Seasonal study of the fauna of bedrock substrates in the wave zones of lakes Huron and Erie

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Quantitative samples of the benthic macrofauna inhabiting bedrock substrates in the wave zone (0- to 2-m depth) at a site on Lake Huron and one on Lake Erie were collected in each season during 1975 and early 1976. The turnover of species between sampling visits was greatest in summer and at depths less than 0.5 m. The fauna at the Lake Huron site was dominated numerically by *Hyalella azteca* (Amphipoda) and larvae of *Stenelmis* spp. (Coleoptera: Elmidae). The density of the fauna appeared to be greatest in winter. The fauna at the Lake Erie site was dominated by *Gammarus fasciatus* (Amphipoda), whose populations were largest in summer and smallest in winter, thus corresponding to the abundance of *Cladophora* in the wave zone. None of the common insect species underwent diapause as larvae at either site.

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Le prélèvement d'échantillons quantitatifs de macrofaune benthique dans des substrats rocheux de la zone de vagues (0- to 2-m de profondeur) en un point du lac Huron et un du lac Erié a permis d'établir que le remplacement des espèces entre les visites se produit surtout en été, à des profondeurs inférieures à 0.5 m; les prélèvements ont eu lieu à chacune des saisons en 1975 et au début de 1976. La faune de la station du lac Huron est dominée par *Hyalella azteca* (Amphipoda) et par les larves de *Stenelmis* spp. (Coleoptera: Elmidae). La densité de la faune semble atteindre son point culminant en hiver. La faune de la station du lac Erié est dominée par *Gammarus fasciatus* (Amphipoda) dont les populations atteignent leur maximum d'abondance à l'été et leur minimum à l'hiver, correspondant ainsi à l'abondance de *Cladophora* dans la zone des vagues. Aucune des espèces communes d'insectes n'a subi de diapause larvaire et ce, ni à l'un ni à l'autre des sites explorés.

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Introduction

A major obstacle to comparative study of benthic faunas in lotic or lentic habitats is the variety of factors which can contribute to the variability among samples. In streams and to a lesser extent in lakes (see reviews in Hynes (1970) and Brinkhurst (1974)), the benthic fauna may change markedly in composition and abundance over short periods of time, especially in summer, as adult insects emerge and other groups migrate or reproduce. Variations in chemical and physical parameters, i.e. water quality, and even very subtle differences in the substrate may greatly increase the variability between otherwise identical samples (Wilhm 1972; de March 1976).

In the wave zone of large lakes, such as the St. Lawrence Great Lakes, other factors, such as the geographical or geological ranges of individual species and differences in the exposure to wave action between sites, further complicate the comparison of samples of benthic communities. Each of these, and possibly other, factors probably contributed to the variation we observed between samples collected from similar wave-zone substrates in each of the Great Lakes during our survey in the summer of 1974 (Barton and Hynes, in preparation). The results of that survey suggested that the wave-zone fauna has potential for use in monitoring water quality but the variability between samples collected from similar substrates precluded us from making any firm statements about local or regional water quality in the Great Lakes.

Therefore, we felt it necessary, as a next step toward testing the usefulness of wave-zone benthic communities as indicators of water quality, to assess the seasonal component of this variability. Toward this end, quantitative samples were collected seasonally from bedrock substrates at a site near Howdenvale, Ontario (44°49′ N, 81°18′ W), on Lake Huron, and near Selkirk, Ontario (42°49′ N, 79°56′ W), on Lake Erie, in 1975 and early 1976. Communities inhabiting bedrock were chosen because of the large number of species present and

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the long-term stability of the substrate which would be relatively unaffected by short-term events such as storms.

The Study Areas

The substrate in the 0- to 2-m zone at Howdenvale was very shallowly shelving limestone pavement with patches of boulders and finer rubble. Immediately along the shore at depths less than 0.5 m, the layer of overlying material was up to 25 cm thick and consisted of tightly packed gravel and angular stones in the cobble to boulder size range. The pavement sloped gradually offshore to a depth of about 1.5 m below water level roughly 100 m offshore, then rose to form a rather smooth ridge about 1 m deep. Further offshore the gradual slope continued and the water was 2 m deep about 250 m offshore. In this deeper portion of the study area, the substrate consisted of areas of pitted limestone pavement alternating with patches of boulders with gravel in all cracks and crevices. Except on 1 May 1975 when the uppermost surfaces of the larger stones at depths to 30 cm were scoured clean, all rock surfaces were covered with a layer of brownish-green aufwuchs up to 3 mm thick. The entire area was subject to continual wave action but was protected from extremely large waves by shoals about 3 km offshore. Ice cover developed in late January 1975, and by late March consisted of a fairly even layer about 35 cm thick extending at least 400 m offshore. All ice disappeared by 1 May.

Limestone bedrock exposed at lake level covered by a low (3- to 4-m), till bluff formed the Lake Erie shore at the study site near Selkirk. In the wave zone this bedrock was mostly covered with boulders, shingle, and gravel out to the 1-m depth contour, about 20 m offshore. Further out the exposed rock was very rough in texture and depth increased to 2 m within 30 m of shore. In midsummer the entire substrate, except for patches of gravel immediately along the water's edge, was covered by thick mats of *Cladophora*. This algal cover began developing in May and generally increased until autumn storms scoured most of the algae away leaving only the basal filaments in crevices on solid stone surfaces. In April and November, the substrates shallower than 25 cm showed evidence of recent scouring. In February 1976, ice cover consisting of fused sheets of fairly smooth ice extended to the horizon. The ice appeared to be grounded by an indistinct rampart at several spots at depths of about 1 m.

Materials and Methods

Quantitative samples of benthic invertebrate communities were collected using the cylinder dip net or quadrat air lift techniques and processed in the manner described by Barton and Hynes (in preparation). Usually duplicate samples were taken on each visit at depths of less than 0.4 m, at 1 m, and at 2 m, although ice, wave conditions, or equipment failures caused several departures from this routine. The placement of the quadrat at a given depth was random but biased somewhat to ensure a close fit to the substrate so that enclosed organisms would not be lost.

Two measures of similarity were used to assess the variation between replicate samples and between sampling dates: coefficient of community (*CC*) and percentage similarity of community (*PSc*) (Johnson and Brinkhurst 1971). The taxonomic units used in the calculations were those listed in Barton and Hynes (in preparation). All samples taken on each date were combined to calculate similarity coefficients between dates.

Coefficient of community was calculated as: $CC = [c/(a + b - c)] \times 100$, where a is the number of taxa in the first sample, b is the number of taxa in the second sample, and c is the number of taxa common to both.

Percentage similarity of community was calculated as: $PSc = 100 - 0.5\,\Sigma|a' - b'| = \Sigma \min(a', b')$, where a' and b' are, for each species, the percentage of the total number of animals in each of the samples being compared.

Results

Howdenvale

Of the 149 taxa collected at the Howdenvale site, 28 were taken on all six visits in 1975. Dominant forms included *Hyalella azteca*, *Ephemera simulans*, *Stenonema fuscum*, *Stenelmis* (two species), and *Pseudosmittia*.

Figure 1 summarizes the community composition and gives ranges of density estimates for the three depths sampled on each date. Similarity coefficients between replicate samples (Table 1) indicated that while the variation in percentage composition of the samples decreased slightly with depth, the number of rare species increased slightly. Coefficients calculated between dates (Table 2) indicated that the variation in community composition was greatest in summer. At the 1- and 2-m depths, the consistently high proportions of *H. azteca* and *Stenelmis* spp. tended to minimize the fluctuations in percentage composition due to turnover of other insect taxa. *PSc* values calculated for each of the major groups of organisms (Table 3) showed that most of the variation in community composition between dates occurred in the less abundant groups such as 'lower phyla' (i.e. *Hydra*, Tricladida, and Nematoda), Oligochaeta, Mollusca and, in summer, the insects.

Estimates of density at the shallowest and greatest depths averaged about 2500 organisms/m^2 but were lower at 1 m, about 1500/m^2. This is probably due to the rather monotonous substrate, but wave-induced motion was also most severe at that depth, which hampered sampling efforts to some extent. The data suggest that overall density may

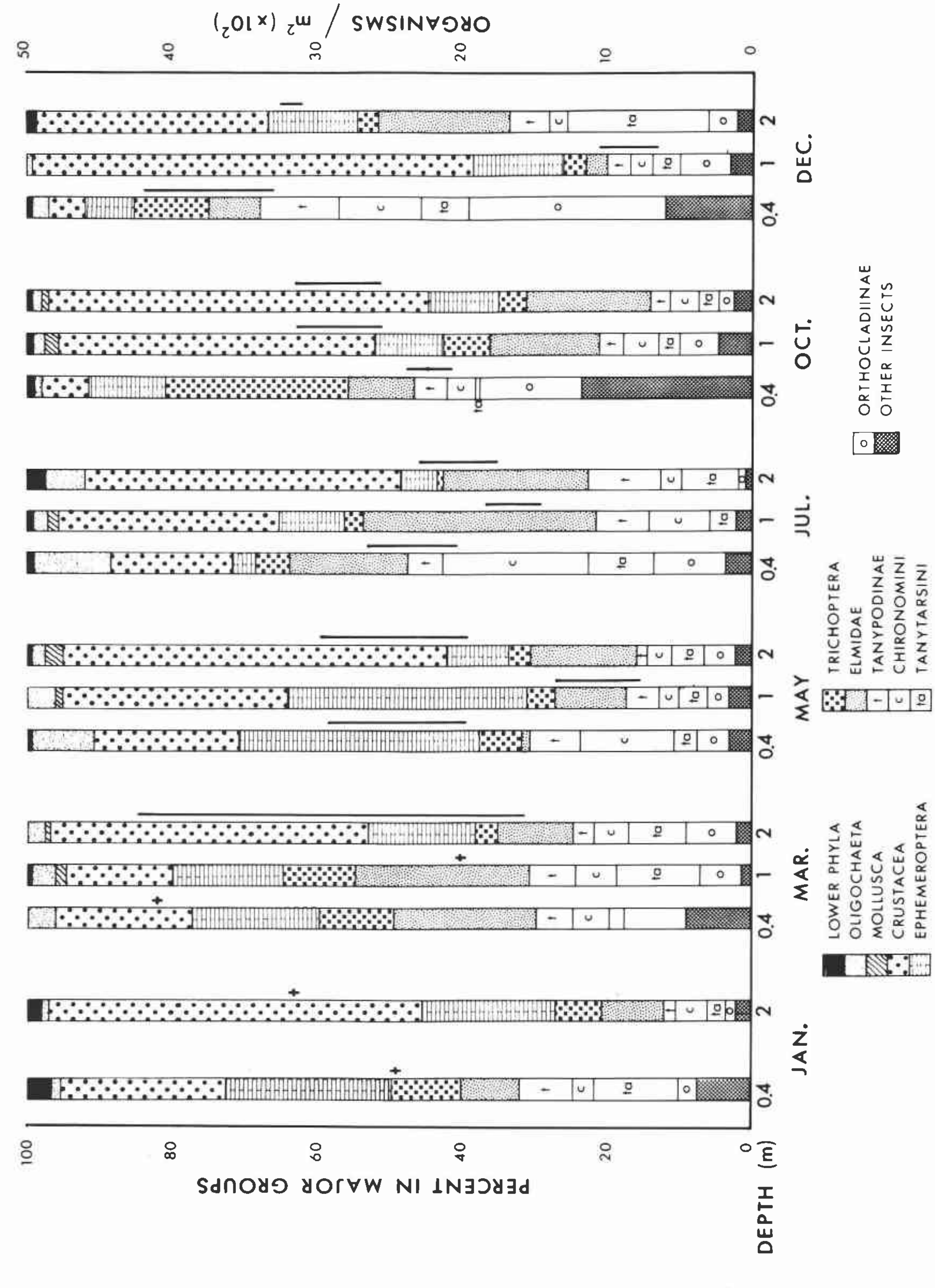

FIG. 1. Community composition expressed as percent of individuals in major groups and estimates of invertebrate density from samples collected at Howdenvale, Lake Huron, 1975. Vertical lines indicate the range of density estimates from two or more samples; (+) indicates single samples.

TABLE 1. *CC* and *PSc* replicate samples, at three depths from Lake Huron

	0.4 m		1 m		2 m	
Date	*CC*	*PSc*	*C*	*PSc*	*CC*	*PSc*
21 March	48	63	—	—	47	62
					50	66
					48	73
1 May	46	38	42	72	53	63
11 July	56	74	48	48	33	64
21 October	59	77	42	72	72	95
15 December	66	83	55	82	59	84
$\bar{X}$	55	67	47	68	52	72

TABLE 2. *CC* and *PSc* between adjacent sampling dates, at three depths from Lake Huron

	0.4 m		1 m		2 m	
Date	*CC*	*PSc*	*CC*	*PSc*	*CC*	*PSc*
10 January						
	51	61	—	—	38	67
21 March						
	52	38	48	56	58	75
1 May						
	30	19	39	55	44	69
11 July						
	41	32	42	56	38	72
21 October						
	52	53	49	71	62	75
15 December						
$\bar{X}$	45	41	44	60	48	72

TABLE 3. *PSc* for major taxonomic groups between adjacent sampling dates, Lake Huron

	10 Jan.	21 Mar.	1 May	11 Jul.	21 Oct.	15 Dec.
Lower phyla	20	67	47	82	14	
Oligochaeta	07	41	39	30	39	
Mollusca	56	47	54	62	37	
Crustacea	79	80	76	79	96	
Ephemeroptera	71	75	21	36	69	
Trichoptera	64	58	20	18	57	
Coleoptera	61	63	55	75	80	
Tanypodinae	89	95	60	61	62	
Chironomini	70	51	32	39	44	
Tanytarsini	88	58	60	41	36	
Orthocladiinae	33	37	28	26	69	
Other insects	88	39	29	07	72	
All taxa	70	67	50	55	74	

be higher in winter than in summer but more samples are needed to clarify this trend. The numbers of organisms in each sample at a given depth on each date were generally fairly close, especially from July through December, even though the surficial substrates were seldom identical. The potential range of invertebrate density on different substrates was demonstrated by the three 0.2-m^2-quadrat samples at a depth of 2 m on 21 March. Cobble- to boulder-sized rubble on pavement yielded 317 animals; deeply cracked pavement with gravel in the cracks, 641; and unbroken, pitted pavement, 853.

Selkirk

Many of the species collected at Howdenvale were also collected at the Selkirk site. The density of the benthic fauna was similar at both sites in summer but much lower at Selkirk in winter (Fig. 2). The variation in species compositions of replicate samples was greater at the Lake Erie site but the overwhelming abundance of *Gammarus fasciatus* reduced the variation in percentage composition (Table 4). The density of the population of *G. fasciatus* closely paralleled the growth pattern of *Cladophora*, which peaked in late summer when thick mats covered all solid substrates in the study area.

Wave action during autumn storms, followed by ice cover in winter, eliminated the algal mat from the shallowest depth during the cold months of the year.

While the seasonal pattern of variation in species composition of the fauna at Selkirk resembled that at Howdenvale, the abundance of *Gammarus* in summer reversed the pattern of percentage similarity (Table 5).

The samples collected on 19 November suggested that a severe autumn storm the week before had greatly reduced the wave-zone populations of all species. The very motile *G. fasciatus* had possibly reentered the study area during the week following the storm. The shallowest depth sampled seemed to have lost the smallest proportion of its fauna, probably owing to reduced scouring as large waves would have actually broken in somewhat deeper water. Under ice cover in February, most groups had regained their former abundances at the 1- and 2-m depths, but *Gammarus* populations had

TABLE 4. *CC* and *PSc* between replicate samples, at three depths from Lake Huron

	0.4 m		1 m		2 m	
Date	*CC*	*PSc*	*CC*	*PSc*	*CC*	*PSc*
17 April	28	62	28	47	33	76
5 August	—	—	28	94	34	93
19 November	22	75	—	—	21	96
$\bar{X}$					29	88

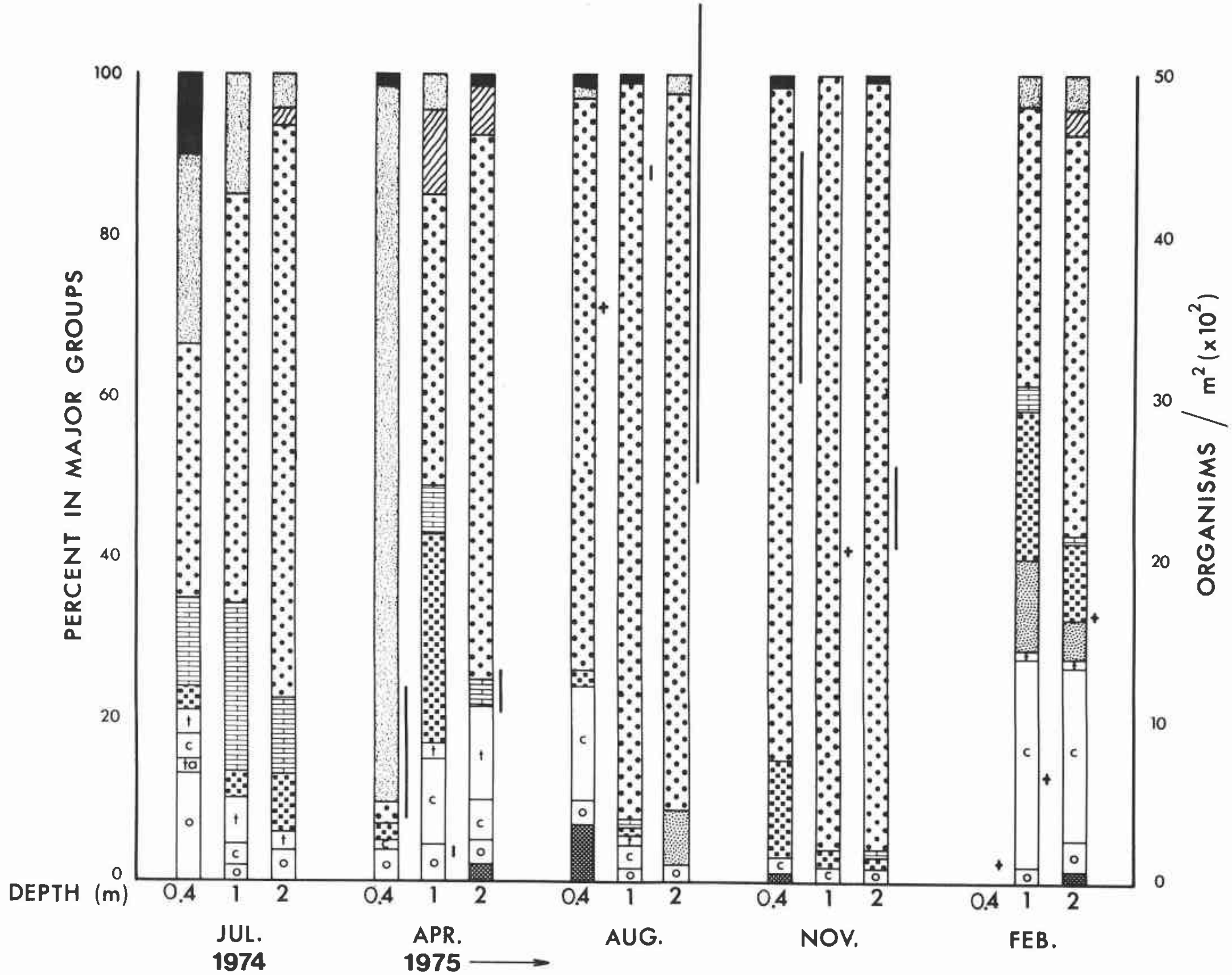

FIG. 2. Community composition expressed as percent of individuals in major groups and estimates of invertebrate density from samples collected at Selkirk, Lake Erie, July 1974 to February 1976. Vertical lines indicate the range of density estimates from two or more samples; (+) indicates single samples. Legend as in Fig. 1.

TABLE 5. *CC* and *PSc* between adjacent sampling dates, at three depths from Lake Huron

	0.4 m		1 m		2 m	
Date	*CC*	*PSc*	*CC*	*PSc*	*CC*	*PSc*
3 July						
	18	9	10	39	31	69
17 April						
	32	4	21	38	22	67
5 August						
	24	75	9	90	19	89
19 November						
	23	10	24	35	31	53
14 February						
$\bar{X}$	24	24	16	50	26	70

continued to decrease and at 0.3 m the abundance of all groups was very low.

The life cycles of the abundant insect species at both Howdenvale and Selkirk were direct, i.e., young larvae appeared soon after adult emergence. None of these larvae underwent diapause, but were active throughout the year (D. R. Barton and H. B. N. Hynes, unpublished data).

Discussion

The seasonal pattern of abundance of the total benthic community at Selkirk resembled that which has been frequently observed along the shores of lakes, namely, summer highs and winter lows. Berg (1938) concluded that these fluctuations were due to migrations by most species in response to changes in temperature, available food, and possibly dissolved oxygen. This does not entirely explain the situation at Selkirk, however, where the differences in the density of invertebrates between sampling dates were almost entirely due to fluctuations in the abundance of *Gammarus*. The abundance of other wave-zone species did not appear to decline, and in some cases (e.g. Tubificidae in April) increased, in the very shallowest water in winter.

Clearly the most important species on solid substrates in the wave zones of lakes Erie and Ontario are *G. fasciatus* and *Cladophora glomerata*. Clemens (1950) found that *G. fasciatus* populations in Lake Erie increased from April through October except for a small decrease in July when overwintering adults died, and then decreased through the winter. The nearly identical annual cycle of *Cladophora* growth in the Great Lakes (Bellis and McLarty 1967; Herbst 1969; Taft and Kishler 1973) suggests that *G. fasciatus* is preadapted to exploit the recent expansion of *C. glomerata* in the lower lakes. Clemens felt that the decline of *G. fasciatus* populations in autumn was the result of the cessation of reproduction brought on by decreasing water temperatures coupled with increased fish predation and sudden temperature changes during storms. Our data suggest that the autumn decline within the wave zone is more directly linked to the elimination of optimum habitat when the algal mats are detached by storm waves. The algal mats appear to be important to *Gammarus* (and other invertebrates) in that they greatly increase the available surface area for attachment and the food supply in the form of epiphytic diatoms and invertebrates as opposed to serving as a direct source of food. Indeed, with the exception of *Sigara* sp. (Kosluscher and Minshall 1973), no invertebrates have been reported to feed directly on *Cladophora* in significant amounts.

The lack of significant differences in the abundance of the nonamphipod fauna at Selkirk during different seasons may be the result of the small number of samples collected. The relatively low mean *CC* value (27.7) with the much higher mean *PSc* value (77.6) for all replicate samples indicates that the 0.2-m^2 sample size used was inadequate for reliably estimating the number of species present, but gave a good estimate of the percentage abundance of the commoner species, especially in summer and at the 2-m depth.

At Howdenvale, the more diverse fauna was apparently more evenly distributed spatially at each depth (mean $CC = 51.5$ for all replicate samples). The samples revealed a seasonal pattern of total faunal abundance similar to that in streams (reviewed by Hynes 1970; also see MacKay and Kalff 1969; Williams and Hynes 1974) of maximum densities in early winter. Our total density estimates were similar to those reported on similar substrates in Lake Erie by Krecker and Lancaster (1933) and Shelford and Boesel (1942) (within limits imposed by the sampling techniques used in those early studies) and in Alberta streams by Radford and Hartland-Rowe (1971*b*), but much lower than in more productive streams such as those studied by Barber and Kevern (1973) and Williams and Hynes (1974).

Considering the results of studies of the vertical distribution of invertebrates in the substrate of streams (Coleman and Hynes 1970; Radford and Hartland-Rowe 1971*a*; Hynes 1974), it is apparent that the density of the invertebrate fauna at Howdenvale, and to a lesser extent at Selkirk, is limited by the shallowness of the inhabitable substrate. It should be noted that wide and rather sudden fluctuations in invertebrate standing stocks at the substrate surface, commonly observed in streams because of the upward migration of one or several species, were not recorded in this study in bedrock areas. Much of the variability between samples from unconsolidated substrates in our 1974 survey may be the result of such migrations. Also noteworthy is the fact that none of the common insect species at Howdenvale appeared to spend any considerable portion of the year in diapause, especially as larvae. These observations suggest that species which require deep substrates for some part of their development cannot survive on exposed bedrock lakeshores, but those which are active through most of the year may be successful.

In general then, a sampling effort sufficient to collect most of the invertebrate species present on any given date (except in midsummer) on predominately bedrock substrates along the shores of the Great Lakes would probably yield most of the species present at any other time of the year. Both the relative and absolute abundance of those species, however, may vary considerably with season, especially from May through September. It appears that a greater sampling effort is needed to estimate the total number of species inhabiting *Cladophora*-covered substrates, but less effort is required to estimate the percentage composition of the fauna. On bedrock substrates in the wave zone of Lake Erie, summer sampling indicates very high levels of invertebrate production while winter collections suggest much lower levels. In bedrock areas which are less physically variable at different seasons, standing stocks are more uniform year-round.

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BARBER, W. E., and N. R. KEVERN. 1973. Ecological factors influencing macroinvertebrate standing crop distribution. Hydrobiologia, **43**: 53–75.

BELLIS, F. J., and D. A. MCLARTY. 1967. Ecology of *Cladophora glomerata* (L.) Kutz in southern Ontario. J. Phycol. **3**: 57–63.

BERG, K. 1938. Studies on the bottom animals of Esrom Lake. K. Dan. Vidensk. Selsk. Naturvidensk. Math. Afd. **9**: 1–255.

BRINKHURST, R. O. 1974. The benthos of lakes. MacMillan, London.

CLEMENS, H. P. 1950. Life cycle and ecology of *Gammarus fasciatus* Say. Contrib. J. Theodore Stone Lab. No. 12.

COLEMAN, M. J., and H. B. N. HYNES. 1970. The vertical distribution of the invertebrate fauna in the bed of a stream. Limnol. Oceanogr. **15**(1): 31–40.

DE MARCH, B. G. E. 1976. Spatial and temporal patterns in macrobenthic stream diversity. J. Fish. Res. Board Can. **33**: 1261–1270.

HERBST, R. P. 1969. Ecological factors and the distribution of *Cladophora glomerata* in the Great Lakes. Am. Midl. Nat. **82**: 90–98.

HYNES, H. B. N. 1970. The ecology of running waters. University of Toronto Press, Toronto.

JOHNSON, M. G., and R. O. BRINKHURST. 1971. Associations and species diversity in benthic macroinvertebrates of Bay of Quinte and Lake Ontario. J. Fish. Res. Board Can. **28**: 1683–1697.

KOSLUCHER, D. G., and W. G. MINSHALL. 1973. Food habits of some benthic invertebrates in a northern cool-desert stream (Deep Creek, Curlew Valley, Idaho–Utah). Trans. Am. Microsc. Soc. **92**(3): 441–452.

KRECKER, F. H., and L. Y. LANCASTER. 1933. Bottom shore fauna of western Lake Erie: a population study to a depth of six feet. Ecology, **14**: 79–93.

MACKAY, R. J., and J. KALFF. 1969. Seasonal variation in standing crop and species diversity of insect communities in a small Quebec stream. Ecology, **50**(1): 101–109.

RADFORD, D. S., and R. HARTLAND-ROWE. 1971*a*. Subsurface and surface sampling of benthic invertebrates in two streams. Limnol. Oceanogr. **16**(1): 114–120.

——— 1971*b*. A preliminary investigation of bottom fauna and invertebrate drift in an unregulated and a regulated stream in Alberta. J. Applied Ecol. **8**(3): 883–903.

SHELFORD, V. E., and M. W. BOESEL. 1942. Bottom animal communities of the island area of western Lake Erie in the summer of 1937. Ohio J. Sci. **42**: 179–190.

TAFT, C. E., and W. J. KISHLER. 1973. *Cladophora* as related to pollution and eutrophication in western Lake Erie. Water Resources Center, Ohio State University Project Completion Report No. 332X, 339X.

WILHM, J. 1972. Graphic and mathematical analyses of biotic communities in polluted streams. Annu. Rev. Entomol. **17**: 223–252.

WILLIAMS, D. D., and H. B. N. HYNES. 1974. The occurrence of benthos deep in the substratum of a stream. Freshwater Biol. **4**: 233–256.