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The Colonization Cycle of Freshwater Insects

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Summary. This paper summarizes the recent research on problems of the so-called colonization cycle as one aspect of the migration and flight behaviour of freshwater insects. New results are presented and the applied methods described and discussed. In general the research on this phenomenon shows that the colonization cycle can not only be seen as a type of compensatory flight behaviour, but also as an expression of the winter survival strategy of water insects in high mountainous areas. It opens up the possibility of exploiting ecologically different biotopes such as living in coastal streams and oligohaline brackish water estuaries.

1 Introduction

In 1954, I proposed the hypothesis that adult aquatic insects compensate for the gradual downstream movements of the larvae by flying upstream. At that time, I was not aware of Mottram's paper (1932) in which he had previously observed and described this phenomenon. I am grateful to Dr. J.M. Elliott (Freshwater Laboratory, Windermere) for having called my attention to this paper in November 1980 when he wrote: "I discovered this paper in one of our older, and often forgotten, boxes in the library."

There have been contradictory opinions about the water insect's colonization cycles. Einsele (1960) rejected the hypothesis: he wrote that at first sight, it is a very fascinating picture, but does not correspond at all with the facts (in German). Ruettimann (1980) believes that the nymphs themselves compensate for their downstream drift by upstream migration and that these nymphal migrations make an adult upstream flight superfluous. Neither author investigated the flight behaviour of the adults, however, Schwoerbel (1969) judged that no consistent colonization cycle had been proven, which was correct at that time. During the last decade, several ecologists have attempted to corroborate the hypothesis with new and quantitatively comparable methods for determining the flight behaviour and flight direction of adult freshwater insects.

A number of quantitative investigations were carried out by Madsen et al. (1972, 1973, 1976, 1977) in Danish running waters. All these investigations were carried out by the same method using a layer of sticky adhesive substance on transparent polyethylene sheets (Madsen et al. 1973). The sheets were set up transversely over the stream, using a wooden frame or wires, with one sticky side facing upstream and the other downstream.

Another method of analysing the flight direction of freshwater insects above the water surface is to use the window trap, as described by Chapman and Kinghorn (1955). This method was used for the analysis of colonization cycles by Müller (1973) in the woodland river Kaltisjokk, near the Arctic Circle in Swedish Lapland, and by Lingdell and Müller (1979) and Müller and Mendl (1979, 1980) in coastal areas of the Gulf of Bothnia.

In a comparative study, we demonstrated (Mendl and Müller 1979) that the type of trap developed by Malaise (1937) is the most suitable for studies on the flight behaviour of freshwater insects. In an excellent field study, Roos (1957) was the first to describe the application of this type of trap in his investigation of the river Ammerån in northern Sweden. The results presented here are based on catches in Malaise traps of the bilateral type, which made it possible to determine the flight direction of adults above running water.

2 The Colonization Cycle

Many investigators have observed that freshwater adult insects, especially mayflies, show an upstream-directed flight behaviour (Schoenemund 1930; Verrier 1956; Macan 1957; Russev 1959, 1972, 1973; Pearson and Kramer 1972; Göthberg 1972). The first adequate method of measurement was carried out by Roos (1957), who was able to demonstrate that the adults of *Cheumatopsyche lepida* and *Rhyacophila nubila* had a flight behaviour directed against the flow of the river Ammerån. All these observations can be defined as compensation flights above running waters.

Recent investigations have shown that directed flight movements can be seen not only as compensation flights above running waters, but that they can also occur between different biotopes (Mendl and Müller 1978; Müller and Mendl 1979, 1980; Lingdell and Müller, 1979, 1981; Engblom et al. 1981; Dahlberg et al. 1981; Nilsson 1981) in order to utilize optimal conditions for eggs and young nymphal stages. The possible types of colonization cycles are discussed in the present paper.

The localities of the present investigations are shown in Fig. 1: the northern mountain area (Abisko), the Swedish woodland region (Messaure), the coastal areas of the Gulf of Bothnia (Ängerån) and the lower reaches of the river Dalälven. Figure 1 also shows the geographical positions of the investigation sites of Roos (1957: Ammerån) and of Madsen et al. (1973) on streams in Jutland.

2.1 The Colonization Cycle as Compensatory Flight Behaviour in Running Waters

Table 1 shows the results that have been reported for different methods such as window traps, adhesive transparent plastic sheets and Malaise traps.

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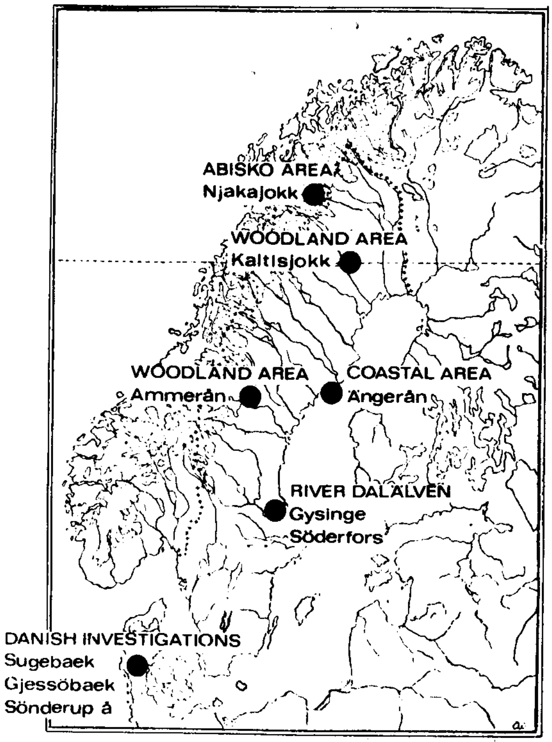

Fig. 1. Investigation localities in several biotopes in Scandinavia

All these investigations, concentrated in Jutland (Denmark) and Sweden, clearly show an upstream-directed flight of the insect above the water surface. These results may be complemented by recent investigations carried out in the river Dalälven (60°15′N, 16°40′E) at the gysinge and Söderfors rapids.

A Malaise trap was placed in the lower half of each rapid. At Gysinge, the trap was at work from 5 May to 30 June and at Söderfors from 5 May to 15 October 1980; the traps were emptied at intervals of 10–14 days.

The dominating insect groups in both rapids were caddisflies, non-biting midges and blackflies, which are mainly supported by the rich food resources from the lake-like parts of the river Dalälven upstream from the rapids. These conditions support an abundance of net-spinning caddisflies and other passive feeders.

This fact is also demonstrated by the high number of caddisfly species *Cheumatopsyche lepida* in the Malaise trap at Söderfors (Fig. 2). Of a total catch of 11,507 individuals, 8,914 (77.5%) were captured in the downstream side of the trap. Of all the mayflies captured at Gysinge rapids, 90% were *Leptophlebia marginata* and *L. vespertina* (Fig. 3). The upstream-directed flight behaviour is clear even in these insects.

In the Söderfors rapids, *Baetis rhodani* is the dominant mayfly species (Fig. 4). This species also showed flight movements directed against the direction of the water current. A similar flight behaviour was shown by the adults of the stonefly *Nemoura cinerea* in the Gysinge rapids (Fig. 5).

Table 1. Survey of measurements of upstream and downstream flight movements of freshwater insects by means of window traps (A), transparent adhesive plastic sheets (B) and Malaise traps (C)

Species	River/stream	Country	Method	Author
Ephemeroptera				
Baetis rhodani Pict.	Sugebaek	Denmark	B	Madsen et al. (1973)
B. vernus L.	Sugebaek	Denmark	B	Madesn et al. (1973)
Ephemerella ignita Poda	Sugebaek	Denmark	B	Madsen et al. (1973)
Caenis rivolorum Etn.	Sugebaek	Denmark	B	Madsen et al. (1973)
C. rivolorum Etn.	Sönderup Å	Denmark	B	Madsen et al. (1977)
Ephemerella ignita Poda	Sönderup Å	Denmark	B	Madsen et al. (1977)
Baetis spp.	Sönderup Å	Denmark	B	Madsen et al. (1977)
Leptophlebia marginata L.	Ängerån	Sweden	A–C	Lingdell and Müller (1979)
L. vespertina L.	Ängerån	Sweden	A–C	Engblom et al. (1981)
B. subalpinus Bgtss.	Ängerån	Sweden	A–C	Engblom et al. (1981)
Plecoptera				
Brachyptera risi Klap.	Sugebaek	Denmark	B	Madsen et al. (1973)
B. risi Klap.	Gjessöbaek	Denmark	B	Madsen and Butz (1976)
Nemoura cinerea Retz.	Sugebaek	Denmark	B	Madsen et al. (1973)
N. flexuosa Aub.	Sugebaek	Denmark	B	Madsen et al. (1973)
Amphinemura borealis Mort.	Ängerån	Sweden	A	Mendl and Müller (1979)
Leuctra digitata Kemp.	Ängerån	Sweden	A	Mendl and Müller (1979)
Nemoura cinerea Retz.	Ängerån	Sweden	A	Mendl and Müller (1979)
A. borealis Mort.	Ängerån	Sweden	C	Mendl and Müller (1979)
N. avicularis Mort.	Ängerån	Sweden	C	Dahlberg et al. (1981)
N. cinerea Retz.	Ängerån	Sweden	C	Dahlberg et al. (1981)
Protonemura meyeri Pict.	Ängerån	Sweden	C	Dahlberg et al. (1981)
Isoperla grammatica Poda	Ängerån	Sweden	C	Dahlberg et al. (1981)
Trichoptera				
Cheumatopsyche lepida Pict.	Ammerån	Sweden	C	Roos (1957)
Rhyacophila nubila Zett.	Ammerån	Sweden	C	Roos (1957)
Philopotamus montanus Don.	Kaltisjokk	Sweden	A	Müller (1973)

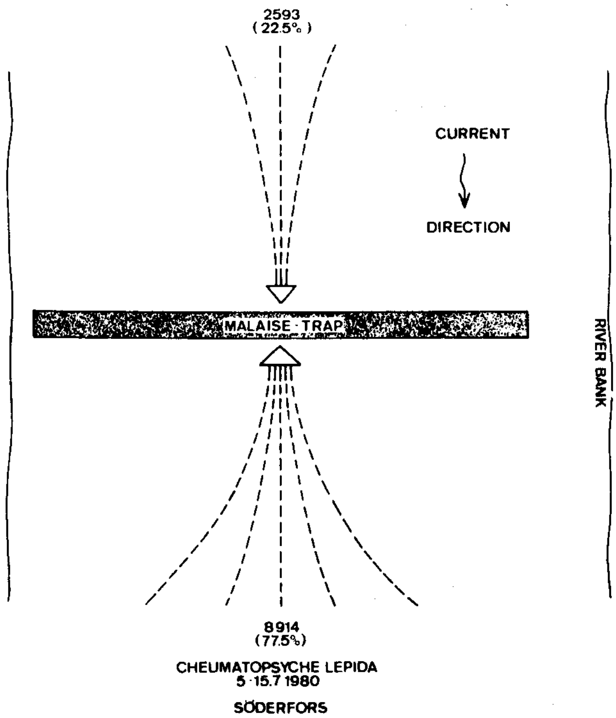

Fig. 2. Upstream and downstream flight movements of the caddisfly *Cheumatopsyche lepida* in the Söderfors rapids in the river Dalälven in July 1980

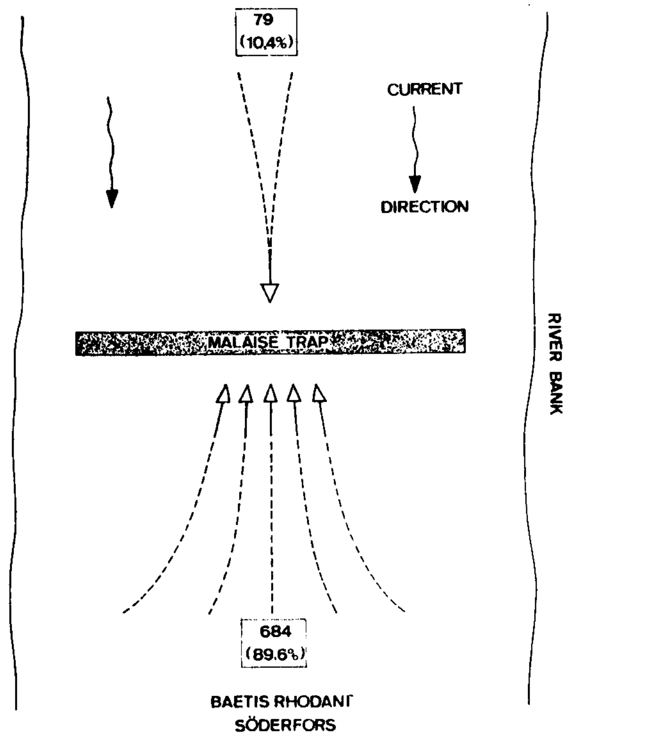

Fig. 4. Upstream and downstream flight movements of the mayfly *Baetis rhodani* in the Söderfors rapids in the river Dalälven in summer 1980

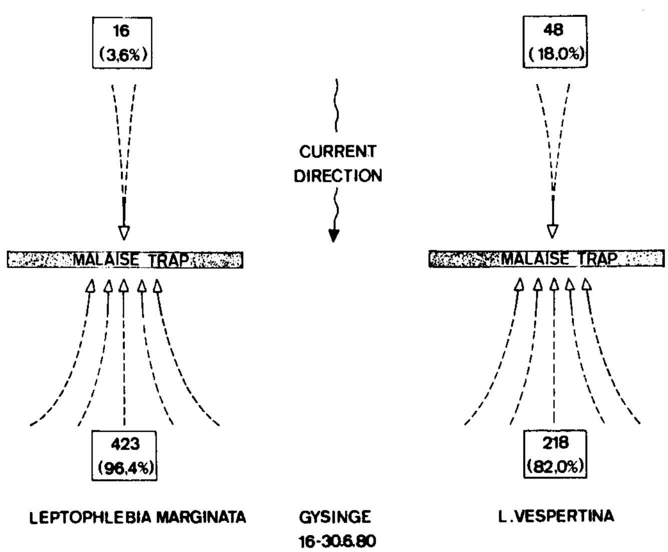

Fig. 3. Upstream and downstream flight movements of the mayfly species *Leptophlebia marginata* and *L. vespertina* in the Gysinge rapids in the river Dalälven in June 1980

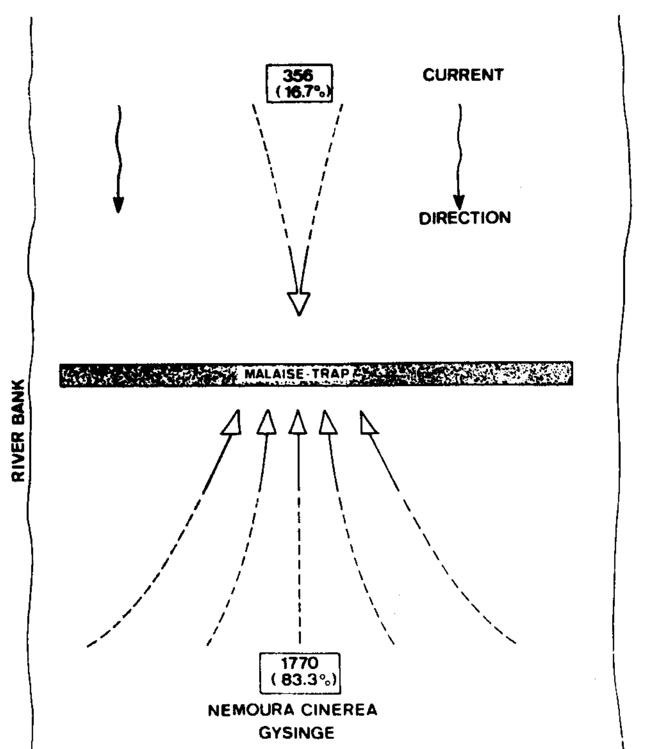

Fig. 5. Upstream and downstream flight movements of the stonefly *Nemoura cinerea* in the Gysinge rapids in the river Dalälven in June 1980

2.2 Flight Movements Between Different Biotopes

2.2.1 Observations in the Mountain Region of Norther Sweden

In a recent study (Mendl and Müller 1978) we described a special type of colonization cycle that occurs between a small mountain lake and the stream below this lake. The lake's outflow is bottom-frozen from November to May and the nymphs go through their first stages in the lake. After the ice breaks up, large numbers of nymphs drift into the stream below and are distributed in running water biotopes. We postulate that in order to oviposit the adults fly back to the lake, which offers stable hydrographical conditions for surviving the winter. We also believe that this type of colonization cycle reflects the winter survival strategy of the dominant stonefly, *Amphinemura standfussi*. Figure 6 shows a schematic survey of this type of colonization cycle.

In the area where this investigation was carried out, we found many small springs that had a rich abundance of stonefly nymphs in early summer. From 19 May to 23 September 1976 , we filtered the total water quantity from one of these springs. The waterflow of this spring empties into the small stream Njakajokk and the distance between the spring and Njakajokk is about 80 m. This part of the spring outflow is bottom-frozen from December to May and communication between the biotopes is impossible in the winter period. The spring can also be seen as a refuge for the nymphs in winter. After the thaw, the nymphs that have spent the winter in the spring are distributed by downstream drift to suitable biotopes in the stream. Table 2 shows the results of drift measurements for the year 1976.

It is remarkable that as many as 2,404 stonefly nymphs were captured in such a small area of water. From the spring to the trap we measured 2.2 m^2, which is equal to 1,093 nymphs/m^2.

In both the biotopes described, the animals use perennial waters such as the lake or the spring for their larval development. Therefore, we may consider this type of colonization cycle as a survival mechanism for the animals under these extreme climatic conditions.

2.2.2 The Colonization Cycle Between a Coastal Stream and Its Estuary

In the previous section we reported that under the extreme environmental conditions to which the freshwater insects are exposed in the high mountain area, the adults were able to lay their eggs in secure conditions. A similar situation was found in coastal areas of the Gulf of Bothnia. The investigations were made during 1977–1980 in the mouth of the small coastal stream Ängerån and its estuary. Figure 7 shows the transition from the fresh water to the estuary, with successively increasing salinity. In investigations over a whole year we observed that many freshwater insect nymphs drift from the Ängerån into the estuary and adapt themselves to the prevailing estuarine oligohaline conditions (Lingdell and Müller 1979; Müller 1980; Müller and Mendl 1980; Danielsson and Müller 1981). Table 3 shows the number of drifting insects at the mouth of the Ängerån, based on 234 observation days in 1978–1979.

Many of these insect species are not able to develop in the brackish water as eggs or nymphs, e.g. the mayflies *Leptophlebia vespertina*, *L. marginata*, *Heptagenia fuscogrisea*, *Baetis subalpinus*, and the stoneflies *Taeniopteryx nebulosa*, *Amphinemura borealis*, *Protonemura meyeri*, *Isoperla grammatica* and *Leuctra digitata*. Our hypothesis was that the adults fly back to the freshwater stream to oviposit. This thesis was confirmed by extensive control of the flight by means of a Malaisetrap set up across the river mouth (Engblom et al. 1981; Dahlberg et al. 1981; Nilsson 1981).

Table 2. Stonefly nymphs drifting from a spring in the Abisko area in the summer of 1976 (19 May–23 September)

Species	May	June	July	August	September	Total
Nemurella picteti	5	1,280	72	–	–	1,357
Nemoura sahlbergi	–	212	186	2	–	400
Amphinemura standfussi	–	42	243	72	–	357
Nemoura cinerea	–	24	93	34	–	151
Diura nanseni	–	33	96	–	–	102
Isoperla obscura	–	17	20	–	–	37
Total catches	5	1,608	710	108	–	2,404

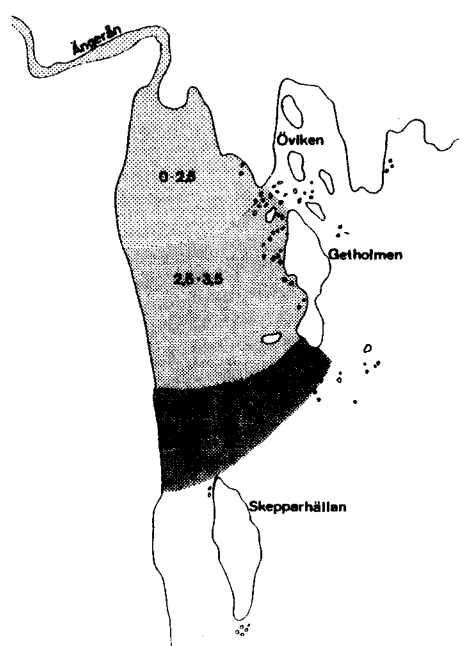

Fig. 7. Yearly mean of salinity in the Ängerån estuary (according to Müller-Haeckel and Sjöberg 1981)

Table 3. The outdrift of invertebrate nymphs at the mouth of the river Ängerån (200 m^3 filtered river water/day)

Group	Number	%
Ephemeroptera	20,854	30.5
Plecoptera	4,747	6.9
Trichoptera	3,398	5.0
Chironomidae	9,102	13.3
Simuloidea	28,533	41.8
Other species	1,760	2.5
Total	68,394	

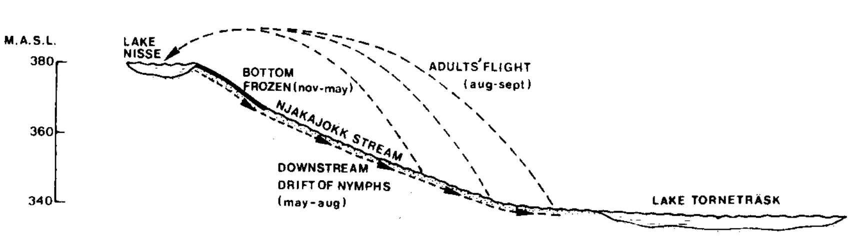

Fig. 6. Schematic view of the colonization cycle in the Njakajokk stream system, near Abisko, Swedish Lapland

Table 4. Numbers and percentages of Malaise-trapped insects flying upstream and downstream at the river mouth (May–October 1980)

Species	Upstream		Downstream	
	Number	%	Number	%
Ephemeroptera				
Leptophlebia marginata	29	90.6	3	9.4
L. vespertina	182	98.4	3	1.6
Heptagenia fuscogrisea	52	94.5	3	5.5
Baetis subalpinus	3,775	96.0	159	4.0
Plecoptera				
Amphinemura borealis	11,319	79.2	2,077	20.8
Leuctra digitata	1.659	68.7	755	31.3
Isoperla grammatica	313	76.5	96	23.5
Coleoptera				
Galerucella nymphaea	320	69.0	143	31.0

These investigations proved that there is a clear tendency for the adults to fly from the estuary to the coastal stream, supposedly to oviposit in the freshwater areas (Table 4).

The extensive investigations carried out at the mouth of the Ängerån, in the eastuary and in the aerial phase of the insects also made it possible to answer Schwoerbel's doubts about 'closed' colonization cycles. Table 3 shows the outward drift of nymphs at the mouth of the Ängerån. In a paper by Danielsson and Müller (1981), we described the zonation of invertebrates in the estuary, especially the distribution of limnobionts, and Table 4 demonstrates the flying behaviour of the imagos to the coastal stream. Table 5 lists the freshwater insects, which are shown in the present investigations to have a 'closed' colonization cycle.

3 Discussion

Since the first interpretation of the phenomenon of a colonization cycle (Müller 1954), the development of new methods and investigations in different geographical areas has extended our knowledge of the migration behaviour of freshwater insects. To quantify the adults, flight behaviour three methods have been used. A comparison of window traps and Malaise traps shows clear differences, and the high number of stoneflies captured in the Malaise trap strikingly demonstrates its effectiveness (Mendl and Müller 1979; Dahlberg et al. 1981). When these methods are compared with the use of adhesive plastic sheets, the latter method (Madsen et al. 1973) captures a high number of insects, but our opinion is that preparation, conservation and determination of the captured insects are more difficult than with the other methods.

In particular, the investigations of Madsen (1977) give convincing evidence for compensation flight in running waters of many freshwater insects. The results from the river Dalälven confirm the investigations of Madsen and are in accordance with the earlier theoretical interpretation of Müller (1954).

An interesting investigation has been carried out by Lehmann (1970) who analysed the flight behaviour of the caddisfly *Philopotamus montanus*. These observations were made over a period of ten days in northern Sweden in the woodland stream of Kaltisjokk near the Arctic Circle.

At the mouth of the stream, there were about one-third the number of females found in the upper reaches. In the lower part most of the females were immature, whereas most of the females in the upper reaches had laid their eggs. From this distribution of immature to mature (or females after oviposition) it was concluded that the females transported their eggs in a direction against the current of the running water. This is in accordance with the investigations of Roos (1957) and of Bird and Hynes (1981).

In a recent work Bird and Hynes (1981), using sticky traps placed across a stream in southern Ontario, found that the mayfly *Baetis intercalaris* and the caddisfly *Lyphe diversa* flew upstream in accordance with the concept of the colonization cycle. They also found that other species of caddisflies flew more randomly along the stream. It is interesting that Bird and Hynes only found females in the upstream flying phase.

Investigations over the last few years demonstrate that the flight movements of freshwater insects not only occur as compensation flight above running waters, but also as an aspect of wintersurvival strategies, as in the case of the investigations in the mountain area of northern Sweden, or they allow the exploitation of different biotopes, which we demonstrated in coastal areas of the Gulf of Bothnia.

Figure 8 shows a schematic system of the flying behaviour

Table 5. Closed colonization cycles between the coastal stream Ängerån and its estuary for some mayflies and stoneflies. A = Observed and measured in the drift at the river mouth, B = Observed and measured by means of bottom samples and colonization boxes and C = Measurement of adults by means of a Malaise trap at the mouth

Species	A	B	C	Authors
Ephemeroptera				
Leptophlebia marginata	+	+	+	Lingdell and Müller (1979, 1981); Engblom et al. (1981)
Leptophlebia vespertina	+	+	+	Lingdell and Müller (1979, 1981); Engblom et al. (1981)
Heptagenia fuscogrisea	+	+	+	Lingdell and Müller (1979, 1981); Engblom et al. (1981)
Baetis subalpinus	+	+	+	Lingdell and Müller (1979, 1981); Engblom et al. (1981)
Cloeon simile	+	+	+	Lingdell and Müller (1979, 1981); Engblom et al. (1981)
Plecoptera				
Amphinemura borealis	+	+	+	Müller and Mendl (1979); Mendl and Müller (1979)
Nemoura avicularis	+	+	+	Dahlberg et al. (1981); Mendl and Müller (1981)
Nemoura cinerea	+	+	+	Dahlberg et al. (1981); Mendl and Müller (1981)
Leuctra digitata	+	+	+	Müller and Mendl (1979, 1980); Dahlberg et al. (1981)
Protonemura meyeri	+	+	+	Dahlberg et al. (1981)
Isoperla grammatica	+	+	+	Dahlberg et al. (1981)

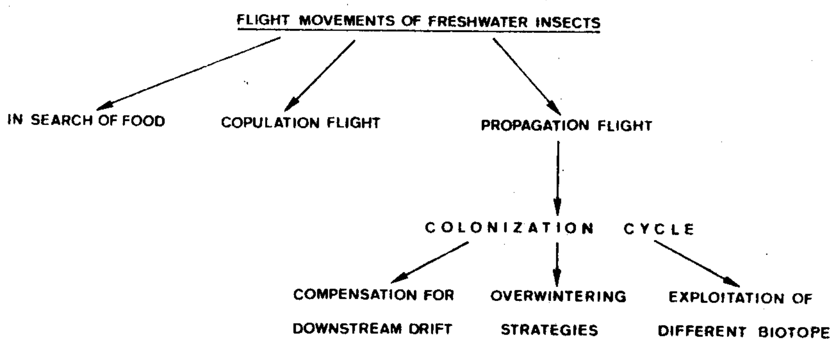

Fig. 8. Interpretation of flight movements of freshwater insects

of freshwater insects, in which the colonization cycle occupies a central place in the insects' flight behaviour. Future research is aimed at the elucidation of the orientation mechanisms that make it possible for the females to find suitable localities for oviposition.

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