973	18-21 December 1973	31 December 1973 – 5 January 1974	14-18 January 1974	28 January – 1 February 1974	11-15 February 1974	25 February – 1 March 1974	11-15 March 1974	25-29 March 1974	8-13 April 1974	21-26 April 1974	6-9 May 1974	20-23 May 1974	3-6 June 1974
Sta. 1	*G*	199	**743**	**661**	5	72	7		16	6	12	5	**23**	**22**	4	16	5	25	13	5
	E	0	**0**	**1**	0	0	0		0	0	0	0	**0**	**0**	0	0	0	0	0	0
Sta. 2	*G*					36		3	0	2		11	1	2	14	2	13	1	0	0
	E					0		0	0	0		0	0	0	0	0	0	0	0	0
Sta. 2a	*G*								61	63	8	20	45	53	82	76	289	53	3	
	E								0	0	0	0	0	0	0	0	0	0	0	
Sta. 3	*G*	3			4	1	1		0	0	2	2	4	2		2	4	2	0	1
	E	0			0	0	0		0	0	0	0	0	0		0	0	0	0	0
Sta. 4	*G*					3		0	1		1		0			9	2	3	0	9906
	E					0		0	0		0		0			0	0	0	0	
Sta. 5	*G*	9	9	5	**15**	5	2		29	5	1	1	1	1	5	**14**	0	4	9	0
	E	0	3	1	**1**	0	0		2	0	0	0	1	0	0	**0**	0	0	0	0
Sta. 6	*G*					51		16	9	6	1	4	10	0	1	2	0	2	0	4
	E					7		3	2	2	2	5	6	3	1	0	4	2	1	2
Sta. 7	*G*					25	0		0	**0**	4	1	0	2	1	**4**	0	0	0	3
	E					42	0		0	**1**	2	1	0	0	0	**2**	1	0	0	2
Sta. 8	*G*					0		0	0	5	0		0		0	4	0	0	0	0
	E					0		0	0	0	1		0		0	0	0	0	0	0
Sta. 9	*G*					0		0	0		0			0		0	0	0	1	0
	E					0		1	0		0			0		1	0	0	0	0
Sta. 10	*G*	1	4	0	0	0	**0**	**0**	0	0	0	0	0	0	0	0	0	0	1	0
	E	5	31	4	7	8	**1**	**0**	7	0	0	1	0	0	0	0	0	4	0	0
Sta. 11	*G*					0		0	0					0	0	0	0	1	0	0
	E					0		1	0					0	1	6	3	9	0	8
Sta. 12	*G*	0	0	0		0	0		0	0	0	0	0	0	0		0	0	0	0
	E	3	0	1		1	8		7	1	0	0	3	0	0		1	1	0	0

TABLE IV

Continuation of previous page.

YEAR 2																		
17-20 June 1974	1-4 July 1974	15-18 July 1974	29 July – 2 August 1974	11-15 August 1974	26-29 August 1974	15-18 September 1974	8-10 October 1974	7-8 November 1974	30 November – 3 December 1974	11-14 January 1975	7-11 February 1975	6-9 March 1975	10-14 April 1975	7-10 May 1975	31 May – 7 June 1975	29 June – 5 July 1975	6-10 August 1975	5-8 September 1975
29	11	**2459**	25	1099	14	34	11	16	45	23	22	105	57	50	68	11	75	18
0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	3	0	0	1	1	2	11		3	42	3	9	7	0	3	17	0	1
0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
2	27	232	9	20	5	38	86		69	270	714	19	135	236	102	67	31	0
0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
2	2	0	12	14	0	13	16		55	5	11	8	2	3	5	9	27	5
0	0	0	0	0	0	1	1		1	0	0	0	0	0	2	0	0	0
9042	4600	1249	65	62	15	74	19	26	109	142	9	23	6	1	**18429**	**4200**	132	335
	0	0	0	0	0	0	0	0	0	0	0	1	0	0			1	0
2	735	17	**695**	88	11	12	13	19	10	4	2	7	29	0	46	707	53	9
0	4	0	**57**	7	1	0	0	0	0	0	0	0	0	0	0	50	4	0
0	4	1	0	1	10	3			15	4	5	8	7	4	4	22	17	9
0	3	11	7	11	17	3			15	5	5	0	1	3	0	9	0	7
1	1	0	0	5		5	7		0	1	0	46	1	0	9	18	7	5
0	1	0	0	7		5	6		2	0	0	0	0	0	27	6	15	16
6	6	2	5	1	0	1			1	0	2	0	0	0	6	0	0	2
0	7	3	26	2	0	2			1	2	0	2	6	0	607	3	6	39
0	0	1	0	2	0	0			7	0	2	0	0	0	1	25	16	0
0	0	1	0	0	0	0			0	0	1	0	1	1	0	17	3	1
0	0	0	0	0	0	1	1	1	0	2	2	1	0	1	3	241	3	1
22	0	5	8	1	0	9	5	10	7	6	0	1	0	0	39	1832	15	19
0	0	0	0	0	0	0			0	0	0	1	0	1	1	0	0	0
5	2	1	41	14	3	0			0	1	0	1	0	2	1	7	43	110
0	1	1	0	0	0	0			0	0	0	0	0	1	1	7	2	0
0	2	2	4	0	1	3			1	8	0	1	1	0	5	5	28	1

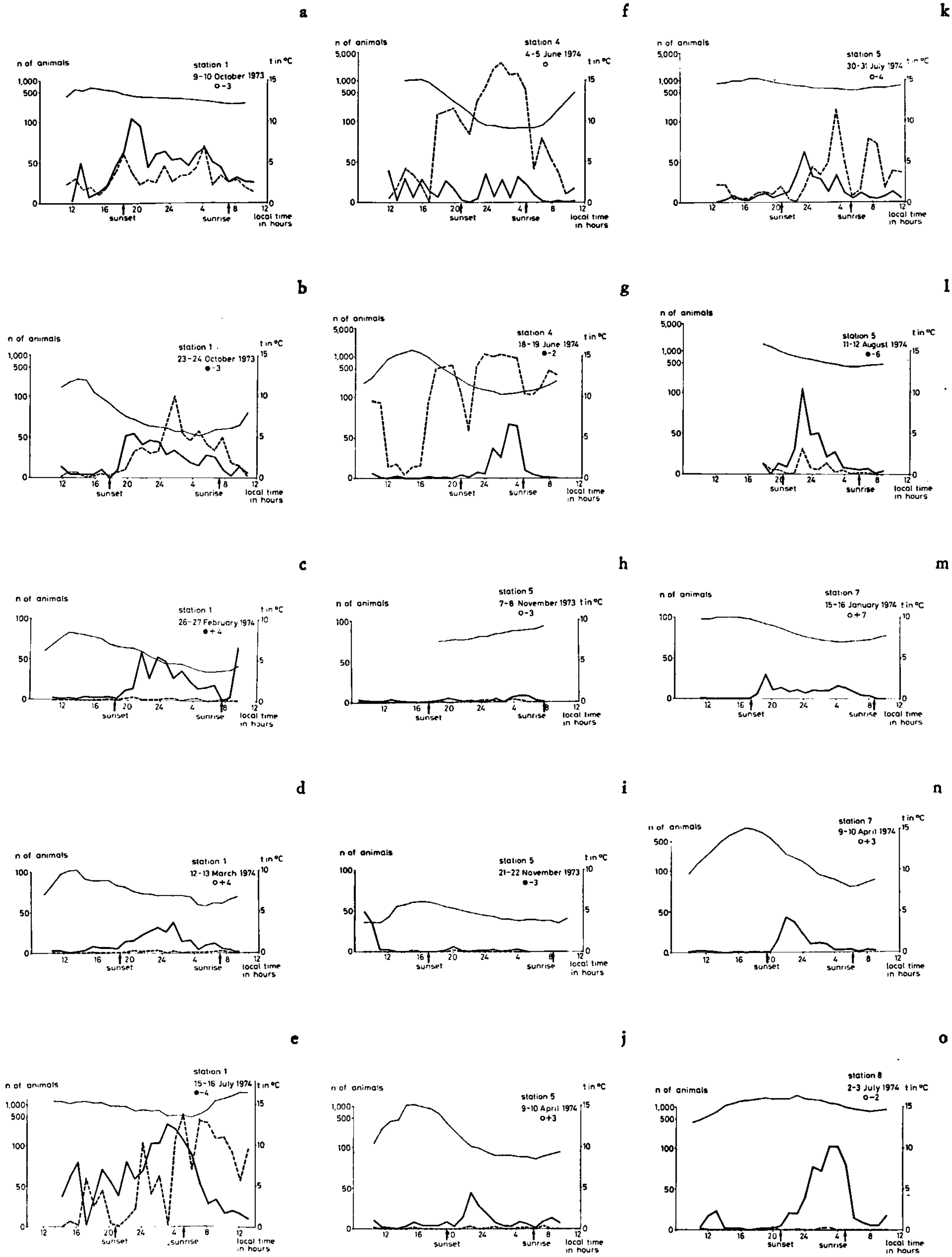

Fig. 12. Diel variation in drift (solid line) and upstream migration (broken line) of gammarids at different stations at various dates. Water temperature is shown by the thin line. Phase of the moon (e.g. 0-3 means: sampling date three days before full moon), sampling date and station number are indicated. (The scale of the number of animals is logarithmic above 100.)

Likewise, in upstream migrating gammarids the percentage of *Gammarus* declined steadily in downstream direction during the first year. The second year, however, the proportion of *E. berilloni* in the upstream migration catches at station 8 increased to almost 100 percent, but slightly diminished at most other stations. At station 8 the percentage of *Gammarus* in the total gammarid population was lower in the second sampling year compared with the first one, which might explain the low percentage of upstream migrating *Gammarus* at this station in the last year.

Species composition of upstream migrating gammarids corresponded more closely to that of the standing crop than to the composition of drift catches, but did by no means directly reflect it.

Differences in migratory behaviour between *G. fossarum* and *G. p. pulex* seem to exist (table V), but were not investigated very thoroughly because of the time-consuming identifications involved. At station 1 a lower percentage of *G. fossarum* was found in the migrating populations than one would expect from species composition of the standing crop. Besides, we found a relatively high percentage of *G. fossarum* in the upstream migration samples compared with the percentage of *G. fossarum* in the drift samples.

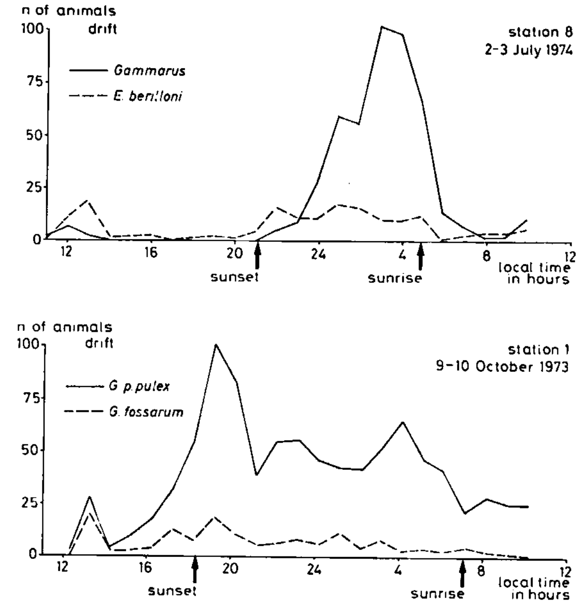

Fig. 13. Diel variation in drift (number of animals) of *G. p. pulex*, *G. fossarum* and *E. berilloni* at certain dates and stations.

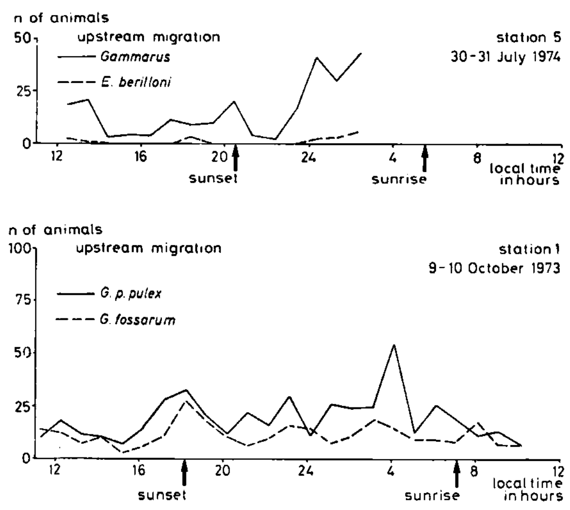

Fig. 14. Diel variation in upstream migration (number of animals) of *G. p. pulex*, *G. fossarum* and *E. berilloni* at certain dates and stations.

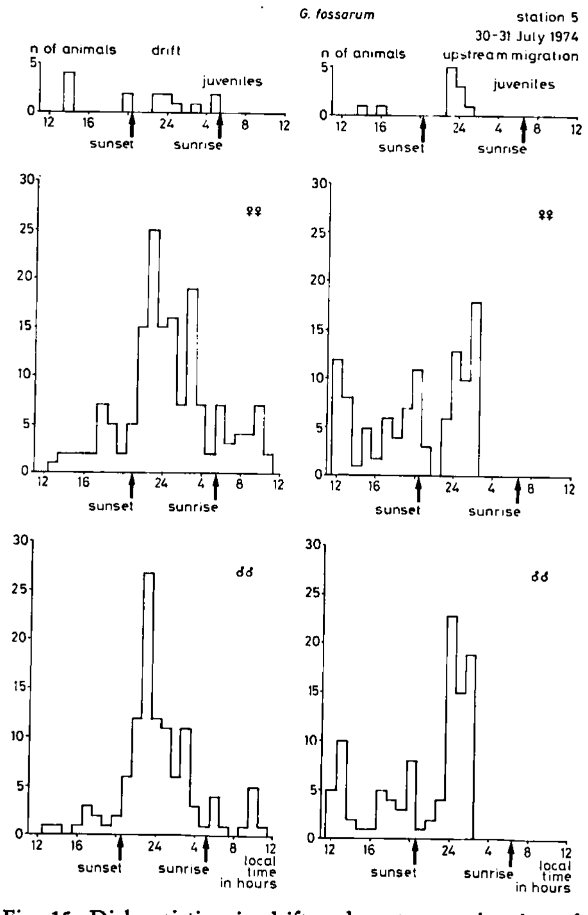

Fig. 15. Diel variation in drift and upstream migration of juvenile, female and male *G. fossarum* at station 5, 30-31 July 1974.

4.1.6. *Structure of migrant populations*

Comparing the mean size of the migrating populations with the mean size of the standing crop (table VI), it is obvious that migrating animals do not constitute a random selection from the standing crop at a given place. However, differences in size between standing crop and either drifting or upstream migrating populations are not constant (see also section 4.2.4). Since migration is a very complicated behaviour and consists of different groups of animals (accidental and non-accidental migration), this phenomenon was to be expected.

From the data presented in table VI certain regularities can be perceived, which have to be verified by more thorough experiments: firstly, the mean size of the standing crop is smaller than that of both drifting and upstream migrating populations; secondly, upstream migrants are sometimes larger (*G. p. pulex* in table VI), other times smaller (*G. fossarum* in table VI) than drifting animals; and finally, in periods of high drift activity, animals drifting during daytime are smaller than those drifting at night. (Fig. 18: Mean cephalic length during the night is 0.82 mm (SD 0.26 mm), while mean cephalic length during the day is 0.55 mm (SD 0.20 mm). The difference between the mean cephalic length of drifters at night vs. that by day is very highly significant, variances do not differ significantly.)

Sex ratio proved to be a rather problematic population parameter in our standing crop research (Goedmakers, 1981), since it shows a wide variation. Also Steenbergen et al. (unpubl.) were confronted with this problem and did not succeed in drawing conclusions about sex ratio of migrating animals. To investigate (fluctuations in) sex ratio, we would have needed a totally different sampling program.

4.1.7. *Sexual activity*

The sampling method confines the animals sometimes for considerable time within the migration nets and disturbs them when the nets are emptied. Therefore we do not consider the number of precopulations in our migration catches a very good measure for the sexual activity of the migrating populations. Generally speaking, the large number of captured animals makes it impossible to even count the number of precopulations.

The percentage of ovigerous females provides

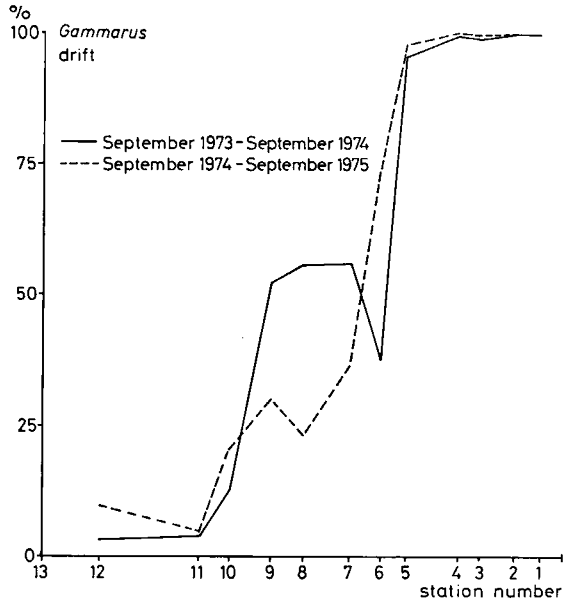

Fig. 16. Microgeographic variation in percentage of *Gammarus* found in the total number of drifting gammarids during the first and the second sampling year.

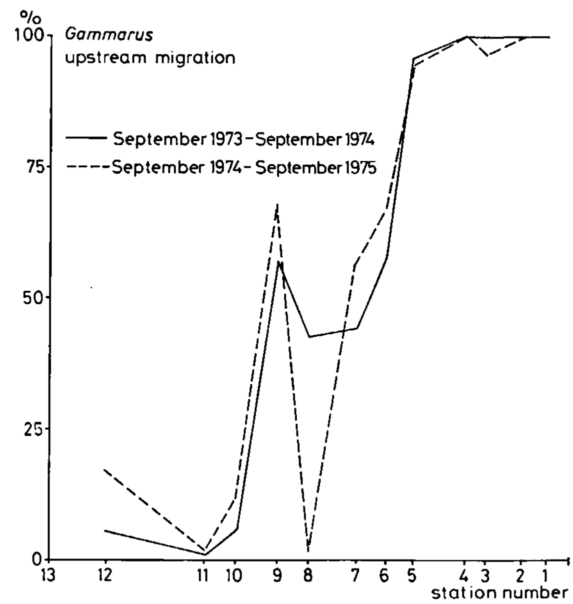

Fig. 17. Microgeographic variation in percentage of *Gam marus* found in the total number of upstream migrating gammarids during the first and the second sampling year.

TABLE V

Differences in migratory behaviour between *G. fossarum* (*f*) and *G. p. pulex* (*p*), compared with the species composition of the standing crop, at station 1.

	number of animals				percentage *G. fossarum*		
	upstream migration		drift				
	p	*f*	*p*	*f*	upstream migration	drift	standing crop
9-10 October 1973	464	279	925	152	38	14	63
5-6 December 1973	3	4	308	70	57	19	60
31 December 1973 - 1 January 1974	8	8	35	28	50	44	61
30-31 January 1974	7	5	228	72	42	24	65
26-27 February 1974	9	14	324	117	61	27	64
6-7 May 1974	10	15	904	167	60	16	83
20-21 May 1974	2	11	43	68	15	61	93
2-3 June 1974	3	2	14	12	40	46	85
17-18 June 1974	16	13	105	71	45	40	63
1-2 July 1974	6	5	52	23	45	31	63
30-31 July 1974	14	11	39	84	44	68	92

a better measure for the sexual activity of both drifting and upstream migrating populations. Although our sampling program was not suitable to draw definite inferences due to the diverse aspects of migration activity (viz. accidental versus non-accidental), the preliminary conclusion can be drawn that the percentage of ovigerous females in the migrating populations is larger than in the standing crop (table VII). A χ^2 test of observed and expected numbers of ovigerous females in standing crop and migrating populations was significant at the 2.5% level, which means that we may conclude that percentages of ovigerous females differ in standing crop and migrating populations.

4.1.8. *Catastrophic drift*

It is generally accepted that environmental disasters like a suddenly increasing pollution or extreme floodings may cause catastrophic drift (Waters, 1972). Our data support this hypothesis as far as pollution is concerned. Thus, in August 1974 (table III) we found an enormous number of animals (60% of them dead) in our drift nets at station 8, owing to an acute case of pollution (probably by some pesticide). This same phenomenon is illustrated by the absence of any gammarid population at station 13 for many months after drums with oilwaste had been dumped upstream of this station. These pollution cases have to be considered as causes of accidental drift, since they were clearly not initiated by the (dead) animals themselves in order to take refuge from pollution. (Although theoretically the animals might have fled at first for the pollution by swimming away, this kind of behaviour is very improbable for gammarids that always react thigmotactic.)

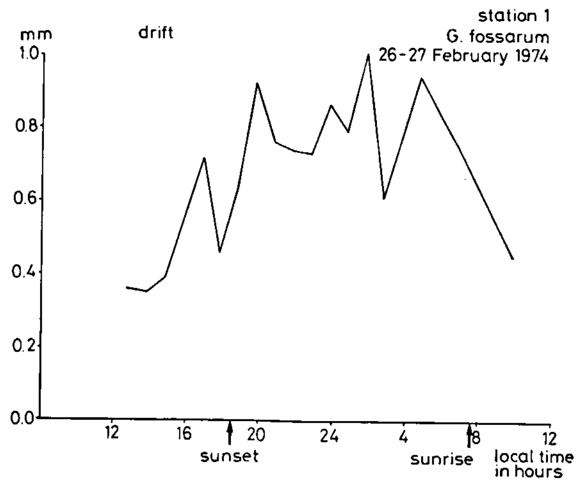

Fig. 18. Diel variation in size (mean cephalic length in mm) of drifting *G. fossarum* at station 1, 26-27 February 1974.

TABLE VI

Size differences between the standing crop and migrating populations. Data showing a significant difference between drift and upstream migration are printed in bold type. An asterisk indicates significant difference between standing crop and migration sample.

		standing crop	drift	upstream migration
G. p. pulex				
Sta. 1	*n* of animals (♀♀, ♂♂, juvs.)	96	250	158
9-10 October 1973	mean cephalic length (mm)	1.10	1.18*	1.18*
	SD of mean cephalic length (mm)	0.19	0.23*	0.25*
	n of males	57	150	101
	mean cephalic length (mm)	1.20	**1.27***	**1.33***
	SD of mean cephalic length (mm)	0.15	0.22*	0.24*
G. fossarum				
Sta. 1	*n* of animals (♀♀, ♂♂, juvs.)	167	21	81
9-10 October 1973	mean cephalic length (mm)	0.90	**1.11***	**0.98***
	SD of mean cephalic length (mm)	0.15	0.28*	0.22*
	n of males	64	11	25
	mean cephalic length (mm)	1.04	1.21*	1.19*
	SD of mean cephalic length (mm)	0.09	0.26*	0.20*
E. berilloni				
Sta. 10	*n* of animals (♀♀, ♂♂, juvs.)	209	413	190
28-29 June 1975	mean cephalic length (mm)	0.69	**0.83**	**1.01**
	SD of mean cephalic length (mm)	0.20	**0.26**	**0.18**

On the other hand, spates in our opinion do not cause a considerable catastrophic drift. Our data on migration clearly show, on the contrary, that drift activity decreases during periods of flooding (fig. 1). The animals take shelter in the substrate and become very inactive, which makes them difficult to catch even for standing crop samples. This shelter-seeking might be responsible for the sometimes drawn, but not always justified (when taking the sampling program into account) conclusion that after floodings the abundance of stream invertebrates is diminished. Likewise, Lehmkuhl & Anderson (1972) state that the decrease in benthic populations by spates may be more apparent than real.

Experiments with people wading across the river, within 1 m upstream of the drift nets, showed that even disturbing the substrate did not dislodge the animals. We never found any animals in our drift nets after these experiments at various stations. Gammarids seem capable of clinging to the substrate again quickly after a physical disturbance of the riverbed forcing them into the current. Therefore, the effect of cattle drinking or trucks crossing through the river can be neglected as a cause of catastrophic drift.

4.1.9. *Environmental factors*

From the above findings emerges that migration patterns are the result of a complicated combined action of various environmental factors with distinct periodical fluctuations. Environmental factors show diel, lunar or seasonal variation patterns which may result in a periodical behaviour of gammarids. But also more irregular events, like a sudden case of pollution or different weather conditions in distinct years have an effect. The influence of environmental factors separately is considered in section 4.2.5.

4.1.10. *Conclusions*

The migration survey clearly demonstrated the complicated nature of drift and upstream migration. Only some very general conclusions can be drawn, due to the diverse results from this type of research. This does not inspire great confidence

TABLE VII

Sexual composition of the standing crop and migrating populations at station 1 on 9-10 October 1973.

	standing crop	drift	upstream migration
total catch (for migration samples during 24 hours)	263	1077	743
% *G. p. pulex*	36.5	85.9	62.4
G. p. pulex			
% males	59.4	57.1	55.4
% ovigerous females	17.7	18.7	25.2
% females	22.9	21.6	18.3
% juveniles	0.0	2.6	1.1

in many of the data from literature and emphasizes the necessity of being very careful with a generalization of observations specific to particular times or places.

Some conclusions, however, may safely be drawn. Upstream migration in times of high activity occurs along the riverbanks, whereas drift takes place in different parts of a cross-section, depending on the locality. We found a distinct microgeographic variation in both drift and upstream migration, although the range of this variation was larger for *Gammarus* than for *E. berilloni*. Population densities at various stations and throughout the year are not directly correlated to migration rates. Seasonal variation in upstream migration was very clear, with a concentration of activity in early summer, while drift was fluctuating less markedly. There is a distinct diel migratory actvity pattern, with a peak in upstream migration usually around sunrise and a peak in drift around sunset. Catastrophic drift is the result of a change in the physicochemical conditions of the environment affecting the animal physically (pollution), but is not brought about by a physical disturbance of the bottom.

4.2. Continuous measurement of migration

We learned much from the extensive sampling of migrating gammarids, as was described in the previous sections. Amongst other things, it gave us a rough idea about migration patterns throughout the river system and throughout the year. But, unfortunately, few answers were given to questions like: why do certain animals migrate at a certain station at that special time of the year in that specific direction. Even with the enormous quantity of data at hand, we were not able to correlate migration to environmental factors or to particular population characteristics in detail.

It would have been logical to undertake laboratory experiments as is often done to investigate migration (Meijering, 1972; Girisch & Dennert, 1975; Dieleman, 1977; 1979). We felt, however, that laboratory conditions would influence the behaviour of gammarids to such an extent that conclusions might appear very clear, but would in fact be wide open to dispute. Therefore we searched for a field situation which had the advantages of laboratory conditions without its drawbacks, to fill in the gaps in our knowledge after the described migration survey.

We set up a program of continuous measurement of migration activity and environmental factors at three sampling stations situated less than 100 m apart: stations 4, 4a and 4b (Goedmakers, 1980). The gammarid population at these three stations consisted almost entirely of one species: the share of *G. fossarum* in the standing crop varies between 95 and 100%. Since the stations lie close together, weather conditions at all three are the same. Other environmental conditions, however, are largely different. Station 4b (springbrook) is the most stable, while station 4a (small tributary, flowing through open grassland, sometimes heavily polluted by the waste of surrounding farms) is very unstable.

From 11 May to 6 July 1975 and from 6 to 17 June 1976 [2]), when according to our migration survey results the highest peaks in migration activity could be expected, we emptied each hour both drift and upstream migration nets placed in the Slack (station 4), the tributary (station 4a) and the springbrook (station 4b). Once an hour we also measured temperature, oxygen content, conductivity and pH of the water at the three sites. Temperature, pressure and humidity of the air were registered continuously. Light conditions were measured during daytime with a lux meter and continuously registered during twilight and night by means of a photomultiplier connected to a recorder (Goedmakers, 1980).

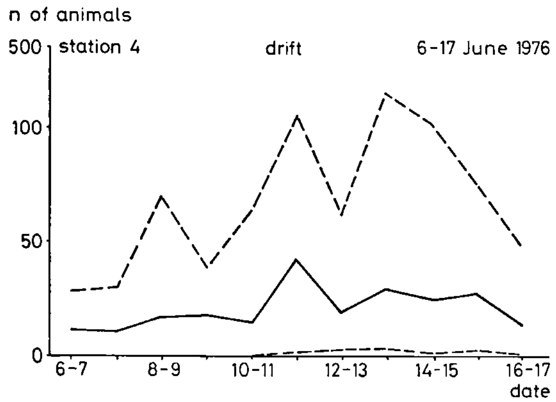

Fig. 19. Diel drift of gammarids at station 4 from 6 to 17 June 1976. Mean hourly catches (solid line) with maximal and minimal catch (broken lines) at certain dates. Diel periods from 12-12 hours local time are averaged. (The scale of the number of animals is logarithmic above 100.)

The volume of the animals trapped every hour in the migration nets was measured in a graduated cylinder with a gauze bottom (Goedmakers & Pinkster, 1977). If a sample contained less than 15 ml of gammarids, the animals were counted. Once a week all samples collected in twenty-four hours were preserved in 70% alcohol and stored for further examination in the laboratory.

To be able to compare different catches, we had to convert volumetric data into numbers of animals. We used two computation methods [3]): firstly, multiplication by a factor resulting from the regression analysis of samples of which both volume and number were known, and secondly, multiplication by a factor resulting from the weighted mean

$$\frac{\Sigma n_h + \Sigma n_d}{\Sigma v_h + \Sigma v_d}$$

of samples of a certain date and hour of which both volume and number were known [4]), in which

n = the number of animals in a migration sample;
v = the volume of the migration sample;
h = sampling hour;
d = sampling date.

Both methods gave almost the same results, although numbers of animals computed by the second method were in general somewhat lower (figs. 37 to 42). When it is not especially indicated in the figures, the first computation method was used.

In 1975 we encountered many problems. Measuring instruments often failed, thus leaving us with incomplete data on environmental factors. There were periods of heavy rainfall and floods that made interpretation of results sometimes difficult and caused many extra breakdowns of our measuring instruments. And lastly the human factor: the long sampling period left us sometimes understaffed, which made us switch to a four-hourly sampling scheme. In 1976 most instruments worked all the time, weather conditions were rather stable with no rain and we were able to sample every hour.

2) In 1976 France introduced summer time, therefore phenomena linked with sunrise and sunset shifted one hour in local time compared with 1975.

3) In both computation methods we treated data on drift and upstream migration of all three sampling sites separately.

4) Since we expected a variation in size of the migrating animals during the day (see section 4.1.6 and fig. 18) as well as a seasonal variation in size of the migrating animals, due to a changing composition of the standing crop (Goedmakers, 1981) we took both sampling hour and date into account to compute the weighted mean of the relation between volume and number.

4.2.1. *Habitat differences*

Both drift and upstream migration patterns are largely different at the three sampling stations (figs. 19 to 24). In the springbrook (station 4b) both drift and upstream migration fluctuate at a rather high level. The river Slack itself shows very high peaks in upstream migration activity, but drift fluctuates around a low level. In the tributary (station 4a), both drift and upstream migration are very irregular, while the number of animals involved is more or less intermediate between that in the Slack and in the springbrook.

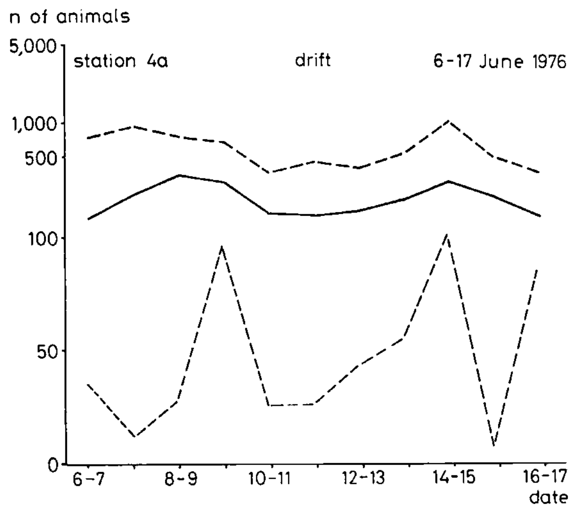

Fig. 20. Diel drift of gammarids at station 4a from 6 to 17 June 1976. Mean hourly catches (solid line) with maximal and minimal catch (broken lines) at certain dates. Diel periods from 12-12 hours local time are averaged. (The scale of the number of animals is logarithmic above 100.)

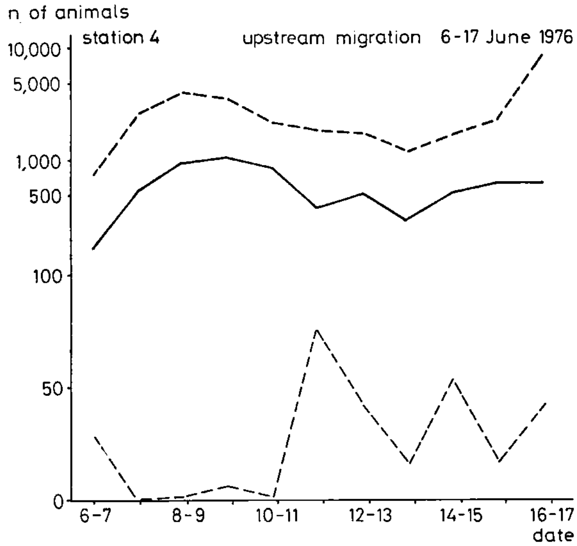

Fig. 22. Diel upstream migration of gammarids at station 4 from 6 to 17 June 1976. Mean hourly catches (solid line) with maximal and minimal catch (broken lines) at certain dates. Diel periods from 12-12 hours local time are averaged. (The scale of the number of animals is logarithmic above 100.)

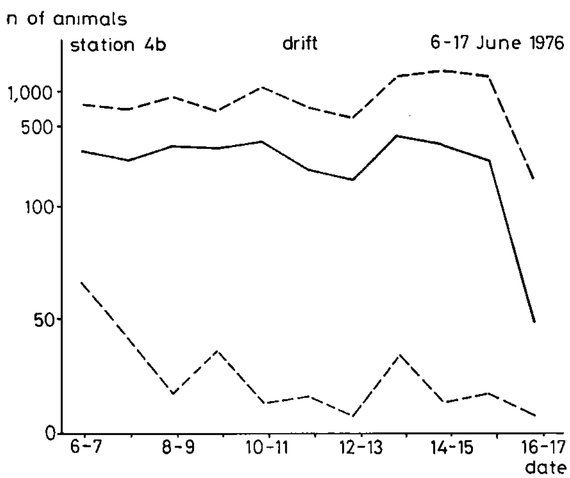

Fig. 21. Diel drift of gammarids at station 4b from 6 to 17 June 1976. Mean hourly catches (solid line) with maximal and minimal catch (broken lines) at certain dates. Diel periods from 12-12 hours local time are averaged. (The scale of the number of animals is logarithmic above 100.)

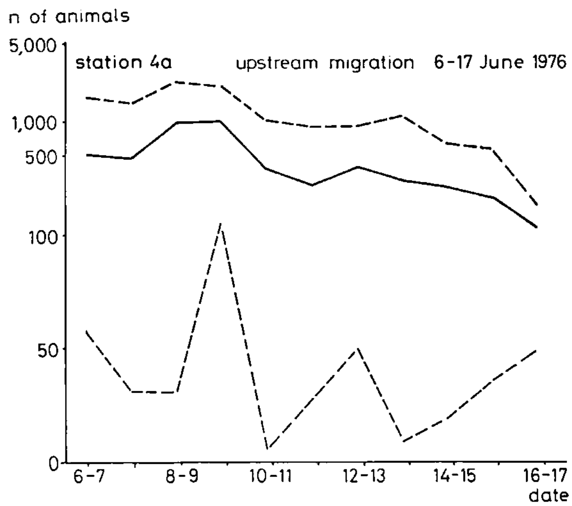

Fig. 23. Diel upstream migration of gammarids at station 4a from 6 to 17 June 1976. Mean hourly catches (solid line) with maximal and minimal catch (broken lines) at certain dates. Diel periods from 12-12 hours local time are averaged. (The scale of the number of animals is logarithmic above 100.)

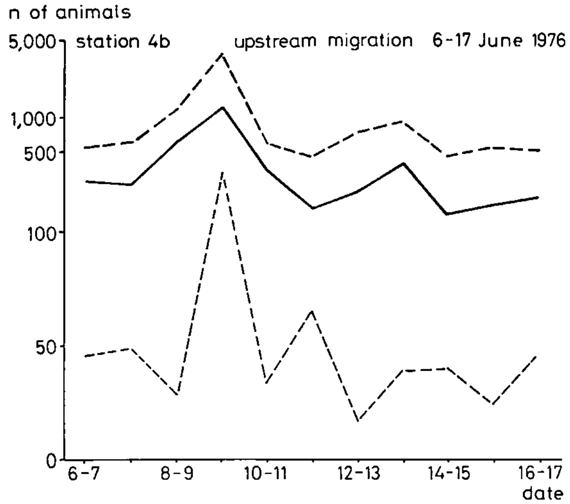

Fig. 24. Diel upstream migration of gammarids at station 4b from 6 to 17 June 1976. Mean hourly catches (solid line) with maximal and minimal catch (broken lines) at certain dates. Diel periods from 12-12 hours local time are averaged. (The scale of the number of animals is logarithmic above 100.)

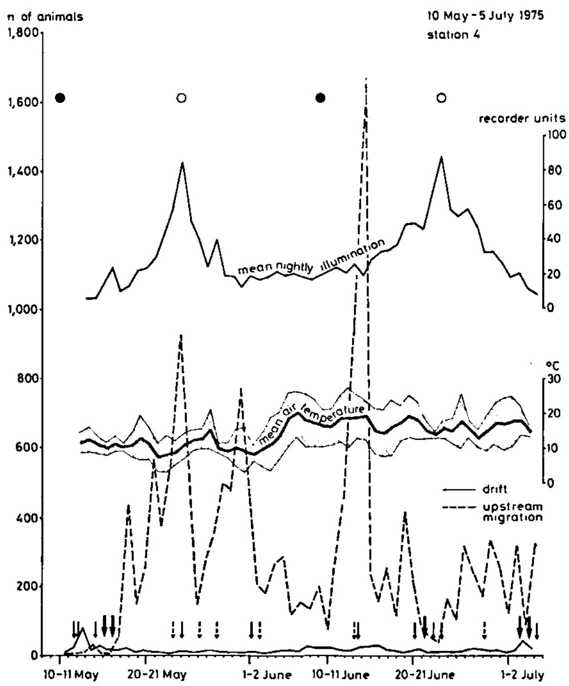

Fig. 25. Diel means of drift and upstream migration of gammarids at station 4 (diel periods from 12-12 hours local time averaged), of air temperature with its standard deviation (diel periods of 1-24 hours local time averaged), and mean nightly illumination (periods from 23-3 hours local time averaged) from 10 May-5 July 1975. Dates with little, moderate or heavy rain are indicated by different arrows; the phase of the moon is indicated as well.

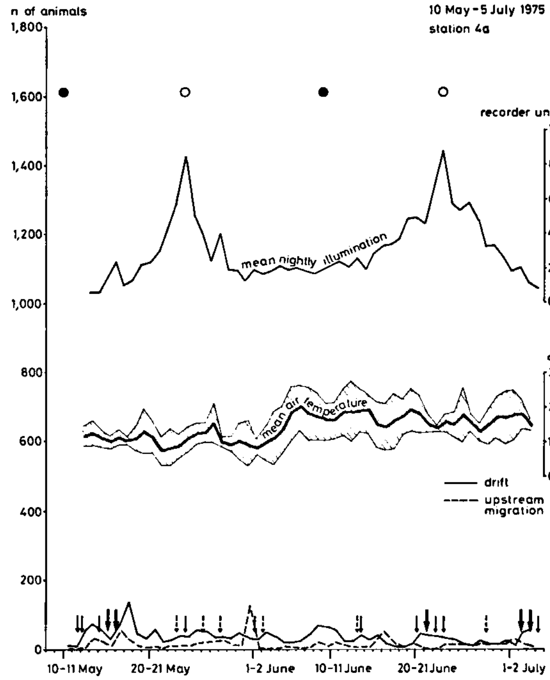

Fig. 26. Diel means of drift and upstream migration of gammarids at station 4a (diel periods from 12-12 hours local time averaged), of air temperature with its standard deviation (diel periods of 1-24 hours local time averaged) and mean nightly illumination (periods from 23-3 hours local time averaged) from 10 May-5 July 1975. Dates with little, moderate or heavy rain are indicated by different arrows; the phase of the moon is indicated as well.

4.2.2. *Day to day variation*

We found no evidence that the lunar cycle had a determining effect on migration behaviour. Our data justify, however, the conclusion that a bright night diminishes migration activity [5]) (figs. 25 to 30). Only data on drift at station 4 in 1976 show a slightly, but significantly increased drift activity during a clear night.

The most important fluctuations in migratory activity can be attributed to changes in the diel range or diel mean value of water temperature. A large diel variation together with a rise of the water temperature on bright, warm days after a relatively cold period brings about a rise in migratory activity [6]). This phenomenon is more evident

[5]) Total diel numbers of drift catches at all three stations, and of upstream migration at station 4b showed a significant negative correlation with nightly illumination in 1975.

[6]) The beginning of the sampling period in 1976 came just after a relatively cold spell. At all three stations water

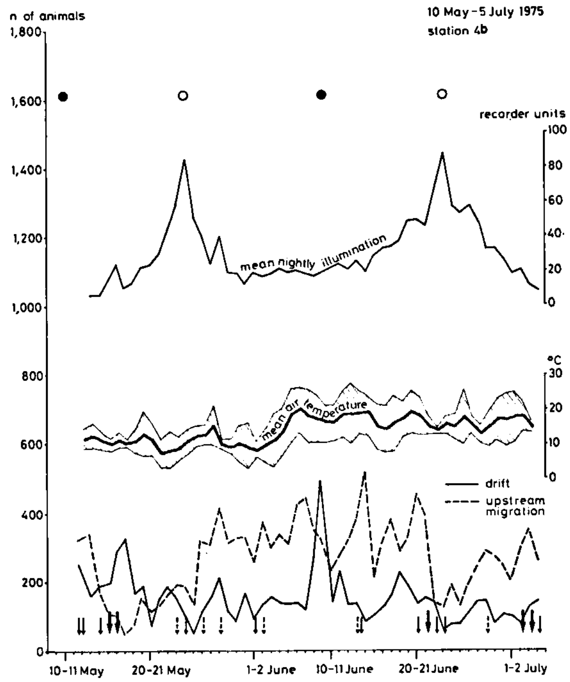

Fig. 27. Diel means of drift and upstream migration of gammarids at station 4b (diel periods from 12-12 hours local time averaged), of air temperature with its standard deviation (diel periods of 1-24 hours local time averaged) and mean nightly illumination (periods from 23-3 hours local time averaged) from 10 May-5 July 1975. Dates with little, moderate or heavy rain are indicated by different arrows; the phase of the moon is indicated as well.

in upstream migration than in drift, which corresponds to our findings on seasonal variation in section 4.1.3.

Rain has a strong negative influence on upstream migration, that may last several days (figs. 25, 26 and 27, in particular the period from 20 to 23 June 1975). It increases drift activity in the hours immediately following heavy rain, but the general effect is negative, although being much smaller than it is on upstream migration (see for instance figs. 26 and 27 the period from 20 to 23 June 1975 and figs. 45 to 50 mentioned in section 4.2.5.3).

We were not able to quantify pollution continuously. (Data on oxygen content or saturation of the water with oxygen could not be used, since the normal diel fluctuation in this environmental factor was far too large to be able to discern a variation caused by pollution. Conductivity proved to be very stable and changed only after heavy rainfall.) Therefore we did not succeed in correlating pollution and migratory activity, although we sometimes found an increased number of drifting gammarids when the turbidity of the water or the stench of muck water indicated pollution.

A comparison of the results of 1976 and 1975 shows the crucial importance of temperature. Migratory activity is larger during the second year. This can be attributed completely to higher water temperatures.

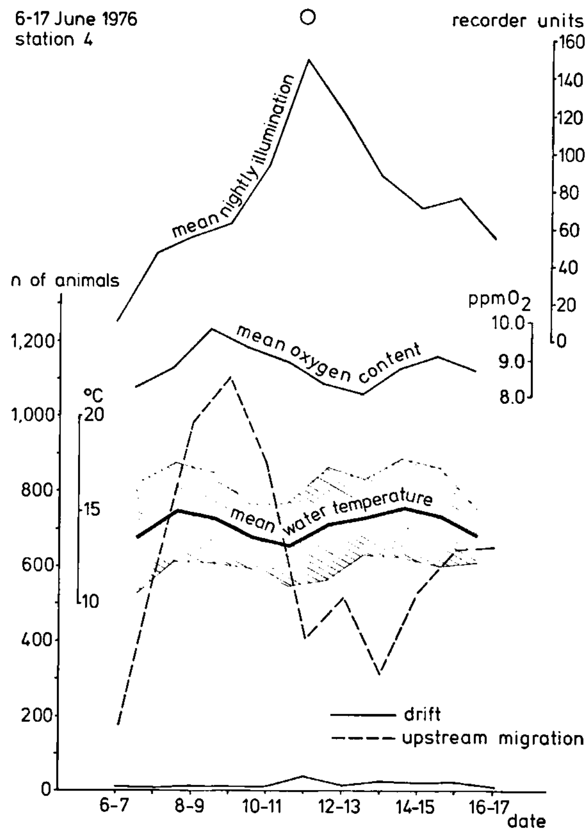

Fig. 28. Diel means of drift and upstream migration of gammarids (diel periods from 12-12 hours local time averaged), of water temperature and its standard deviation and of oxygen content (diel periods of 1-24 hours local time averaged) and mean nightly illumination (periods from 24-4 hours local time averaged) at station 4 from 6-17 June 1976. The phase of the moon is indicated as well.

temperatures showed a large diel variation and increasing mean values. Upstream migration activity grew rapidly in that period at all three sampling sites (figs. 28, 29 and 30).

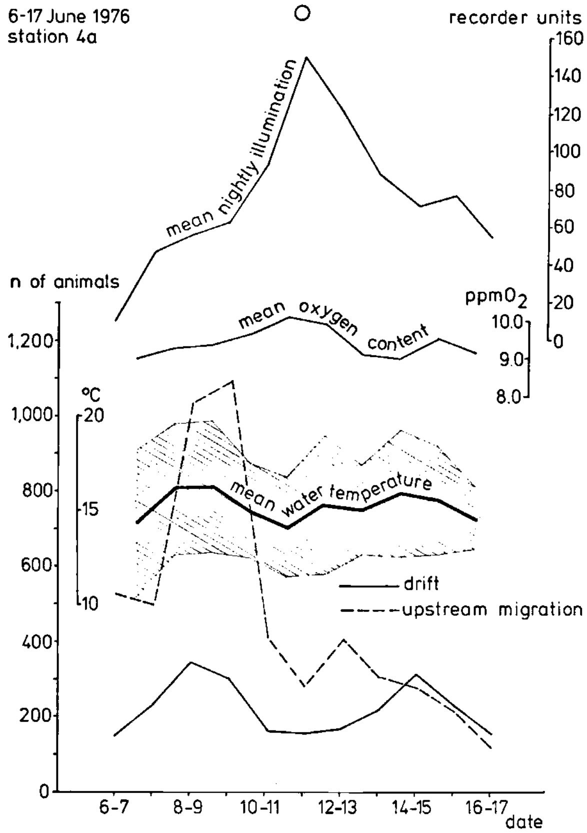

Fig. 29. Diel means of drift and upstream migration of gammarids (diel periods from 12-12 hours local time averaged), of water temperature and its standard deviation and of oxygen content (diel periods of 1-24 hours local time averaged) and mean nightly illumination (periods from 24-4 hours local time averaged) at station 4a from 6-17 June 1976. The phase of the moon is indicated as well.

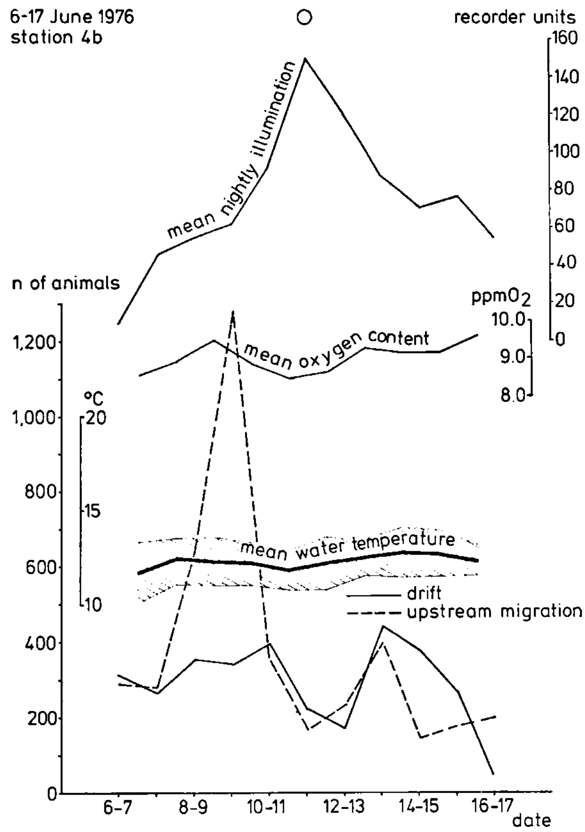

Fig. 30. Diel means of drift and upstream migration of gammarids (diel periods from 12-12 hours local time averaged), of water temperature and its standard deviation and of oxygen content (diel periods of 1-24 hours local time averaged) and mean nightly illumination (periods from 24-4 hours local time averaged) at station 4b from 6-17 June 1976. The phase of the moon is indicated as well.

4.2.3. *Diel variation*

The diel variation is especially conspicuous in the upstream migration at station 4 (figs. 34 and 40). The diel patterns of both upstream migration and drift are essentially the same for stations 4 and 4a (figs. 31, 32, 34, 35, 37, 38, 40 and 41). Peaks in upstream migration occur around or just before sunrise, when water temperatures reach a minimum, although upstream migration in the tributary is also found in the beginning of the night. Drift, however, often reaches its highest peak around sunset (figs. 31, 37 and 38).

In the springbrook (station 4b), drift showed no diel variation in 1975 (fig. 33), but in 1976 (fig. 39) we found it reaching a peak a few hours after sunrise. Also the diel variation in upstream migration had an exceptional character in the springbrook, as it concentrated around sunset instead of sunrise (figs. 36 and 42). Probably the very small fluctuations in water temperature, together with the exceptional chemical composition of the water at this site (a very stable, moderate oxygen content night and day; a minimum in pH a few hours after sunrise; a very high conductivity; see Goedmakers, 1980: fig. 30) could explain this difference between migratory activities in the springbrook and in the Slack or the tributary.

As this example shows, it is not light, but changes in water conditions, that might constitute the most important factor in diel variation of migration. Of course the changes in water conditions are frequently indirectly caused by changes in light conditions.

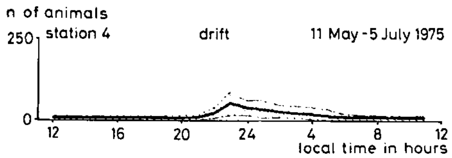

Fig. 31. Diel variation in drift of gammarids at station 4 (period from 11 May to 5 July 1975 averaged), in mean hourly catches (mean number and its standard deviation) at a certain time of the day.

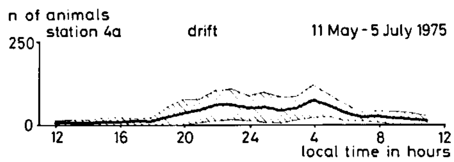

Fig. 32. Diel variation in drift of gammarids at station 4a (period from 11 May to 5 July 1975 averaged), in mean hourly catches (mean number and its standard deviation) at a certain time of the day.

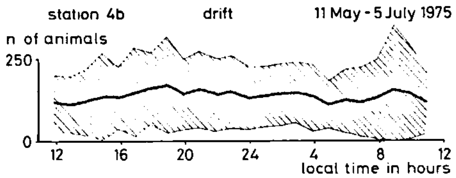

Fig. 33. Diel variation in drift of gammarids at station 4b (period from 11 May to 5 July 1975 averaged), in mean hourly catches (mean number and its standard deviation) at a certain time of the day.

4.2.4. *Structure of migrant populations*

During two twenty-four hour periods in 1975 the size of the migrating animals was measured (Bosch, unpubl.). The data on mean size of the migrating populations were compared with those of the standing crop (table VIII).

The mean size of the standing crop is smaller than that of the migrating part of the population. The composition of the upstream migrating population and the drifting population is quite dissimilar. The standard deviation in size of the drifting animals is larger than that of the upstream migrants. This is an obvious result from the differences between upstream migration and drift: the first being purely non-accidental and the second consisting of both accidental and non-accidental behaviour. In the Slack (station 4) the drifters are smaller in mean size than the up-

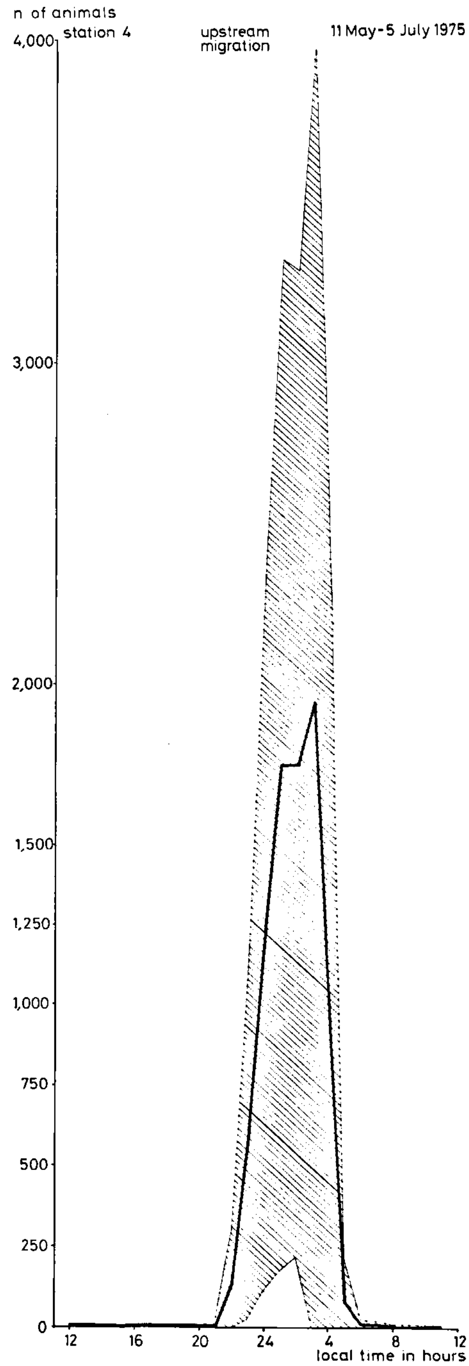

Fig. 34. Diel variation in upstream migration of gammarids at station 4 (period from 11 May to 5 July 1975 averaged), in mean hourly catches (mean number and its standard deviation) at a certain time of the day.

stream migrants; in the tributary (station 4a) the drifters are larger and in the springbrook (station 4b) drifters and upstream migrants have about the same rather large mean size. Drift in the Slack itself could show the closest resemblance to the standing crop, because it consists largely of accidental drift.

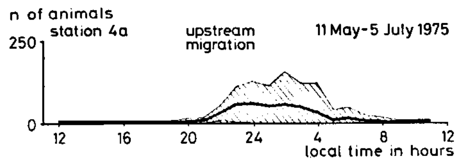

Fig. 35. Diel variation in upstream migration of gammarids at station 4a (period from 11 May to 5 July 1975 averaged), in mean hourly catches (mean number and its standard deviation) at a certain time of the day.

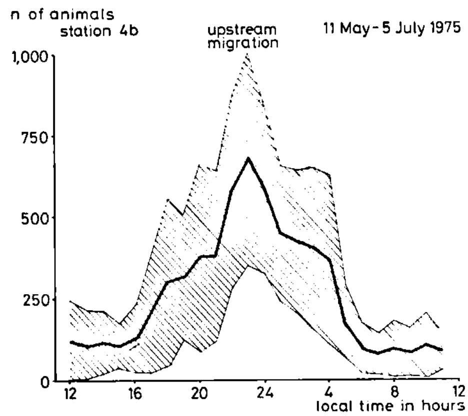

Fig. 36. Diel variation in upstream migration of gammarids at station 4b (period from 11 May to 5 July 1975 averaged), in mean hourly catches (mean number and its standard deviation) at a certain time of the day.

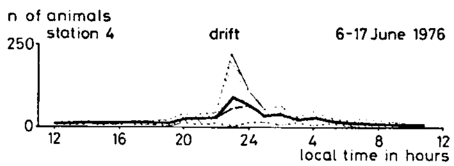

Fig. 37. Diel variation in drift of gammarids at station 4 (period from 6 to 17 June 1976 averaged). Mean hourly catches in number of animals based on a computation (see section 4.2) after a regression analysis (solid line) and with the weighted mean (broken line) collected at a certain time of the day are compared. The standard deviation of the mean hourly catches computed after a regression analysis is indicated as well.

Except on 31 May-1 June 1975 at station 4, animals that drift at night are often significantly smaller than those drifting during the day, while the mean size of upstream migrants is usually larger at night (table IX). A comparison of peak hours with the other hours (Bosch, unpubl.) showed that sometimes drifting animals were

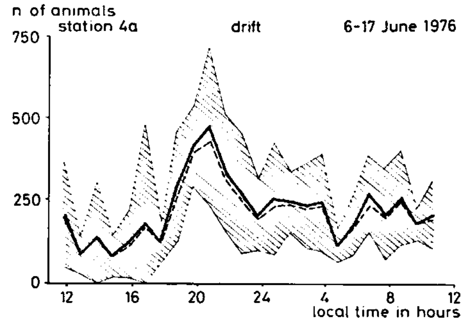

Fig. 38. Diel variation in drift of gammarids at station 4a (period from 6 to 17 June 1976 averaged). Mean hourly catches in number of animals based on a computation (see section 4.2) after a regression analysis (solid line) and with the weighted mean (broken line) collected at a certain time of the day are compared. The standard deviation of the mean hourly catches computed after a regression analysis is indicated as well.

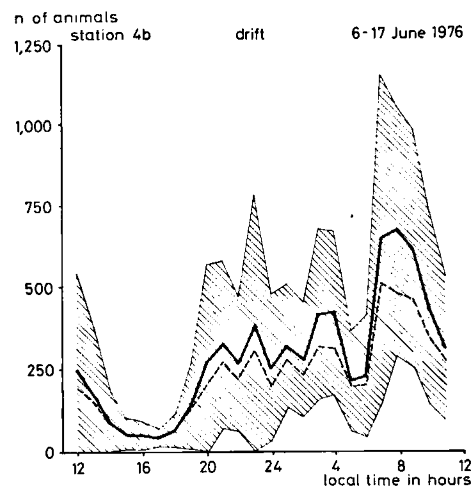

Fig. 39. Diel variation in drift of gammarids at station 4b (period from 6 to 17 June 1976 averaged). Mean hourly catches in number of animals based on a computation (see section 4.2) after a regression analysis (solid line) and with the weighted mean (broken line) collected at a certain time of the day are compared. The standard deviation of the mean hourly catches computed after a regression analysis is indicated as well.

TABLE VIII

Size differences between the standing crop and migrating populations. During the night of 4-5 July 1975 it was raining; at these dates the standing crop sample was collected by electrofishing. Data showing a significant difference between drift and upstream migration are printed in bold type. An asterisk indicates significant difference between standing crop and migration sample.

	standing crop			drift			upstream migration		
	n of animals	mean cephalic length (mm)	SD of cephalic length (mm)	*n* of animals	mean cephalic length (mm)	SD of cephalic length (mm)	*n* of animals	mean cephalic length (mm)	SD of cephalic length (mm)
31 May – 1 June 1975									
Sta. 4	144	0.91	0.26	201	**0.92**	**0.25**	970	**1.07***	**0.20***
Sta. 4a	111	0.90	0.22	1064	**1.05***	0.20	330	**1.00***	0.19*
Sta. 4b	118	0.80	0.28	2129	**1.06***	**0.22***	2555	**1.03***	**0.18***
4-5 July 1975									
Sta. 4	348	0.78	0.29	439	**0.90***	**0.25***	837	**1.01***	**0.17***
Sta. 4a	223	0.82	0.23	1267	**1.02***	**0.20***	183	**0.93***	**0.17***
Sta. 4b	217	0.88	0.24	2482	**1.01***	**0.20***	2003	**1.03***	**0.18***

larger in peak hours, though generally they tend to be smaller in those hours. Upstream migrants were larger or of more or less the same mean size during peak hours compared to sizes during hours of low activity.

Data on Q (= number of animals/volume of a migration sample) for 1976 (table X) illustrate the same phenomenon. Upstream migration activity involves larger animals at peak hours (a low value of Q indicates that samples contain many large-sized animals).

4.2.5. *Environmental factors* (figs. 43, 44 and Goedmakers, 1980: fig. 30)

The enormous amount of data on migration collected in the course of our continuous measurement enabled us to correlate migratory actvity with certain environmental factors. A comparison of 1975 and 1976 was very useful for testing our conclusions. Several environmental factors influence each other, but nevertheless it is possible to classify them into groups of a specific character: external factors occurring occasionally (rain, pollution), year-to-year weather differences, and environmental factors of a certain periodic duration (diel, lunar or seasonal). The range of a factor may be as important as its actual value or level.

In sections 4.2.2 and 4.2.3 the influences of environmental conditions on day-to-day and diel variations in migration are discussed. The differences in migration patterns between various habitats are caused by large differences in environmental conditions between the three habitats of stations 4, 4a and 4b.

4.2.5.1. Temperature.

High water temperatures and a large diel fluctuation of water temperature do increase migratory activity. Although fluctuations in the springbrook are much smaller than in the Slack, a change in fluctuation there had the same effect as in the Slack. The higher level of water temperatures in the tributary may be the cause for the higher drift rates at station 4a.

4.2.5.2. Oxygen.

The oxygen content of the water reaches a minimum soon after sunset in the tributary and in the Slack. In the springbrook the concentration of oxygen is constant throughout the twenty-four hours of the day; only the percentage saturation with oxygen rises somewhat in the middle of the day. Although abundant aquatic vegetation is present in the springbrook, its influence seems much smaller than that of all the algae and microorgan-

TABLE IX

Differences in size between night and day of drifting and upstream migrating populations. During the night of 4-5 July 1975 it was raining. Figures printed in bold type indicate a significant difference between mean cephalic lengths at night and those by day.

	drift		upstream migration	
	4-21 hour local time	21-4 hour local time	4-21 hour local time	21-4 hour local time
	mean cephalic length (mm)	mean cephalic length (mm)	mean cephalic length (mm)	mean cephalic length (mm)
31 May – 1 June 1975				
Sta. 4	**0.79**	**0.97**	**0.93**	**1.10**
Sta. 4a	1.04	1.05	0.96	1.01
Sta. 4b	**1.07**	**1.01**	**1.01**	**1.06**
4-5 July 1975				
Sta. 4	**0.99**	**0.86**	**0.93**	**1.02**
Sta. 4a	**1.04**	**1.00**	0.94	0.92
Sta. 4b	**1.03**	**0.98**	1.02	1.04

isms that cover the gravel and pebbles at stations 4 and 4a. Our hypothesis is that a low oxygen concentration at night between these substrate particles where the animals live makes them leave their biotopes and thus increases their chance to drift during the night.

Changes in oxygen conditions during our sampling period did not tell us very much. Levels of oxygen content of stations 4, 4a and 4b were too much alike to relate them to differences in migration patterns.

4.2.5.3. Conductivity.

Originally we were under the illusion that oxygen concentration and conductivity could be used as measures for pollution. Both the fallibility of our measuring instruments and the rather minor influence pollution had on these factors rendered it impossible to measure pollution continuously.

The influence of rain on the conductivity is very distinct. Due to the heavy ionic load of surface run-off, the conductivity of the water increases almost immediately after it starts to rain at all three stations. As we stated above, drift increases at such times and upstream migration decreases (figs. 45 to 50).

4.2.5.4. pH.

The pH level of the springbrook is lower than that of stations 4 and 4a. The pH slowly decreases during the night in the springbrook and reaches a mimimum a few hours after sunrise. Due to photosynthesis it starts to rise again during the day. Thus pH in the springbrook is higher at night than during daytime.

In the Slack and the tributary pH is more or less constant; in 1975 we found the maximum around sunrise in the Slack, while the data for 1976 showed the minimum around sunrise in the tributary and a very peculiar minimum in the middle of the day for the Slack.

Here again the fallibility of our measuring instruments makes the interpretation of our results a hazardous exercise. But since pH is the outcome of many processes occurring in water, a simple correlation of pH and migration would, as a general rule, be impossible anyway.

4.2.2.5. Light.

As we discussed above (section 4.2.3), the diel variation of drift in the springbrook probably indicates that the influence of light on migration is of only secondary importance.

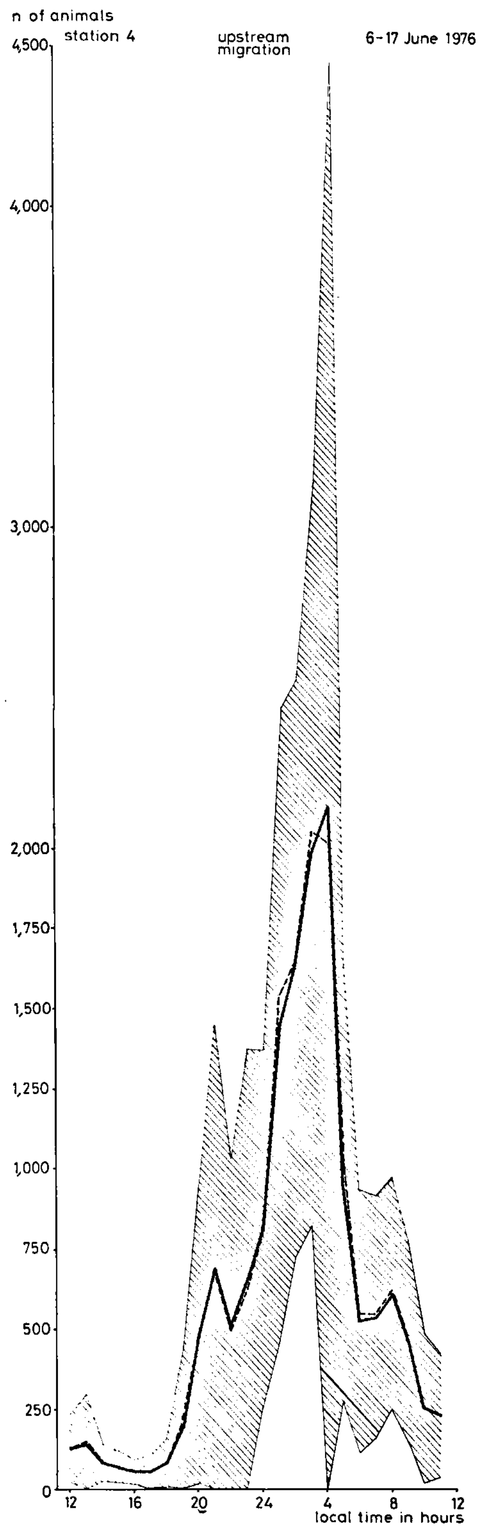

Fig. 40. Diel variation in upstream migration of gammarids at station 4 (period from 6 to 17 June 1976 averaged). Mean hourly catches in number of animals based on a computation (see section 4.2) after a regression analysis (solid line) and with the weighted mean (broken line) collected at a certain time of the day are compared. The standard deviation of the mean hourly catches computed after a regression analysis is indicated as well.

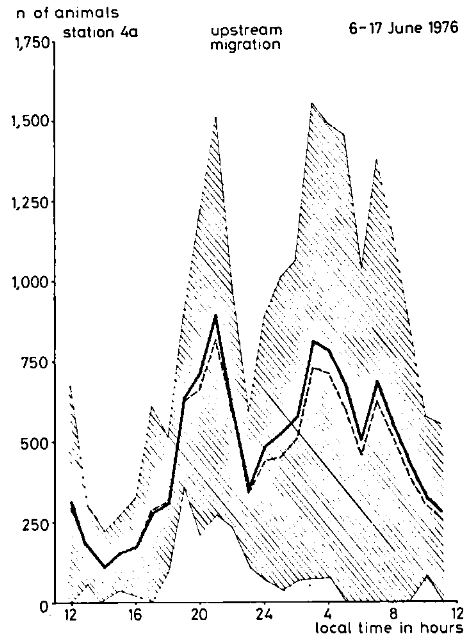

Fig. 41. Diel variation in upstream migration of gammarids at station 4a (period from 6 to 17 June 1976 averaged). Mean hourly catches in number of animals based on a computation (see section 4.2) after a regression analysis (solid line) and with the weighted mean (broken line) collected at a certain time of the day are compared. The standard deviation of the mean hourly catches computed after a regression analysis is indicated as well.

We also concluded that bright nights might exert a positive influence on drift in the Slack and a negative one on upstream migration. The most probable explanation for this phenomenon would be that accidental migration (drift in the Slack is for the most part due to accidental migration) is influenced in a different way by moonlight than is non-accidental migration.

4.2.5.6. Current velocity.

Only during part of the sampling period in 1975 current velocity was measured. The results indicate a rise in current velocity at station 4a immediately after heavy rainfall, at station 4 after one or two days, and at station 4b with an interval of about six days. More research would be necessary to verify these results.

This delayed effect of heavy rain on current velocity seems to corroborate our hypothesis in section 4.1, viz. that a physical disturbance of the streambed by the scouring effect of floods is not responsible for catastrophic drift, but rather the change in chemical composition of the water causes an increase in drift after heavy rain (cf. figs. 45 to 47; conductivity rises immediately at all three stations, see section 4.2.5.3).

4.2.5.7. Standing crop.

The composition of the standing crop influences the structure of migrant populations (sections 4.1.6 and 4.2.4). It seems plausible, when assuming that only a part of the population living at a certain spot migrates, that a different structure of the standing crop causes different migration patterns, just like dissimilar environmental conditions.

In the above-mentioned sections we discussed our results and drew some preliminary conclusions. Differences between the standing crop and migrating populations need to be investigated in a more quantitative way to be able to draw any definite conclusions on their interrelation.

TABLE X

Diel fluctuation in weighted mean of size (measured in number of animals/ volume of migration sample) for upstream migrants at stations 4, 4a and 4b, over the period from 6 to 17 June 1976. Peak hours are printed in bold type; hours at which migration activity was lowest are indicated by *.

	Sta. 4		Sta. 4a		Sta. 4b	
sampling hour	*m*	*Q*	*m*	*Q*	*m*	*Q*
0-1	1	35	6	22	7	22
1-2	–	–	6	25	9	26
2-3	–	–	4	27	8	27
3-4	1	23	3	29	8	27
4-5	2	33	5	28	8	28
5-6	4	31	6	28	4	28*
6-7	3	27	5	29	7	32
7-8	2	29	5	30	6	29
8-9	5	30	6	28	6	32
9-10	8	28	4	28	7	29
10-11	9	32	5	28	9	29
11-12	10	32	6	29	8	29
12-13	8	35	8	28	7	29
13-14	8	35	7	32*	6	21
14-15	8	37	9	31	7	23
15-16	7	33	8	31	6	36
16-17	7	38*	6	35	7	31
17-18	8	39	8	33	8	33
18-19	8	31	4	34	6	30
19-20	8	27	3	28	5	23
20-21	6	29	4	**28**	7	**27**
21-22	6	26	5	26	8	25
22-23	7	26	7	29	6	27
23-24	3	28	4	25	6	24

$Q = \frac{\Sigma n_h}{\Sigma v_h}$ (of samples of a certain hour of which both volume and number are known), in which:

n = number of animals in a migration sample;

v = volume of the migration sample;

h = sampling hour;

m = number of cases in which both the number of animals was counted and the volume of the sample measured.

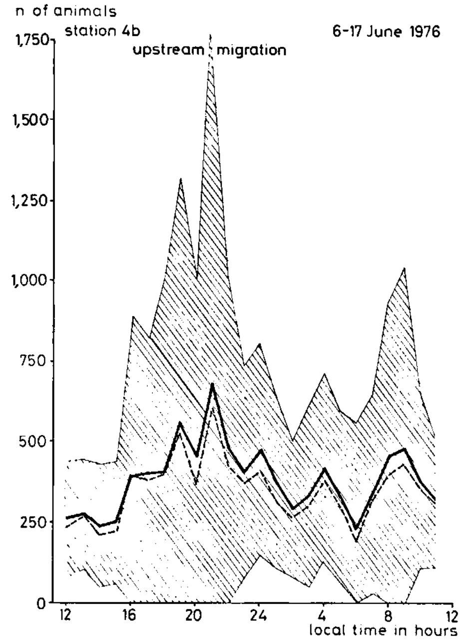

Fig. 42. Diel variation in upstream migration of gammarids at station 4b (period from 6 to 17 June 1976 averaged). Mean hourly catches in number of animals based on a computation (see section 4.2) after a regression analysis (solid line) and with the weighted mean (broken line) collected at a certain time of the day are compared. The standard deviation of the mean hourly catches computed after a regression analysis is indicated as well.

4.2.6. *Conclusions*

The results of our continuous measurement of migration throw some light on the very complex differences found between various stations and between distinct times of the year. Furthermore, our results show that experiments under laboratory conditions make it indeed very difficult to get an adequate insight into migration patterns, since very small differences in environmental conditions change the behaviour of gammarids to a large extent.

Temperature is the most important catalyst of non-accidental migration. Changes in chemical composition of the water increase drift and diminish upstream migration, perhaps by influencing accidental and non-accidental migration differently. Light seems to be a less important factor than is usually assumed (Müller, 1974), but light conditions at night seem to have a differential effect on accidental and non-accidental migration. Moonlight affects the first type of migration positively and the second one negatively.

Our conclusions in section 4.1.10 are neatly supported by our results in the present section: there is a concentration of upstream migratory activity in the beginning of summer due to the significantly large effect of temperature changes on bright, warm days; the more smoothly fluctuating drift activity is due to the smaller effect of temperature and several other environmental factors upon both the accidental and non-accidental parts of drift activity.

The concentration of upstream migration around sunrise might be caused by the predominant influence of temperature, while the drift peak around sunset might be caused by the changes in chemical composition of the water at that time.

Mean size of migrating animals is definitely larger than that of the standing crop. The standard deviation of the size of the drifting population is larger than that of the upstream migrating one.

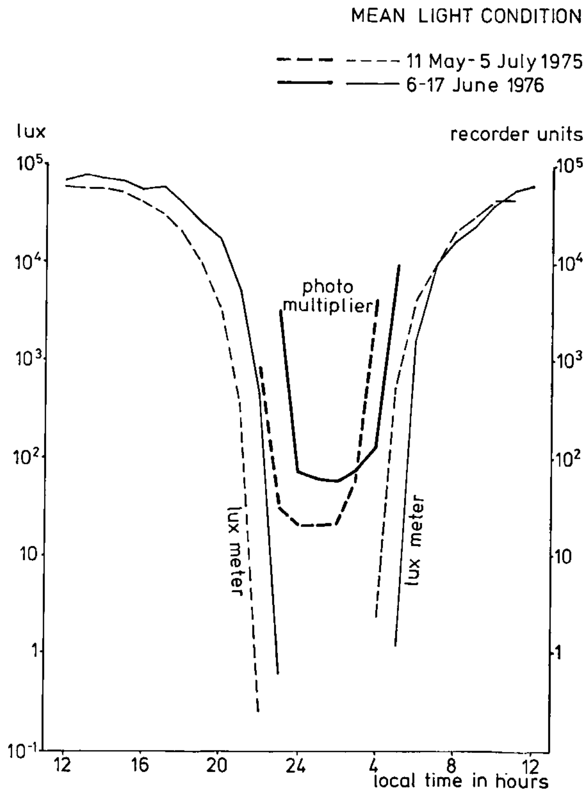

Fig. 43. Diel variation in mean illumination (data averaged over sampling period indicated) at station 4 (the conditions at stations 4a and 4b are identical). The first and the second sampling year are compared.

Upstream migrants are larger in the periods within which this type of behaviour is concentrated. Drifters are mostly smaller during the night and at peak hours. This might be explained by a high percentage of old, dying animals in accidental drift, since we observed that during daytime the percentage of those senile gammarids was rather large in drift samples (during the day most drift is accidental).

4.3. Marking experiments

In order to investigate whether migration in up- or downstream direction is a constant behaviour of certain parts of the population, we marked

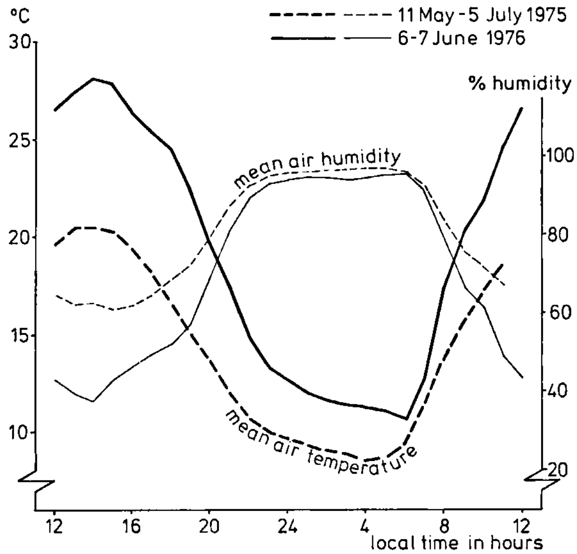

Fig. 44. Diel variation in mean air temperature and mean humidity (data averaged over sampling period indicated) at station 4 (the conditions at stations 4a and 4b are identical). The first and the second sampling year are compared.

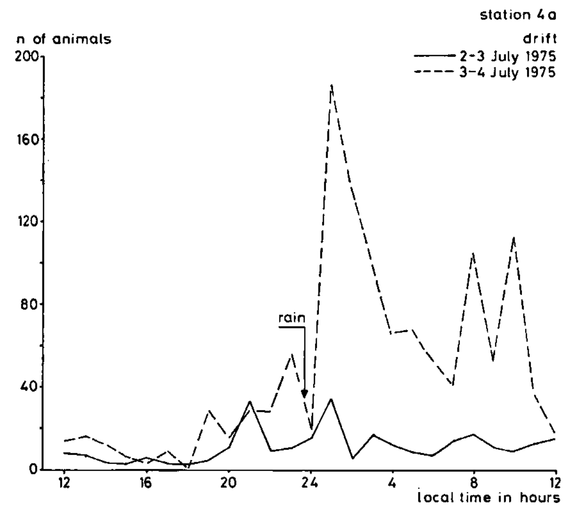

Fig. 46. Diel variation in drift for two consecutive days at station 4a, showing the influence of heavy rains. In the night of 3 July 1975 it started to rain.

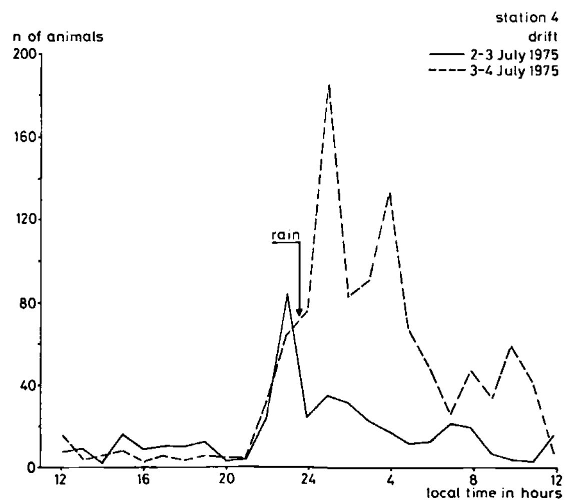

Fig. 45. Diel variation in drift for two consecutive days at station 4, showing the influence of heavy rains. In the night of 3 July 1975 it started to rain.

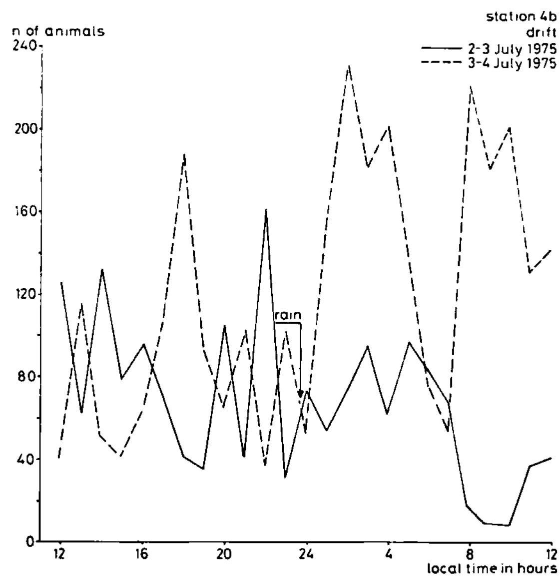

Fig. 47. Diel variation in drift for two consecutive days at station 4b, showing the influence of heavy rains. In the night of 3 July 1975 it started to rain.

animals caught migrating in up- and downstream direction with different colours of paint. After being marked they were released in the middle between the drift net and a newly placed upstream migration net (fig. 51). (For details of the marking method see Dennert et al., 1969.)

The experiments were carried out at station 4b (with animals that were collected at that same station) since at this station we were able to seal off the whole streambed with our nets and thus could capture all migrating animals, either marked or unmarked. In 1975 the animals were released in a sort of basin placed in the stream between the drift net and the second upstream migration net, immediately after they had been marked with paint. The basin had detachable sides made of fine metal gauze. Thus the water could flow through wire sides of the basin, whilst the animals were prevented from escaping. The purpose of this procedure was to return the animals immediately after they had been painted to their natural surroundings, and release them all at the same moment from the basin by removing its detachable sides. However, it did not prove to be a particularly successful procedure, since the animals could climb out of the basin. The second year we kept the animals in a bucket until we had the desired number of them marked, after which they were released all at the same moment between the drift net and the second upstream migration net.

We collected the animals that were to be marked during hours of more pronounced activity. Thereby we hoped to increase the proportion of non-accidental migration.

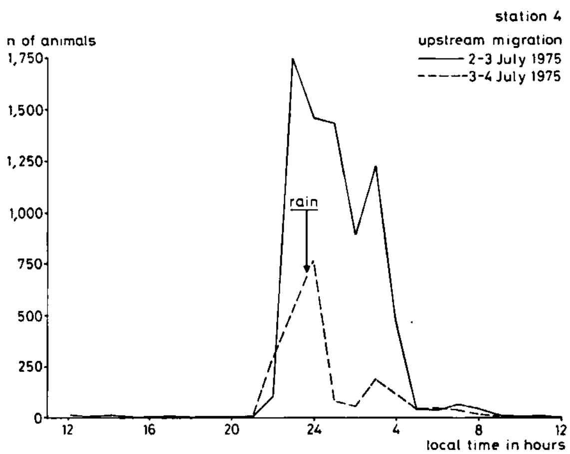

Fig. 48. Diel variation in upstream migration for two consecutive days at station 4, showing the influence of heavy rains. In the night of 3 July 1975 it started to rain.

Some of the problems that rise when marking gammarids with paint are:

a. One runs the risk of painting their walking or swimming legs instead of their metasome, thus making it difficult for them to move actively; this means that more painted animals would be found drifting than was to be expected.
b. The moulting of gammarids, which involves the shedding of their carapace together with the paint. It is not known whether animals like to drift or migrate upstream at a certain stage of their moulting cycle, therefore we do not know if moulting makes the number of marked animals in either drift or upstream

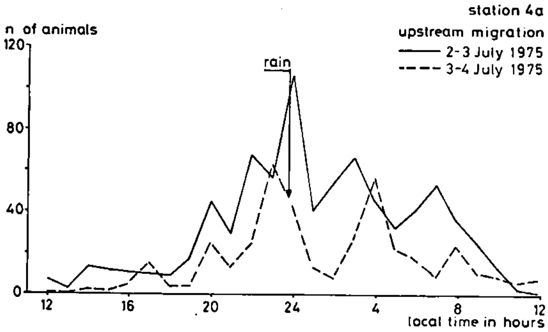

Fig. 49. Diel variation in upstream migration for two consecutive days at station 4a, showing the influence of heavy rains. In the night of 3 July 1975 it started to rain.

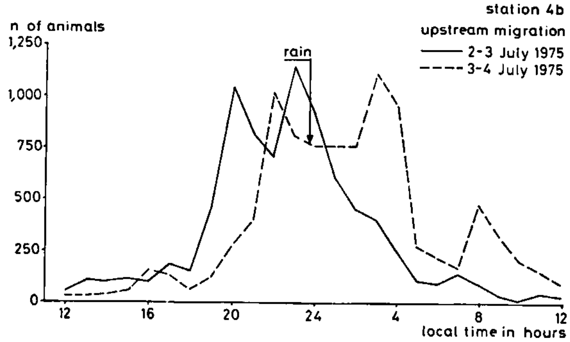

Fig. 50. Diel variation in upstream migration for two consecutive days at station 4b, showing the influence of heavy rains. In the night of 3 July 1975 it started to rain.

TABLE XI

Marking experiments at station 4b. The numbers of animals indicated are the numbers recollected during 24 hours after the release of 1000 marked drifters and 1000 marked upstream migrants, that had been collected the previous night.

		marked and recollected	
		drift	upstream migration
22-24 June 1975	drift	247	55
	upstream migration	94	99
13-15 June 1976	drift	56	24
	upstream migration	27	55
Total catch of drifting and upstream migrating animals (marked and unmarked).			
22-24 June 1975		5087	10570
13-15 June 1976		9581	4502

migration relatively high or normal. (We expect no distinct heterogeneity, since both drifting as well as upstream migrating animals were found with a dot of paint on their backs after a period of up to ten days. If migration would only take place at a certain stage of their moulting cycle, this would not have happened.)

c. The time of the day at which the animals were collected before they were being marked; for drifting animals particularly this may make some difference due to the percentage of accidental drift. (Because we collected migrating animals during hours when migration was at its peak, this might not have a very important influence.)
d. The extent of migration on the day the painted animals were found again in the migration traps: when either drift or upstream migration activity has in- or decreased while animals were painted, the number of animals found again in drift or upstream migration may be relatively too high or too low; this may influence the conclusions in relation to the constant nature either of drift or of upstream migratory behaviour.

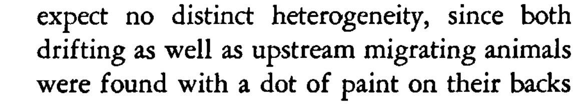

Fig. 51. Situation at station 4b for marking experiments. Drifters and upstream migrants were collected in the drift net and the first upstream migration net, respectively. They were marked with paint and released in the middle between the second upstream migration net and the drift net. Later they were recaptured either in the original drift net or in the second upstream migration net.

4.3.1. *Upstream migration*

The number of upstream migrants found migrating upstream again the following day was in both years twice as high as the number of drifters found migrating upstream (table XI). In 1976, however, out of 1000 marked upstream migrants 55 were found to migrate upstream again during the twenty-four hours after release of the marked animals, while in 1975 the number was 99. The reason for this lower number in 1976 might be found in a sharp decline of ustream migratory activity between the time the animals were collected and the time they were released again.

In 1975, the number of upstream migrants found drifting the following period was about as high as the number found migrating upstream again, while in 1976 it was half as high. This difference may have been due to a relatively high number of animals damaged by the marking procedure in 1975, as we were yet inexperienced in this technique. This could have brought about that many animals landed in the drift net, not being able to resist the action of the current.

4.3.2. *Drift*

The number of drifters found drifting again was much higher in 1975 than in 1976. The large number of drifters the first year could be explained by the same reason as supposed for the high number of upstreamers found drifting in the following period in that same year 1975: animals were drifting because they were hampered in their movements by the paint with which they were marked.

The number of animals that changed their behaviour from drifting to migrating upstream was in 1975 twice as large as in 1976. This might be the result of the same decrease in upstream migratory activity in 1976, as that we held responsible in the previous section for a relatively low number of upstreamers found migrating upstream again in 1976.

Nevertheless, we can give no explanation for the relatively low numbers of marked animals drifting in 1976, in spite of the large drift activity in 1976 compared with that of 1975.

4.3.3. *Conclusions*

Many animals that migrated in a certain direction before they were marked, migrated again in the same direction after they were marked. The results for drift are partly due to accidental drift, which makes recollected numbers for drift always higher than for upstream migration. This means that both drift and upstream migration are constant types of behaviour. This fact increases at the same time the likelihood that non-accidental drift is quite another type of behaviour than non-accidental upstream migration.

REFERENCES

BAKER, R. R., 1978. The evolutionary ecology of animal migration: i-xxi, 1-1012 (Hodder and Stoughton, London).

BESCH, W., 1966. Driftnetzmethode und biologische Fliesswasseruntersuchung. Verh. int. Ver. Limnol., **16**: 669-678.

BOSCH, W., unpubl. Onderzoek aan drift en opstroomse migratie bij Gammarus fossarum in de Slack. (Doctoraalverslag Instituut voor Taxonomische Zoölogie, Univ. Amsterdam, 1978).

BOURNAUD, M. & M. THIBAULT, 1973. La dérive des organismes dans les eaux courantes. Annls. Hydrobiol., **4** (1): 11-49.

DENNERT, H. G., A. L. DENNERT, P. KANT, S. PINKSTER & J. H. STOCK, 1969. Upstream and downstream migration in relation to the reproductive cycle and to environmental factors in the amphipod, Gammarus zaddachi. Bijdr. Dierk., **39**: 11-43.

DIELEMAN, J., 1977. Circatidal activity and the annual migration cycle in an estuarine population of Gammarus zaddachi Sexton, 1912. Crustaceana, Suppl. **4**: 81-87.

——, 1979. Swimming rhythms, migration and breeding cycles in the estuarine amphipods Gammarus chevreuxi and Gammarus zaddachi. In: E. NAYLOR & R. G. HARTNOLL eds., Cyclic phenomena in marine plants and animals: 415-422 (Pergamon Press, Oxford).

GIRISCH, H. B. & H. G. DENNERT, 1975. Simulation experiments on the migration of Gammarus zaddachi and Gammarus chevreuxi. Bijdr. Dierk., **45** (1): 20-38.

GOEDMAKERS, A., 1980. Population dynamics of three gammarid species (Crustacea, Amphipoda) in a French chalk stream. Part I. General aspects and environmental factors. Bijdr. Dierk., **50** (1): 1-34.

——, 1981. Population dynamics of three gammarid species (Crustacea, Amphipoda) in a French chalk stream. Part II. Standing Crop. Bijdr. Dierk., **51** (1): 31-69.

GOEDMAKERS, A. & S. PINKSTER, 1977. Migration of freshwater gammarids, 16 mm film, Institute of Taxonomic Zoology, University of Amsterdam.

GOEDMAKERS, M. J., unpubl. Migratieonderzoek in de Slack van sept. 1974 tot sept. 1975. (Doctoraalverslag Instituut voor Taxonomische Zoologie, Univ. Amsterdam, 1979).

HUGHES, D. A., 1970. Some factors affecting drift and upstream movements of Gammarus pulex. Ecology, **51** (2): 301-305.

HYNES, H. B. N., 1972. The ecology of running waters (2nd ed.): i-xxiv, 1-555 (Liverpool University Press, Liverpool).

LEHMANN, U., 1967. Drift und Populationsdynamik von Gammarus pulex fossarum Koch. Z. Morph. Ökol. Tiere, **60**: 227-274.

LEHMKUHL, D. M. & N. H. ANDERSON, 1972. Microdistribution and density as factors affecting the downstream drift of mayflies. Ecology, **53** (4): 661-667.

MEIJERING, M. P. D., 1972. Experimentelle Untersuchungen zur Drift und Aufwanderung von Gammariden in Fliessgewässern. Arch. Hydrobiol., **70** (2): 133-205.

——, 1977. Quantitative relationships between drift and upstream migration of Gammarus fossarum Koch, 1835. Crustaceana, Suppl. **4**: 128-135.

MÜLLER, K., 1974. Stream drift as a chronobiological phenomenon in running water ecosystems. Ann. Rev. Ecol. Syst., **5**: 309-323.

STEENBERGEN, H., M. J. VAN HEZEWIJK & F. SCHURING, unpubl. Onderzoek naar de populatieopbouw en de migratieactiviteit van gammariden in de Slack. (Doctoraalverslag Instituut voor Taxonomische Zoologie, Univ. Amsterdam, 1979).

WATERS, T. F., 1962. A method to estimate the production rate of a stream bottom invertebrate. Trans. Am. Fish. Soc., **91** (3): 243-250.

——, 1965. Interpretation of invertebrate drift in streams. Ecology, **46**: 327-334.

——, 1972. The drift of stream insects. Ann. Rev. Entom., **17**: 253-272.

WATERS, T. F. & J. C. HOKENSTROM, 1980. Annual production and drift of the stream Gammarus pseudolimnaeus in Valley Creek, Minnesota. Limnol. Oceanogr., **25** (4): 700-710.

WILLIAMS, D. D. & H. B. N. HYNES, 1976. The recolonization mechanisms of stream benthos. Oikos, **27**: 265-272.

Received: 27 June 1981