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

PART IV. REVIEW AND IMPLICATIONS

by

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ABSTRACT

The results of the investigations on environmental factors, standing crop and migration patterns of *Gammarus pulex pulex* (Linnaeus, 1758), *G. fossarum* Koch in Panzer, 1836, and *Echinogammarus berilloni* (Catta, 1878) in the river Slack (Pas-de-Calais, France) are linked to get a picture of gammarid life in a small chalk stream.

Gammarids appear to live in clusters, here called microgeographic races, with more or less unpopulated areas between them. By non-accidental migration they are able to colonize new areas. The locomotory activity necessary to feed and reproduce causes (and is reflected in) accidental migration.

The different ways in which the three species respond to environmental factors can be explained by their different origin. *G. p. pulex* and *G. fossarum* are both species originating from eastern Europe, the first one euryecious, the second cold stenothermous; *E. berilloni* is an euryecious animal with a distribution centre in southwestern Europe.

The concept of ecological zonation is strongly supported by our investigations. The three species can be used as a helpful tool in bioassays, since they demand different environmental conditions.

The three freshwater species compete for the same limited resource: space. They often occupy the same ecological niche. This invalidates the competitive exclusion principle (s.l.: competitors can not coexist permanently): competitive exclusion is only one of the solutions for animals sharing resources.

RÉSUMÉ

On réalise une synthèse des résultats des recherches entreprises dans la rivière Slack (Pas-de-Calais, France) sur les facteurs du milieu, le «standing crop» et les migrations de *Gammarus pulex pulex* (Linnaeus, 1758), *G. fossarum* Koch in Panzer, 1836, et *Echinogammarus berilloni* (Catta, 1878), afin d'obtenir une image sur la vie des Gammares dans un ruisseau calcaire.

Il semble que les Gammares vivent en groupes, que nous allons appeler ici races microgéographiques, séparées par des aires plus ou moins non-peuplées. Ils sont capables de coloniser des aires nouvelles par migration non-accidentelle. La migration accidentelle reflète (et est provoquée par) l'activité locomotrice nécessaire en vue de l'alimentation et de la reproduction.

Les trois espèces répondent aux facteurs du milieu de manière différente, ce qui peut s'expliquer par leur origine différente. *G. p. pulex* et *G. fossarum* sont des espèces orien-

tales, la première euryoeque, la seconde sténotherme d'eau froide; tandis que *E. berilloni* est une espèce méridionale et euryoeque.

La notion de zonation écologique est nettement confirmée par nos recherches. Les trois espèces peuvent être utilisées comme bioindicateurs pour la détermination de la qualité des eaux, car les conditions de l'environnement qui leur sont nécessaires diffèrent d'une espèce à l'autre.

Les trois espèces sont en compétition pour une ressource limitée: l'espace. Souvent, elles occupent la même niche écologique. Ceci contredit le principe de l'exclusion compétitive: cette exclusion est seulement une des solutions qui permettent aux animaux de partager les ressources du milieu.

CONTENTS

1. INTRODUCTION

The apparent contradiction between the often stable zonation of limnic gammarid species (Minckley & Cole, 1963; Roux, 1967; Besch, 1968; Meijering, 1971; Vincent, 1971) and the high migration rates often shown by the same species (Waters, 1965; Lehmann, 1967, Elliott & Minshall, 1968; Hultin, 1971; Meijering, 1972) induced the present research program. It consisted of three parts: a study of environmental conditions (Goedmakers, 1980a), standing crop (Goedmakers, 1981) and migration patterns (Goedmakers & Pinkster, 1981) of three freshwater gammarid species in a French chalk stream. With this program we wanted to solve the question when, how, and why freshwater gammarids realize short-term fluctuations in their microgeographic

distribution area. In the present paper the results of the three previous parts are linked to get a picture of what is happening during a gammarid life cycle in a small stream like the river Slack (Pas-de-Calais, France).

Since we started our investigations with only a very slight and superficial knowledge of gammarid distribution and environmental conditions in the river Slack (Stock et al., 1966), we could neither choose methods that would give us more than a qualitative insight, nor focus on only certain aspects of gammarid ecology. We attempted to get an overall picture first, but we realize that many questions remain to be answered.

In this paper, the last of a series of four, our results are reviewed and conclusions are drawn on the population dynamics of freshwater gammarids and their impact on other fields of ecology. A comparison with other findings and hypotheses reveals to what extent our model of gammarid life in a small river is supported by other investigations.

It is common nowadays for scientific research, fortunately, to be judged amongst others by the criterion of social utility. Useful as this demand may be for scientific research at large, it can considerably hamper research on specialized fields. Social relevance is easily demonstrated for some short-term or fashionable topics like for instance pollution, but it is much more difficult to establish when a subject like autecology is under discussion. In my opinion, however, autecology in the long run will prove to be very useful and even indispensable for pollution studies. Therefore, I readily concur with the view of Waters (1979) stressing in his paper on future research requirements in particular the great need for basic life history studies.

2. ACKNOWLEDGEMENTS

3. LIFE PATTERNS

Three gammarid species live in the limnic reaches of the river Slack: *Gammarus pulex pulex* (Linnaeus, 1758), *G. fossarum* Koch in Panzer, 1836, and *Echinogammarus berilloni* (Catta, 1878). Distinct populations of a single species sometimes show remarkable differences in sexual activity, fecundity and size (Goedmakers, 1980b; Goedmakers, 1981). We concluded that gammarids live together in clusters (Goedmakers, 1980b; see also section 5), with more or less unpopulated or barren areas between them. By means of non-accidental migration they are able to colonize new habitats in these barren areas.

At station 3 [1] the mean size of the standing crop did not increase after the mass upstream migration at the more downstream station 4 of relatively large animals in early summer [2]. On the contrary, the drop in mean size of the standing crop at station 4 was very clear, in particular during the summer of 1975 [3]. Population densities remained the same at both stations [4]. The fact that mass upstream migration has no effect on either population density or population structure of upstream stations, constitutes additional evidence that migration is used for the colonization of formerly barren areas.

We found no proof for large scale migration of gammarids throughout the whole river Slack, although individual animals are very well able to travel considerable distances over difficult trajects. *E. berilloni* for instance is found regularly at stations 3 and 4, which means passing a three meters high man-made waterfall by crawling upstream. The same species was sporadically found even as far upstream as stations 2, 2a and 1, situated about 3 km from its normal distribution area in this stream.

The population density at a certain locality may vary considerably. Since peaks in population densities are not associated with peaks in juvenile production [5], these changes of population density must be attributed to the ability of gammarids to

[1] Goedmakers (1981): section 5.3.1.2 and fig. 24.
[2] Goedmakers & Pinkster (1981): table IV and section 4.2.4.
[3] Goedmakers (1981): fig. 25.
[4] Goedmakers (1981): table II.
[5] Goedmakers (1981): section 5.5 and fig. 59.

move around extensively. They can hide in the substrate and swim or crawl very easily to other sites within, or even outside, the area occupied by the population.

Non-accidental migration involves animals with a larger mean size than that of the standing crop [6]. Larger animals seem better equipped to migrate and colonize new areas. They are better capable of swimming against the current or of resisting being swept away by it than juveniles. Juveniles live hidden in the substrate, but can sometimes be found in accidental migration together with very old animals. The relatively large percentage of ovigerous females we found in migrating populations [7], would indicate a very efficient means of colonizing new habitats.

Different life stages may require special demands upon environmental conditions. For animals living in an area with tidal influences, migration provides the means to meet the needs of different life stages (Dennert et al., 1969; Girisch et al., 1974). We found no evidence that gammarid migration in fresh water serves this purpose.

Migration does not play a role in an active search for sexual partners, firstly because both males and females take part in migration in roughly the same numbers [8], secondly because population densities of the standing crop are far too high to necessitate a migratory search for sexual partners. The correspondence of maximum seasonal drift (in insects) and pupation (Cloud & Stewart, 1974; Elliott & Tullett, 1977) has no counterpart in the migration patterns of gammarids.

Lack of space and shelter alone can not explain migration rates, since no correlation was found between either drift or upstream migration and population density [9]. Our data certainly did not prove the existence of a density-dependent migration as postulated by Walton et al. (1977).

Adequate supplies of food [10] were always available at the localities where the animals were collected, although lack of it might be one reason why some areas remain barren. (Some localities that we did not use as sampling stations because we could hardly collect any gammarids there, were also characterized by the absence of decaying plants or detritus.) Therefore, search for food is probably not an important cause of migration. Foraging and other locomotory activities are often considered causes of (accidental) drift (Waters, 1972; Bournaud & Thibault, 1973; Müller, 1974; Hynes, 1975; Hiroki, 1980). In their opinion, diel changes in activity patterns are reflected by diel changes in drift. We agree that there appears to be a certain correlation between the two phenomena, but our results clearly show that the foraging or reproductive activity of an animal is only a minor cause of migration. We found a large microgeographic, seasonal and diel variation in migratory activity, while patterns of drift and upstream migration differed. This fact, together with our results from marking experiments [11], shows that migration is for the greater part non-accidental. The colonization of implanted (artificial) substrates by small animals first (Nilsson & Sjöström, 1977; Bournaud et al., 1978) might reflect normal locomotory activity necessary for day-to-day survival.

We agree with most authors that migration is an important way to (re)colonize other habitats (Waters, 1972; Elliott & Corlett, 1972; Bournaud & Thibault, 1973; Müller, 1974; Williams & Hynes, 1977; Williams, 1977). Non-accidental migratory behaviour must have been selected during evolution since it proved to be a successful strategy for gammarids. Active migratory behaviour enables gammarids to colonize new areas and to regain the territory lost by downstream accidental migration.

Several authors compare numbers of drifting and upstream migrating animals (Bournaud & Thibault, 1973; Meijering, 1972; 1974; 1977). In our opinion this quantitative type of research is a little premature in the light of our results. We found a very large microgeographic variation in both drift and upstream migration [12], while also

[6] Goedmakers & Pinkster (1981): sections 4.1.6 and 4.2.4.
[7] Goedmakers & Pinkster (1981): section 4.1.7.
[8] Goedmakers & Pinkster (1981): table VII.
[9] Goedmakers & Pinkster (1981): section 4.1.2 and figs. 8 and 9.

[10] Goedmakers (1980a): section 7.1 and table I.
[11] Goedmakers & Pinkster (1981): section 4.3.3.
[12] Goedmakers & Pinkster (1981): section 4.1.2 and 4.2.1.

the seasonal variation in migration patterns was quite large [13]. Especially the results of continuous measurement of migration [14] at three stations lying within a hundred meters of each other clearly show the complexity of migratory behaviour. The main question is not the fact whether (or not) the animals are able to keep their place in a river (gammarids obviously are able to do this), illustrating this fact with an equal or corresponding number of drifting and upstream migrating animals, but the way how they manage to keep their place.
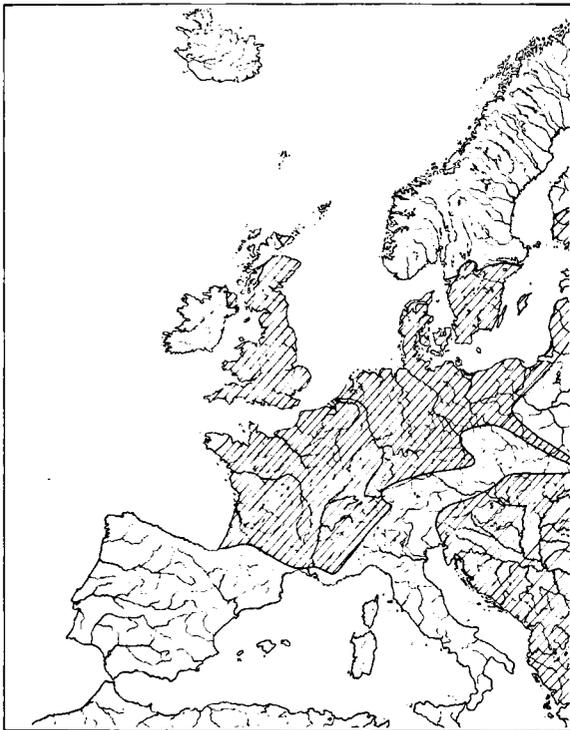
Fig. 1. Distribution of *G. p. pulex* in western Europe.

Essentially, *G. p. pulex*, *G. fossarum* and *E. berilloni* have largely alike life histories [15]. They differ in numbers of batches offspring and number of eggs in one batch, but the low numbers of batches offspring a female *E. berilloni* produces is compensated by the high number of eggs she carries in her broodpouch.

Fecundity of both *G. fossarum* and *E. berilloni*

was smaller in the second sampling year (September 1974—September 1975) than in the first one (September 1973—September 1974) [16], while both species showed a larger percentage of ovigerous females in the second year [17], the second year being warmer than the first. When fecundity is multiplied by the percentage of ovigerous females to get a standard for the reproduction in a certain year, this value is smaller for *G. fossarum* (192 and 160, respectively) and larger for *E. berilloni* (310 and 393, respectively) in the second year.

These differences, caused by a distinct response to environmental factors, can be explained by the different origin of both species and the resulting distribution areas (figs. 1, 2 and 3). *E. berilloni* is a southwestern European euryecious species, *G. p. pulex* and *G. fossarum* are both eastern European species, euryecious and cold stenothermous, respectively (Pinkster, 1978). This explains their different migratory behaviour as well. *E. berilloni* migrates in far lower numbers than *Gammarus* in the river Slack, although its migratory behaviour was more strongly pronounced in the second, warm sampling year [18]; it was able to shift its upper border upstream in the second year [19].

The importance of chance in life processes has always to be kept in mind. Fluctuations in ecological features can not be correlated always to variations in environmental conditions, although much research is necessary before it is possible to exclude a correlation with environmental conditions. Another important fact is the difference between individuals of one species, which can seriously affect conclusions on life processes. In our case the large number of animals investigated will have diminished the influence of this fact.

4. ZONATION AND BIOASSAY

The three gammarid species inhabiting the limnic reaches of the river Slack are rather evenly distributed over the different habitats in this stream. *G. p. pulex* lives in the most unstable

[13] Goedmakers & Pinkster (1981): section 4.1.3.
[14] Goedmakers & Pinkster (1981): section 4.2.
[15] Goedmakers (1981): section 5.3.

[16] Goedmakers (1981): table X, *f* calculated.
[17] Goedmakers (1981): tables IV and V, sta. 1-15.
[18] Goedmakers & Pinkster (1981): section 4.1.5.
[19] Goedmakers (1981): section 5.2.4.

Fig. 2. Distribution of *G. fossarum* in western Europe.

Fig. 3. Distribution of *E. berilloni* in western Europe.

habitats, *G. fossarum* occupies the most stable and unpolluted upper and middle reaches, while *E. berilloni* is found in the middle and lower part of the Slack [20]. During the second sampling year (September 1974—September 1975), when water temperatures were rather high compared with the first one (September 1973—September 1974), *E. berilloni* and *G. fossarum* moved a little upstream [21]. At a very unstable locality, station 1, where *G. p. pulex* and *G. fossarum* coexist, the percentage of *G. fossarum* decreased [22]. The distribution of gammarid species is clearly related to environmental conditions [23]. This makes our three gammarids good indicator species of ecological zonation.

The concept of ecological zonation (Illies & Botosaneanu, 1963; Botosaneanu, 1979) is founded on the existence of gradients in environmental conditions, whereas animal and plant communities in aquatic environments show rather abrupt changes. Our results confirm this. We were not able to make a sharp distinction in abiotic conditions between the upper and middle region of the Slack [24]. Gammarids, however, could discriminate between the upper and middle region of this river. They even distinguished several zones in the middle reaches: one with and one without *G. fossarum*. *G. fossarum* is only sporadically found below station 9, while the middle reaches stretch to station 12.

Obviously, pollution has a large impact on environmental conditions in such a small river. In the discriminant analyses of our environmental data pollution was often selected as the factor that could explain most of the differences between the various localities [25]. The accumulation of pollution going downstream coincides, however, with the normal downriver succession in abiotic conditions. Therefore, we did not find a distribution pattern of gammarid species that was disrupted by pollution, although pollution may have enlarged the distribution area of both *G. p. pulex* and *E. beril-*

[20] Goedmakers (1981): section 5.2.2.
[21] Goedmakers (1981): section 5.2.4 and fig. 16.
[22] Goedmakers (1981): section 5.2.4 and fig. 5.
[23] Goedmakers (1981): section 5.6.
[24] Goedmakers (1980a): section 7.4.
[25] Goedmakers (1980a): table VII.

loni and shortened the stretch of the river where *G. fossarum* can thrive.

Gammarids are often used in biological water quality studies (Sládeček, 1973). They can, however, be of much more value to bioassays than they are now. Most of the times only the genus (Ghetti & Bonazzi, 1977) or even the family (Tuffery & Verneaux, 1968; Lagauterie & Leroux, 1977; Cairns & Dickson, 1971) is used, which makes only a subdivision possible into very polluted or unpolluted to moderately polluted water. Sometimes morphologically similar but ecologically different species like *G. p. pulex* and *G. fossarum* are used as one category. Thereby a lot of useful information about the sites they occupy is lost. Sometimes an euryecious species is used instead of a stenoecious one (Verneaux, 1976), which makes the discriminating value of such a category much lower.

In our opinion a thorough investigation of the taxonomy of species used in bioassays is imperative. After our study of the ecology of *G. p. pulex, G. fossarum* and *E. berilloni* and with the description of morphological characteristics of different life stages at hand, these species could be used more effectively in bioassays, even by technicians not particularly trained to do this kind of work. The fact that gammarids spend their whole lifetime in water, that they are easy to collect and do not need a quantitative sampling program to know whether conditions have changed (the occurrence or dominance of species with certain environmental claims is sufficiently informative) makes them helpful means in bioassays. In particular with regard to checking and controlling water quality in a defined area they might be very useful creatures to local (water) authority boards.

5. MICROGEOGRAPHIC RACES

Our study shows that differences between populations of the same gammarid species living at various localities are often considerable. The mean length, fecundity, and percentage of ovigerous females differs largely within one species [26]. There might even exist a clinal variation in these features [27].

[26] Goedmakers (1981): figs. 38, 39, 55 and 56.
[27] Goedmakers (1981): section 5.3.4.2.

Since environmental conditions are very much the same at different stations, especially in the upper and middle reaches of the Slack, we concluded that differences between populations must have a genetic and not only a phenotypic basis (Goedmakers, 1980b). The mean length, fecundity and percentage of ovigerous females could all have been influenced by the composition of a population, thereby resulting in only seemingly large differences between populations. But, in particular, the changing relation from station to station between fecundity and length of ovigerous females proved that a difference in composition of a population can not be the sole cause of different population characteristics.

These facts made us postulate the concept of a patchy distribution of gammarids in the river Slack, consisting of rather isolated populations. Because of the possible genetic basis of differences between the gammarid populations, we called them microgeographic races (Goedmakers, 1980b). They are an example of the interaction groups Den Boer (1979) distinguishes within a population living in a certain geographic area.

6. COMPETITION AND THE PRINCIPLE OF COMPETITIVE EXCLUSION

Before drawing conclusions from our results it is necessary to define what we mean, when using concepts like niche, competition and the principle of competitive exclusion. Different authors mean quite different things with the same words, which makes general conclusions difficult to compare. For a history of the principle of competitive exclusion, see Den Boer (1980).

We use the definition of a niche as given by Ayala (1970). In his opinion the concept "niche" encompasses all relationships between the organism and its environment. (This is a broader sense of the niche than that of Elton, 1927. He used the concept niche for the place of an animal in his biotic environment, his relations to food and enemies.) The impossibility of measuring all variables by which the environment can be defined, and the changing relationships depending on e.g. life stage of an animal, make this niche concept useless. Quantitative or qualitative statements about the niche of an individual or species can be

made only by referring to one (or more) specified component(s) of the ecological niche, as Ayala (1970) rightly points out.

We follow the reasoning of Birch (1957; 1979) who gives "competition" the following restricted meaning: competition occurs when a number of animals (of the same or of different species) utilize common resources, the supply of which is short; or if the resources are not in short supply, competition occurs when the animals seeking that resource nevertheless harm one another in the process. Although much used, it is no clear definition. Therefore it might be better to refer to the definition of Bakker (1961) with the same meaning: Competition is a manifestation of the struggle for existence in which two or more organisms of the same or of different species exert a disadvantageous influence upon each other because their more or less active demands exceed the immediate supply of their common resources. This means that in our opinion predation and parasitism do not constitute examples of competition, although they may have the same effect. Also natural selection and competition are different concepts. Natural selection can take place without competition. It is the result of a differential reproduction that can be caused by many factors, one being competition.

The principle of competitive exclusion means to some authors, that no two species can coexist when they occupy the same niche. This is a true but trivial statement, because in our definition of niche no two species, not even two individuals occupy the same niche. A more meaningful formulation of the competitive exclusion principle is: two species can not coexist if they share resources essential for the survival of the species; in other words if they compete for the same essential limited resource, usually food or a place to live (Ayala, 1970). If this is the only factor that regulates their population densities, the principle holds true. However, often the principle is used in a much broader (inaccurate) sense: competitors can not coexist permanently.

Our three gammarid species share the same essential resources, places to live. Most of the time they live not segregated over different habitats (e.g. station 1 is inhabited by *G. fossarum* and

G. p. pulex, without even the possibility of segregation to different microhabitats; the same holds true for station 6, where *G. fossarum* and *E. berilloni* live together unsegregated), although they may have preference for some kind of microhabitats. (From observations on feeding gammarids we expect no difference in the food they eat, but more research would be necessary to be sure that they share the same essential resource, food.)

The three species occupy different ecological niches when temperature fluctuations and other abiotic factors, like oxygen content of the water and conductivity, are taken into account. These ecological niches, however, show a large overlap: at station 1 *G. fossarum* and *G. p. pulex* coexist in equally large numbers; at stations 6, 7 and 8 both *G. fossarum* and *E. berilloni* thrive.

The animals harm each other in their search for a place to live. This is evident in our laboratory experiments, where gammarids kept together in a basin vigorously attack each other if not enough shelter is present. We observed these fights also in the field. The large number of damaged animals [28] found at station 6 is probable the result of a lack of hiding places at this station.

This means that some populations of the three species share the same ecological niche, while harming each other at those places for the same essential resource. Since they do not show an increased migration rate at those stations (migration rates at station 6 for instance are even exceptionally low), we feel justified to conclude that our gammarids show both intra- and interspecific competition.

Their relative abundance changes only when environmental conditions alter considerably: the comparatively high temperatures of 1974 enlarged the distribution area of *E. berilloni* and made *G. fossarum* decrease its range [29]. These results invalidate the principle of competitive exclusion

[28] Goedmakers (1981): section 5.3.5.2.
[29] The relative abundance of *E. berilloni* and *G. fossarum* could also have been changed by differences in reproductive success. We found no relation between population density and reproductive cycles (Goedmakers, 1981: section 5.5 and fig. 59). Therefore we concluded that the differences in reproductive success (see Goedmakers, 1981: section 5 page 40) for both species in the two consecutive sampling years could not explain the shifts in microgeographic distribution.

(s.l.): species are very well able to compete and coexist in nature; extinction of one or more species is only one of the outcomes of competition. Species that show some kind of self-regulation are perfectly able to coexist permanently, although competing (De Bruyn, 1980).

In our case abiotic factors restrict the distribution area of the competing gammarid species. Other gammarid species solve distributional problems in other ways. The replacement of indigenous species in the Netherlands by the gammarid *G. tigrinus* Sexton, 1939, is an example of a difference in reproductive success (Pinkster et al., 1977), while the estuarine gammarids in the river Slack avoid a potential competition (Pinkster & Broodbakker, 1980) by living segregated over different microhabitats.

As suggested above (see section 4) there might exist a clinal variation in some population characters. This would mean that our microgeographic races show different population characteristics combined with a gradual change in the environmental conditions provoked by natural selection. Even if this turns out to be true it would not contradict or materially affect our conclusion on the competitive exclusion principle.

Competition, as we said, is only one way natural selection is evidenced, but natural selection can act quite independently of competition. If our microgeographic races were to show the postulated clinal variation, this would be caused by abiotic and perhaps biotic (parasitation and predation) environmental factors and not by competition, the reason for this being that it did not change the feeding habits of our gammarids, nor did it give them a preference for certain microhabitats. A form of natural selection that increases for example fecundity of a certain microgeographic race at certain localities, might change its competitive force at those particular places. An increase of fecundity may mean a strategy to win the battle, but does not necessarily mean a final victory.

The special situation at station 9 needs some explication, although our lack of data does not enable us to provide ultimate proof for our hypothesis. The nearby springbrook, inhabited by *G. fossarum*, offers a reservoir of gammarids that can migrate immediately to a barren area. The low population density at station 9 in September 1973 (we did not succeed in collecting a kick-sample of one hundred animals), might indicate that before that time a catastrophe has expelled or killed all gammarids at this station. Conditions might have changed recently so that gammarids were recolonizing this locality. By consultation of neighbouring farmers a severe case of pollution seems the most plausible explanation.

The colonization by *G. fossarum* from the springbrook could take place very rapidly since migration rates in springbrooks are large during the entire year, compared with those in the main stream. Conditions at station 9 fall well within the ecological niche (temperature, oxygen content, conductivity) of *G. fossarum. E. berilloni* was not able to colonize station 9 so fast. Migration rates of this species are smaller and there was no nearby population to replenish the population at station 9. In the long run *E. berilloni* invaded this station; until March 1978 the population consisted for 50% of *E. berilloni*; in the warm summer of 1978 practically 100% of the population consisted of *E. berilloni*, while the temperature conditions chased *G. fossarum* away (Steenbergen et al., unpubl.).

Our former conclusion that gammarids, competing for the same space, can live together, fits perfectly the reconstruction of events at station 9. At first, places to live were not limited. Every animal capable of thriving under the conditions at station 9 could colonize it. The colonization chances for *G. fossarum* were greater in the beginning; then *E. berilloni* followed. Only a change in environmental conditions drove *G. fossarum* away, after both species had inhabited the locality in large densities and had been engaged in competition.

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