THE ECOLOGY OF MORECAMBE BAY

IV. INVERTEBRATE DRIFT INTO AND FROM THE RIVER LEVEN

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Invertebrate drift can originate from both lenitic and lotic systems. Drift material from lakes is chiefly plankton which is washed out via outflows (Woltereck 1908; Chandler 1937). This planktonic drift food often supports a dense community of filter and vortex feeders in the outflow biozone (Knöpp 1952; Muller 1956; Illies 1956). Invertebrate drift is also a normal feature of lotic systems and is chiefly aquatic in origin (see references in Elliott 1967; Ulfstrand 1968; Bishop & Hynes 1969; Waters 1969). Pools and lakes act as catching basins for drifting invertebrates, and many of the animals soon succumb to silt deposition, wave action in lakes, and unsuitable temperature (Needham 1930; Beauchamp 1932; Dendy 1944).

The overall purpose of the present investigation was to assess the importance of invertebrate drift in the River Leven, one of the large rivers flowing into Morecambe Bay. This short investigation is part of the Feasibility Study for the proposed Morecambe Bay Barrage. If the barrage is built, the present Leven estuary and part of the bay will become freshwater. As drifting invertebrates are potential colonizers of these freshwater areas, it is important to know the qualitative and quantitative composition of the invertebrate drift in the river. It seemed necessary to sample the invertebrate drift from: (a) Windermere into the River Leven and (b) the Leven into the estuary.

SAMPLING STATIONS AND METHODS

The River Leven is the outflow of Windermere (Fig. 1) and flows south-west for about 5·5 km before it is brackish (upper tidal limit is near Low Wood Bridge). Although the overall gradient from source to mouth is not very steep (fall $<1\%$), there are several stony sections with a steep gradient and a fairly fast current.

Drift samples were taken at the lake outflow in June and July, and at Low Wood Bridge in May, June and July 1969. Physical conditions at the two stations are given in Table 1. Surface nets (Elliott 1967) were used at both stations. The number of nets and the sampling times were different in each month. This procedure ensured that samples were taken at different points across the river and at different times of the day (the number of nets per month and the sampling periods are given in Table 1). Sampling times were also arranged so that comparisons could be made between day and night catches. The most extensive sampling was at the lake outflow in June (five nets across outflow and each net emptied three times in 16·5 h), and at Low Wood Bridge in May (three nets across river and each net emptied four times in 14 h). All samples were taken during periods of low discharge (average total discharge over a year = 56 800 m^3/h). In each month, the volume of water passing through the drift samplers was about 1% or less of the total discharge at the sampling point (Table 1).

INVERTEBRATE DRIFT FROM THE LAKE

Copepoda and Cladocera were predominant in the drift samples at the lake outflow (Table 2). Other taxa were poorly represented in the samples and all, except larvae of *Chaoborus* sp., were non-planktonic (Table 2b). As Copepoda and Cladocera were so numerous in the samples, total numbers were estimated indirectly. Sub-samples were removed from the catches and over 200 animals were counted in each sub-sample. These counts were used to determine the percentage composition of the total catch for each net. In June, *Cyclops* spp. (including *C. leuckarti* (Claus) and *C. strenuus abyssorum* Sars) and *Daphnia hyalina* were jointly predominant in the catch near the bank (net 1), but *D. hyalina* was clearly predominant in the other catches across the outflow (nets 2–5). In July, *Cyclops* spp. contributed the largest percentage to the total catch both near the

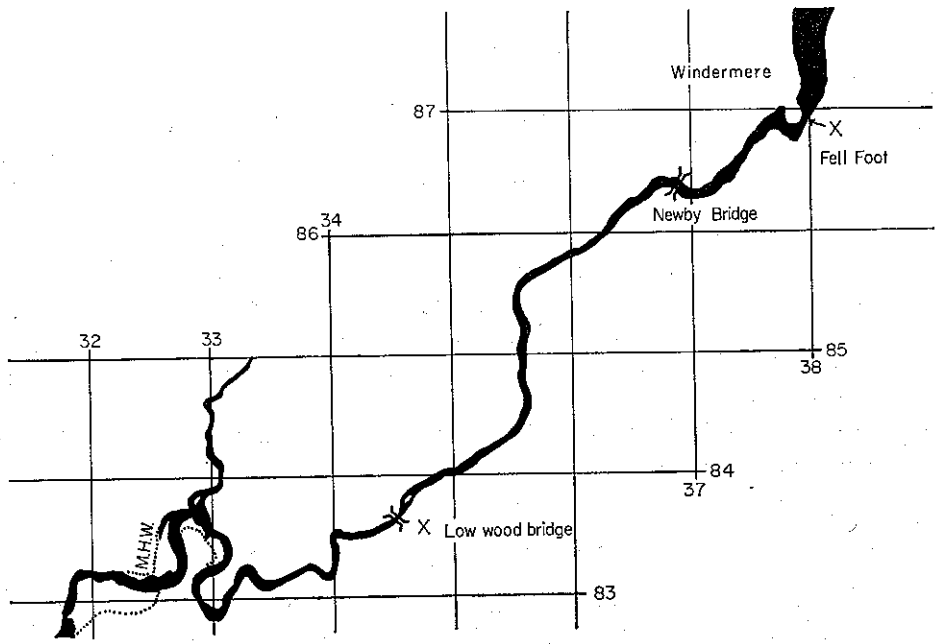

FIG. 1. Map of River Leven showing position of sampling stations (×).

bank (net 1) and near the middle of the outflow (net 5). The total volume of Copepoda and Cladocera in each drift sample increased markedly with increasing distance from the bank (i.e. from net 1 to net 5) in June but not in July (Table 2a). This discrepancy between months was possibly due to the lower discharge at the outflow in July (see Table 1).

It was assumed that 1 ml of Copepoda and Cladocera contained about 1000 animals (based on equivalents given in Ward 1896, and Ricker 1937), and that the drift samples were representative of the total drift at the lake outflow. Therefore, it was possible to estimate total numbers of plankton drifting out of the lake (Table 3a). The estimated day total was greater than the night total for all species except *Chaoborus* sp. in June. A comparison of total numbers per hour for day and night revealed that the drift rate was greatest at night for *Chaoborus* sp., about the same in day and night for *Bosmina coregoni*, and greatest during the day for all other species (Table 3b).

Although very large numbers were drifting out of the lake, no planktonic species were

Table 1. *Conditions at the sampling station*

	Lake outflow			Low Wood Bridge		
Date, 1969	5–6 June	22 July		27–28 May	26–27 June	15–16 July
Time (BST)	15.30–08.00	15.00–21.00		21.30–11.30	19.00–01.00	19.00–07.00
Duration (h)	16·5	6		14	6	12
Water level (height above O.D., m)	39·26	39·17		3·86	3·94–3·99 (tidal variations)	3·67–4·30
Total discharge (m^3/h)	31583	18440		23636	32703	11003
Water velocity near mouth of net (m/s)						
Net 1 (near bank)	0·18	0·18	Net 1 (north)	0·83	0·88	–
Net 2	0·18	–	Net 2 (centre)	1·10	–	0·52
Net 3	0·27	–	Net 3 (south)	1·10	1·20	0·81
Net 4	0·30	–				
Net 5 (midstream)	0·28	0·13				
Volume of water sampled by all nets (m^3/h)	305	78·2		256·3	176	112·5
% of total discharge sampled	0·97	0·43		1·09	0·54	1·02
Water temperature (° C)	12·1–14·6	16·1–16·2		10·6–12·6	15·5–16·3	17·9–20·5

found in the drift samples at Low Wood Bridge. Therefore, under discharge conditions at the time of sampling, most of the plankton drifting out of the lake must have either died, been eaten, been filtered by macrophytes, or remained in pools. This is probably not the case during periods of high discharge. A surface net was used at Low Wood Bridge for about 30 min during a period of high discharge in May. The catch included several specimens of *Diaptomus gracilis*, *Cyclops* spp., *Daphnia hyalina* and *Bosmina coregoni*. A plankton net was also used at Low Wood Bridge in June, and caught nauplii and viable eggs of Copepoda. Therefore, some planktonic species do survive the journey down the River Leven and would rapidly colonize a freshwater reservoir at the mouth of the Leven estuary.

Table 2. *Invertebrate drift at lake outflow*

(a) *Copepoda and Cladocera: % composition of total catch*

	5–6 June					22 July	
	Net 1	Net 2	Net 3	Net 4	Net 5	Net 1	Net 5
Copepoda							
Diaptomus gracilis Sars	2·3	6·0	6·4	12·4	9·6	10·0	4·3
Cyclops spp.	45·1	12·4	7·4	6·4	4·4	45·4	50·8
Cladocera							
Daphnia hyalina Sars	49·9	78·2	80·8	74·4	80·8	36·2	24·5
Bosmina coregoni (Baird)	2·7	3·4	5·3	6·5	5·0		
Sida crystallina (Müller)			0·1	0·3	0·2		
Leptodora kindti (Focke)						6·9	18·2
Bythotrephes longimanus Leydig						1·5	2·2
Total volume of Copepoda and Cladocera (ml)	132	355	1105	2405	3840	45	35
Volume of water through net (m^3/h)	45·4	45·4	68	75·6	70·6	45·4	32·8

(b) *Total catch of other taxa*

	5–6 June				
	Net 1	Net 2	Net 3	Net 4	Net 5
Insecta					
Chaoborus spp.			1	13	1
Limnephilidae spp.		3	1	1	1
Others					
Gammarus pulex L.	1	1	2	4	
Crangonyx pseudogracilis Bousf.	2				
Asellus aquaticus L.				1	
Glossiphonia complanata (L.)			1		
Limnaea peregra (Müller)			1		

Several workers have sampled invertebrate drift at a lake outflow and have found that the quantity of lake plankton rapidly decreases with increasing distance from the outflow. This reduction in drifting plankton is higher when aquatic macrophytes are present below the outflow (Chandler 1937; Ruttner 1956; Beach 1960) and some taxa are eliminated more rapidly than others (Reif 1939; Ruttner 1956). Lake plankton entering the Huron River disappeared almost completely at about 8 km from the outflow in some months, but decreased only 40% over the same distance in other months (Chandler 1937). The total plankton at the station 8 km from the outflow varied from 12/l in July to 16 896/l in November. The influence of lake plankton in Swedish rivers was still significant at 30 km from the lake outflow in a large river with a discharge of about 720 000 m^3/h (Müller 1956), but was insignificant at about 200 m from the outflow in a small stream

with a discharge between 1440–2880 m^3/h (Illies 1956). As the Leven is a short river (5·5 km) with a relatively high discharge (average for year = 56 800 m^3/h), a large quantity of lake plankton is probably swept down the whole length of the river during periods of high discharge.

INVERTEBRATE DRIFT FROM THE RIVER

Table 4(a) lists all species taken in the drift samples at Low Wood Bridge. The differences between the monthly catches probably reflect differences in the benthos, but no definite conclusions can be drawn in the absence of bottom samples. It must be emphasized that the samples were only taken over three months, and therefore other species are probably

Table 3.

(a) *Estimates of total numbers drifting out of lake*

	5–6 June			22 July	
	Day 17 h	Night 7 h	Total 24 h	Total 24 h	
Copepoda					
Diaptomus gracilis	9980	2303	12283	500	All ×10⁴
Cyclops spp.	5500	1905	7405	3350	
Cladocera					
Daphnia hyalina	84730	16160	100890	2560	
Bosmina coregoni	4000	1868	5868		
Sida crystallina	277	23	300		
Leptodora kindti				880	
Bythotrephes longimanus				133	
Insecta					
Chaoborus spp.	184	1442	1626		×1

(b) *Estimates of total numbers drifting per h, 5–6 June*

	Day	Night	
Copepoda			
Diaptomus gracilis	587	329	All ×10⁴
Cyclops spp.	323	272	
Cladocera			
Daphnia hyalina	4984	2309	
Bosmina coregoni	235	267	
Sida crystallina	16	3	
Insecta			
Chaoborus spp.	11	206	×1

predominant in the drift during other months. One notable absentee was *Gammarus pulex*. This species occurs in the River Leven and is usually a major component of invertebrate drift. Its absence from the drift samples at Low Wood Bridge suggests that it is also absent from the stretch of river immediately upstream from Low Wood Bridge. *Gammarus zaddachi* appears to be abundant above and below Low Wood Bridge, and was taken in the drift samples for June and July. This species occurs in brackish water, but can penetrate some distance in fresh water. It would be interesting to know where the populations of *Gammarus pulex* and *G. zaddachi* meet in the River Leven. Dennert *et al.* (1969) studied the movements of *G. zaddachi* in a French river. They found a

Table 4.

(a) *Invertebrate drift at Low Wood Bridge: total numbers and percentage composition in each month*

	May (27–28)		June (26–27)		July (15–16)	
	Nos.	%	Nos.	%	Nos.	%
Plecoptera						
Amphinemura sulcicollis (Stephens)	186	38·6			1	0·06
Nemoura cinerea (Retzius)	1	0·2				
Leuctra inermis Kempny	2	0·4				
Leuctra geniculata Stephens			6	0·6	5	0·32
Perlodes microcephala (Pictet)	2	0·4				
Isoperla grammatica (Poda)	5		2	0·2		
Chloroperla torrentium (Pictet)	2	0·4	3	0·3		
Total Plecoptera	198	41·1	11	1·1	6	0·38
Ephemeroptera						
Ephemerella ignita (Poda)	1	0·2	324	32·0	649	41·4
Caenis rivulorum Eaton	23	4·8	13	1·3	5	0·32
Baetis rhodani (Pictet)	143	30	488	48·3	315	20·1
Heptagenia sulphurea (Müller)			4	0·4	35	2·2
Total Ephemeroptera	167	35	829	82	1004	66·9
Hemiptera						
Sigara dorsalis (Leach)			1	0·1		
Trichoptera						
Rhyacophila dorsalis (Curtis)			1	0·1	107	6·8
Agapetus fuscipes Curtis	1	0·2				
Psychomyia pusilla (Fabr.)	2	0·4	3	0·3		
Hydropsyche instabilis (Curtis)	30	6·2	11	1·1	351	22·4
Total Trichoptera	33	7·0	15	1·5	458	29·2
Coleoptera						
Elmis aenea (P. Müller)—larvae	79	16·4	3	0·3	3	0·19
Elmis aenea (P. Müller)—adults	2	0·4	1	0·1	3	0·19
Oulimnius tuberculatus (Müller)—larvae					2	0·13
Oulimnius tuberculatus (Müller)—adults					2	0·13
Dytiscid larvae			3	0·3		
Palpicorn larvae			2	0·2		
Total Coleoptera	81	16·8	9	0·9	10	0·64
Diptera						
Simulium spp.	1	0·2				
Tipulidae	1	0·2				
Total Diptera	2	0·4				
Non-Insecta						
Gammarus zaddachi Sext.			135	13·4	88	5·6
Asellus aquaticus L.			10	1·0	1	0·06
Erpobdella octoculata (L.)			1	0·1		
Limnaea truncatula (Müller)	1	0·2				
Limnaea peregra (Müller)					1	0·06
Total Non-Insecta	1	0·2	146	14·5	90	5·7
GRAND TOTAL (all groups)	482	100	1011	100	1568	100

(b) *Total catch of fish at Low Wood Bridge*

Lampetra planeri (Bloch) <0·8 cm			16	15·7		
Anguilla anguilla (L.) >15 cm	5	27·8				
Anguilla anguilla (L.) <7·5 cm	11	61·1	86	84·3	23	79·3
Pleuronectes flesus (L.) <3·4 cm					6	20·7
Salmo salar (L.) 2·5 cm	2	11·1				
Total fish	18	100	102	100	29	100

downstream movement at night in all months of the year, and a mass upstream movement in autumn. The repopulation of the up-river reaches in autumn was performed by juveniles assisted by the current reversal during equinoxal spring-tides.

Some fish were also taken in the drift samples and were all caught at night (see Table 4b). A large number of emerging insects were also taken in the drift samples and these are recorded separately (Table 5).

A comparison of day and night catches clearly shows that the drift rate of most species was greatest at night (Table 6). Emergence also occurred chiefly at night in the Plecoptera and Trichoptera, but not in the Ephemeroptera and Chironomidae (Table 7).

Table 5. *Emerging insects taken in the drift samples at Low Wood Bridge*

	May (27–28)		June (26–27)		July (15–16)	
	Nos.	%	Nos.	%	Nos.	%
Plecoptera						
Amphinemura sulcicollis (Stephens)	31	0·22			3	0·27
Protonemura meyeri (Pictet)			1	0·04		
Perlodes microcephala (Pictet)	2	0·01				
Isoperla grammatica (Poda)	2	0·01			1	0·09
Chloroperla torrentium (Pictet)					2	0·18
Total Plecoptera	35	0·24	1	0·04	6	0·54
Ephemeroptera						
Ephemerella ignita (Poda)			2	0·08		
Caenis rivulorum Eaton			11	0·45	3	0·27
Baetis rhodani (Pictet)	38	0·27	303	12·5	44	4·0
Heptagenia sulphurea (Müller)			23	0·95	1	0·09
Total Ephemeroptera	38	0·27	339	13·96	48	4·3
Trichoptera						
Rhyacophila dorsalis (Curtis)	42	0·3	49	2·0		
Glossosoma boltoni (Curtis)	1193	8·6	21	0·86	4	0·36
Agapetus fuscipes Curtis	27	0·19	1691	69·6	111	10·0
Polycentropus flavomaculatus (Pictet)			2	0·08	1	0·09
Psychomyia pusilla (Fabr.)			1	0·04		
Hydropsyche pellucidula (Curtis)			13	0·53	1	0·09
Hydropsyche instabilis (Curtis)			44	1·8	50	4·5
Cheumatopsyche lepida (Pictet)			9	0·37	32	2·9
Silo pallipes (Fabr.)			1	0·04		
Total Trichoptera	1262	9·1	1831	75·3	199	17·9
Diptera						
Chironomidae	12574	90·4	259	10·7	856	77·2
GRAND TOTAL	13909	100	2430	100	1109	100

It was assumed that the drift samples were representative of the total drift under Low Wood Bridge. As both total discharge and volume sampled by surface nets were known (Table 1), it was possible to estimate total numbers of invertebrates drifting out of the river (Table 8). The totals for all groups can be compared with estimates from other localities.

The highest estimate was recorded by Berner (1951) who calculated that 64 million invertebrates drifted under Boonville Bridge (Missouri River, U.S.A.) in 24 hours. Other estimates of total numbers of drifting invertebrates per day are as follows.

800–18 000 in Wilfin Beck, Lake District (Elliott, unpublished)
1025–29 868 in River Yarty, East Devon (Bailey 1966)

1500–32 000 in Walla Brook, Dartmoor (Elliott 1967)
35 000–200 000 in Crosby Gill, River Duddon, Lake District (Elliott & Minshall 1968)
2 629 500–9 048 000 in river in central Swedish Lapland (Ulfstrand 1968)
20 380–366 417 in Speed River, Canada (Bishop & Hynes 1969)
46 060–403 358 in River Leven

As no drift samples were taken in the River Leven during periods of high discharge, the figures for this locality are probably well below the maximum possible values.

Table 6. *Comparison of day and night catches of invertebrate drift at Low Wood Bridge*

	May		June		July	
	Day (Nos./7 h)	Night (Nos./7 h)	Day (Nos./3 h)	Night (Nos./3 h)	Day (Nos./6 h)	Night (Nos./6 h)
Plecoptera						
Amphinemura sulcicollis	4	182			1	
Nemoura cinerea		1				
Leuctra inermis		2				
Leuctra geniculata				6		5
Perlodes microcephala		2				
Isoperla grammatica		5	1	1		
Chloroperla torrentium		2		3		
Total Plecoptera	4	194	1	10	1	5
Ephemeroptera						
Ephemerella ignita	1		13	311	102	547
Caenis rivulorum		23	13			5
Baetis rhodani	3	140	7	481	7	308
Heptagenia sulphurea			1	3		35
Total Ephemeroptera	4	163	34	795	109	895
Trichoptera						
Rhyacophila dorsalis				1	1	106
Agapetus fuscipes		1				
Psychomyia pusilla		2		3		
Hydropsyche instabilis	2	28		10	17	334
Total Trichoptera	2	31		15	18	440
Coleoptera						
Elmis aenea larvae	4	75		3	1	2
Elmis aenea adults		2		1		3
Oulimnius tuberculatus					1	3
Other Coleoptera larvae			1	4		
Total Coleoptera	4	77	1	8	2	8
Non-Insecta						
Gammarus zaddachi			2	133	6	82
Asellus aquaticus			1	9		1

Therefore, there is a very high drift rate at Low Wood Bridge and these drifting invertebrates would rapidly colonize the present estuary if ever it became fresh water. Some species listed in Table 4 would also colonize a freshwater reservoir at the mouth of the estuary. The following species from Table 4 have been found in still water: *Nemoura cinerea, Perlodes microcephala, Isoperla grammatica, Chloroperla torrentium, Ephemerella ignita, Heptagenia sulphurea, Sigara dorsalis, Agapetus fuscipes, Asellus aquaticus, Erpobdella octoculata, Limnaea truncatula* and *L. peregra*.

Although Chironomidae and Tipulidae were not identified to species, it is probable that some species of both groups would colonize a freshwater reservoir.

Table 7. *Comparison of day and night catches of emerging insects at Low Wood Bridge*

	May		June		July	
	Day	Night	Day	Night	Day	Night
Plecoptera						
Amphinemura sulcicollis		31			2	1
Protonemura meyeri				1		
Perlodes microcephala		2				
Isoperla grammatica		2				1
Chloroperla torrentium					2	
Ephemeroptera						
Ephemerella ignita				2		
Caenis rivulorum			10	1	1	2
Baetis rhodani	13	25	277	26	18	26
Heptagenia sulphurea			5	18		1
Trichoptera						
Rhyacophila dorsalis		42	1	48		
Glossosoma boltoni	24	1169		21		4
Agapetus fuscipes		27	46	1645	15	96
Polycentropus flavomaculatus			1	1		1
Psychomyia pusilla				1		
Hydropsyche pellucidula				13	1	
Hydropsyche instabilis			8	36	2	48
Cheumatopsyche lepida			1	8	3	29
Silo pallipes			1			
Diptera						
Chironomidae	7883	4691	43	216	605	251

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SUMMARY

(1) Samples of invertebrate drift were taken at the outflow of Windermere into the river Leven, and at Low Wood Bridge which is close to the upper tidal limit. Physical conditions at the two stations are given.

(2) Very large numbers of planktonic species were drifting out of the lake. Although none of these species was taken in the regular drift samples at Low Wood Bridge, some species of Cladocera and Copepoda were taken at the bridge during periods of high discharge. Therefore some planktonic species do survive the journey down the river Leven and would rapidly colonize a freshwater reservoir at the mouth of the estuary.

(3) Large numbers of lotic invertebrates were taken in the drift samples at Low Wood Bridge, especially at night. These drifting invertebrates would rapidly colonize the Leven estuary if ever it became freshwater. As many species in the drift have also been found in still water, there would also be a rapid colonization of a freshwater reservoir at the mouth of the estuary.

Table 8. *Estimates of total numbers of invertebrates drifting under Low Wood Bridge*

	May		June		July	
	Day (Nos./17 h)	Night (Nos./7 h)	Day (Nos./18 h)	Night (Nos./6 h)	Day (Nos./18 h)	Night (Nos./6 h)
Plecoptera						
Amphinemura sulcicollis	891	16697			294	
Nemoura cinerea		92				
Leuctra inermis		184				
Leuctra geniculata				2222		588
Perlodes microcephala		184				
Isoperla grammatica		459	1111	370		
Chloroperla torrentium		184		1111		
Total Plecoptera	891	17800	1111	3703	294	588
Ephemeroptera						
Ephemerella ignita	223		14443	115194	30000	64355
Caenis rivulorum		2110	14443			588
Baetis rhodani	669	12844	7777	178162	2059	36236
Heptagenia sulphurea			1111	1111		4118
Total Ephemeroptera	892	14954	37774	294467	32059	105297
Hemiptera						
Sigara dorsalis				370		
Trichoptera						
Rhyacophila dorsalis				370	294	12470
Agapetus fuscipes		92				
Psychomyia pusilla		184		1111		
Hydropsyche instabilis	446	2569		4074	5000	39295
Total Trichoptera	446	2845		5925	5294	51765
Coleoptera						
Elmis aenea—larvae	891	6881		1111	294	235
Elmis aenea—adults		184		370		353
Oulimnius tuberculatus					294	353
Other Coleoptera larvae			1111	1482		
Total Coleoptera	891	7065	1111	2963	588	941
Diptera						
Simulium spp.		92				
Tipulidae		92				
Total Diptera		184				
Non-Insecta						
Gammarus zaddachi			2222	49263	1765	9647
Asellus aquaticus			1111	3334		118
Erpobdella octoculata				370		
Limnaea truncatula		92				
Limnaea peregra						118
Total Non-Insecta		92	3333	52967	1765	9883
TOTAL (all groups)	3120	42940	43329	360029	40000	168475

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