Habitat requirements of burrowing mayflies (Ephemeridae:*Hexagenia*) in lakes, with special reference to the effects of eutrophication

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Abstract. *Hexagenia* nymphs are large sediment burrowers that are sensitive to hypoxia. Major declines in some lake populations have been attributed to reduced concentrations of dissolved oxygen near the substrate resulting from eutrophication. This study was carried out on lacustrine populations of *Hexagenia* in the Quebec Eastern Townships (81 sampling sites in 12 lakes). It quantifies the suitability of littoral and sublittoral lake habitats for *Hexagenia* by means of discriminant functions that classify sites, with and without these larvae, in terms of a number of variables that are thought to be related to both sediment oxygen demand, and oxygen supply to sediments. These environmental variables include sediment oxidation-reduction potential, sediment water content (a surrogate of particle size), water column chlorophyll *a* concentration (a measure of lake trophic status), aquatic macrophyte biomass, and two morphometric parameters that reflect the physical energy regime (site exposure, and bottom slope). The biomass of *Hexagenia* was also related, by multiple regression analysis, to the environmental variables. The predictions from the habitat suitability models (discriminant functions and multiple regression models) were compared with independent data from the literature on the distribution and abundance of *Hexagenia*, and found to predict both presence/absence and biomass reasonably well. Furthermore, the models support the contentions made by previous authors that dramatic declines in lacustrine *Hexagenia* populations are the result of eutrophication. In addition, the suitability of a site for *Hexagenia* was positively related to bottom slope and exposure to waves at the site, and negatively related to the abundance of submerged macrophytes, especially when high macrophyte biomass was developed near the substrate.

Key words: *Hexagenia*, habitat requirements, empirical modelling, eutrophication, population declines, macrophyte biomass, sediment redox potential, sediment water content, slope, wave-exposure.

Hexagenia nymphs are among the largest benthic animals from the littoral and sublittoral zones of lakes, and are consumed with high selectivity by perch, walleye, whitefish, and other epilimnetic fish (Clady and Hutchinson 1976, Clemens et al. 1923, Cooper 1941, Johnson 1977, Klaassen and Marzolf 1971, Ryder and Kerr 1978). Some of the best rates of growth for yellow perch (Hayward and Margraf 1987), walleye (P. J. Colby, Ontario Ministry of Natural Resources, personal communication), drum (Swedberg 1968), and white crappie (Siefert 1969) have been associated with high consumption of *Hexagenia* nymphs. Therefore these nymphs can be of considerable importance to energy flow, and knowledge of their habitat requirements is of great importance to lake and fisheries management.

Although *Hexagenia* populations are widespread throughout east-central North America, their abundance in lakes is highly variable. The life-history and population dynamics of *H. limbata* has been described many times (Craven and Brown 1969, Horst and Marzolf 1975, Riklik and Momot 1982, Rutter and Wissing 1975, Schloesser and Hiltunen 1984), but little attention has been paid to the factors underlying the large lake-to-lake variability in abundance. Knowledge of habitat requirement of *Hexagenia* is therefore sketchy despite a considerable number of site-specific studies.

Major declines in some *Hexagenia* populations have been reported (Beeton 1961, 1969, Britt et al. 1973, Jacobsen 1966, Mills et al. 1978), and attributed to reduced bottom dissolved oxygen (DO) concentrations resulting indirectly (during decomposition) from increased biomass of phytoplankton (eutrophication). Because these nymphs are highly sensitive to hypoxia (Eriksen 1963a, 1963b, Hunt 1953, Jacobsen 1966) this hypothesis is plausible, but how consistent it is with other data on the abundance of *Hexagenia* has not been established.

Hexagenia nymphs burrow within the top few centimeters of sediment, and thus it is difficult to assess directly the DO concentration avail-

able to them. Sediment can become deficient in DO owing to aerobic decomposition, and owing to chemical oxygen demand (COD) by reducing substances (S^-, Fe^{++}, NH_4^+, and others), some of which are products of microbially mediated anaerobic decomposition (Brock 1966, Mortimer 1941, 1942, Hutchinson 1957). The ability of hypoxia-sensitive animals to survive in such sediments is largely contingent on their ability to ventilate their burrows by undulatory body movements (Eriksen 1963a, 1963b). They must then "import" sufficient oxygenated water to satisfy their own respiratory demand and to offset the COD of their immediate environment. In addition, ventilatory behavior of benthic nymphs also helps clear directly toxic reducing substances such as sulphide, ammonia, and hydroxylamine (Ikeshoji 1973, 1974). Sediment redox potentials (Eh) are platinum electrode potentials that are influenced by a number of redox systems including oxygen, iron, manganese, sulphur, and others (Stumm and Morgan 1981), and are thus composite measures that reflect the degree of balance between oxidizing and reducing processes (Hutchinson 1957). Thus sediment Eh could prove to be a good indicator of the suitability of sediment conditions for *Hexagenia*. Because sediment is more dense and cohesive than water, and diffusion rates are very slow (Håkanson and Jansson 1981), sediment Eh is more stable temporally and less prone to disruption by probes than is the DO concentration at the sediment-water interface. DO at this interface in the mixing zone of lakes can exhibit a steep microstratification gradient that is virtually impossible to measure without disruption (Brundin 1951, Hutchinson 1957).

A number of limnological variables would be expected to influence the balance between the oxygen demand and the DO supply in sediments, and thus should be determinants of sediment Eh. Oxygen demand in sediments should increase with the biomass of phytoplankton (lake trophic status) and aquatic macrophytes; and the residence time of decomposing organic matter at the sediment-water interface should be greatest where bottom slope and exposure to waves is low. The DO supply should decrease with depth, and increase with wave exposure and bottom slope. The last two factors are related to the exchange of physical energy between water and sediment (Håkanson and Jansson 1983). Thick stands of submerged macrophytes

also reduce mixing, and therefore DO concentrations, at the sediment-water interface (Carpenter and Lodge 1986).

This study tests the hypothesis that habitat suitability for *Hexagenia* nymphs is adversely affected by factors that increase the accumulation of oxygen-demanding substances in the sediment. Low redox potentials in the sediment should indicate an unsuitable habitat. Factors influencing the balance between oxidizing (DO supply) and reducing processes (phytoplankton sedimentation, depth, exposure, slope and macrophyte abundance) should be useful in predicting which sediments can support *Hexagenia*, and perhaps could even predict *Hexagenia* abundance. This hypothesis was tested by linear discriminant analysis and multiple regression on data collected from littoral and sublittoral sites in twelve lakes of the Quebec Eastern Townships. The results were used to develop a multi-factorial habitat model for *Hexagenia* which was validated by comparing its predictions of *Hexagenia* biomass to estimates obtained from the literature.

Methods

All ephemerid nymphs were identified as *Hexagenia limbata* using McCafferty (1975) and Burks (1955).

Eighty-one sampling sites ranged in depth from 1.5 to 12 m. Forty-one sites were in Lake Memphremagog, a dimictic, oligo- to mesotrophic lake on the Quebec-Vermont border, which varies greatly in morphometry and wind exposure along its 45-km length (Duarte and Kalff 1986). The remaining 40 sampling sites were in 11 smaller lakes in the Eastern Townships, Quebec (Appendix 1). These lakes ranged from oligo- to highly eutrophic, and presented a broad range of physical and chemical characteristics (Rasmussen 1988). Sites were chosen to maximize the range of slope, sediment water content (a surrogate of particle size, Håkanson 1977), sediment Eh, and phytoplankton biomass (mg/m^3), as well as the range of combinations between variables, to minimize collinearity. The sites in Lake Memphremagog were sampled monthly from September to October 1984 and from May to August 1985. The other lakes were sampled from May to October 1985.

Fifty-nine of the stations were within the littoral zone (depth < Secchi transparency). These

sites either contained submerged macrophytes or had coarse sediments, both of which interfere with successful operation of an Ekman grab. At these sites the *Hexagenia* nymphs were sampled with 40-cm² plexiglass core tubes pushed 20 cm into the sediment (or as far as sediment thickness permitted) by a SCUBA diver. The core tubes were fitted on top and bottom with plugs to prevent loss of animals. Five of these cores were taken at each station on each of the six sampling dates. The 22 sublittoral stations had softer sediment and no plants. At these stations, three Ekman grab samples (15 × 15 cm) were taken on each date for a total of 18 at each site. Mayfly nymphs from the cores and Ekman grabs were retained by a 0.2-mm screen and were preserved in 5% formalin. Wet weights of blotted larvae were measured to the nearest 0.1 mg. The mean biomass of *Hexagenia* (HBM) was estimated for each site by averaging over the six sampling times.

At each site, slope was measured by echo-sounding along a transect perpendicular to shore as described by Duarte and Kalff (1986). The index of exposure was calculated (on 1:25,000 or 1:50,000 maps) as the contour (circular) integral of the fetch ($\oint$ Fdθ, where F = fetch, or distance to nearest shoreline (Håkanson 1981) for a given angle θ). This circular integral describes the area exposed (or visible) from the sampling site.

Sediment measurements were obtained from undisturbed sediment cores that were obtained by SCUBA diving, capped, and brought directly to the surface. Oxidation-reduction potential (Eh) was recorded by inserting a clean platinum electrode 5 cm into the sediment, and waiting (sometimes several minutes) for readings (mV) to stabilize. Three different core measurements were averaged for each estimate. This procedure was carried out at each site in August and September 1985, and the two estimates were averaged. Cores from the Lake Memphremagog sites were measured again in June 1986, and the estimates obtained were similar to the 1985 values.

Sediment water content (%) was estimated as a surrogate for sediment grain size since fine sediments contain a much higher percentage of water than do coarse sediments (Håkanson and Jansson 1981). A 50-ml sample of wet sediment was weighed and then reweighed after drying at 60°C. The weight lost on drying was then divided by the wet weight of the sample to estimate percent water. This measurement was done five times at each site and averaged.

Forty-seven of the 81 stations contained measurable (>0.05 kg/m² wet weight) quantities of submerged macrophytes. The total biomass of submerged macrophytes was estimated at each of these stations on each sampling date by quadrat sampling. The quadrat, a steel frame enclosing 0.1 m², was tossed from a boat to randomize exact sampling locations with respect to local variability in plant density. A SCUBA diver then removed and bagged the macrophytes that were rooted within each quadrat (5 on each sampling date). The cores for estimating mayfly biomass and sediment water content were taken adjacent to the plant quadrats. The plants were rinsed under running water and weighed fresh, after excess water had been removed in a salad spin-dryer. The estimate of plant biomass for each site was obtained by averaging over the six sampling times. The height of the plant canopy was measured from echo-sounding traces taken at each site.

A number of water quality parameters were also measured at each site. For the littoral stations, these measurements were taken beyond the weed bed so that macrophytes would not interfere with the water column sampling. Conductivity (μS/cm, 25°C), water colour (mg/L Pt as determined by absorbance at 440 nm), Secchi disk transparency (m), and the concentration of chlorophyll *a* were the measurements taken. These estimates were also averaged over all sampling times.

Linear discriminant analysis (SAS) was used to study the relationship between the presence or absence of *Hexagenia* and the environmental factors. Owing to collinearity between the environmental factors, two sets of discriminant functions were developed. The first related the presence/absence of *Hexagenia* to sediment Eh, the chlorophyll concentration (μg/L)$^{0.5}$, and the slope of the bottom (log % slope). The second set of predictors used was the chlorophyll concentration, the slope of the bottom (log % slope), and the exposure estimated for the site (log km²). The ability of the discriminant functions to distinguish between sites with and without *Hexagenia* was assessed by means of a chi-square test on the Wilks' lambda statistic, and the misclassification proportions for both categories are presented.

TABLE 1. Comparison of habitat characteristics for sites where *Hexagenia* were found (H+) to sites where it was not (H−).

Habitat Characteristic	H+ ($n = 57$)			Significant Level of Difference	H− ($n = 24$)		
	Average (1 SE)	Minimum	Maximum		Average	Minimum	Maximum
Sediment Eh (mV)	−94.4 (8.32)	−188	+70	$p < 0.001$	−225 (7.25)	−295	−175
Water column chlorophyll *a* (μg/L)	4.33 (0.32)	1.3	11.0	$p < 0.001$	10.21 (1.43)	3.1	24.0
Secchi disk transparency (m)	4.5 (0.7)	3.0	8.0	$p < 0.05$	2.5 (0.5)	0.9	4.0
Depth (m)	4.41 (0.37)	1.5	10.0	n.s.	4.89 (0.63)	1.0	11.0
Plant biomass (kg/m²)	0.29 (0.04)	0.00	1.61	$p < 0.005$	0.92 (0.20)	0.00	3.05
Plant biomass/plant height (kg/m²)	0.46 (0.052)	0.00	1.07	$p < 0.001$	1.33 (0.18)	0.00	4.35
Slope of bottom (%)	6.45 (0.79)	0.5	25.0	$p < 0.001$	1.74 (0.58)	0.10	11.0
Exposure (km²)	8.93 (1.12)	0.17	35.8	$p < 0.005$	3.53 (1.04)	0.09	22.0
Water colour (mg Pt/L)	6.0 (1.03)	0	31	n.s.	11.8 (2.5)	3	38
Sediment water content (%)	48.8 (2.27)	15	83	$p < 0.001$	77.7 (2.41)	43	91
Conductivity	98 (8.1)	47	265	n.s.	105 (9.5)	65	140

Multiple linear regression was used to study the relationship between *Hexagenia* abundance and a series of hypothesized predictors. The model tested was log(HBM + 0.1) vs. chlorophyll $a^{0.5}$, water colour, depth$^{0.5}$, plant biomass/plant height, log slope (%), log exposure, and a slope × exposure interaction term. The same regression was also tested without the plant biomass variable in order to provide a model that could provide predictions of HBM for situations where information on plant abundance was not available. All variables retained were significant at $p < 0.01$. Sediment Eh was not tested in this model since it was found to have high multicollinearity with the other predictors in the model. This was tested by regressing sediment Eh against the above predictors. Sediment water content was strongly collinear with exposure and slope, and was thus tested in place of these variables and their interaction term. Plant biomass/plant height (kg/m³) was tested in place of plant biomass (kg/m²). In this way variable combinations that resulted in serious collinearity problems (Belsley et al. 1980, Wilkinson 1986) were avoided.

When HBM was the dependent variable, the estimated detection limit, 0.1 g/m², was added to remove zero values and permit log transformation. Log$_{10}$(HBM + 0.1) produced good linear fit, and homoscedastic normally distributed residuals in all of the models tested. Independent variables were transformed when necessary (Box and Tidwell 1962) to meet the requirements of linear regression.

Estimates of *Hexagenia* abundance from the literature that could be associated with limnological data and bathymetric maps were used to test predictions of models generated from this study. Data on western Lake Erie (island area, depth 10 m) were obtained from Beeton (1961, 1969), Britt et al. (1973), Brydges (1971a, 1971b), Carr and Hiltunen (1965), Chandler and Weeks (1945), Loehr et al. (1980), Veal and Osmond (1968), Vollenweider et al. (1974), and Wood (1963). Pre-1968 chlorophyll *a* concentrations for Lake Erie were estimated from total phosphorus values (Beeton 1961, 1969, Chandler and Weeks 1945) using a phosphorus–chlorophyll regression for the lake (Brydges 1971a). Data on Saginaw Bay (center of the inner bay, depth 5 m) were from Beeton (1957), Bierman (1980), Bierman et al. (1984), Glooschenko et al. (1973), Schneider et al. (1969), and Schuytema and Powers (1966). Pre-1970 chlorophyll *a* values for Saginaw Bay were estimated from the total phosphorus using the phosphorus and chlorophyll data of Bierman (1980) and Bierman et al. (1984). Data on Green Bay were from Allen

(1973), Beeton (1969), and Rousar and Beeton (1973). Data on Oneida Lake (central part average of 6-, 8-, and 12-m stations) were from Mills et al. (1978), and Clady and Hutchinson (1976). Pre-1966 chlorophyll values from this lake were estimated from the regression of Rasmussen and Kalff (1987) using Secchi transparency, colour, and conductivity as predictors. Data on Savanne Lake (lake average, mean depth of sites 3.2 m) were from P. J. Colby (personal communication), Riklik and Momot (1982), and Sandhu (1979); on Brandenburg Pond (sites of 1.5- and 2-m depth) from Rutter and Wissing (1975); on Lake Winnipeg (south basin average, mean depth 5 m) from Flannagan (1977) and Janus and Vollenweider (1981); on Simcoe Lake (averages for 2-, 7-, 12-, and 17-m depth zones) from Rawson (1930) and Janus and Vollenweider (1981); on Batchawana Bay (Lake Superior) (average for 10-m depth) from Dermott (1984) and Janus and Vollenweider (1981); on Otsego Lake (averages for 6-, 8-, and 10-m depths) from Harmon and Sohacki (1978); and on a series of lakes from Maine from Davis et al. (1978). Slope and exposure were estimated from published maps. Although the exposure estimates were obtained with the same integration method used for the Quebec lakes when individual sites were specified, the slopes obtained from the bathymetric maps were, of course, somewhat cruder than those measured by echosounding in the Quebec lakes. When data sources provided only average estimates of *Hexagenia* abundance for a basin, or for a depth zone, the corresponding average slopes were estimated. When data sources gave *Hexagenia* abundance only as numbers/m^2, these values were multiplied by 30 mg/larva to yield g/m^2. This was the average wet weight of all the *Hexagenia* larvae collected at the 81 Quebec study sites; it agrees well with the mean value given by Wood (1963) for western Lake Erie. The data on chlorophyll concentration for these lakes, or the other variables that were used to estimate it, were basin averages.

Results

The 81 sites sampled ranged widely in sediment Eh (-295 to $+70$ mV), water column chlorophyll *a* content (1.3 to 24 $\mu g/L$), Secchi disk transparency (0.09 to 8.0 m), submerged plant biomass (0.0 to 3.05 kg/m^2 wet weight), bottom

TABLE 2. Discriminant functions that classify sampling sites that contained *Hexagenia* (H+, $n = 57$) and that did not (H−, $n = 24$) on the basis of habitat characteristics.

a) Classification of H+ and H− on the basis of Eh (mV), water column chlorophyll concentration ($\mu g/L$)$^{0.5}$, and log(% bottom slope).

Linear Discriminant Functions (D)

	D_1	D_2
constant	−15.205	−6.730
Eh	−0.0654	−0.0333
(chlorophyll)$^{0.5}$	+4.586	+3.496
log slope	+2.907	+4.291

Wilks' lambda = 0.377, $\chi^2 = 75.5$, df = 3, $p < 0.0001$
Misclassifications 2/24 for H−; 4/57 for H+

b) Classification of H+ and H− using chlorophyll ($\mu g/L$)$^{0.5}$, log(% slope of bottom), and log(exposure, km^2).

Linear Discriminant Functions (D)

	D_1	D_2
constant	−10.323	−5.565
(chlorophyll)$^{0.5}$	+6.096	+3.849
log slope	−1.653	+1.164
log exposure	−0.0315	+3.160

Wilks' lambda = 0.4222, $\chi^2 = 66.8$, df = 3, $p < 0.0001$,
Misclassifications 3/24 for H−; 5/57 for H+

To predict whether or not a site will contain *Hexagenia*, evaluate both D_1 and D_2. For H+, $D_2 > D_1$, for H−, $D_1 > D_2$.

slope (0.1 to 25%), and exposure (0.09 to 35.8 km^2).

Hexagenia nymphs were found at 57 of these sites. The sites with *Hexagenia* present (H+) differed significantly in many respects from H− sites. H− sites had lower Eh, higher chlorophyll concentrations, lower Secchi disk transparency, lower slopes, less exposure, higher biomass of submerged plants, and sediments with lower water content (Table 1). Depth, conductivity, and water colour were not significantly different between H+ and H− sites; however, between-site variation in water colour and conductivity was only slight relative to the range possible in lakes. Linear discriminant analysis was used to classify H+ and H− sites. Because of collinearities between the variables, they could not all be tested simultaneously. The two best discriminant functions are shown in Table 2. The first discriminates H+

TABLE 3. Matrix of correlation coefficients between variables occurring in regression analyses ($n = 81$).

	Sediment Eh (mV)	Total Zoobenthic Biomass	Plant Biomass $(g/m^2)^{0.5}$	Plant Height (m)	Plant Biomass/ Height	Chlorophyll a $(\mu g/L)^{0.5}$	Exposure area $(km^2)^{0.25}$	Slope $(\%)^{0.5}$	Exposure × Slope	Sediment Water Content	Colour (mg Pt/L)$^{0.5}$	Depth (m)$^{0.5}$
Hexagenia biomass log(g/m² + 0.1)	0.834[c]	−0.094	−0.186	0.287[a]	−0.406[b]	−0.505[b]	0.327[a]	0.544[b]	0.600[b]	0.728[c]	−0.297[a]	−0.228[a]
Sediment Eh	—	−0.123	−0.220[a]	−0.201	−0.365[a]	−0.658[b]	0.323[a]	0.607[b]	0.657[b]	−0.688[b]	−0.327[a]	−0.12
Total zoobenthic biomass		—	0.820[c]	0.620[b]	0.479[b]	0.358[a]	−0.042	0.181	0.133	−0.026	0.170	−0.722[c]
Plant biomass			—	0.641[b]	0.746[c]	0.192	0.262[a]	0.197	0.267[a]	−0.018	0.112	−0.680[b]
Plant height				—	0.074	−0.093	0.056	−0.079	0.055	−0.276	−0.114	−0.693[b]
Plant biomass/height					—	0.189	−0.403[a]	−0.078	−0.238[a]	0.100	0.124	−0.366[a]
Chlorophyll a						—	0.018	−0.334[a]	−0.203	0.335[a]	0.384[a]	−0.190
Exposure area							—	0.053	0.546[b]	−0.279[a]	−0.098	0.203
Slope								—	0.614[b]	0.706[b]	−0.289[a]	−0.154
Exposure × slope									—	0.682[b]	0.227	−0.050
Sediment water content										—	0.304[a]	0.316[a]
Colour											—	−0.197

[a] $p < 0.05$.   [b] $p < 0.01$.   [c] $p < 0.005$.

and H− sites on the basis of sediment Eh, water column chlorophyll a, and bottom slope. The second discriminates on the basis of chlorophyll a, slope, and exposure. Both of these discriminant functions correctly classify over 85% of both H+ and H− sites (Table 2).

The biomass of *Hexagenia* (HBM) ranged from 0.0 to 6.5 g/m² at the 81 sampling sites. For the sites where *Hexagenia* was recorded, the standard error of HBM was 18–34% of its mean value. HBM was strongly correlated with sediment Eh (+) and sediment water content (−), two variables that were themselves negatively correlated. Other variables significantly correlated with HBM were chlorophyll (−), transparency (+), slope (+), exposure (+), the slope × exposure interaction (+), plant biomass/plant height (−), and depth (−) (Table 3).

Although the single variable most strongly correlated to HBM was sediment Eh, the relationship between the two variables was highly non-linear (Fig. 1). *Hexagenia* nymphs were never found at Eh < -190 mV, but when Eh was > -120 mV, they were always found (mean HBM = 2.1 g/m²), and for this Eh range no significant relationship between the two variables was detected. Over the Eh range -190 to -120 mV there was a strong positive relationship between HBM and sediment Eh. Thus the overall pattern is sigmoidal (in fact, almost a step function with a threshold in the Eh range -170 to -140 mV) and the relationship cannot be adequately represented with a linear model. Although sediment Eh made a strong contribution to one of the discriminant functions predicting the presence and absence of *Hexagenia* (Table 2), there was no significant correlation between HBM and Eh for sites with HBM >1 g/m².

In addition to having a complex relationship with HBM, sediment Eh has strong multicollinearity with the other environmental factors tested. It was therefore not included in the multiple regression models predicting HBM. Furthermore, sediment Eh is not often measured in limnological surveys and would thus have limited use as a predictor. When HBM was regressed against a series of limnological predictors other than sediment Eh, a model containing significant contributions from the chlorophyll concentration (−), plant biomass/plant height (−), sediment water content (−), and water depth (−) was obtained (Equation 1, Table 4).
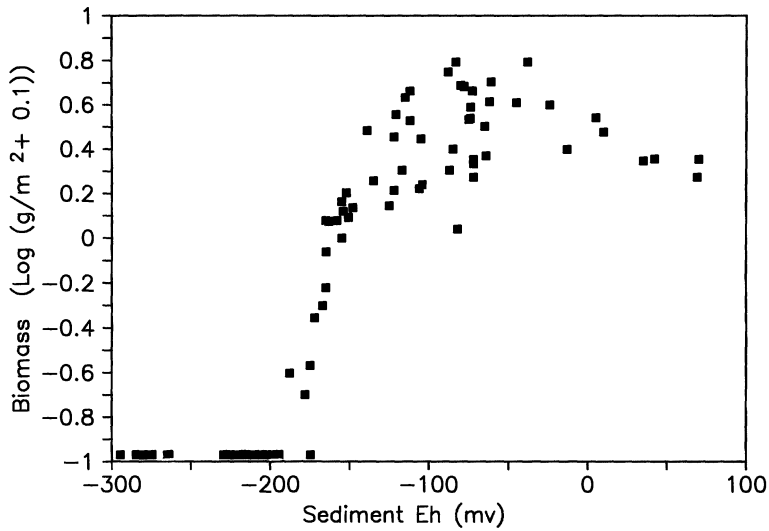
FIG. 1.　*Hexagenia* biomass vs. oxidation-reduction potential of surface sediment at littoral and sublittoral stations in lakes of the Eastern Townships of Quebec.

Water colour was originally tested in this model, but its contribution was not significant, and so it was dropped from the model. When slope, exposure, and exposure × slope were entered instead of sediment water content, with which they were highly collinear, the exposure × slope interaction was highly significant (+) (Equation 2, Table 4), but the precision of the model as measured by the SE of the estimate and the R^2 was reduced. The log slope and log exposure

terms were not significant when the model contained their interaction term, and were thus dropped from the model. When plant biomass was entered instead of its correlate plant biomass/plant height, the precision was again reduced (Equation 3, Table 4). If no plant community indices were entered, the best model obtained was Equation 4 which explained 59% of the variance in log(HBM + 0.1).

Sediment Eh was highly collinear with vari-

TABLE 4.　Multiple regression models predicting the biomass of *Hexagenia* (HBM), obtained from data on 81 sites in 12 lakes in the Eastern Townships, Quebec.

	Equation 1	Equation 2	Equation 3	Equation 4	Equation 5
Hexagenia biomass					
log(g/m² + 0.1)	log(HBM + 0.1)	log(HBM + 0.1)	log(HBM + 0.1)	log(HBM + 0.1)	(Eh + 300)⁰·⁵
Intercept	1.5352	1.4193	1.8469	0.9519	17.953
Chlorophyll *a*					
(μg/L)⁰·⁵	−0.2466	−0.3398	−0.3616	−0.3614	−2.193
Depth (m)⁰·⁵	−0.2890	−0.4554	−0.5717	−0.3044	−0.937
Plant biomass					
(g/m²)⁰·⁵	—	—	−0.0161	—	—
Plant biomass/height					
g/m³	−0.3618	−0.3557	—	—	−1.138
Exposure × slope					
(km²)⁰·²⁵ × (%)⁰·⁵	—	+0.1229	+0.1172	+0.1534	+0.820
Sediment water content (%/100)⁴	−1.6759	—	—	—	—
R^2	0.74	0.70	0.64	0.58	0.81
Standard error of the estimate	0.349	0.378	0.413	0.444	1.558

ables that reflect the trophic status of the lake, the plant biomass, and the physical energy regime. The best model obtained predicted sediment Eh from the chlorophyll concentration (−), plant biomass/plant height, exposure × slope (+), and depth (−), and explained 81% of the variance in the dependent variable (Equation 5, Table 4).

The patterns in the abundance of *Hexagenia* do not simply reflect overall patterns in macrozoobenthic biomass since HBM was not significantly correlated with either macrozoobenthic biomass (Table 3), or non-*Hexagenia* macrozoobenthic biomass. It is conceivable that variation in HBM could be partially related to the biomass of other macrozoobenthic taxa, and this was tested by entering the biomass of non-*Hexagenia* macrozoobenthos into a multiple regression alongside the predictors listed in Equations 1–4. This variable was never found to be significant. Three of the factors (chlorophyll, exposure × slope, and plant biomass) that were negatively related to HBM were shown to have strong positive relationships to macrozoobenthic biomass (Rasmussen 1988, Rasmussen and Kalff 1987).

The ability of Equation 2 to predict the biomass of *Hexagenia* in other lakes was tested by comparing literature estimates of HBM to the predictions from this equation. Although Equation 2 was developed using data obtained from both littoral and sublittoral stations, most of the literature estimates that I found were from sublittoral areas (no macrophytes present). In some cases this absence of macrophytes was not explicitly stated by the authors; however, in applying Equation 2, I assumed macrophytes to be absent when the sampling depth exceeded the Secchi disk transparency. Equation 2 explained 67% of the variance in the literature estimates of HBM, and the standard error of the estimate was 0.393. Thus Equation 2 predicted the literature estimates of *Hexagenia* abundance almost as well as it explained the data from which it was derived. The model is, however, somewhat biased in that it tends to underpredict high values of HBM (Fig. 2). The average observed log(HBM + 0.1) exceeds the predicted values by 0.14 (±0.07, $p < 0.1$) where an unbiased model should give a mean difference of zero. The slope of the observed vs. predicted estimates is 1.2 (±0.14) which, however, is not significantly greater than 1.0. The decreases in

Hexagenia abundance that accompanied eutrophication in western Lake Erie, Saginaw Bay, and Oneida Lake (Beeton 1961, 1969, Britt et al. 1973, Carr and Hiltunen 1965, Jacobsen 1966) were all in reasonable accordance with the predictions of Equation 2. The presence and absence of *Hexagenia* in the literature data set was compared with the classification predicted by the discriminant (Table 2) function based on chlorophyll, slope, and exposure. Six of the seven sites without *Hexagenia* were correctly classified (H−), and 20 of the 24 sites with *Hexagenia* were classified correctly (H+).

Discussion

The results of this study strongly support hypotheses that pronounced declines in the abundance of *Hexagenia* can result from eutrophication (Beeton 1961, 1969, Britt et al. 1973, Carr and Hiltunen 1965, Jacobsen 1966, Mills et al. 1978, Wood 1963). The increased input to the sediments of decomposing plankton contributes to lower Eh levels; this likely is a combined effect of lower DO concentrations and higher concentrations of other reducing substances, some of which (e.g., sulphide) may be directly toxic to the nymphs.

Reversing eutrophication would be expected to improve habitat conditions for *Hexagenia*, and such reversals are the objective behind the management of phosphorus loading through tertiary treatment of point source emissions to watersheds (Loehr et al. 1980). Projected loading rates of phosphorus, after the application of this type of management, have been calculated for western Lake Erie and Saginaw Bay by Bierman (1980) and for Oneida Lake by Ogelsby and Schaffner (1977) (Table 5). From these projected P loadings, mean total P concentrations were predicted from the P loading model of Chapra (1977). These values were in turn used to predict chlorophyll *a* concentrations for western Lake Erie (islands area), Saginaw Bay (inner portion) and Oneida Lake (central region) using P and chlorophyll data measured in these areas (Bierman 1980, 1984, Brydges 1971a, 1971b, Mills et al. 1978). From these chlorophyll estimates and the morphometric data for these areas (cited in methods section) the projected estimates of HBM were obtained using Equation 2. Although significant increases in the biomass of *Hexagenia* would be expected from the proposed manage-
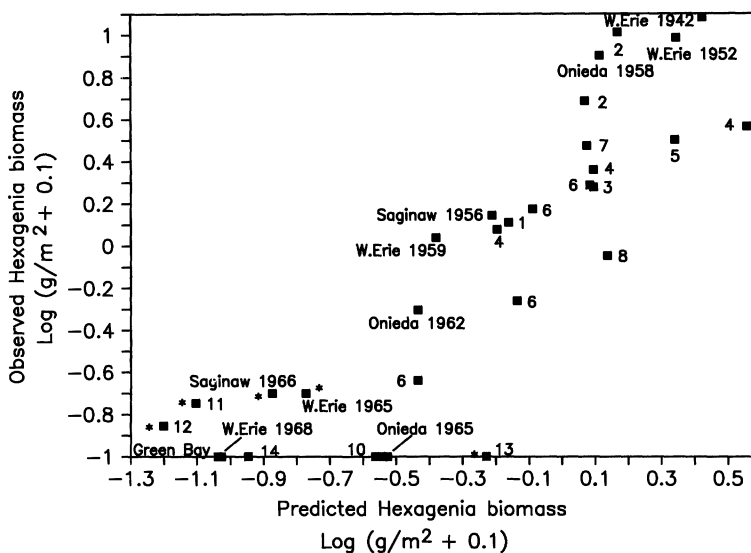
FIG. 2. Literature estimates of *Hexagenia* abundance compared with predictions from Equation 2. Numbered points are from Savanne Lake (1), Brandenburg Pond (2), Lake Winnipeg (South Basin) (3), Simcoe Lake (4), Batchawana Bay (Lake Superior) (5), Otsego Lake (6) and from a series of lakes in Maine (7-14). The points marked by asterisks were incorrectly classified as H− or H+ by the discriminant function (Table 2b).

ment strategy, the predicted HBM for all three of these situations were well below maximum recorded values for *Hexagenia* biomass (Fig. 2).

The hypothesis that submerged macrophytes would exert a negative effect on both the abundance of *Hexagenia* and on the sediment Eh was strongly supported by this study. The macrophytes that achieve high biomass in close proximity to the substrate (*Potamogeton robbinsii, Elodea canadensis, Ceratophyllum demersum,* and *Chara*

spp.) had the greatest effect on both HBM and sediment Eh. This suggests that the main effect of macrophytes on *Hexagenia* involves the reduction of mixing at the substrate–water interface. The direct effect of macrophyte biomass itself on decomposition, and the increase in decomposition rates brought about by increased sedimentation rates in macrophyte beds (Carpenter and Lodge 1986, Wetzel 1983) must also be important contributing mechanisms.

TABLE 5. Phosphorus management objectives and their predicted potential for restoring *Hexagenia* populations, in three basins from which populations have become extinct.

Site	Projected P loadings (g/m²/yr)[a]	Predicted Mean TP (µg/L)[b]	Predicted Mean Summer Chlorophyll *a* (µg/L)[c]	Predicted *Hexagenia* Biomass[d]
Western Lake Erie (Bierman 1980)	4.07	28 (38)	7.0	1.5
Saginaw Bay, Lake Huron (Bierman 1980)	0.40	22 (40)	8.2	0.9
Oneida Lake, N.Y.				
(Ogelsby and Schaffner *in* Mills et al. 1978)	0.56	30.1 (44)	7.8	1.0

[a] Projected P loading regimes were calculated under the assumption that major point source emissions would be reduced to 1 mg/L. This would lead to an approximately 90% reduction in point source P loading (Bierman 1980). No change in diffuse source P loadings were projected.

[b] The Chapra (1977) loading model was used. Values for 1975 in parentheses.

[c] TP–chlorophyll *a* relationships were obtained from data specific to each lake. See text for references.

[d] *Hexagenia* biomass was predicted from Eq. 2 for specific sites (see text) in these three basins. The manner in which these predictions were calculated is described in the methods section.

The importance of exposure and slope as morphometric factors that modify the impact of eutrophication on bottom conditions was also supported by this study. Both HBM and sediment Eh were higher on steep slope sites, and on sites that had greater exposure to waves; this must reflect the importance of the physical energy environment (Håkanson and Jansson 1981). In environments characterized by high physical energy exchange between water and sediment, which is enhanced by both increased exposure and bottom slope, decomposing matter has a high chance of resuspension, and sediments will be well supplied with dissolved oxygen.

Hexagenia limbata is by far the most abundant ephemerid mayfly in east and central North America, but it is not very common in other areas. However, the family Ephemeridae is distributed world-wide with the genus *Ephemera* being abundant throughout the Holarctic region (Needham et al. 1935, Zhadin and Gerd 1961). These larvae are all burrowers, similar in size, morphology, and feeding habits to *H. limbata*. Furthermore, they occupy similar habitats within the littoral and sublittoral zones of oligotrophic to mildly eutrophic lakes, and play a prominent role in the nutrition of many benthivorous fish species (Macan 1970, Zhadin and Gerd 1961). Eriksen (1963a, 1963b) showed that *Ephemera simulans* was slightly less tolerant of hypoxia than *H. limbata,* and that the latter, by virtue of its larger gill lamellae, could generate a slightly higher maximum respiratory current through its tube. The differences between the two species were small, however, and it is possible that the models developed in this study for *H. limbata* will provide a reasonable description of the habitat requirements of other lacustrine ephemerids in other parts of the world.

Acknowledgements

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APPENDIX 1. The biomass of *Hexagenia* at various stations in Lake Memphremagog and other Eastern Townships lakes, and associated limnological variables.

Lake	Slope (%)	Exposure (km²)	Depth (m)	Plant Biomass (kg/m²)	Plant Height above Sediment (m)	Sediment Eh (mV)	Chl-*a* (mg/m³)	Secchi (m)	Total Macrobenthic Biomass (g/m²)	*Hexagenia* Biomass (g/m²)
Memphremagog										
Newport Bay	0.2	3.1	2.5	1.89	2.5	−230	12.0	2.5	118.5	0.0
	1.0	5.8	3.1	0.75	2.2	−154	10.4	3.0	66.0	1.2
	2.0	4.1	4.2	1.52	3.5	−218	10.4	2.9	67.3	0.0
	2.0	5.8	8.0	0.00	0.0	−198	10.4	3.0	23.5	0.0
South Basin	20.0	22.5	4.2	0.00	0.0	+70	6.2	3.5	15.8	2.2
	1.1	2.0	2.5	1.20	2.3	−175	6.0	3.8	40.0	0.0
	1.7	12.3	3.5	0.63	2.5	−121	6.0	3.3	34.9	3.5
	18.0	14.5	3.0	0.00	0.0	+69	6.1	3.3	11.2	1.8
	1.5	16.2	2.6	0.68	2.5	−82	6.8	3.4	53.4	2.1
	4.0	35.8	2.5	0.74	2.0	−106	6.0	3.6	21.7	1.6
	18.0	17.2	4.5	0.00	0.0	+42	5.5	3.8	11.3	2.2
	5.0	20.6	3.0	0.55	2.2	−80	6.2	3.8	37.3	4.8
	1.2	22.0	9.0	0.00	0.0	−203	9.0	3.0	9.9	0.0
	2.0	35.0	10.0	0.00	0.0	−188	6.2	3.6	7.3	0.2
	3.0	12.0	9.0	0.00	0.0	−172	6.0	3.8	10.2	0.3
	0.1	11.0	12.0	0.00	0.0	−195	5.5	3.8	6.3	0.0
Fitch Bay	14.0	6.7	3.5	0.22	2.5	−88	5.5	3.8	29.0	6.5
	2.2	2.6	2.5	0.81	2.0	−112	3.2	3.6	35.4	4.2
	3.8	3.7	1.5	0.51	1.5	−62	3.6	3.6	37.0	4.0
Central Basin	7.0	19.7	3.0	0.00	0.5	−74	4.2	3.8	10.6	2.2
	11.0	24.4	3.8	0.13	1.5	−78	4.5	4.3	12.9	3.4
	0.9	3.8	2.5	0.79	2.5	−125	3.5	4.2	36.1	4.7
	0.3	4.8	3.5	1.65	3.0	−195	4.5	4.2	47.2	1.3
	6.6	12.8	3.2	0.47	3.1	−165	3.5	4.8	25.5	0.0
	1.8	2.1	2.9	1.61	2.9	−155	3.0	5.0	43.3	1.4
	19.0	2.0	2.2	0.01	2.2	−24	3.0	5.0	11.3	3.9
	5.4	16.9	4.0	0.35	4.0	−13	3.4	4.9	18.3	2.4
	0.1	0.5	10.0	0.00	0.0	−190	4.5	4.2	9.9	0.0
	10.5	9.5	9.0	0.00	0.0	−115	4.5	4.2	6.2	0.0
	9.5	23.0	9.5	0.00	0.0	−105	3.5	4.8	3.1	2.7
North Basin	1.5	10.8	2.8	0.44	1.5	−74	3.1	4.9	22.0	3.8
	4.2	3.2	3.2	0.74	2.3	−87	3.0	4.9	27.8	1.9
	3.5	11.9	3.5	0.39	3.0	−64	3.0	5.3	17.5	2.2
	8.0	10.9	3.2	0.29	2.5	+35	3.1	5.0	14.6	2.1
	4.0	5.1	2.5	1.05	2.0	−83	4.1	5.1	72.1	6.1
	3.0	6.2	3.7	0.27	1.0	+10	3.2	5.2	15.2	2.9
	2.0	7.4	2.5	0.46	2.5	−135	3.5	5.3	25.1	1.7
	1.5	8.0	10.0	0.00	0.0	−158	3.0	5.2	3.7	1.1
	6.5	10.5	10.2	0.00	0.0	−139	4.1	4.8	3.7	3.0
	0.5	3.5	9.5	0.00	0.0	−151	3.1	5.3	4.6	1.1
	1.0	15.0	9.0	0.00	0.0	−148	3.1	5.2	3.6	1.3
Brompton	3.0	2.2	1.5	0.45	1.5	−72	1.3	4.2	19.5	2.2
	7.0	11.2	2.1	0.08	1.5	−38	1.3	4.2	15.4	6.1
	1.0	14.0	10.0	0.00	0.0	−167	1.3	4.2	1.9	0.4

APPENDIX 1. Continued.

Lake	Slope (%)	Exposure (km²)	Depth (m)	Plant Biomass (kg/m²)	Plant Height above Sediment (m)	Sediment Eh (mV)	Chl-a (mg/m³)	Secchi (m)	Total Macro-benthic Biomass (g/m²)	*Hexagenia* Biomass (g/m²)
Brome	0.6	6.5	1.8	0.28	1.5	−112	10.1	2.8	36.7	4.5
	5.0	13.6	2.4	0.09	1.5	−104	10.1	2.8	19.9	1.6
	0.5	14.0	7.0	0.00	0.0	−165	10.1	2.8	12.7	0.8
D'argent	18.0	0.9	1.8	0.02	0.5	−65	3.5	2.6	9.3	3.1
	6.0	0.9	2.0	0.52	1.8	−73	3.5	2.6	14.7	4.5
	1.0	0.9	2.0	0.35	1.8	−61	3.5	2.6	20.3	5.0
	0.2	0.9	9.0	0.00	0.0	−198	3.5	2.6	4.2	0.0
Hertel	5.1	0.3	3.5	3.05	0.7	−210	3.0	3.5	42.5	0.0
	11.0	0.3	3.3	0.78	0.5	−196	3.0	3.5	18.4	0.0
	5.0	0.3	3.8	2.45	0.7	−206	3.0	3.5	36.1	0.0
	1.5	0.3	6.0	0.00	0.0	−202	3.0	3.5	8.3	0.0
Magog	0.5	1.8	1.8	1.59	1.7	−265	11.0	2.3	62.6	0.0
	5.2	10.1	2.3	0.83	2.2	−163	11.0	2.3	26.5	1.1
	9.0	10.1	2.3	0.25	2.0	−122	11.0	2.3	24.1	2.8
	0.1	10.1	8.0	0.00	0.0	−265	11.0	2.3	12.4	0.0
	0.1	10.1	8.5	0.00	0.0	−275	11.0	2.3	14.5	0.0
Orford	1.8	0.9	4.0	0.28	3.0	−75	1.6	7.1	7.4	3.3
	4.2	0.7	3.3	0.12	2.0	−85	1.6	7.1	6.1	2.4
	15.0	0.3	4.2	0.05	0.3	−72	1.6	7.1	4.2	1.8
	14.0	1.2	5.0	0.13	3.0	−72	1.6	7.1	4.5	2.1
	6.0	1.2	9.0	0.00	0.0	−165	1.6	7.1	4.2	0.5
Roxton Pond	0.8	1.7	2.2	1.30	1.2	−225	8.5	2.3	21.8	0.0
	0.5	1.7	5.5	0.00	0.0	−215	8.5	2.3	11.6	0.0
Silver	12.0	0.7	4.0	0.03	0.5	−117	3.5	5.8	18.7	1.9
	2.2	0.7	2.0	0.64	0.6	−175	3.5	5.8	20.1	0.2
	14.0	0.5	4.0	0.03	0.4	−122	3.5	5.8	10.2	1.5
	25.0	0.7	4.0	0.00	0.0	−45	3.5	5.8	7.5	4.0
	8.5	0.7	9.0	0.00	0.0	−155	3.5	5.8	2.5	0.9
Waterloo	8.6	1.3	1.2	1.32	0.8	−280	24.0	0.9	42.8	0.0
	0.9	1.3	1.0	1.22	0.8	−264	24.0	0.9	36.8	0.0
	0.4	0.1	1.0	1.39	0.8	−295	24.0	0.9	43.4	0.0
	0.1	1.3	4.5	0.00	0.0	−285	24.0	0.9	3.7	0.0
Drolet	5.0	2.1	2.3	0.13	1.5	+5	5.5	3.8	19.1	3.4
	0.5	2.1	2.4	0.34	2.1	−152	5.5	3.8	27.1	1.5
	1.5	2.1	10.0	0.00	0.0	−178	5.5	3.8	2.9	0.1
Bromont	1.0	0.2	1.6	2.90	1.2	−200	9.6	2.1	85.6	0.0
	0.1	0.2	6.0	0.00	0.0	−220	9.6	2.1	7.3	0.0