Differences in Littoral Fauna Due to Fluctuating Water Levels Below a Hydroelectric Dam

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Water level fluctuations below a hydroelectric dam on the Connecticut River produce a freshwater "intertidal" zone. Along a transect in this zone from high to low water mark benthic invertebrates increased markedly in density and taxonomic diversity. Community composition shifted from chironomid–oligochaete predominance on the most exposed sites to mollusc predominance on the least exposed sites.

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Les fluctuations du niveau de l'eau en aval d'un barrage hydroélectrique dans la rivière Connecticut produisent une zone "intertidale" d'eau douce. La densité et la diversité des animaux benthiques augmentent notablement le long d'une coupe transversale entre les haut et bas niveaux dans cette zone. La prédominance chironomides–oligochètes des communautés les plus exposées fait place à celle des mollusques aux endroits les moins exposés.

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THIS note describes benthic macroinvertebrate communities on periodically exposed substrates below a hydroelectric dam on the Connecticut River in central Massachusetts.

Hydroelectric dams have transformed the Connecticut River from its original free-flowing state to a stair-step series of long narrow ponds. Hydroelectric power generation is often not continuous, but generally occurs only during hours of high power demand (1000–2000 hr). During daytime, water levels rise above dams and fall below. At night, sluice gates are closed, ponds fill, and the water level below dams drops. Fluctuating water levels are most pronounced during summer and early autumn months, when the natural flow of the river is low and no water at all may be released for up to 14 hr per week day and nearly 42 hr on weekends (U.S. Geological Survey discharge data).

Water level fluctuations of this sort are responsible for the periodic exposure of the littoral zone, producing a freshwater "intertidal" zone which is somewhat analogous to the marine "intertidal." The "intertidal" zone of rivers differs from its marine counterpart in that 1) the tidal period is irregular, but usually diel, 2) the medium is fresh rather than salt water, 3) degree of exposure is related to season, being most pronounced during summer, and 4) the zone is of recent origin, so that sufficient time has not elapsed to allow the evolution of a well-adapted indigenous fauna.

While some workers have studied the fauna of freshwater systems subjected to periodic drying, such as vernal ponds (Hoff 1943), intermittent streams (Moon 1956), and lacustrine shoreline zones subjected to periodic flooding (Moon 1935), none of these systems has tidal periods shorter than one month. In most cases, the period is annual.

Materials and methods — Our primary sampling site was a bar 425 m long and approximately 70 m wide located 10 km below the Turner's Falls dam in Montague, Mass. The bar is completely submerged during periods of high discharge and is exposed during low flow. Tidal amplitude is approximately 1.0 m at the bar and 2.0 m immediately below the dam. Substrate is a uniform mixture of sand and gravel, approximately equally divided by weight into 0–1, 1–5, and >5 cm diameter size classes. The organic content of the substrate (loss on ignition) is 0.2% by weight or about 3.8 g/m^2. Vascular plants are rare on the bar. Attached algae were not studied.

A transect running from the high water mark past the low water mark was established and divided into four zones, designated 1–4, which were exposed 70, 40, 13, and 0% of the time in summer, respectively. Macroinvertebrates in each zone were sampled semi-monthly from July to mid-September, 1971, with a 500 cm^2 cylindrical metal sampler (Whitley 1962). The sampler was pushed 10 cm into the substrate and the sediment within the sampler was removed, then taken to the laboratory for sorting and analysis. One sample was taken at each site on each sampling date. Large molluscs were sampled separately by means of a series of ten 50 m^2 circular plots per zone.

All samples were sorted by elutriation (Lauff et al. 1968). Only those organisms retained on a 0.5-mm mesh screen were processed. Animals were identified to genus where possible, using standard keys (Ward and Whipple 1959, Pennak 1953). Standing crop data for five sampling dates were averaged to yield mean summer standing crops for each zone on the transect. Biomass (ash-free dry weight) of selected faunal categories was computed as the difference between oven dry weight (95 C for 24 hr) and weight of ash (550 C for 2 hr).

While only one transect was sampled in this study, the bar is very homogeneous in appearance and is similar to other bars in this section of the river. Selected quantitative samples taken at other sites on the bar were similar in composition to samples taken from our transect, which suggests that our transect is representative of the habitat which we purport to describe.

In order to determine the vertical distribution of organisms in the substrate, the fauna was also sampled by allowing buried metal cylinders (cans 17.5×10.5 cm) to become colonized over two 4-week periods (July–September). Cylinders were filled with substrate from zone 1 and were placed in the other zones in pairs. Top and bottom halves of the cans were sorted separately to determine the vertical distribution of the fauna and to evaluate the efficiency of our primary sampling method. Coleman and Hynes (1970) performed similar experiments on inundated substrates in the Speed River, Ont., and found no diminution of invertebrate numbers to a depth of 30 cm in the sediments. Our results, however, indicated that approximately 81% of the organisms on our transect were distributed in the upper 7.5 cm of sediment. The numbers per m^2 and the percentages in the upper 7.5 cm in the various zones were:

Zone	1	2	3	4	Total
Number/m^2	1689	1020	2243	9277	3557
Percent in upper 7.5 cm	94	71	66	91	81

Since we sampled to a depth of 10 cm, we feel we removed the bulk of organisms present at our sites.

Results and discussion — Our results clearly show that benthic invertebrate communities of periodically exposed areas were lower in density and diversity than communities in continuously flooded areas. Pronounced increases in diversity, biomass, numbers, and number of taxa occurred from zones 1–3 (Fig. 1). Zone 4, which was never exposed, was not significantly different from zone 3, which was exposed 13% of the time. This suggests that the benthic community may tolerate brief periods of exposure without significant change. The greatest discontinuity occurred between zones 3 and 2, where biomass was reduced by an order of magnitude (Table 1). Much of this change in biomass can be attributed to the intolerance of unionid molluscs to exposure.

The discontinuity between zones 2 and 3 can also be documented by changes in community composition (Table 2). With the exception of chironomids, insects were extremely rare in zones 1 and 2. Those insects which were present were probably washed onto the site during periods of inundation. *Amnicola*

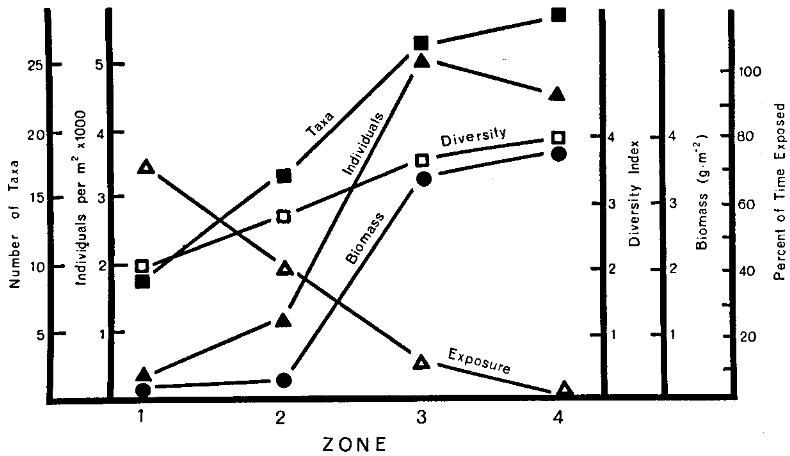

FIG. 1. Distribution of benthic macroinvertebrates along transect in the Connecticut River.

TABLE 1. Mean standing crops (Grams ash-free dry weight/m²) of selected faunal categories along the Connecticut River transect. Values in lower rows are percentages of total biomasses in the various zones.

Taxon	Zone 1	2	3	4
Mollusca				
Amnicola sp.	–	0.14	2.0	1.3
	<1	36.7	56.1	35.2
Gyraulus sp.	0	0.10	0.15	0.07
	0	26.0	4.3	1.9
Lampsilis sp.	0	0	0.92	1.8
	0	0	26.4	49.1
Pisidium sp.	–	0.001	0.008	0.006
	<1	0.2	0.2	0.2
Ligumia sp.	0	0	0.15	0.25
	0	0	4.4	6.5
Total	–	0.24	3.2	3.4
	<1	62.9	91.4	92.9
All other taxa	0.11	0.14	0.30	0.26
	99	37.1	8.6	7.1
Total biomass (g/m²)	0.11	0.38	3.5	3.7

sp. was the only mollusc found in significant numbers in zones 1 and 2. In zones 3 and 4, molluscs predominated, comprising over 90% of the biomass and approximately 68% of the numbers present. *Lumbricus terrestris* was collected only in zones 1 and 2. Our transect, therefore, had characteristics of a terrestrial–aquatic continuum.

It is unlikely that stable, productive freshwater communities can become established in the periodically exposed biotope, the marine analogue of which is highly productive. Fluctuating water level ecosystems are often productive and attain a high degree of "pulse stability" provided that the community present is adapted to the frequency and magnitude of fluctuation present (Odum 1969). This degree of adaptation requires time measurable on the evolutionary time scale. Sufficient time has not been available for the evolution of complex communities suited to this freshwater intertidal biotope — a recent artifact of Man's activities.

Alteration of shallow water habitats is a cost which must be evaluated when assessing the environmental impact of water level manipulation

TABLE 2. Check list and numbers/m² of "intertidal" fauna along transect. Each number in parentheses indicates the percentage of the total community in each zone represented bk the given taxon.

Taxon	Zone[a] 1	2	3	4
Platyhelminthes				
Dugesia sp.	0	0	44(0.8)	76(1.6)
Rhabdocoela[b]				
Nematoda	26(6.7)	376(30)	56(1)	84(1.8)
Sp. 1	13	340	28	60
Sp. 2	13	36	28	24
Annelida	207(54)	36(2.8)	309(5.9)	482(10.4)
Oligochaeta				
Sp. 1	7	16	112	68
Sp. 2	187	4	172	324
Sp. 3	0	0	20	48
Lumbricus terrestris	13	16	0	0
Hirudinea				
Helobdella sp.	0	0	5	12
Arthropoda	134(35)	600(47)	980(19)	1124(24.2)
Hydracarina	0	0	52	12
Cladocera	0	0	4	4
Amphipoda				
Hyallela azteca[b]				
Odonata				
Gomphus sp.	0	0	4	0
Coleoptera				
Anchycteis sp.	0	4	8	20
Agabus sp.	0	4	0	0

(*Continued*)

TABLE 2. Check list and numbers/m² of "intertidal" fauna along transect. Each number in parentheses indicates the percentage of the total community in each zone represented by the given taxon. — *(Concluded)*

Taxon	Zone[a] 1	2	3	4
Neuroptera				
Climacia areolaris[b]				
Ephemeroptera				
Stenonema sp.	0	0	0	12
Ephemerella sp.	0	0	20	24
Tricorythodes sp.	7	0	76	156
Caenis sp.	0	0	12	4
Paraleptophlebia sp.[b]				
Ephoron sp.	0	0	0	4
Trichoptera				
Limnephilus sp.	0	4	4	20
Molanna sp.	0	0	0	4
Hydropsyche sp.[b]				
Lepidostoma sp.	0	0	0	4
Cheumatopsyche sp.	0	0	12	48
Tascobia sp.	0	0	4	0
Orthotrichia sp.	0	0	4	4
Unidentified pupae	0	0	16	16
Rhyacophila sp.[b]				
Diptera				
Tipulidae				
Erioptera sp.	0	4	0	0
Pedicia sp.	0	8	0	0
Helius sp.	0	8	0	0
Antocha sp.	0	12	0	0
Chironomidae	127	556	764	792
Simuliidae[b]				
Mollusca	20(5.2)	256(20)	3884(74)	2880(62)
Gastropoda				
Physa sp.	0	8	4	12
Gyraulus sp.	0	4	52	28
Ferrissia sp.	0	0	220	228
Amnicola sp.	13	240	3520	2524
Pelycypoda				
Sphaeridae				
Pisidium sp.	7	4	52	36
Sphaerium sp.[b]				
Musculium sp.[b]				
Unionidae				
Lampsilis sp.	0	0	32	52
Ligumia sp.	0	0	0.23	0.37
Anodonta sp.	0	0	4	0
Elliptio sp.[b]				
All taxa	387	1268	5273	4646
Total taxa present	9	17	27	29
Total individuals[c]	58	318	1318	1168
Diversity index[d]	1.97	2.78	3.62	3.96

[a]Percent exposure times by zone: 1, 70%; 2, 41%; 3, 13%; 4, 0%.
[b]Taxa present but not collected in quantitative samples.
[c]Absolute number of individuals collected (for diversity computations).
[d]Taxonomic diversity index (D) = $(S-1)/\log_e N$, where S = number of taxa present and N = number of individuals.

programs. The total cost must of course be assessed in terms of the entire river ecosystem. Our study treated only a portion of the system — the benthic invertebrates of exposed areas. The significance of this effect on the whole ecosystem is a function of the total area exposed, which in turn depends upon channel morphometry. While we do not know the area of the Connecticut River which is periodically exposed, approximately half of the 400 linear miles of the river is subjected to periodic drawdown. Effects of water level fluctuations should also be assessed in terms of primary and secondary productivity, fish migration and spawning behavior, sedimentation rates, waste assimilation capacity, and other whole system properties.

The problem of periodic exposure could be partially alleviated by low flow augmentation — the storage of spring runoff and its subsequent release during periods of low discharge. This remedy, however, trades main stem littoral stability for instability elsewhere, e.g. tributary reservoirs. Furthermore, restoration of mean historical discharge rates is effected at the expense of the whole riverine ecosystem (Brower 1971). Finally, while water level fluctuations induced by main stem hydroelectric generation can be minimized by a modified program of low flow augmentation, the problem will persist and, in fact, intensify, if pumped storage systems proliferate in the drainage basin.

In summary, our data clearly show that water level fluctuations resulting from conventional hydroelectric power generation may prevent the establishment of normal benthic invertebrate communities on periodically exposed areas. The total environmental cost of this practice should, however, be assessed in the context of the entire riverine ecosystem.

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