A Hydrological Model for Predicting the Effects of Dams on the Shoreline Vegetation of Lakes and Reservoirs

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ABSTRACT / The species richness of shoreline vegetation of unregulated lakes in Nova Scotia, Canada, is known to increase as a function of catchment area, a topographic variable governing water level fluctuations. Predictions based on catchment area however, fail to account for richness patterns at the margins of lakes enlarged by dams. Here, we compare the vegetation and hydrological regimes of regulated and unregulated systems. Hydrological regimes of regulated systems deviated from natural systems of similar catchment area by being either hypovariable or hypervariable for both within-year and among-year fluctuations in water level. Plant communities of dammed systems were less diverse, contained more exotic species, and were, with one exception, devoid of rare shoreline herbs. Data from "recovering," or previously dammed systems indicated that shoreline communities can be restored upon return of the appropriate hydrological regime. Using observed within-year and among-year water level fluctuation data, we propose a general model for the maintenance or restoration of diverse herbaceous wetlands on shorelines of temperate lakes or reservoirs. Managers can manipulate the within-year water level variation within prescribed limits (1–2 m), while ensuring that among-year variation (SD of summer levels) is less than 25% of within-year variation. This preliminary model is based on data from low-fertility, temperate lakes in river systems. To calibrate the model, plant community data from other regions are needed, as are long-term water-level data for unregulated lakes, data which are essential but largely lacking in many areas.

Human alteration of hydrological regimes has replaced glacial or tectonic processes as the primary agency of lake formation (Moss 1988) and has left few large rivers free-flowing (Dynesius and Nilsson 1994). The unmodified systems required to establish long-term hydrological and ecological relationships are becoming increasingly uncommon, and this affects our ability to develop wetland ecology into a predictive science. The hydrology of large rivers has been most affected since their flow offers greatest potential for hydroelectricity (Stanford and Ward 1992). For similar reasons, lakes with large catchment areas have been sought to serve as head ponds or reservoirs. Thus, for both rivers and lakes, much information on the premodified states of large catchment area systems has been lost.

The impact of dams upon aquatic systems has been well documented (references in Moss 1988, Fraser 1972), although the information on fish and invertebrates outweighs that on plants. Indeed, most of the instream flow recommendations and water rights are designed to satisfy the needs of individual fish species (Richter and others 1996). Studies have established that damming leads to changes in shoreline vegetation (e.g., Nilsson 1978, Keddy 1985, Obot 1986, Nilsson and Keddy 1988, Wilcox and Meeker 1991, Nilsson and others 1991, Nilsson and Jansson 1995), but a need remains for predictive models that relate "biologically relevant hydrological parameters" (Richter and others 1996) to diversity and structural patterns of shoreline wetland plant communities. In the case of reservoirs that already exist, models should allow us to estimate the properties of the original vegetation as a guideline for possible restoration of the plant community. In the case of newly proposed dams or reservoirs, models should allow us to predict the consequences of various hydrological scenarios.

KEY WORDS Catchment area, Regulated lakes, Shoreline restoration, Rare plants, Exotic plants, Diversity

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Environmental Management Vol. 22, No. 5, pp. 723–736

Our objective is to develop a general model applicable to the hydrological management of lakes and reservoirs in temperate zone regions. Our starting point is a series of hydrologically unaltered lakes in Nova Scotia for which a set of equations relating lake properties to vegetation has already been developed (Hill and Keddy 1992). The main conclusion for unaltered lakes was that the amplitude of lake water-level fluctuations, as estimated from catchment area, is the best predictor of species richness patterns of both common and rare shoreline plants. This finding reinforced our understanding of factors governing richness of shoreline wetlands and was consistent with an earlier mechanistic model by Keddy and Reznicek (1986), which proposed how water-level fluctuations can enrich species pools. Normal water-level fluctuations prevent establishment of woody plants and extreme draw-downs allow periodic recruitment from shoreline seed banks. For unregulated lakes, the Hill and Keddy (1992) model indicated that species richness increases with increasing amplitude of seasonal water-level fluctuation. If fluctuations are sufficiently great, however, the hypervariable conditions might cause a reduction in richness as plant tolerance levels are exceeded. Such extremes were not represented in the set of 37 unregulated lakes that formed the original model. However, more extreme conditions are represented in regulated lakes. Therefore, a broader, more encompassing model that includes regulated lakes is required. This research develops patterns using unregulated lakes, then expands the scope to include regulated systems. Our three main aims are to: (1) describe the general patterns of vegetation change; (2) test the above prediction of decreased diversity in hypervariable conditions; and (3) develop a general predictive model that relates water level fluctuations to vegetation richness patterns.

Methods

Fifty lakes were selected from southern Nova Scotia, including 37 unregulated lakes described in Hill and Keddy (1992) and 13 regulated lakes. Lakes were selected in a nonrandom manner so that a wide range of lake surface areas and catchment areas were represented. Lakes were also selected so that most common management regimes were represented. Regulated lakes included those that are currently used as head ponds and storage reservoirs and lakes that have been regulated in the past. For currently regulated lakes, original shoreline positions are lower than current shorelines and an approximation of the difference can be obtained from the head height of the dam structure (Appendix 1). For lakes regulated in the past, shoreline positions approach those of the lakes before regulation (personal communication with local residents).

Inventories of all plant species from 1 m below the waterline to 1 m above the shrub line were made for each lake. One straight shoreline, one sheltered bay, and an exposed point were selected from 1:50,000 scale topographic maps for both sides of the long axis of each lake as described in Hill and Keddy (1992). For each lake, both species richness and species frequency were recorded. Species frequency values were sums for all species of the number of occurrences of each species over the six sites surveyed per lake. In the present study, patterns among shrubs and the following five herb groupings were considered: annuals, exotic species, upland herbs, rare Atlantic coastal plain herbs, and all herbaceous species (Appendices 2–5).

Lake environmental variables such as catchment area, lake surface area, elevation, and water chemistry (color, pH, alkalinity, conductivity, and concentrations of Ca, Cl, and Fe) were measured as described in Hill and Keddy (1992). Shoreline variables such as shore width and shore sediment composition were found to account for a portion of the variation in richness patterns in the previous study (Hill and Keddy 1992); however, since these features are greatly affected by damming, their present values in any altered system are not indicative of predam values and are thus of no use in estimating the state of the original vegetation.

To test for overall differences in shoreline vegetation among sets of lakes, Mann-Whitney U tests (Siegel 1956) were used to compare richness and frequency between groups of lakes, and to calculate *P* values. Stepwise (forward) multiple regression (model II; Sokal and Rohlf 1995) was performed to obtain predictive models for species richness patterns from combinations of the ten environmental variables listed above using Statsgraphics (1991) software. The regression equations, calculated using only the data from unregulated lakes, were then used to estimate what the original richness patterns in regulated systems might have been before water-level regulation.

Water-level data were obtained from the Nova Scotia Power Corporation and Environment Canada. Means and standard deviations were hand calculated from recorded values or operation curves. Dam histories are given in Appendix 1 and were provided by the Seaforth Engineering Group and from personal interviews with residents and Nova Scotia Power Corporation employees.

Table 1. Differences in shoreline vegetation between unregulated and hydrologically regulated lakes[a]

	Lake class		
Vegetation grouping	Unregulated ($N = 37$)	Regulated ($N = 13$)	P
Annuals[b]			
Richness	1.78	2.54	NS
Frequency	3.92	6.31	<0.10
Exotic herbs[c]			
Richness	0.08	2.00	<0.001
Frequency	0.08	4.00	<0.0001
Upland herbs[d]			
Richness	1.03	3.00	<0.01
Frequency	1.49	7.54	<0.01
Rare herbs[e]			
Richness	1.49	1.00	NS
Frequency	3.22	1.62	NS
All herbs			
Richness	56.6	62.5	NS
Frequency	150.0	173.9	NS
All shrubs			
Richness	21.7	20.4	NS
Frequency	63.8	55.8	<0.05

[a] Significance for unpaired samples assessed by Mann-Whitney U tests.

[b] List in Appendix 2.

[c] List in Appendix 3.

[d] List in Appendix 4.

[e] List in Appendix 5.

Results

Vegetation Patterns

Comparison of vegetation. Table 1 compares the vegetation of two classes of lakes: those that have never been regulated to our knowledge (the 37 unregulated lakes examined in Hill and Keddy 1992) and those that have, at some time during their history, been regulated (see Appendix 1). The 13 regulated lakes had higher species richness, higher frequencies of exotic and upland herb species, and lower frequencies of shrubs than the unregulated lakes (Table 1).

In the foregoing analysis, both classes of lakes contain lakes varying widely in the size of their catchment areas. Since catchment area exerts a major effect upon vegetation patterns (Hill and Keddy 1992), we extracted two extreme subgroups from the 37 unregulated lakes for comparison with the regulated lakes: lakes with catchment areas less than 2000 ha and lakes with catchments greater than 50,000 ha. The 12 lakes with small catchment areas have fewer numbers of herbs ($P < 0.001$) and fewer rare plants ($P < 0.001$) than do the nine lakes of large catchment area (Table 2). The regulated lakes were, as a group, more like high-catchment-area lakes. In particular, both regulated systems and large-catchment-area lakes had double the numbers and frequencies of annuals than were observed in the small-catchment-area lakes. Regulated lakes also had more exotic species than both large- and small-catchment-area lakes—a mean of 2 as opposed to <0.1 (Table 2).

The regulated lakes can also be subdivided into two categories. Table 3 compares regulated lakes with existing dams ($N = 8$) to those lakes ($N = 5$) that had been dammed but had returned to natural fluctuations upon collapse or removal of the dam. These lakes are "recovering" (Gore 1985), since without human intervention, plant communities and shoreline characteristics have been in transition from their dammed state (prevalent for 30–65 years) to a state governed by natural level fluctuations for 23–38 years (at the time of survey). Recovering lakes have significantly higher richness and frequency values for all herbs and rare herbs and higher frequencies of annuals than recovering systems (Table 3).

To consider smaller groupings of regulated lakes with existing dams, small sample sizes necessitate a descriptive, nonstatistical approach. The subset of dammed lakes with large catchment areas is of most concern because these are often the systems selected by managers to generate hydroelectricity since they offer greatest flow rates. Dammed systems of large catchment area are managed in two main ways: as head ponds or storage reservoirs. Head ponds have stabilized water levels (hypovariable levels, $N = 2$), whereas storage reservoirs ($N = 2$) have hypervariable water levels and are drawn down to maintain head pond levels, thus ensuring peak flow rates. Hypervariable reservoirs appear to have higher frequencies of annuals, upland species, and herbaceous species than hypovariable head-ponds (Table 4). No rare species were present in either class of dammed large catchment area lakes. The differences between head ponds and storage reservoirs illustrate the difficulty in comparing regulated and unregulated lakes: regulated lakes themselves represent a number of extreme states of water levels and vegetation.

Finally, large-catchment-area unregulated lakes were selected to match recovering lakes (Table 5). Despite the discrepancies in catchment area between the two lake classes, insights may be gained. First, recovering lakes appear to have similar numbers of rare species as those lakes that have never been regulated. Second, the highest numbers of annuals, exotic species, and upland herbs seem to occur in the recovering lake class. Both observations suggest recovering lakes are in transition between the dammed and unregulated states.

Regression models for potential flora. Regression models were made from data from unregulated lakes to achieve

Table 2. Differences in shoreline vegetation between lakes of small and large catchment areas[a]

	Unregulated lakes				P (unregulated vs regulated lakes)	
	Small catchment area ($N = 12$) (<2,000 ha)	Large catchment area ($N = 9$) (>50,000 ha)	P	Regulated lakes ($N = 13$)	Small catchment area	Large catchment area
Annuals						
Richness	1.50	2.44	0.024	2.54	0.213	1.00
Frequency	2.50	5.89	0.001	6.31	0.016	0.778
Exotic herbs						
Richness	0.08	0	0.441	2.00	0.016	0.012
Frequency	0.08	0	0.441	4.00	0.014	0.012
Upland herbs						
Richness	1.08	1.67	0.268	3.00	0.028	0.198
Frequency	1.58	2.33	0.257	7.54	0.029	0.214
Rare herbs						
Richness	0.08	3.66	<0.001	1.00	0.033	0.002
Frequency	0.08	9.33	<0.001	1.62	0.030	<0.001
All herbs						
Richness	44.8	72.0	<0.001	62.5	0.015	0.132
Frequency	111.3	190.2	0.001	173.9	0.015	0.422
All shrubs						
Richness	21.7	22.4	0.363	20.4	0.348	0.348
Frequency	69.3	61.7	0.165	55.8	0.005	0.269

[a] P values are from Mann-Whitney U tests.

Table 3. Shoreline vegetation of currently dammed and recovering lakes

	Dammed ($N = 8$)	Recovering ($N = 5$)
Annuals		
Richness	1.88	3.60
Frequency	4.37	9.50[a]
Exotic herbs		
Richness	1.00	2.60
Frequency	1.25	3.80
Upland herbs		
Richness	2.25	4.40
Frequency	5.50	11.40
Rare herbs		
Richness	0.25	2.20[b]
Frequency	0.25	3.80[b]
All herbs		
Richness	51.80	79.60[a]
Frequency	133.40	237.40[a]
All shrubs		
Richness	19.50	21.80
Frequency	53.00	60.40

[a] Mann-Whitney $P < 0.05$.

[b] $P < 0.01$.

Table 4. Shoreline vegetation of headponds and storage reservoirs[a]

	Head ponds (hypovariable)		Storage reservoirs (hypervariable)	
	Vaughan	Gavels	Raynard	Rossignol
Annuals				
Richness	3	0	2	3
Frequency	3	0	7	9
Exotic herbs				
Richness	1	0	2	0
Frequency	1	0	2	0
Upland herbs				
Richness	4	1	4	6
Frequency	4	1	12	22
Rare herbs				
Richness	0	0	0	0
Frequency	0	0	0	0
All herbs				
Richness	47	41	49	58
Frequency	97	95	121	174
All shrubs				
Richness	18	24	20	15
Frequency	58	70	47	38

[a] Sample sizes are too small for significance tests.

a standard for what can be expected in the flora of any lake in an unregulated state. These models were then used to estimate the potential diversity of dammed and recovering lakes.

Of the ten environmental variables (lake catchment area, lake surface area, elevation, and seven lake chemistry variables), catchment area and lake water color accounted for 49% of the observed variation in the total number of herbaceous species in regulated lakes (Figure 1). Recovering lakes, which fall to the left of the best

Table 5. Shoreline vegetation of lakes recovering from dams and of lakes with no history of dams[a]

	Recovering lakes			Unregulated lakes			
	Parr	Molega	Ogden	Rounding	Ponhook	Bennett	Kejimkujik
Catchment area (× 1000 ha)	25.0	29.5	26.2	27.4	107.4	107.6	68.4
Annuals							
Richness	6	2	4	1	2	3	4
Frequency	12	5	10	3	6	7	6
Exotic herbs							
Richness	10	0	1	1	0	0	0
Frequency	12	0	1	1	0	0	0
Upland herbs							
Richness	5	2	7	0	3	1	2
Frequency	17	2	16	0	4	2	5
Rare herbs							
Richness	6	3	4	2	5	7	4
Frequency	14	9	10	6	9	18	8
All herbs							
Richness	105	64	83	72	81	70	71
Frequency	285	155	240	204	191	186	205
All shrubs							
Richness	22	20	24	13	23	23	19
Frequency	58	58	64	40	47	75	45

[a] Sample sizes are too small for significance tests.

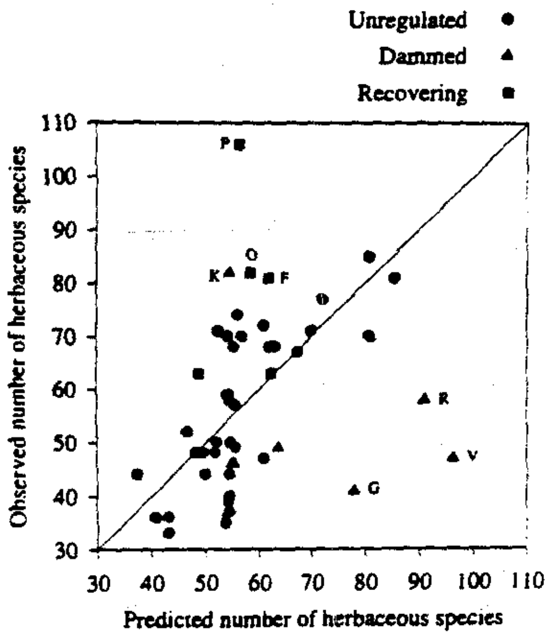

Figure 1. Observed and predicted numbers of herbaceous shoreline species. The number of predicted species was generated from the following equation: species richness of all herbs = 2.98×10^{-4} catchment area (ha) -5.758×10^{-2} color (total color units) + 54.7, $N = 37$, $P < 0.01$, R^2 (adj) = 0.49. Initials correspond to the following lakes: F, Fanning; G, Gavel; K, Kempt Back; O, Ogden; P, Parr; R, Rossignol; and V, Vaughan.

fit line, have more species than predicted from environmental variables. Dammed lakes, with one exception, have fewer herbaceous speces than predicted. The three that are most deviant (G, Gavel; R, Rossignol; and V, Vaughan) are all large catchment area systems with comparatively small floras. The exception among the dammed lakes (K, Kempt Back) is atypical in its regulation pattern. Spring high water levels are let go rapidly at the start of summer to allow for fish migration, mimicking the timing of large fluctuations typical of unregulated high-catchment-area lakes.

A regression model calculated for rare herbaceous species accounted for most of the variation in richness patterns in unregulated lakes (R^2 (adj) = 0.82). However, the complexity of this model (five variables: catchment area, water color, water pH, bedrock granite, and drainage capability of perimeter soils) obscured the importance of the most important variable, lake catchment area. A simple univariate model was therefore used, using lake catchment area alone and accounting for 67% of the variation in rare species richness (Figure 2).

The three lakes with the largest catchment areas (>100,000 ha) in the regulated state (G, R, and V) all have fewer rare species than expected by comparing with unregulated lakes (Figure 2). The calculated loss of an estimated five to six rare species, including species that are globally imperiled (Appendix 5), underestimates the real losses since the total shoreline survey distance was only between 1/100 to 1/20 of the total

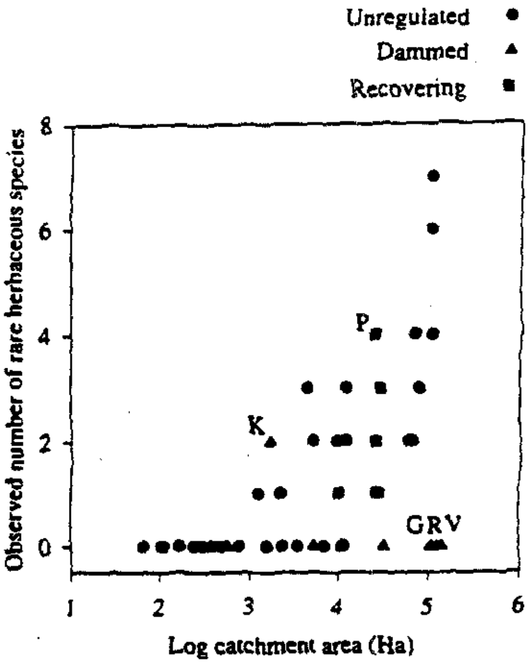

Figure 2. Observed numbers of rare herbaceous shoreline species as related to log catchment area. Initials are as in Figure 1.

shoreline lengths of the various lakes. As for the recovering lakes, they lie in an intermediate position, with Parr Lake (P) supporting a high number of rare species. Interestingly, Kempt Back Lake (K), a dammed lake, has one rare coastal plain herb (*Utricularia subulata*) as well as a rare species of wider distribution (*Eleocharis olivacea*), demonstrating that habitat suitable for some rare species can be created and maintained artificially.

Hydrology

Comparison of different classes of lakes. The problem with any pairwise comparison is that lakes differ naturally owing to geology, position in the drainage basin, range of exposures, etc. To understand the impact of regulation on water level variation, we began by comparing two large catchment area lakes of the same river system where the upstream lake was unregulated (Kejimkujic) and the lake immediately downstream from it (Rossignol) had been regulated for more than 60 years. Kejimkujic is in a national park and is unique in this region in having daily records of water-level fluctuations available for ten years. Records over the same time period were available for the reservoir, Rossignol. There are no historical plant data for the original shorelines in the Rossignol area, but according to the models in this paper and in Hill and Keddy (1992), given its large catchment area (127,000 ha), it would have had one of the most striking coastal plain communities in the province. Rossignol became Nova Scotia's largest reservoir when a dam constructed in the 1920s submerged the shorelines of five lakes.

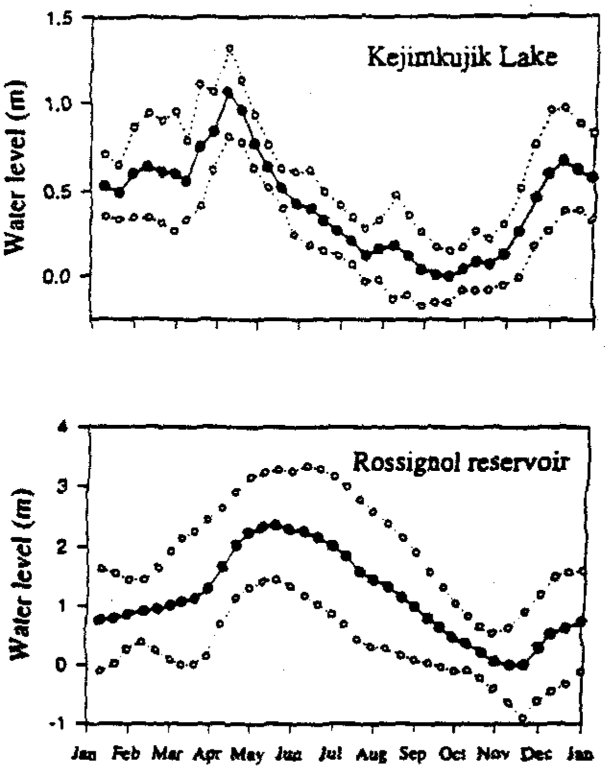

Figure 3. Seasonal water-level fluctuations in an unaltered high-catchment-area lake having many rare species (Kejimkujik) and in a high-catchment-area reservoir (Rossignol). Solid circles are mean values for ten years of data. Open circles above and below mean values indicate position of standard deviations from each mean. Mean levels are expressed in relation to height above the mean low water level for each waterbody.

There are three main differences in the seasonal fluctuation patterns of the unregulated (Kejimkujik) and regulated (Rossignol) systems (Figure 3). The first is a temporal shift in draw down. The mean seasonal time course, calculated using ten years of data, shows that in the unregulated lake, water levels begin to fall in April and reach a minimum in September, which is still within the growing season. In contrast, water levels do not begin to fall in the reservoir until late May and do not reach their minimum until November, well beyond the growing season. The second difference is an absolute increase in the seasonal draw-down of water level in the regulated lake. In Kejimkujik, mean water levels drop by 1.06 m over the summer; in Rossignol, levels drop by 2.2 m from spring to fall, more than twice that of the unregulated lake and 1.8 times more than expected given the larger catchment area of the reservoir (see Figure 4 model, below). The third difference is

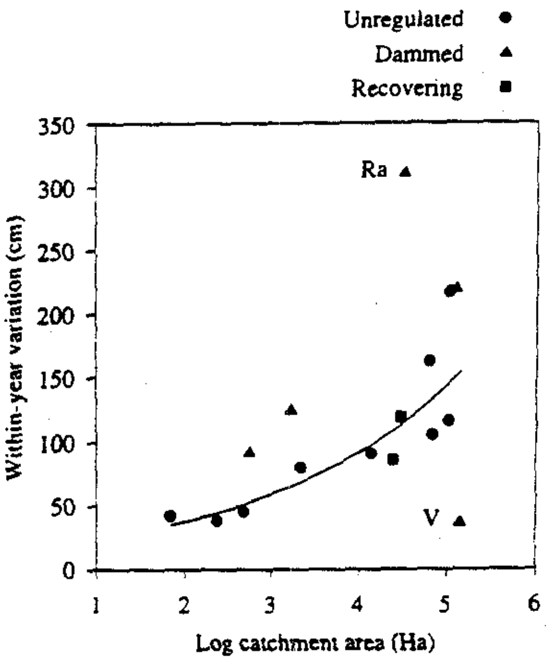

Figure 4. Within-year water-level variation as related to log catchment area [$y = \exp(2.72 + 0.45 \log \text{catchment area})$, $R^2 = 0.86$, $P < 0.001$). The model was constructed from only the nine unregulated lakes in Table 6, although dammed lakes have been added to the figure as triangles. Three of the five reservoirs fall outside the 95% confidence region around this relationship. Initials correspond to Raynard (Ra) and Vaughan (V) lakes.

Table 6. Within-year variation of lake water levels (spring high minus summer low) for unregulated and regulated systems

Lake	Catchment area (× 1000 ha)	Variation (m)
Unregulated[a]		
Janes	0.07	0.42
Somes	0.24	0.38
Halfway	0.49	0.45
Beaverhouse	2.26	0.80
Salmon	ca 14.0	0.91
Pearl	63.0	1.63
Wilson	107.0	1.17
Bennett	107.6	2.17
Kejimkujik	68.4	1.06
Recovering		
Fanning	29.9	0.86
Parr	25.0	1.20
Dammed		
Mink	0.57	0.92
Kempt Back	1.71	1.25
Raynard	33.5	3.11
Rossignol	126.1	2.20
Vaughan	144.1	0.36

[a] Variation in cm = exp (2.72 + 0.45 catchment area), $R^2 = 86$.

an increased among-year variation (ten years of record for each lake) in water level in the regulated lake. In Kejimkujik, the standard deviation from the mean water level in August is 24 cm, this figure is 1.0 m for Lake Rossignol. Any one of these changes would substantially alter a plant community. Together, these alterations to the hydrological regime appear to have eliminated the rare coastal plain plants found in the unregulated system and to have favored upland plant species.

A second comparison of hydrological regimes was made between the different kinds of reservoirs. There are two basic management strategies for maintaining water flow to tubines. In the case of Rossignol, a large reservoir was created, and it both stores water and serves as the head pond. In contrast, where there are many upstream lakes, flow may be drawn from these to maintain levels of a single head pond lake (e.g., Vaughan) that provides optimal flow for the hydroelectric turbines. As a result, level changes of upstream reservoir lakes (e.g., Raynard) that provide for the head pond, are large and unpredictable. We compared Vaughan and Raynard as representatives of two extreme states in reservoir management (Figure 4). Water levels of Vaughan (V), the head-pond reservoir, are nearly stable. There is very little change in within-year variation (0.36 m), and among-year variation is small (August standard deviation 0.11 m, $N = 4$ years). In contrast, Raynard (Ra) has large variation in levels within a given year (3.11 m) and among years (SD of 1.27, $N = 4$ years). Neither lake displays a temporal shift in drawdown judging from the previous unregulated seasonal pattern of Kejimkujik (Figure 3). Historically, both lakes did support rare coastal plain plants (Keddy 1985), although neither do now, even though nearby unregulated lakes of similar catchment area do.

Predicting water-level fluctuations. Data on among-year fluctuations are particularly challenging to obtain since long-term records are needed. In Figure 3, we were fortunate to have been able to present a comparison as Kejimkujik Lake is the only Nova Scotian unregulated lake for which long-term water-level records are known (although records for streams and rivers are fairly common). Such records are vital, however, if lakes are to be compared.

To construct a model with which to predict within-year amplitudes, we measured the amplitude of water-level fluctuations in 12 lakes as recorded spring maximum minus August low-water level. Table 6 shows that unregulated lakes had within-year fluctuations ranging from 0.38 to 2.17 m. The lakes with large numbers of rare plants (Keddy 1985, Hill and Keddy 1992) were the ones with within-year changes between 1.06 and 2.17 m. This change in within-year fluctuation can be predicted in unregulated lakes from the log of the catchment

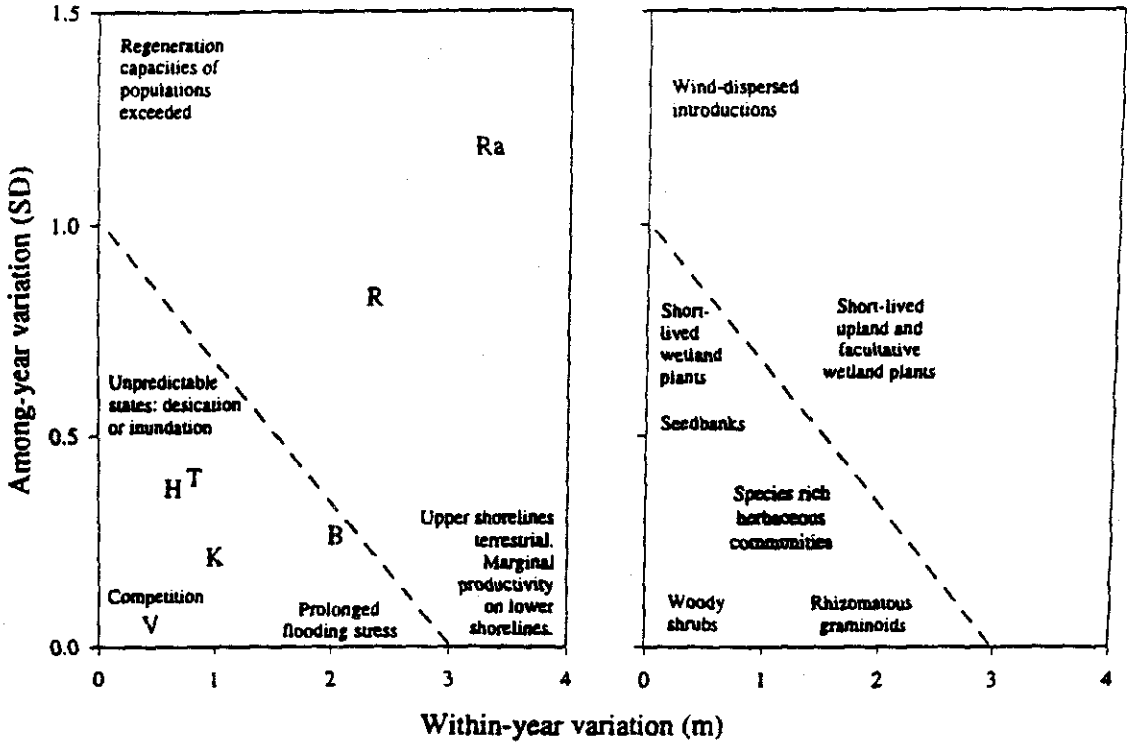

Figure 5. The effects of water-level variation upon shoreline vegetation. The stippled area contains lakes whose hydrological regimes produce rich floras, while hypo- and hypervariable zones represent impoverished systems. Rich floras with many rare species occur in unregulated lakes with high catchment areas such as Kejimkujik (K) and Bennetts (B), both lakes with intermediate water level fluctuations (1-m changes in amplitude within years and 0.5-m variation among years). In contrast, hypovariable lakes such as unregulated lakes with small catchment areas and head ponds (e.g., V, Vaughan) lose many species through competitive exclusion by shrubs. Hypervariable lakes such as storage reservoirs (above the dashed line, e.g., Ro, Rossignol and Ra, Raynard) lose species and are subject to invasion by exotic species. The stippled area is therefore the desirable management target. Increased catchment area can push lakes into the region of high richness, but reservoir construction can push lakes into the hypervariable state. Data on Long Island pondshores (H, House Pond and T, Third Pond) from Schneider (1994).

area, but regulated lakes fall off the regression line (Figure 4).

General Model

Consider two key hydrological variables: within- and among-year variation in water level. There are scant data on amplitude and among-year variation in unregulated lakes; however, we have postulated states of vegetation based upon the existing data for known cases (Figure 5). At the bottom left of Figure 5 are lakes with stable water levels and negligible within or among-year variation. Lake Vaughan, a head-pond reservoir, represents this region, as would two thirds of unregulated lakes: those that have small catchment areas. Such lakes have a few shoreline herbs, but no rare species and no exotics (Hill and Keddy 1992). At higher levels of within and among-year variation, one finds the region with maximum richness of native species and maximum abundance of rare species. This region is represented by Kejimkujik Lake and would include all other unregulated lakes of large catchment area (greater than 50,000 ha, 5.4% of lakes in the study region). Finally, we have the region where variation is great both within and among years; here rare species are absent and exotics and/or upland species are represented. Rossignol and Raynard, large-catchment-area storage reservoirs, represent this class of waterbodies. Interestingly, Raynard has greatest within-year (Table 6, Figure 4) and among-year variation (1.27 vs 1.0 m, SD for Raynard vs. Rossignol) and has correspondingly lower plant richness and abundance than Rossignol (Table 4).

Discussion

Changes in hydrological regimes are known to change the composition of shoreline plant communities (Toner and Keddy 1997, Nilsson and Jansson 1995), and the results of this study indicate that vegetation changes on lake shorelines are predictable consequences of water-level variation. Artificially decreasing the amplitude of water-level fluctuations, as is the common goal of head-pond management for hydroelectricity, will lead to a loss of species, which is predicted by the empirical relationships in the Hill and Keddy model (1992) and is consistent with the mechanisms of the Keddy and Reznicek model (1986). What could not be predicted from these earlier works, but is demonstrated in the species-richness patterns from storage reservoir lakes in the current study, is that increasing the fluctuation of water levels to extreme values may lead to a decline in the species richness of all herbs, a loss of the rare plant component, and an invasion of shorelines by exotics. The first two processes appear to be reversible, since "recovering" (Gore 1985) lakes that had been dammed for long periods (30–65 years) but have been unregulated for 23–38 years, have shoreline communities that include populations of rare Atlantic coastal plain species.

The mechanisms underlying these patterns are various. At low amplitudes of within-year fluctuation in head ponds, shrubs and other large species dominate the shoreline and exclude many smaller species (Keddy 1989, Wisheu and Keddy 1994, Holt and others 1995). Moreover, the lack of low water periods prevents the regeneration of various Atlantic coastal plain wetland plants from buried seed (Keddy and Reznicek 1982). At the other extreme, the scenario is more complex. The large seasonal fluctuation in water level that is typical of storage reservoirs appears to select against many wetland species, the rare coastal plain species in particular. While coastal plain plant populations may require, in some instances, low-water-level years to provide extensive areas of drawn-down and suitable habitat, few coastal plain species are obligate dryland species (Reznicek 1994) and the extensive upper shoreline zones of storage reservoirs are too xeric in summer. At lower shoreline stations, plants experience the stresses associated with flood duration and shortened growing season (Kozlowski 1984, Toner and Keddy, 1997). These two stresses at upper and lower shoreline zones should not preclude the development of a highly diverse wetland community at mid-shore zones. However, in addition to the great within-year variability in water levels, we have noted much greater among-year variability in regulated storage reservoirs than in comparable unregulated systems. The year-to-year unpredictability may select against rare coastal plain plants, especially since they are typically slow-growing (Gaudet and Keddy 1988) and would not be likely to survive year-to-year shifts in substrate water status ranging from xeric to submerged.

Are these differences in vegetation simply the result of differences between the hydrological regimes of regulated and unregulated systems or are there irreversible changes associated with the submergence of the plant community by damming? Can hydrological regimes be managed so that diverse shoreline communities establish even along dammed lakes? One obstacle is the elimination of the original plant community when shorelines are submerged by damming. Keddy (1985), for example, has reported on the disappearance from Lake Vaughan of rare species after water levels were dammed to a height of 9 m. However, if dams were removed or hydrological regimes were manipulated, it is likely that propagules from unregulated lakes directly upstream would bring about the succession of a diverse flora at the new shoreline level. The role of hydrochory of seeds in river systems is well documented (Nilsson and others 1993), and an additional propagule source for Lake Vaughan is the yearly flotilla of ice-disrupted ramets including the rare Atlantic coastal plain species *Hydrocotyle umbellata*, *Sabatia kennedyana*, and *Panicum rigidulum* var *pubescens*. These ramets settle on upper shorelines in spring floods and could be a main source of shoreline revegetation.

A second obstacle or long-term change caused by damming is the replacement of a stabilized shoreline with a new, erodible shoreline (Smith and others 1987). Shorelines along storage reservoirs are barren and contain little stabilized peat, which may slow the revegetation process. However, there are two examples in this study of diverse floras with rare species developing on new shorelines in systems with appropriate hydrological regimes. One example is the diverse shoreline on the currently dammed Kempt Back Lake. A second is the recovering lake, Parr, which has had four distinct shoreline positions since 1930 (unregulated pre-1930, regulated with dredged outflow 1930–1960, dam removed 1960, outflow infilled 1978 to present, Appendix 1). Current shorelines of this lake support diverse wet-meadow plant communities with rare species. Even though the substrate composition of new shorelines is different from original shorelines, depauperate floras in many currently regulated systems are likely enforced by their current hydrological regimens and are not a legacy of the original disruption caused by the damming.

More exotic species were observed in regulated systems than in unregulated systems. The overall contribution of these species to the total flora, however, is small (2.4%) in comparison with values (6%–30%) for various river communities in France and the northwestern United States (Planty-Tabacchi and others 1996). Nilsson and Jansson (1995) suggest that the invasion by exotic plants of riparian corridors may be rapid in temperate regions but not in boreal regions where the available pool of such species is low. In the present study, the distribution of exotics was patchy and highest values were found on regulated lakes with more farming in the surrounding catchment area. In contrast, no exotics were found on the shorelines of the largest reservoir, Rossignol, which is surrounded by forested land. Rossignol has the largest number of nonwetland, upland species (8% of total complement) of all the lakes studied. Exotic and upland species may invade margins of regulated lakes using a combination of attributes common to many weedy species, namely, reproductive plasticity, tolerance of ruderal conditions (e.g., desiccation and soils with low organic matter), and persistent seed banks and/or long-distance seed dispersal. The inability of exotic species to colonize the shorelines of unregulated systems may indicate a community level resistance to invasion by exotic species as has been postulated for other systems with limited among-year variation in water-level fluctuations (McIntyre and others 1988). Conversely, exotics may simply not be able to produce sufficient propagule densities on shorelines of unregulated lakes, which in the study region are infertile (Moore and others 1989, Holt and others 1995) and subject to periodic flood events during the growing season (Hill and Keddy 1992).

Water-level fluctuations influence countless biological processes ranging from microbial processes and habitat fertility (Pinay and Naiman 1991, Reddy and Patrick 1975) to the composition of the plant (Nilsson and Keddy 1997), Toner and Keddy 1997), amphibian (Real and others 1993), and fish communities (Stanford and Ward 1992, Kinsolving and Bain 1993). We showed previously that the relative magnitude of seasonal water-level variation was related to the area of the drainage basin, the catchment area that funnels water into the study lakes (Hill and Keddy 1992). Here, we have quantified this relationship and have identified how two kinds of regulated systems, head ponds and storage reservoirs, deviate from their unregulated counterparts. Our contention that populations of nationally rare and imperiled Atlantic coastal plain species have been extirpated from large-catchment-area lakes by damming is supported by predam herbarium records for Tusket River lakes (Keddy 1985) and by the absence of rare species from all large-catchment-area dammed lakes investigated and their presence at all unregulated lakes of similar catchment size.

Given the overriding importance of water-level fluctuation patterns to the structure of the shoreline plant community, there is clearly scope for management within dual constraints: that of meeting hydroelectricity requirements and that imposed by the tolerance limits of wetland plants. At present, some hydroelectric generating systems do accommodate fish and recreational needs, and this could easily be broadened to include the restoration of extirpated plant communities. In the case of Lake Rossignol, five large catchment area lakes, whose species compositions were never recorded, were submerged to form one huge reservoir that now supports a depauperate flora and no known rare plants. Given the empirical relationship between catchment area and species richness of all herbs and of rare plants in particular, one could anticipate that if a hydrological regime similar to the original were restored, a more diverse flora that contained rare plants could succeed. The shoreline communities on the recovering lakes examined here are testaments to this process, as recovery has met the requirements not only of a few target species but rather a diversity of common wetland and rare Atlantic coastal plain species. Since the recovery processes of succession on recovering shorelines was not followed, these lakes present only circumstantial evidence for the process. Another line of evidence, however, is presented by the small-catchment-area lake, Kempt Back Lake, which by chance is regulated so that its hydrological regime conforms to a lake of much larger catchment area. Damming has almost doubled the expected seasonal water-level fluctuations (0.65 m expected, 1.25 m observed), so that they match those expected in a lake approximately 30 times larger in catchment area size. Unlike many storage reservoirs, however, Kempt Back Lake water is released in early summer as dictated by local fish migration ordinances. The overall result is that the lake shorelines have a higher than expected herb species richness and populations of two rare plants that are unusual on lakes of small catchment area. This lake shows clearly that artificial regimes imposed on small-catchment-area lakes can mimic natural fluctuation patterns of unregulated large-catchment-area lakes and can maintain rare plant populations.

The identification of the importance of the landscape variable, catchment area, can facilitate conservation efforts that can be preferentially directed toward unregulated lakes of large catchment area (Hill and Keddy 1992). In this study, we have asked the follow-up question: how does the hydrology and vegetation of regulated systems differ from that of their unregulated counterparts? The answer involves two main hydrological parameters, the amplitude of within-year water-level fluctuations and the among-year variation in water levels. These two variables are stressors of plant communities and as such can be potentially manipulated to direct shoreline community composition.

A summary model displays the zone where maximum richness of wetland plants and rare species should occur within herbaceous shoreline communities (Figure 5). The zone is defined by within- and among-year water-level variation. The oval of maximum richness is drawn around three states: low within-year/high among-year variation, moderate within- and among-year variation, and high within-year/low among-year variation. Data on systems representing these states are rare at present due to the absence of long-term records of water levels. However, the oval is also defined by the exclusion of hydrological patterns typical of systems known for low richness and rarity values. Such excluded systems are unregulated, low-catchment-area lakes (Hill and Keddy 1992) and regulated head ponds, which both have low values for within- and among-year water-level variation, and regulated storage reservoirs, which exhibit high within- and among-year water-level variation.

Within-year and among-year water-level variations can potentially be tools to manage shoreline plant community composition and structure. If both within- and among-year variation is reduced, wet-meadow species disappear owing to stabilized water levels that narrow shore width and allow establishment of robust and woody vegetation (Toner and Keddy 1997). If water levels are unpredictable from year to year, then communities need to become reestablished from dormant propagules (Keddy and Reznicek 1986). When this occurs without a concomitantly large within-year water-level variation to jeopardize recruitment, a highly diverse community should result. Conversely, if water levels in the growing season are fairly constant from year to year (low SD, less than 25% of within-year fluctuation), greater seasonal water-level variation may be required to prevent the loss of species due to competitive exclusion. High winter and spring water levels followed by low summer and fall levels reduce the growing season for both aquatic and dryland species. Competition among the remaining wetland species may be offset by overwinter ice disturbance and periodic flooding during the growing season (Hill and Keddy 1992, Toner and Keddy 1997). Manipulation of both within-year and among-year water-level fluctuations to high values should exceed both the tolerance and recruitment capabilities of most wetland plants, so that low-diversity systems are formed that include either increased numbers of upland or exotic species.

We recognize that we have only a few data points with which to base Figure 5. However, given the rate of hydrological alteration of landscapes by humans and the huge areas involved (Stanford and Ward 1992, Dynesius and Nilsson 1994), there is increased pressure to make preliminary predictions and recommendations of water-level management for biodiversity. Riparian plant communities are exceptionally diverse and their proper management can preserve not only the species involved but their ecological functions in providing migration corridors, reducing sediment erosion, and preserving water quality (Naiman and others 1993, Large and Petts 1996). There is some evidence to suggest that maintaining native plant communities helps in resisting the spread of alien species (McIntyre and others 1988). However, this may be an effect of the combined selective forces associated with the original disturbance regime (Planty-Tabacchi and others 1996).

In the study region, high species richness along lakes with large catchment areas appears to be maintained through the stress and disturbance regime governed by within-year water-level fluctuations ranging from 1 to 2 m of draw-down. Corresponding among-year variation appears to be low (e.g., SD of 0.24 m, or 24% of the mean within-year value, Lake Kejimkujik) but scant data are available from unregulated systems. In contrast with modified systems managed to deliver peak flow for hydroelectricity, long-term water-level data are rare for most unregulated lakes, and our preliminary recommendations for plant community management are perforce rudimentary. We therefore invite wetland ecologists to add points to Figure 5 to determine how shoreline plant communities of other regions fit this model and to test whether large among-year water-level variations can generate diversity patterns similar to those associated here with large within-year water-level changes. Further work is needed to identify hydrological regimes that maintain natural vegetation and those critical points where natural diversity patterns are changed.

Acknowledgments

We thank John Houck of Seaforth Engineering Group, Burpee Brittain, David Freeman, Hugh Richardson, Nick Stow, Rick Swaine, and various employees of Nova Scotia Power Corporation for providing data on dams to prepare Appendix 1. Rochelle Lawson and Adrian deBruyn kindly assisted with manuscript preparation. Funding was provided by the Natural Sciences and Engineering Research Council of Canada.

Appendix 1. Summary of information on dams used in this study

Lake	Catchment area (× 1000 ha)	Head (m)	Operating function	Construction type	Regulation device	Date installed	Date deteriorated
Vaughan	144	9.1	Head pond	Concrete	Tainter gates	1929	
Gavel	109	9.1	Head pond	Concrete	Tainter gates	1929	
Raynard	33.5	7.6	Storage	Earth with timber core	Stop logs	1929	
Mink	0.6	2	Storage	Earth with timber core	Stop logs	1930	
Kempt Back	1.7	1	Storage	Timber crib	Stop logs	1930	
Rossignol	126	17	Storage and head pond	Concrete	Sluice gates	1920s	
Harmony	1.6	3	Saw mill	Timber crib	Stop logs	1872	
Grafton	5.3	3	Fish hatchery	Earth	Stop logs	1938	1995
Molega	29.5	2	Storage	Timber crib	Sluice gates	1885	1950
		2	Recreation	Timber crib	Stop logs	1950	1965
		2	Recreation	Concrete infill	Free overflow	1965	
Hoopers	10.4	2	Sawmill	Concrete	Sluice gates	pre-1928	~1960
Ogden	26.2	4	Storage	Earth with timber core	Sluice gates	1930	1960
		4	Storage	Concrete infill	Free overflow	1978	
Parr	25.0	4	Storage	Earth with timber core	Sluice gates	1930	1960
		4	Storage	Concrete infill	Free overflow	1978	
Fanning	29.9	3	Head pond for industries	Earth with timber core	Stop logs	1910	1965
		3	Head pond for industries	Infilled	Free overflow	1965	

Appendix 2. Annual species recorded from shorelines and used in this analysis

Bartonia virginica (L.) BSP.
Bartonia paniculata (Michx.) Muhl.
Bidens frondosa L.
Conium maculatum L.
Eleocharis acicularis (L.) R. & S.
Eleocharis olivacea Torr.
Gerardia neoscotica Greene
Impatiens capensis Meerb.
Oxalis stricta L.
Polygonum puritanorum Fern.
Utricularia subulata L.

Appendix 3. Herbaceous exotic species recorded from shorelines and used in this analysis

Cardamine pratensis L.
Cerastium vulgatum L.
Conium maculatum L.
Convolvulus sepium L.
Hypochoeris radicata L.
Leontodon autumnalis L.
Oxalis stricta L.
Prunella vulgaris L.
Plantago major L.
Ranunculus repens L.
Solanum dulcamara L.
Taraxacum officinale Weber.
Trifolium repens L.
Tussilago farfara L.
Vicia cracca L.

Appendix 4. Herbaceous upland species recorded from shorelines and used in this analysis

Agrostis scabra Willd.
Anaphalis margaritacea (L.) Benth & Hook.
Bidens frondosa L.
Erechtites hieracifolia (L.) Raf.
Gerardia neoscotica Greene
Panicum lanuginosum Ell.
Potentilla simplex Michx.
Solidago graminifolia (L.) Salisb.

Appendix 5. Rare herbaceous species recorded from shorelines and used in this analysis[a]

Coreopsis rosea Nutt., nationally imperiled and globally rare
Panicum rigidulum Bosc ex Nees var. *pubescens* (Vasey) Lelong, nationally imperiled
Eleocharis tuberculosa (Michx.) Roemer and Schultes, nationally critically imperiled
Eupatorium dubium Willd., nationally rare
Hydrocotyle umbellata L., nationally imperiled
Lachnanthes caroliana (Lam.) Dandy, nationally critically imperiled
Lophiola aurea Ker-Gawl, nationally imperiled
Panicum dichotomiflorum Michx. var. *puritanorum* Svenson, provincially rare
Platanthera flava var. *flava* (L.) Lindl., nationally critically imperiled
Sabatia kennedyana Fern., nationally threatened and globally rare
Scirpus longii Fern., globally imperiled
Utricularia subulata L., nationally imperiled
Woodwardia areolata (L.) T. Moore, nationally imperiled

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[a] The rare species are all elements of the Atlantic coastal plain flora (Roland and Smith 1969. Keddy and Wisheu 1989). Their designations follow Maher and others (1978) and Argus and Prior (1990).

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