Structure of the Microarthropod Community In Lake Ontario Beach Debris[1]

Compliments
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ABSTRACT

The microarthropod community of the beach debris, or drift line, on the southeast shore of Lake Ontario was investigated during summer and fall of 1970 to determine the species composition and the influence of drift components and vertical location on community structure. Structural characteristics measured included the arthropod species and volume diversities, habitat diversity, and 3-dimensional ordination.

The drift line was composed principally of decaying fish (*Alosa pseudoharangus* Wilson), herbaceous plant fragments, and driftwood. Some species were clearly associated with either the decomposing alewives or the plant debris; others were common to both. Alewife fauna had a lower average species diversity and arthropod volume diversity that that of the plant debris, although alewives supported a much greater arthropod saprovore volume until late fall; values for mixed debris were intermediate. Burial of drift materials by sand had a major effect on species composition, but little or no effect on species diversity or arthropod volume diversity. Species diversity, richness, and equitability were not correlated with the diversity of components in the natural drift line. General comparisons showed the drift line community to be very dissimilar to that of nearby cottonwood leaf litter, which had a higher species diversity.

On the shores of any sizable body of water there is usually an area of debris deposited by the action of waves in rows parallel with the shoreline. This debris is variously known as a drift line, windrow, jetsam, or flotsam. Except in the case of thick algal drift which remains wet for long periods of time, and except for an occasional hardy beach plant, the drift line has no primary productivity.

The size, composition and position of such drift lines can vary greatly. The animal component, when present, is almost exclusively decaying fish, although in some instances the amount of dead invertebrate material may be significant. The plant component usually contains fragments of emergent vegetation, driftwood, and other materials of terrestrial origin, and sometimes algae or uprooted benthic plants. In addition, non-biodegradable human artifacts, especially plastics, tend to accumulate in this zone. Drift lines in a *Spartina* salt marsh, composed mainly of straw from emergent vegetation, may be 2–5 ft (0.6–1.5 m) wide and 0.5–2 ft (0.2–0.6 m) deep, compared to maritime sandy-beach drift lines which are rarely over 2 ft (0.6 m) wide and several inches deep (Barnes and Barnes 1954). The latter size range is also characteristic of those on the Great Lakes. Dimensions and position on the beach depend on both the slope of the shore and the extent of wave action. The latter is determined partially by tidal patterns in maritime situations (Barnes and Barnes 1954) and by storm patterns on fresh-water beaches (Cowles 1899).

Early investigations of fresh-water drift line arthropods dealt with periodic accumulations of terrestrial insects in windrows on Lake Michigan following continuous onshore winds (Needham 1900, 1904, Snow 1902) with little or no mention of a resident drift-line fauna. Shelford (1913) also described such accumulations, but a short account was also given of larger decomposers and predaceous animals associated with drift line carrion.

Only certain segments of the resident fauna have been studied in detail. Jaques (1915) supplied information on the beetle fauna of fish carrion on Lake Erie, listing 21 species. As part of a study of spider succession in Lake Michigan sand dunes, Lowrie (1948) recorded 17 species from the open beach or drift line, although some were believed to be accidentals. The biology of muscoid flies breeding in fish carrion was investigated by Herms (1907), who considered flies as the principal organisms responsible for fish decomposition.

Fewer studies have dealt with the arthropod fauna of maritime drift, but they have been more intensive and analytical. The structure of the spider fauna in both saltmarsh and sandy-beach drift has been examined in North Carolina (Barnes and Barnes 1954) and England (Duffey 1968). Backlund (1945) made a classical ecological study of sea wrack on the Scandanavian coast, but the fauna of such accumulations of decaying algae is quite distinct from that of other drift habitats.

A relatively recent peculiarity of the drift lines along the Great Lakes, especially Lake Ontario, is the accumulation of large numbers of dead alewives, *Alosa pseudoharangus* (Wilson), following the annual spring dieoff. The magnitude of the dieoff varies from year to year with changes in the population densities (Brown 1968; Smith 1970). One of the important consequences of such a dieoff is the decrease in the recreational value of beach areas where the fish accumulate and decompose (Wilson 1968).

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The recreational impact and regular deposition of the drift line on Lake Ontario suggest a need for a better understanding of its ecology. Our study involved the arthropod segment of the drift line community, with particular reference to mites and small insects (microarthropods). Specifically our objectives were (1) to determine the composition of the resident microarthropod fauna, and (2) to determine the effect of drift composition and vertical location, relative to sand surface, on microarthropod community structure.

Methods

Study Site

The study area was located on the southern portion of a narrow sandy barrier beach at the east end of Lake Ontario, on the Lakeview Game Management Area, Town of Ellisburg, Jefferson Co., NY. This has been designated a "natural beach" by the State of New York and is protected from development and most recreational uses (Wilson 1970). A conspicuous character of the site is the almost continuous presence of a dense, sharply defined row of cottonwood saplings, ca. 2–3 m wide, which runs parallel with the shore and marks the upper limit of open beach. Although still present, the depth of the row of cottonwoods was reduced by severe wave activity during 1973–74. These saplings mark the inland extent of wave action and drift deposition during late fall storms and consequently correspond to the "maximum winter storm line" described by Cowles (1899) on the more extensive Lake Michigan beaches.

The formation of drift lines begins when a large mass of herbaceous and woody material is deposited on the shore after the lake ice melts in the spring. This is gradually moved farther inland by storms. Soon afterwards the annual alewife dieoff results in the accumulation on the lower beach of large numbers of fish which undergo the initial stages of decomposition by fly larvae. The remains then are washed farther inland and mix with the plant debris. This main mass of drift, which is the subject of the present study, will be referred to as the primary drift line. Secondary drift lines are those deposited later in the season when the water level is receding. These are usually rather homogeneous masses of driftwood fragments, algae, or terrestrial insect accumulations.

Sampling

Two methods of sampling were employed on a 500 m section of beach marked at 100-m intervals. The 1st involved the collection of all drift materials within a circular metal frame of 710 sq cm inside area. These will be referred to as area samples. On June 20, 1970, when the primary drift line was well formed, 4 area samples were taken at random from each 100 m section (a total of 20 samples). Collections of one sample/section were initiated Aug. 1, and were continued every other week through Oct. 24, with the last sample taken Nov. 21. On Sept. 26, 4 area samples of cottonwood litter on a stabilized dune 75 m from the beach were taken for comparison with the drift fauna.

The 2nd method involved the packaging of presorted, arthropod-free materials in nylon 0.6 cm mesh bags (litter bags) similar to those used in leaf litter decomposition studies (Crossley and Hoglund 1962, Heath et al. 1966). Fourteen litter bags were prepared for each of the following categories of drift material: (1) alewives collected after initial decomposition by fly larvae; (2) herbaceous material (emergent plant fragments); (3) a mixture by air-dry wt of 40% fish, 40% wood fragments, 20% herbaceous material. These were placed in the primary drift line Aug. 1. Beginning Aug. 14, 2 bags/category were collected in each sampling period.

Arthropods were extracted from both types of samples in Tullgren funnels. One day was allowed for air drying and 2 days for drying with a suspended 7.5-w bulb. After extraction, litter bags were weighed and area samples were sorted into components to determine the percentage by weight of fish, wood and herbaceous fragments.

Analytical Methods

Community structure was analyzed on the basis of numerical species diversity (referred to simply as species diversity) and volumetric species diversity (referred to as volume diversity). A rough volume estimate for the various developmental stages of each species was calculated by treating them as oblate spheroids, measuring average length and width, and including a factor based on how closely the cross-sectional shape approached a circle. Species diversities (H') were calculated using the Shannon-Weiner function, as modified by Lloyd, Zar, and Karr (1968), and are based on natural logarithms. Volume diversities were calculated in the same way, using volume per species, instead of numbers per species. The volume diversity index was used as a rough indication of the arrangement of biomass among the various drift-line microhabitats defined below.

In addition, a measure of species richness and equitability was made for each area sample based on the formulae of Menhinick (1964) and Pielou (1969), respectively. Habitat diversity was measured for each area sample based on the air-dry wt of each component. Simple correlations were then attempted with species diversity, richness, and equitability to see if relationships existed.

To analyze the effect of drift composition on the arthropod community structure, and to understand temporal trends, we treated the following arrangements of drift materials as distinct microhabitats. Their respective faunas were considered separate microcommunities, as defined by Dindal (1973):

A. Litter Bag Microhabitats

1) Herbaceous LB (herbaceous litter bags)
2) Fish LB (fish litter bags)
3) Mixed LB (mixed litter bags)

B. Natural Drift Microhabitats
1) Fish Drift (≥70% fish remains)
2) Herbaceous Drift (≥ 70% herbaceous fragments)
3) Woody Drift (≥70% wood fragments)
4) Mixed Drift (no component making up > 70% of the air-dry wt).

Each area sample was categorized in one of the last 4 microhabitats, resulting in unequal sample sizes. All 7 were then placed in a simple 3-dimensional ordination based on faunal similarity coefficients (SC), using the method of Bray and Curtis (1957). Two of the 3 factors used in measuring similarity—relative frequency and relative density—were calculated with their formulae. The 3rd—relative dominance—was calculated as the fraction of the total arthropod volume attributable to the species in question.

Results

On June 20, the primary drift line was about 6–8 m inshore from the water line and 3–6 m from the cottonwood saplings. The water level, measured by a reference stake in a nearby pond outlet, then dropped steadily until Oct. 24, when it was 56 cm lower and the drift line was 20–25 m from the shore line. During this time the drift was essentially unmoved by wave action. By Sept. 26 much of the drift line, including litter bags, had been dispersed

Table 1.–Relative density (RDe), relative frequency (RF) and relative dominance (RDo) of microarthropods most commonly collected from the primary drift line.

	FISH LB			FISH DRIFT			HERB. LB			HERB. DRIFT			WOODY DRIFT			MIXED LB			MIXED DRIFT		
	RDe	RF	RDo	RDe	RF	RDo	RDe	RF	RDo	RDe	RF	RDo	RDe	RF	RDo	RDe	RF	RDo	RDe	RF	RDo
ARACHNIDA																					
ORIBATEI																					
Zygoribatula sp.	.03	.07	.00	.09	.14	.00	.00	.04	.01	.21	.10	.01	.22	.08	.03	.01	.07	.00	.27	.09	.04
Macrocheles merdarius (Berl.)	.25	.09	.00	.01	.04	.00	.00	.07	.01	.01	.03	.00	.05	.03	.01	.10	.07	.02	.03	.06	.00
Macrocheles ontariensis Norton	.00	.04	.00	.00	.10	.00	.00	.03	.00	.00	.05	.00	-	-	-	.00	.03	.00	.00	.04	.00
M. perglaber Filip. & Pegaz.	.00	.02	.00	.00	.01	.00	-	-	-	-	-	-	-	-	-	-	-	-	.00	.02	.00
Gamasodes bispinosus (Halb.)	-	-	-	.00	.03	.00	-	-	-	-	-	-	-	-	-	-	-	-	.01	.03	.00
Amblyseius salish Chant & Hans.	.01	.04	.00	.03	.05	.00	.00	.03	.00	.01	.03	.00	.09	.03	.00	.01	.05	.00	.06	.06	.00
Arctoseius cetratus (Selln.)	.00	.01	.00	.00	.01	.00	.00	.06	.00	.00	.02	.00	.00	.03	.00	.00	.03	.00	.00	.02	.00
Hypoaspis sp.	.00	.01	.00	-	-	-	.01	.07	.02	-	-	-	-	-	-	.01	.05	.00	-	-	-
MESOSTIGMATA																					
PROSTIGMATA																					
Tydeus tuttlei Baker	.00	.03	.00	.01	.03	.00	.00	.04	.00	.09	.05	.00	.18	.03	.00	.01	.04	.00	.11	.05	.00
Microtydeus sp.	.56	.02	.00	.71	.03	.00	.22	.06	.01	.38	.03	.00	-	-	-	.34	.04	.01	.12	.02	.00
Tarsonemus sp.	.00	.03	.00	.01	.03	.00	.09	.06	.02	.00	.05	.00	.01	.06	.00	.05	.04	.00	.02	.02	.00
Bakerdania tarsalis (Hirst)	.00	.04	.00	.00	.01	.00	.15	.07	.04	.00	.02	.00	.02	.03	.00	.01	.04	.00	.01	.03	.00
Pseudopygmephorus sp.	.00	.02	.00	-	-	-	.13	.06	.03	.00	.02	.00	.00	.01	.00	.03	.04	.00	.00	.01	.00
Pediculaster sp.	.01	.03	.00	.00	.01	.00	.21	.06	.06	-	-	-	.00	.02	.00	.07	.06	.00	.00	.02	.00
Siteroptes	-	-	-	-	-	-	.02	.02	.00	-	-	-	-	-	-	.01	.02	.00	-	-	-
Raphignathus gracilis (Rack)	.00	.04	.00	.00	.02	.00	.00	.02	.01	.01	.08	.00	.00	.02	.00	.00	.02	.00	.00	.03	.00
ACARIDEI																					
Tyrophagus putrescentiae (Shrank)	-	-	-	-	-	-	.00	.01	.00	-	-	-	-	-	-	.04	.02	.01	.01	.01	.00
INSECTA																					
COLEOPTERA																					
Anthicus spp.[b]	.00	.04	.10	.00	.08	.01	-	-	-	.01	.03	.73	.01	.05	.17	.00	.03	.04	.01	.05	.10
Omosita colon Linn.[b]	.05	.10	.60	-	-	-	-	-	-	-	-	-	.00	.02	.15	.01	.05	.44	.01	.03	.19
Dermestes spp.[a]	.00	.03	.19	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
DIPTERA																					
Fannia sp.[a]	.00	.03	.02	.00	.03	.02	-	-	-	-	-	-	.00	.01	.00	.00	.02	.20	.00	.01	.13
other diptera[a]	.01	.05	.06	.09	.08	.97	-	-	-	.02	.05	.11	.01	.05	.42	.00	.01	.14	.00	.03	.39
COLLEMBOLA																					
Hypogastrura matura (Nic.)	.01	.04	.00	.01	.05	.00	.01	.05	.08	.08	.06	.04	.25	.08	.14	.08	.06	.05	.26	.05	.08
Proisotoma minuta (Tullberg)	.03	.04	.00	.00	.02	.00	.08	.07	.20	.07	.06	.01	.08	.07	.01	.21	.06	.02	.03	.05	.00
PSOCOPTERA																					
Liposcelis spp.	.01	.07	.00	.02	.07	.00	.00	.05	.03	.08	.06	.02	.02	.03	.00	.00	.05	.00	.01	.04	.01
LEPIDOPTERA																					
Tineidae[a]	.00	.03	.00	.00	.02	.00	.00	.03	.42	-	-	-	.00	.01	.02	.01	.02	.07	.04	.04	.02
OTHERS	.03	.08	.03	.02	.14	.00	.08	.03	.06	.03	.26	.08	.06	.34	.05	.00	.08	.00	.00	.19	.04

[a] larvae only

[b] adults and larvae

and partially buried by sand movement, although its position was still obvious. By Oct. 24 the remaining litter bags were buried under 5–10 cm of sand; the natural drift materials were still shallowly buried and still detectable on the surface. The water level had risen again by Nov. 21, and stormy weather brought the waves to within a few decimeters of the primary drift line.

During the study, 42 species of mites (20 families), 8 species of spiders (4 families), and 43 species of insects (16 families) were extracted from the samples. Those occurring in 5 or more samples are given in Table 1, along with their relative density, frequency, and dominance per microcommunity.

In no case was the mean species diversity of a litter bag microcommunity significantly different from its natural drift counterpart (Table 2). Both fish categories had significantly lower diversity than all other categories, but no other significant differences were observed. The mean species diversity of the mixed drift categories, both natural and litter bags, were intermediate between the fish and herbaceous categories. The average diversity of the cottonwood leaf litter fauna (H′ = 1.046) was significantly higher ($\alpha = .01$) than all drift microcommunities.

Volume diversities showed less distinct differences, although as with species diversity the litter bag microcommunities and their natural drift counterparts were not significantly different. The relationships between the litter bag microcommunities are the same as for species diversity, with Mixed LB intermediate. In the natural categories this relationship does not hold. The Woody Drift is relatively high in species diversity but low in volume diversity.

The similarity coefficients of all possible microcommunity pairings, used to construct the ordination, are given in Table 3. The most similar are the Mixed Drift and Woody Drift; the most different are the Herbaceous LB and Fish Drift. The 3-dimensional relationships are more clearly seen in Fig. 1, where the units shown are dissimilarities (the compliment of similarities). None of the litter bag microcommunities are very close to their respective natural drift counterparts. The cottonwood litter fauna, not included above, showed very low similarity with all drift faunas, being highest (SC = 0.043) with the Mixed Drift. Thirty-six species of mites and 6 species of insects were collected from the litter, of which only 4 and one, respectively, occurred in the drift.

No correlation was found between the habitat diversity of the area samples and the species diversity, species richness, or equitability of their fauna. Attempts were also made using differential weighting schemes for the various drift components, but no correlations were significant.

The decomposition rates for the litter bag microhabitats were quite different. By Oct. 24 an avg. 60.2% of the original weight of the fish bags remained, compared to 83.8% in the herbaceous bags and 69.2% in the mixed bags.

Discussion

It has been shown that mite communities of decomposing plant materials can vary considerably between available microhabitats (Aoki 1967). The number of available microhabitats in the primary drift line on Lake Ontario is a function of both drift composition and vertical location.

In terms of drift composition, essentially 2 types of materials were present: (1) alewives in the later stages of decomposition (Fish LB, Fish Drift); and (2) relatively intact, protein-poor plant materials (Herbaceous LB, Herbaceous Drift, Woody Drift). In terms of drift placement, the litter bags represented a somewhat unnatural situation where the organic matter was buried by sand up to 10 cm deep, yet was not dispersed. This created a microhabitat capable of retaining high moisture levels. In the natural drift materials, dispersal of the debris, in

Table 2.–Comparison of mean diversities of driftline microcommunities by Student's *t*-test.

	Fish LB	Fish drift	Herb. LB	Herb. drift	Woody drift	Mixed LB	Mixed drift
SPECIES DIVERSITY	.449	.357	.673	.603	.623	.601	.565
Fish LB		NS	**	*	*	*	*
Fish Drift			**	*	**	*	**
Herb. LB				NS	NS	NS	NS
Herb. Drift					NS	NS	NS
Woody Drift						NS	NS
Mixed LB							NS
VOLUME DIVERSITY	.347	.272	.531	.418	.347	.450	.430
Fish LB		NS	*	NS	NS	NS	NS
Fish Drift			**	*	NS	*	*
Herb. LB				NS	*	NS	NS
Herb. Drift					NS	NS	NS
Woody Drift						NS	NS
Mixed LB							NS

NS No significant difference.
* Significant at 0.05 level.
** Significant at 0.01 level.

Table 3.—Similarity coefficients of beach driftline microcommunities based on 3-factor importance values.[a]

	Fish LB	Fish drift	Herb. LB	Herb. drift	Woody drift	Mixed LB	Mixed drift
Fish LB	.479		.328	.438	.380	.644	.482
Fish Drift			.266	.474	.445	.408	.515
Herb. LB				.348	.286	.546	.316
Herb. Drift					.539	.463	.530
Woody Drift						.454	.783
Mixed LB							.544

[a] Range from 0.0 (completely different communities) to 1.0 (identical communities); procedures after Bray and Curtis (1957).

conjunction with shallower and less complete burial, created a microenvironment which was much drier and presumably had greater temperature extremes.

Effects of Drift Composition

Several of the saprovores, such as larvae of *Anthicus* spp. and *Omosita colon*, were associated only with microhabitats containing fish. These beetles have been reported from vertebrate carrion by many authors. Others associated primarily or exclusively with the fish carrion included larvae of *Fannia* sp., *Dermestes* spp., and acalypterate muscoids. Predators in this category included *Gamasodes bispinosus*, *Macrocheles perglaber*, and *M. merdarius*. To our knowledge, the latter 2 species were previously recorded only from manure-related habitats.

Saprovores found primarily in plant drift materials included the mite families Pyemotidae and Tarsonemidae, along with the tydeid *Tydeus tuttlei*. These are all known or suspected to be fungus feeders (Cross 1965, Wallwork 1967). Collembolans were also associated, for the most part, with plant fractions of the drift, and these too are primarily fungivores or feed on plant material attacked by fungi (Hale 1967). Certain predaceous species, such as *Arctoseius cetratus* and *Hypoaspis* sp., reached relative abundance only in plant debris.

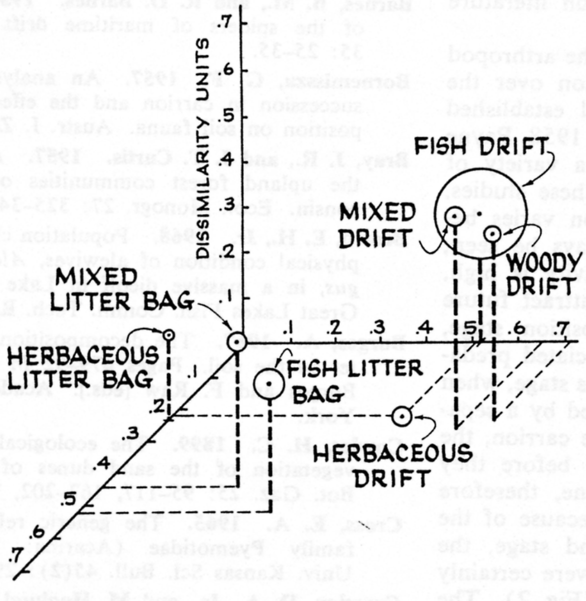

FIG. 1.—Ordination of drift mocrocommunities based on importance values. (Area of circles proportional to average arthropod volume of each site.)

There was apparently no correlation between the diversity of drift materials and the diversity of species, species richness, or equitability, even when a system of habitat weighting was applied. Such a correlation with habitat structure has been shown for birds and desert rodents (Karr 1968, MacArthur 1964, Rosenzweig and Winakur 1969). There was, however, a significant difference between the overall diversity of the plant-dominated and fish-dominated microcommunities, the former being higher. It was expected that species diversity in the mixed drift categories would be even higher because of the presence of both energy sources, but they were intermediate.

Average volume diversities showed generally the same relationships with drift composition as did species diversities. The lower volume diversity of the fish microcommunities indicates that a higher percentage of the total volume (and presumably biomass and energy) was tied up in relatively few species. Volume was more evenly distributed among the species in the plant microcommunities.

Effects of Drift Location

The vertical location of drift materials had a great effect on a number of species. The predators *Gamasodes bispinosus, Macrocheles perglaber* and *Amblyseius salish*, along with the saprovores *Zygoribatula* sp., *Tydeus tuttlei*, *Anthicus* spp., *Fannia* sp. and *Liposcelis* spp. were all considerably more abundant in the natural drift materials, which remained on or near the sand surface. Others, such as the saprovores *Proisotoma minuta, Omosita colon* larvae, *Tarsonemus* sp. and the species of Pyemotidae, reached high numbers only in the buried litter bags. This was also true of the predators *Raphignathus gracilis, Macrocheles merdarius, Arctoseius cetratus* and *Hypoaspis* sp. The last species, as well as the saprovore *Siteroptes* sp. were not found in any collections of natural drift. An analogous shift in species composition has been noted by Payne et al. (1968) when decaying baby pigs are buried, instead of left on the soil surface. The grouping of the litter bag microcommunities away from the natural drift

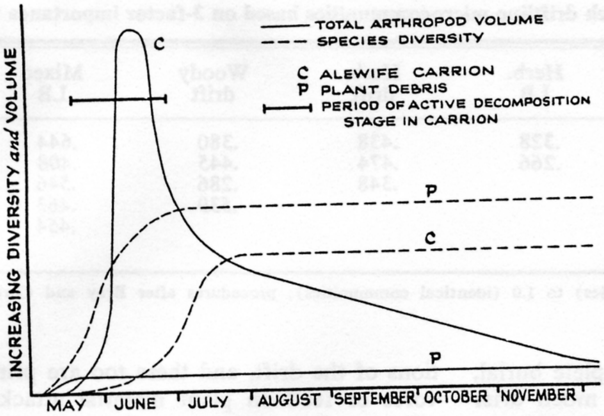

FIG. 2.—Speculative temporal changes in arthropods associated with alewife and plant debris microcommunites.

faunas in the ordination is evidence of the effect of deeper burial and lack of natural dispersion in the former.

The absence of significant differences in means between the litter bag and corresponding natural drift microcommunities indicates that drift location had little effect on species diversity or volume diversity.

Temporal Structure Changes in Natural Drift Microcommunities

Several factors complicated an analysis of fauna succession in the natural drift materials during decomposition. The most important is that natural materials are mixed to a high degree, which does not allow collection of relatively pure fish or plant debris in a random fashion. The seasonal changes suggested here (Fig. 2) for species diversity and total arthropod volume are based as much on literature and speculation as on the data collected.

The fact that there is a succession in the arthropod communities inhabiting vertebrate carrion over the course of decomposition has been well established (Bornemissza 1957, Walker 1957, Reed 1958, Payne 1965, Payne et al. 1968). Although a variety of vertebrate animals have been used in these studies, and the categorization of the succession varies between authors, 3 main stages can always be seen; (1) a fresh stage, when bacterial activity is high, bloating occurs, and chemical stimuli attract future decomposers; (2) an active decomposition stage, dominated by fly larvae with their associated predators and parasites; and (3) a dry-remains stage, when the skin and its derivatives are consumed by a separate fauna. With regards to the alewife carrion, the 1st 2 stages were generally completed before they were mixed with the primary drift line, therefore prior to the initiation of this study. Because of the predominance of fly larvae in the 2nd stage, the species diversity and volume diversity were certainly very low, with total volume very high (Fig. 2). The rate of weight loss is greatest in this stage (Payne 1965).

After the active decomposition, the rate of weight loss and total volume decreased, species and volume diversities increased, and the microcommunity changed from one numerically dominated by large insects to one dominated by microarthropods. By late November, total volumes were at their lowest and weight loss was probably very slow, but relatively high species and volume diversities were maintained.

Decomposition and faunal succession in decomposing plant remains with relatively high carbon: nitrogen ratios take a great deal more time than in animal carrion, probably lasting many years (Burges 1967). Changes in arthropod community structure observed in this study may be only a result of seasonal population fluctuations and microclimatic changes involved in burial and dispersal of the debris. The rate of colonization of plant debris washed ashore after the lake ice melted was probably dependent on the degree of microbial preconditioning. Most saprophagous microarthropods feed either directly on fungi or on plant material after it is invaded by fungi (Wallwork 1967, Hale 1967). Since insect larvae were not dominant in this microcommunity, the large scale fluctuation in total volume was not evident; low values were maintained throughout the study. Species and volume diversities in the plant microcommunity remained relatively constant, but at higher levels than in the alewife microcommunity.

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