The Lake Pend Oreille Aquatic

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Abstract

This study compares the species composition, biomass, and the influence of substrate composition on an aquatic macrophyte community in the meso-oligotrophic Lake Pend Oreille, Idaho under two winter drawdown regimes. Mean dry aquatic macrophyte biomass significantly increased in the drawdown zone (1.4 - 3.5 m) from 39.9 $g{\cdot}m^{-2}$ under a 3.5 m drawdown in 1990 to 99.2 $g{\cdot}m^{-2}$ and 103.7 $g{\cdot}m^{-2}$, respectively under 2.1 m drawdowns in 1998 and 1999. Mean aquatic macrophyte biomass deeper than 3.5 m did not significantly increase, suggesting the increased biomass in the drawdown zone can at least partially be attributed to decreased winter mortality. Myriophyllum sibiricum, Chara spp., and Potamogeton richardsonii dominated the aquatic macrophyte community under the 3.5 m winter drawdown, while Chara spp., £ berchtoldii, and£. crispus dominated under higher winter water levels. The exotic Myriophyllum spicatum was present at one sample station and most prevalent in depths between 3.9- 5.1 m. M. micatum attained mean *maximum* densities in excess of 900 $g{\cdot}m^{-2}$ by August, 1999 (one year after it was first observed). Logistic regression indicated a higher probability of finding clay and cobble substrates in the drawdown zone. On these clay substrates, there were significantly lower densities of aquatic vegetation (17.9 $g{\cdot}m^{-2}$) than on sand (86.6 $g{\cdot}m^{-2}$) or silt (129.0 $g{\cdot}m^{-2}$) substrata and few plants were observed on cobble substrata.

Table Contents

List of Tables

List of Figures

Introduction

Drawdowns can greatly influence the distribution, density, and species composition of aquatic macrophyte communities. Drawdowns may directly influence aquatic vegetation through exposure of both above-ground vegetation and beneath-ground root and rhizome systems to desiccation, under either freezing or hot conditions (Cooke 1980). Indirect effects of drawdowns include alteration of physical habitat through the formation of frost heaves on de-watered sediments and subsequent mechanical damage to root systems (Renman 1989) as well as de-watering and consolidation of exposed substrates (Cooke 1980). Water level fluctuations may also influence substrate particle size distribution (Gracia Prieto 1995). Sediment particle size is an important factor in determining the distribution of aquatic macrophytes (Unni 1977, Anderson 1978, Sand-Jensen and Sondergaars 1979) by controlling the availability of root attachment surfaces, intra-sediment chemistry, and nutrient dynamics (Anderson and Kalff 1988).

The response of aquatic macrophyte communities to seasonal de-watering (lake drawdown) has been the focus of many studies (Lantz et al. 1964, Hunt and Jones 1972, Nichols 1975a, Wilcox and Meeker1991). However, most studies have emphasized the use of drawdown as a lake management technique to control nuisance aquatic vegetation (Mathis 1965, Manning and Sanders 1975, Nichols 1975b, Goldsby et al. 1978, Cooke 1980, Tazik et al. 1982) and as a result, have taken place in mesa-to eutrophic systems (Cooke and Gorman 1980, Siver et al. 1986). Fewer studies have taken place in meso-oligotrophic or oligotrophic water bodies (Rorslett 1985, Hellsten and Riihimaki 1996), or studied effects of higher winter water levels on an aquatic macrophyte community after exposure to multiple winter drawdowns.

The importance of aquatic macrophytes to the autotrophic community of freshwater lakes and rivers has been well-established (Hutchinson 1975, Home and Goldman 1994). Aquatic macrophyte communities influence both physical and biogeochemical lake processes. Carpenter and Lodge (1986) provide a comprehensive review of the role of submersed macrophytes in lake ecosystems including; (1) physical processes, such as light extinction, water flow, substrate accretion and composition, and temperature; and (2) biogeochemical processes, such as oxygen production/consumption, dissolved inorganic and organic carbon cycling, and sediment-water nutrient dynamics. Aquatic macrophytes also serve as a food source and provide habitat for littoral fauna (Soszka 1975, Weaver et al. 1997). Aquatic macrophytes may reach nuisance densities as lake enrichment becomes more prevalent. These nuisance levels of aquatic vegetation may hinder water-based recreation and become aesthetically unpleasing (Tarver 1980, Falter and Burris 1996). Therefore, any anthropogenic changes to the lake littoral zone *(i.e.* lake level manipulations) and subsequently to the aquatic macrophyte community are of both ecological and economic importance.

The objectives of this study were to:

(1) Describe Lake Pend Oreille's littoral sediment and water column pysico-chemistry;

(2) Describe the aquatic macrophyte community in Lake Pend Oreille and its response to an experimental increase in winter lake elevation from 625 m

(typified by 1990 winter drawdown) to 626.7 m msl (typified by 1998-99 winter drawdown);

(3) Compare overall biomass of aquatic vegetation in the drawdown zone (the depths of the littoral zone from Om to 3.5 m) and in the permanently wetted depths of the littoral zone (depths greater then 3.5 m) in 1990 vs. 1998-99;

(4) Describe composition of the aquatic macrophyte community under both drawdown regimes (1990 and 1999); and

(5) Investigate relationships between substrate particle size, depth, and macrophytes in 1999.

Site Description

Lake Morphometry

The meso-oligotrophic Lake Pend Oreille lies in the glacially formed Purcell Trench in the panhandle of northern Idaho. Approximately 90% of the surface-water inflow and close to 90% of the total nitrogen and phosphorus loads to Lake Pend Oreille are from the Clark Fork River (Frenzel 1993), draining much of Montana west of the Continental Divide, into the northeast comer of the lake (Fig. 1). Lake Pend Oreille is divided into several basins: the deep relatively poorly flushed southern end with a mean hydraulic retention time greater than 10 years (Falter et al. 1992); the deep central basin with its steep shorelines; the shallow northern basin (mean hydraulic retention time less than 1 year; Hoelscher et al. 1993); and the lake's shallow outlet arm. Lake morphometry is an important factor influencing the spatial distribution of aquatic macrophytes in Lake Pend Oreille.

Lake Pend Oreille proper is a 383 km^2 (94641 acres) lake with mean and maximum depths of 164 m (538 ft) and 357 m (1171 ft), respectively (USGS 1996). It is Idaho's largest and deepest lake. Shoreline length of the lake proper is approximately 310 km with a maximum width of 10 km and low ratios of littoral area/lake volume to pelagic area/lake volume. The lake's outlet arm is the Pend Oreille River, exiting from the northwest comer of the lake. Mean and maximum depths of the outlet arm are 7.4 m and 48 m, respectively. Shoreline length of the outlet arm is about 152 km (USGS 1996). The outlet arm is impounded by Albeni Falls Dam on the Washington-Idaho border. Lake Pend Oreille is an important recreational and residential water body for the area, supporting moderate shoreline development on the northern half of the main lake and the outlet arm as well as seasonally heavy recreational use.

Lake Pend Oreille lies in a 59324 km^2 watershed. Major bedrock types in the watershed are Belt series and Kaniksu batholith (Savage 1965). Much of the watershed is forested (83% of the watershed) consisting mainly of coniferous tree species (Hoelscher et al. 1993). Developed lands (barren and impervious surfaces) in the early 1990's accounted for approximately five percent of the watershed, while agriculture and grazing comprised smaller percentages of total watershed use (EWU 1991). Population growth around Lake Pend Oreille is steadily increasing from about 15587 in the 1960's to 26622 in 1990 and a projected population of 35081 by 2010 (Hoelscher et al. 1993).

History of Winter Lake Drawdowns on Lake Pend Oreille

From 1966 to 1994, an annual winter drawdown controlled by the Albeni Falls outlet dam lowered lake water levels 3.0 m to 3.7 m (lake elevation of 625 m mean sea level (msl)) from mid-November through April, for spring flood control and winter power production. Maximum summer water level has been controlled at 628.6 m msl from 1952 to the present. The Idaho Department of Fish and Game (IDF&G) had concerns that winter drawdowns of 3.5 m were de-watering much of the preferred spawning substrate for winter lake-spawning kokanee (Onchorhynchus nerka). These concerns prompted experimental winter drawdowns of 2.1 m (higher winter lake levels of 626.3 m - 626.7 m msl rather than 625 m) in an effort to enhance kokanee spawning gravel and survival. The IDF&G also wanted to determine whether higher winter water levels would improve over-winter survival of warmwater fishes (*e.g.,* pumpkinseed (Lepomis gibbosus), black crappie (Pomoxis nigromaculatus), and largemouth bass (Micropterus salmoides)) in the outlet arm of Lake Pend Oreille by providing additional littoral habitat. These fishes prefer habitat of shallow waters with zero velocity, and dense vegetation. Over-winter fish habitat for these fishes had been consequently limited by winter drawdown (Dupont 1994). Any increase in aquatic macrophyte densities in these backwater areas as a result of higher winter water levels could increase available winter habitat and habitat complexity.

Materials and Methods

SamJ.!le Stations

Nineteen stations on the outlet arm and on Lake Pend Oreille proper were sampled for aquatic macrophytes in 1998 and 1999 (winter drawdown of 2.1 m). Six stations located on the outlet arm and the northern-most basin of the lake had earlier been sampled for aquatic macrophytes in 1990 (winter drawdown of 3.5 m). Drawdown regime analysis is restricted to the six stations with data in all three of these years (Fig. 1). The six sample stations were River Kilometer (RK) 0.8, 4.4, 18.5, and 26.6 on the outlet arm, and Kootenai and Sunnyside Bays. These sites are conducive to macrophyte growth (shallow depths and well-lit, fine substrate) and therefore most likely to respond to higher winter water levels.

Sediment and Water <u>Physico-Chemistry</u>

Sediment

To describe lake sediment chemistry, we sampled lake sediments at eight sample stations in July, 2000 in Lake Pend Oreille (LPO) proper and its outlet arm. LPO proper stations included Bottle, Ellisport, Idlewilde, and Scenic Bays. Outlet arm stations were RK 0.8, 4.4, 18.5, and 26.6. Three to nine replicate sediment samples were obtained at each site using a Petite Ponar Dredge (225 cm^2). Samples were cleaned of all vegetation, placed in storage containers, and stored in the dark on ice until processing. Analyses were performed at the Analytical Sciences Laboratory, University of Idaho. Analyses included the determination of sediment total phosphorus, percent nitrogen, percent organic carbon, percent carbon, and percent organic matter.

Water Column Physico-Chemistry

We measured selected physical and chemical water quality variables at all 19 stations in July-September, 1998 and July-October, 1999. A complete list of variables measured is in Tables 1 and 2. We also measured total phosphorus and nitrate-nitrogen at all 19 sample stations in July-October, 1999 as follows. Three replicate water samples were taken at each station using a 2-liter Kemmerer water sampler. Samples were placed in a I-liter Cubitainer, fixed with 2 ml $H2SO_4$ and stored in the dark on ice until processing. Quality Assessment/Quality Control (QA/QC) analyses included field and laboratory spikes. Field spikes were obtained by retrieving duplicate water samples from six randomly selected stations (three for nitrate-nitrogen and three for total phosphorus each month). One water sample was divided into two 1 1 cubitainers. One cubitainer was spiked while the other was used as a control. Nitrate-nitrogen was determined according to Standard Methods Procedure 4500-N.B, and total phosphorus was determined according to Standard Methods Procedure 4500-P.C (APHA 1992).

Aquatic Macrophyte Collection and Laboratory

Aquatic macrophytes were sampled August 1990 and July through September in 1998 and 1999. Therefore, aquatic macrophyte data used in the drawdown regime analysis were restricted to samples collected in August (the period of maximum macrophyte biomass) in all three sampling years. Using a bathymetric map of Lake Pend Oreille and its outlet arm (USGS 1996), sample stations were established along the depth contours of the littoral zone. Depth zones were designated A through D as follows: A = 0 m (full summer level) - 1.4 m depth; B = 1.4 m- 3.5 m; C = 3.5 m- 7.0 m; and D = 7.0 m - 11.0 m depth. Samples were taken along a transect running perpendicular to the shoreline at increasing depths until all strata were sampled. We collected plants in 1990 with a Peterson Dredge (900 cm^2), taking four to eight replicate plant samples from each stratum per site. A Petite Ponar Dredge (225 cm^2) was used in 1998 and 1999 to obtain eight replicate plant samples from each stratum per site.

Plant samples obtained in 1990 and 1999 were carefully washed to remove any detritus, sediment, and epiphytic algae. Samples were then separated and identified to species. Plant identification followed the manual Flora of the Pacific Northwest (Hitchcock and Cronquist 1973). The Standard Methods Procedure (10400 D.3) for oven dry weight (**ODW** as $g\text{-}m^{-2}$) or biomass, was used to obtain percent species composition by weight and total ODW per grab by depth to estimate areal biomass (APHA 1992). Total areal biomass per grab was determined for aquatic macrophytes sampled in 1990, 1998, and 1999. All mean biomass values include grabs in which no plants were collected *(e.g.,* if eight grabs were retrieved and 3 grabs contained no plants then 3 zero values were entered when computing mean biomass).

Substrate Coml!osition Data Collection

Substrate particle size was visually determined for each plant grab using the modified Wentworth Scale (Hynes 1972). This scale classifies substrate ranging from clay-sized (< 0.004 mm) to boulder-sized (>256 mm) particles. Other qualitative physical properties such as sediment consolidation and color were also recorded.

Statistical Analysis

Sediment

We used analysis of variance (ANOVA) to evaluate overall between-site differences in measured sediment parameters. The Ryan-Einot-Gabriel-Welsch Multiple Range Test was used for multiple comparisons among sites. Sediment nutrient values were log-transformed prior to analysis to meet statistical assumptions (K.leinbaum et al. 1998).

Aquatic Macrophytes

Aquatic Macrophyte Community Dynamics. Mean aquatic macrophyte biomass values for the 19 selected sample stations are reported to describe temporal and spatial patterns of aquatic macrophyte biomass in Lake Pend Oreille proper and its outlet arm. Percent species dominance was calculated for 1999 sample stations. Statistical analyses of mean biomass values were not performed due to the inability to accommodate homogeneity of variance. Percent dominance was calculated by pooling the species data for each station as follows:

$$\text{Percent dominance} = (r'N) \times 100 \tag{1}$$

where 'n' is the total biomass of a given species and 'N' is the total biomass of all individual samples.

Drawdown Regime Analysis. To analyze the aquatic macrophyte community response to higher winter water levels we divided the littoral area into two zones, drawdown and permanently wetted. The drawdown zone was defined as the depths of the littoral zone that were previously de-watered during winter drawdowns of 3.5 m and now permanently wetted under higher winter water levels (winter drawdown of 2.1 m). The drawdown zone encompassed the depths between 1.4 m to 3.5 m.

Aquatic macrophyte biomass in the permanently wetted areas of the littoral zone (depths greater than 3.5 m) were analyzed to determine the temporal response of the aquatic macrophyte community in areas not de-watered during either drawdown regimes. This depth stratum had never been subjected to winter drawdown, and therefore served as a control to determine if an observed increase in biomass occurred over the entire littoral zone or only in the drawdown zone.

Between-year and among-site differences in mean aquatic macrophyte biomass in the drawdown zone and in the permanently wetted depths of the littoral were evaluated using analysis of variance (ANOVA). The Ryan-Einot-Gabriel-Welsch Multiple Range Test was used for multiple comparisons among years. Aquatic macrophyte biomass values were log-transformed prior to analysis to meet statistical assumptions (Kleinbaum et al. 1998). To take into account differences in sampling areas (dredge size of 900 cm^2 in 1990 and 225 cm^2

in 1998-99) between years, 1998 and 1999 biomass measurements were given 1/4 the weight (variance weighting) of the 1990 biomass measurements prior to the analysis. Sample stations were not randomly selected because of the need to ensure the areas analyzed were suitable macrophyte habitat; therefore, inferences based on statistical analyses cannot be made to the entire lake and pertain only to specific stations.

Community composition and diversity. Due to the inherent difficulty in analyzing multi-species community data (Smith et al. 1990), several methods were used to compare community composition in the drawdown zone in 1990 and 1999. Species percent dominance was calculated as described above. Percent frequency was calculated by pooling the species data for all six sites for 1990 and 1999 as follows:

$$\text{Percent frequency} = \} \qquad 100 \tag{2}$$

where '*f*' is the number of samples in which a given species was recorded and 'F' is the total number of samples. Percent dominance is based on abundance (biomass) whereas percent frequency is based on the number of samples in which a species was recorded.

Kulczynski's Index ofDisimilarity (CAP 1999) was used to compute station dissimilarity values to define temporal variation in species composition and abundance between sample stations in 1990 and 1999. Rare species (frequency of occurrence less than 5% in both years) were deleted from the data matrix prior to analysis, as these occurrences can usually be attributed to chance rather than to an indication of ecological conditions (Gauch 1982). Aquatic macrophyte biomass for each species was averaged over replicate samples for each sample station to reduce variation (Gauch 1982) and later used as abundance values in the computation. Abundance data were double-square-root transformed (McRae et al. 1998) to allow less abundant species to contribute to between-site dissimilarities.

Dissimilarity values were calculated as follows:

Kulczynski's Index of Dissimilarity: $D_{jk} = 1 - \left(\frac{1}{2}\left(\frac{W}{A} + \frac{W}{B}\right)\right)$ (4)

where A is the sum of species abundance's at station j, B is the corresponding value at station k, and W is the sum of the minimum values for each species when comparing both stations. Computed values are on a scale from O to 1 where a dissimilarity value of 1 would indicate completely different community composition and abundance between stations j and k, and a dissimilarity value of O would indicate identical community composition and abundance between stations j and k.

The Kulczynski's Dissimilarity matrix was then used in cluster analysis using Ward's Minimum Variance method. Standard Euclidean distance measures were not used in the cluster analysis due to poor performances of these measures (Ludwig and Reynolds 1988). The hierarchical clustering method was used to produce a dendrogram showing any meaningful clustering of stations. For example, if 1990 sample stations clustered together but separately from 1999 stations, then community structure would be different between these years indicating different macrophyte communities between the two drawdown regimes.

Substrate Composition

To elucidate relationships between substrate composition, depth and aquatic macrophyte biomass we classified each plant grab's sediment content into one of five substrate categories. Each grab was classified as either (1) "clay "; (2) "silt"; (3) "sand"; (4) "gravel"; or (5) "cobble".

Binary logistic regression analysis was performed to determine if depth was a significant predictor of substrate. The probability of observing a substrate particle size class at a given depth can then be determined for any significant relationships as follows:

$$P(substrate) = \frac{\exp^{(\hat{\beta}_0+\hat{\beta}_1 x)}}{1+\exp^{(\hat{\beta}_0+\hat{\beta}_1 x)}} \qquad (5)$$

where $\hat{\beta}_0$ and $\hat{\beta}_1 x$ are coefficients derived from logistic regression and 'exp' is e raised to the given power.

No aquatic macrophytes were found on "gravel" or "cobble" substrate classes. Therefore only mean aquatic macrophyte biomass on "clay", "silt", and "sand" substrate classes were compared using ANOVA and the Ryan-Einot-Gabriel-Welsch Multiple Range Test for pair-wise comparisons. Aquatic macrophyte biomass values were log-transformed prior to analysis to accommodate homogeneity of variance. All statistical analyses were performed using the SAS GLM and LOGISTIC procedures (SAS Institute Inc. 2000) and STATISTICA (Statistica for the Macintosh 1994) computing software.

Results

Sediment and Water Physico-Chemistry

Sediment

Lake sediment chemistry analyses determined that total sediment phosphorus ranged from 395.0 $\mu g \cdot g^{-1}$ - 1563.3 $\mu g \cdot g^{-1}$ · Scenic Bay had significantly higher total phosphorus (1563.3 $\mu g \cdot t^{1}$) than other stations (Table 3). Mean percent nitrogen ranged from 0.0 % at RK18.5 to 0.4 % at Bottle and Idlewilde Bays. Mean percent organic carbon ranged from 0.8 % at RK.18.5 to 7.5 % at Scenic Bay; mean percent carbon ranged from 0.7 % at RKI 8.5 to 8.4 % at Scenic Bay; and mean percent organic matter ranged from 1.4 % to 12.9 % at RK.18.5 and Scenic Bay, respectively.

Water Column Physico-Chemistry

Lake Pend Oreille is a meso-oligotrophic water body characterized by moderately high water clarity and low nutrient concentrations. Mean secchi depth ranged from 5.6 m - 12.0 min August, 1998 and from 3.8 m - 8.9 min August, 1999. Mean total phosphorus and nitrate-nitrogen concentrations at selected sample stations in August, 1999 ranged less than 7 μgT^{1} (detection limit) - 7 μgT^{1} and from 21.5 μgT^{1} - 40.25 $\mu g\text{-}r^{1}$, respectively (Tables 1 and 2).

Mean percent recovery (QA/QC) for total phosphorus and nitrate-nitrogen field spikes were 101.8% and 74.1%, respectively. Mean percent recovery for laboratory spikes of total phosphorus and nitrate-nitrogen were 90.8% and 94.5%, respectively.

Aquatic Macrophytes

Aquatic Macrophyte Community Dynamics

Mean aquatic macrophyte biomass from the 19 selected sample stations on Lake Pend Oreille proper and its outlet arm ranged from 0.0 g·m^{-2} at Warren Island to 276.0 g-m^{-2} at RK0.8 in 1998 and from 0.0 g-m^{-2} at Maiden Rock to 188.7 g-m^{-2} at RK.16.1 in 1999 (Fig. 2 and 3). Mean aquatic macrophyte biomass declined from northern lake stations *(e.g.,* CFR and BOT) to southern lake stations *(e.g.,* IDL and SCE) in both years. No apparent trend in biomass was observed in the outlet arm.

Twenty-five macrophyte species from 14 families were present in Lake Pend Oreille proper and its outlet arm in 1999 (Table 4). Two dominant species in the outlet arm and Lake proper stations in July, 1999 were Potamogeton crispus (comprising 47% and 32% of the community in the outlet arm and Lake proper, respectively) and Elodea spp. (comprising 17% and 22% of the community in the outlet arm and Lake proper, respectively). In August, the two dominant species in the outlet arm were Elodea spp. and r. crispus (each comprising 26% of the macrophyte community). Myriophyllum sibiricum dominated (40%) the aquatic macrophyte community in the outelt arm stations in September. In August and September, the two dominant species in the Lake Pend Oreille proper stations were Chara spp. and P. berchtoldii (comprising 26% and 22% in August and 31% and 27% in September, respectively; Fig. 4).

Drawdown Regime Analysis

Mean dry aquatic macrophyte biomass, in the drawdown zone (1.4 m - 3.5 m), significantly increased ($p = 0.01$) from 39.9 $g{\cdot}m^{-2}$ in 1990 to 99.2 $g{\cdot}m^{-2}$ and 103.7 $g{\cdot}m^{-2}$ in 1998 and 1999, respectively (Fig. 5A). Mean aquatic macrophyte biomass among stations and stationsxtime interaction were not significant ($p = 0.23$ and 0.08, respectively); therefore, we investigated the effects of time on biomass independently of site. Mean aquatic macrophyte biomass in the permanently wetted littoral (depths greater than 3.5 m) were not significantly different ($p = 0.72$) in 1990 (70.3 $g{\cdot}m^{-2}$) when compared to 1998 and 1999 (185.0 $g{\cdot}m^{-2}$ and 157.1 $g{\cdot}m^{-2}$, respectively; Fig. 5B).

Community Composition and Diversity

Community composition changed in the drawdown zone in 1990 when compared to 1999 (Table 5). The four dominant aquatic macrophytes in 1990 were Myriophyllum sibiricum (30.1%), Chara spp. (29.3%), Potamogeton richardsonii (23.9%), and P. foliosus (6.3%). In 1999, Chara spp. (27.4%), r_. berchtoldii (25.3%), r_. crispus (23.6%), and Elodea spp. (12.7%) (E. canadensis and E. nutallii) dominantated the drawdown zone. Community composition in the described drawdown zone does not include the exotic Myriophyllum spicatum. This species was abundant at RK 0.8 in 1999 (maximum densities exceeded 900 $g{\cdot}m^{-2}$ oven dry weight) in depths between 3.9- 5.1 m; however, it occurred less frequently and at lower densities in the 1.0 - 3.5 m depth range which includes the described drawdown zone (1.4 - 3.5 m).

The dominant species frequency of occurrence also changed between years. For example, in 1990, the three dominant aquatic macrophyte species also occurred most frequently. In 1999, however, Elodea spp. occurred more frequently (47.9%) than _e. crispus (8.3%). All other macrophyte species comprised small proportions of the community. Potamogeton crispus, _e. praelongus, and Drepanocladius were not found in 1990 in depths between 1.4 m and 3.5 m; however, they were present in depths below 3.5 min 1990. These three species were present between 1.4 m and 3.5 min 1999 after 3 years of higher winter water levels. Potamogeton zosteriformis was not found in 1990, but was present in the 1.4 - 3.5 m drawdown zone in 1999. Potamogeton robbinsii was present in the drawdown zone in 1990 and absent in 1999. Ceratophyllum demersum, Tillaea aquatica, and P. pectinatus were major species that showed no or little response to a change in winter water levels.

Cluster analysis of Kulczynsk:i 's dissimilarity values revealed two meaningful clusters (Fig. 6). Most stations within a year (stations under a similar drawdown regime) tended to cluster together. Shannon's ff Diversity Index was also calculated for each station in 1990 and 1999. Index calculations were based on the total number and biomass of species present at each station. Mean Shannon's ff Index did not significantly differ between 1990 and 1999 (t-test, p = 0.64).

Substrate Coml!osition

Results of the binary logistic regression indicated that depth was a significant predictor of four of the five-substrate categories (Table 6). Silt was the only non-significant category (p = 0.12). The probability of observing "clay" and "cobble" increased as depth decreased; whereas, the probability of observing "gravel" and "sand" decreased as depth decreased (Fig. 7).

Mean aquatic macrophyte biomass was significantly lower ($p < 0.0001$) on "clay" substrate types (mean dry biomass= 17.9 $g \cdot m^{-2}$) compared to "silt" and "sand" substrate classes which had mean aquatic macrophyte biomass of 129.0 $g \cdot m^{-2}$ and 86.6 $g \cdot m^{-2}$, respectively (Fig. 8).

Discussion

Sediment and Water Physico-Chemistry

Sediment

Lake sediments play a large role in nutrient cycling and dynamics in many lakes and reservoirs (Horne and Goldman 1994). Heathwaite (1994) demonstrated that increased human development often leads to an increase in sediment and nutrient export from land to adjacent waterbodies and these changes are reflected in lake sediments. Lake Pend Oreille is phosphorus-limited (Woods 1993); therefore, any potential sources of phosphorus *(i.e.,* sediments) can potentially contribute to biological productivity. However, aerobic sediment conditions in Lake Pend Oreille retain sediment phosphorus in a biologically unavailable form *(i.e.,* as ferric phosphate). Total mean sediment phosphorus measured in Lake Pend Oreille ranged from 395 $\mu g \cdot g^{-1}$ at Idlewilde Bay to 1563.3 $\mu g \cdot g^{-1}$ at Scenic Bay, July, 2000. These values are likely influenced by the degree of human development at these two bays. Idlewilde Bay is located on a state park and as a result, has little human development. Scenic Bay however, is located on a town (Bayview, Idaho) and has a significant amount of housing development, house docks, and intense boating activity that may have contributed to the observed differences. Except for Scenic Bay, total phosphorus (TP) concentrations in Lake Pend Oreille are similar to those reported by Rattray et al. (1991) for the oligotrophic Lake Taupo, New Zealand (TP range= 234 - 700 µg·t ^{1}) . However, they are lower than the range reported by Ostrofsky (1987) for 66 lakes in the eastern U.S. representing a broad range of lake types from oligotrophic to eutrophic (TP range= 1329 - 9212 µg·g-^{1}) .

Water Column Physico-Chemistry

Due to its deep aerobic water column acting as a nutrient trap (Falter et al. 1992), Lake Pend Oreille is able to dilute much of the effects of the sizeable nutrient loading from the Clark Fork River. Nutrient concentrations (total phosphorus and nitrate-nitrogen) and water transparency (secchi depth) in Lake Pend Oreille proper appear not to have changed from 1990 through 1999. Mean total phosphorus and nitrate-nitrogen concentrations at selected sample stations in August, 1999 ranged less than 7 µgT ^{1} (detection limit) to 7 µgT^{1} and 21.45 µgT ^{1} - 40.25 µg-r^{1}, respectively. Mean concentration of total phosphorus in Lake Pend Oreille proper in 1989-90 ranged from 5 µgT ^{1} - 10 µg-r' (Woods 1993). Summer secchi depth readings in Lake Pend Oreille proper ranged from about 5.0 - 11.0 min 1989-90 (Woods 1993). Mean summer secchi depth ranged from 5.6 - 12.0 min August, 1998 and from 3.8 - 8.9 min August, 1999. Low secchi depth readings observed by Woods (1993) were measured during spring runoff when turbid inflows entered the lake *via* the Clark Fork River and were not due to an increase in biological production.

Aquatic Macrophytes

Aquatic Macrophyte Community Dynamics

Mean aquatic macrophyte biomass (oven dry weight (ODW)) from the 19 selected sample stations on Lake Pend Oreille proper and its outlet arm ranged from 0.0 $g \cdot m^{-2}$ at Warren Island to 276.0 $g \cdot m^{-2}$ at RK0.8 in 1998 and from 0.0 $g \cdot m^{-2}$ at Maiden Rock to 188.7 $g \cdot m^{-2}$ at RK.16.1 in 1999. The lack of aquatic plants at Warren Island and Maiden Rock are likely a function of lake morphometry (littoral slope) and substrate. Both stations were characterized by steep littoral slopes and a substratum dominated by medium to large cobble. The lack of root-attachment surface and low nutrient levels in coarse substrates (Barko and Smart 1986) likely limited macrophyte colonization at these sites.

Higher densities of aquatic macrophytes in sample stations located at the northern end of the lake were also influenced by lake morphometry and the Clark Fork River. The northern lake area has a shallower mean depth, a more gradual littoral slope, and receives an annual spring influx of fine sediments and nutrients from the Clark Fork River providing high quality aquatic macrophyte habitat compared to southern lake areas.

Common species in Lake Pend Oreille and its outlet arm included Potamogeton spp., Elodea, spp., Chara spp., and Myriophyllum spp. Falter and Olson (1990) found similar aquatic macrophyte species in Lake Pend Oreille proper and its outlet arm in 1989-90 which included M. sibiricum, Chara spp., Potamogeton spp., and Elodea canadensis.

Drawdown Regime Analysis

Mean aquatic macrophyte biomass (ODW) in the drawdown zone significantly ($p = 0.01$) increased from 39.9 $g \cdot m^{-2}$ in 1990 to 99.2 $g \cdot m^{-2}$ and 103.7 $g \cdot m^{-2}$ in 1998 and 1999, respectively. This overall increase in aquatic macrophyte biomass in the drawdown zone showed increased survival and spatial expansion of aquatic macrophytes into depth strata under the new regime of year-round submersion with higher winter water levels. We found no significant increase in aquatic macrophyte biomass in the permanently wetted littoral (deeper than 3.5 m) that supports this hypothesis. The lack of significant increase in biomass in the permanently wetted littoral suggests that the observed increase in aquatic macrophyte biomass in the drawdown zone was not due to site enrichment or any other physico-chemical changes that may have occurred between 1990 and 1998-99. Improvements in residential and commercial wastewater treatment systems surrounding the lake may ,have decreased potential site enrichment in higher density developments around the lake. For example, there has been a decrease in the number of shoreline residences with septic systems impacting the lake since 1977 (Lawlor 1993). And recently, a three-lagoon sewage collection and treatment system was developed for the north-east area of the lake that eliminated several more residential and commercial septic tank systems, thereby reducing potential nutrient leaching into the lake.

The increase in aquatic macrophyte biomass in the drawdown zone under higher winter water levels might be expected in relatively deep lakes with high transparency. Higher water levels increase the amount of available habitat and light does not rapidly become a limiting factor so a net increase of littoral volume ensues. Conversely, higher water levels may reduce the standing crop of aquatic macrophytes in shallower water bodies with low transparency. In these latter systems, high water levels can increase sedimentation, and decrease light penetration through wave re-suspension of sediments (Woltemade 1997), thereby reducing available habitat for aquatic vegetation. Lake Pend Oreille is clearly a lake in the former category.

Community Composition and Diversity

Higher winter water levels have a species-specific effect on aquatic macrophyte communities. Different species have different tolerances to de-watering and exposure to dry conditions (Hudon 1997). Different community composition would therefore be expected under different levels of winter drawdown. Three of the four dominant species present under higher winter water levels were either absent (P. crispus) or represented a very minor proportion of the macrophyte community (Elodea spp. and_E. berchtoldii) in the 1.4 m - 3.5 m drawdown depth zone in 1990. Elodea spp. primarily spreads *via* stem fragmentation whereas P. crispus propagates primarily from dormant apices (turions; Nichols and Shaw 1986). Wave action and anthropogenic disturbances (e.g., boat traffic) may lead to the dispersal of these vegetative structures into newly created habitat. The spatial expansion of these species from 1990 to 1998-99 into the new permanently wetted littoral zone may have been facilitated *via* the propagation of vegetative reproductive structures. Furthermore, these two species can overwinter as evergreen plants under ice cover, and grow quickly with spring warming (Nichols and Shaw 1986), thereby obtaining an advantage early in the growing season when competing for light. Hestand and Carter (1975) also documented shifts in dominant species under higher water levels following an overwinter drawdown. Hellsten and Riihimaki (1996) found different aquatic plant species composition in the regulated Lake Ontojarvi compared to the unregulated Lake Lentua. Average winter drawdown in Lake Ontojarvi was about 3.4 m. The aquatic macrophyte community in Lake Ontojarvi was comprised of species that had adapted to the level of disturbance caused by lake regulation.

Chara spp. was the only dominant member of the drawdown zone under both drawdown regimes in Lake Pend Oreille. Charophytes are often pioneering species and their oospores will remain viable after extended periods of dry and freezing conditions (Proctor 1967, Bates and Smith 1994). These characteristics may account for its dominance both in the exposed area of the littoral zone after overwinter drawdown (1990) and its continued dominance with higher winter water levels in Lake Pend Oreille (1999). The movement of _e_. crispus, _e_. praelongus, and Drepanocladius from the permanently wetted littoral (depths > 3.5 m) into the drawdown zone with higher winter water levels, suggests that the earlier 3.5 m winter drawdown limited the shoreward distribution of these taxa. In 1999, _e_. crispus occurred less frequently than Elodea spp. although the former was a more dominant species (occurred in higher densities) in the community. This is likely because P. crispus was found in dense monospecific stands, while, Elodea spp. occurred in more samples, but at lower densities.

Some species showed no response to higher winter water levels. C. demersum represented a small (0.4%) but constant proportion of the community under both drawdown regimes. Since C. demersum lacks true roots, currents and wave action can move it between depth zones and as a result, it will be relatively unaffected by winter drawdowns and subsequent increases in winter water levels. Nichols (1975a) also found _C. demersum show no response to overwinter drawdown and no preference to water level in the Chippewa Flowage, Wisconsin. However, Hestand and Carter (1975) found a disappearance of C. demersum upon refilling of shallow Lake Ocklawaha following a 1.5 m overwinter drawdown from September to February. Lake morphometry, winter conditions, and species mix likely influence the response of individual species to higher water levels. For example, the Chippewa Flowage is a large reservoir with interconnected bays. Isolated areas of the reservoir experience different water level changes as surface water connection with the flowage is cut off. As a result, some areas experience less than a 2 m drawdown while other areas experience up to a 9 m drawdown. The areas that experience relatively stable water levels apparently provide refugia for populations of aquatic plants. Whereas Lake Ocklawaha, a shallow reservoir in central Florida, has the entire lake littoral area affected by water level fluctuations, thereby reducing the chance of shallow water refugia. Hestand and Carter (1975) further noted that plant cover of Hydrilla verticillata increased following winter drawdown. Hydrilla may have acted synergistically, through competition for resources, with winter drawdown to reduce densities of C. demersum.

Cluster analysis indicated that different aquatic macrophyte communities were present in the drawdown zone in 1990 compared to 1999. These communities differed in community composition and overall biomass (as described above). I believe that biomass of species present (overall increase in biomass in the drawdown zone) and species composition (spatial expansion of species into the new permanently wetted littoral under higher winter water levels) both contributed to the dichotomy of the two communities. However, with such extreme spatial heterogeneity of aquatic plant communities (France 1988), I do expect that a few sample stations would cluster with stations under a different drawdown regime.

Substrate Com}!osition

Logistic regression showed the probability of observing "clay" and "cobble" decreased as depth increased and the probability of observing "gravel" and "sand" increased as depth increased. With water level fluctuation, finer particles will be transported before large particles (Home and Goldman 1994), therefore increasing the probability of leaving cobble-sized particles in the drawdown zone. The higher probability of finding cobble substrates in shallow water in this study reduced the amount of available plant habitat in the drawdown zone.

Substrate composition was influenced by both overwinter drawdown and by the dominant bottom morphology of sample stations in this study. The increased probability of observing clay and cobble substrate types in shallow depths are likely a direct result of years (since 1966) of exposing littoral sediments to drying and desiccation.

Four of the six sample stations were located in the outlet arm of Lake Pend Oreille. The outlet arm has some lotic characteristics, having unidirectional flow (velocities up to 8 $cm \cdot s^{-1}$ Dupont 1994) and the presence of an old river channel as the deepest area (thalweg). As depth, current velocity, and slope increase in the thalweg, the substrate shifts to a sand and gravel composition because these larger substrate particles are less likely to be moved by the current. Falter et al. (1991) also cited the direct effects of morphometry and velocity on substrate deposition and accumulation as limiting factors of aquatic macrophyte colonization in the Pend Oreille River, Washington immediately downstream of Lake Pend Oreille. Carlson (1995) compared aquatic macrophyte densities in two sloughs in the Pend Oreille

River, Washington and concluded that lower aquatic macrophyte densities in one slough was primarily a function of morphometry *(i.e.,* steeper littoral slope).

Highest biomass was found on silt and sand substrates for two likely reasons (1) the probability of observing sand increased as depth increased; therefore, plants on this substrate were removed from effects of wave action and winter drawdown; and (2) low nutrient levels and limited nutrient diffusion rates in coarse substrates such as gravel (Barko and Smart 1986). Anderson and Kalff (1988) found that silt substrate supported significantly higher biomass than did sand or organic sediments and that these three categories all supported higher biomass than gravel. Madsen and Adams (1989) found maximal aquatic macrophyte biomass on silt substrata in a eutrophic stream (Badfish Creek, Wisconsin). Aquatic macrophyte densities were low on gravel and lowest on sand. Badfish Creek was dominated by r_. pectinatus, a species also found in Lake Pend Oreille.

Ecological and Management Implications

Years of winter drawdown have altered the physical habitat for aquatic macrophytes in many areas of Lake Pend Oreille through sediment alterations such as consolidation, erosion, and depositional processes. Sediment consolidation occurs as exposed flocculent sediments dry out and compact. For example, Plotkin (1979) conducted a series of artificial lake drawdowns on experimental lakes. After 6 weeks desiccation, exposed sediment in all test lakes were consolidated and sediment depth decreased by 50%. The sediments in the test lakes remained firm 6 months after refilling. This consolidation can influence aquatic plant growth. For instance Plotkin (1979) noticed slower growth rates of Elodea densa in the compacted sediments compared to flocculent sediment. Our study did not directly measure sediment consolidation; however, consolidated clay sediments were common in shallower depths *(i.e.,* the drawdown zone) and these sediments provided relatively poor aquatic plant habitat.

Increasing the permanently wetted littoral area through higher winter water levels has led to an overall increase in aquatic macrophyte density and resulted in the spatial expansion of species from deep-water communities to shallow-water communities in Lake Pend Oreille. The spatial complexity and abundance of the resulting plant community will benefit aquatic and semi-aquatic biota which utilize these vegetated littoral areas. For example, yellow perch (Perea flavescens) are often more dominant in dense, species-rich vegetation beds that are structurally complex (Weaver et al. 1997). Liter (1991) collected fish densities up to 5.2 fish·m-^{2} in heavily vegetated areas while sampling with pop nets in the Pend Oreille River, Washington, and concluded that heavily vegetated areas were important fish habitats, especially for juvenile centrarchids. Aquatic macrophyte communitites in the Pend Oreille River, Washington also contained higher density and diversity of zooplankton species than in adjacent open waters (Carlson 1995). For example, Carlson (1995) determined mean zooplankton densities measured in aquatic macrophyte beds to be 43 organismsT^{1} in late August compared to 3 organismsT^{1} in adjacent open water.

These backwater areas also represent important fish habitat in the outlet arm of Lake Pend Oreille (Dupont and Bennett 1991). Dupont (1994) concluded that many warmwater fishes in the outlet arm of Lake Pend Oreille are limited by overwintering habitat, primarily vegetated areas of low velocity. The observed increase in aquatic plant densities may increase the amount of overwintering habitat and possibly increase winter survival of the warmwater fish community. Furthermore, aquatic macrophytes provide an important substrate for aquatic invertebrates (Soszka 1975) and therefore can increase the food supply for species that forage in these areas. The dominant macrophyte species found under higher winter water levels in Lake Pend Oreille represent important habitat and food sources for migratory waterfowl. For example, turions and seeds produced by£. crispus and _E. canadensis are important food for many waterfowl species (Rogers and Breen 1980, Nichols and Shaw 1986).

In managing Lake Pend Oreille, a balance must be attained between improving littoral habitat (providing a diverse aquatic macrophyte community) versus the possibility of nuisance aquatic plant growth (dense monospecific stands) as a result of high winter water levels. Extremely dense aquatic plant growth not only impedes recreation (Hestand and Carter 1975), but also decreases bass (Micropterus salmoides) growth rates as a result of decreased forage efficiency (Engel 1987).

Development of the Exotic Myriophyllum spicatum

The invasive, nonindigenous species (Myriophyllum spicatum L.) was first observed in Albeni Cove on the outlet arm of Lake Pend Oreille in the summer of 1998. The patchy distribution of **M.** spicatum in the 1.0 - 3.5 m depth range and subsequent exclusion from the drawdown regime analysis should not minimize the effects this species can have on surrounding littoral habitats. For example, mean *maximum* densities within monospecific plant beds exceeded 900 $g{\cdot}m^{2}$ oven dry weight by August, 1999. These densities are higher than values reported for milfoil in the Pend Oreille River, Washington, which reached densities near 600 $g{\cdot}m^{-2}$ (Getsinger et al. 1997). This species has the potential to spread rapidly throughout this system. For instance Eurasian watermilfoil spread at a rate of3.7 ha-yr in the Pend Oreille River, Washington immediately downstream of Albeni Falls Dam and has become a severe nuisance throughout this 55 km river reach (Gibbons et al. 1983, Falter et al. 1991). Winter drawdown has been used successfully to control this species (Goldsby and Bates 1978, Siver et al 1986) in some systems; however **M.** micatum occurs deeper than 5 min the outlet arm of Lake Pend Oreille reducing much of the benefit of a 3.5 m winter drawdown as a control method. Possible management of this system could include utilizing a winter drawdown of 3.5 m every few years (since consecutive winter drawdowns have shown to provide little additional macrophyte control compared to the initial drawdown; Nichols 1975b) to control nuisance aquatic vegetation and maximize the available wetted littoral for aquatic biot

Summary

- Highest mean densities of aquatic macrophytes were found in northern lake stations and declined at mid- and southern lake stations. Aquatic macrophytes most commonly found in Lake Pend Oreille proper and its outlet arm were£_ crispus, Elodea spp., M. sibiricum, and Chara spp.
- Mean aquatic macrophyte biomass (oven dry weight) significantly increased in the drawdown zone from 39.9 $g \cdot m^{-2}$ in 1990 (winter drawdown of 3.5 m) to 99.2 $g \cdot m^{-2}$ and 103.7 $g \cdot m^{-2}$ in 1998 and 1999, respectively (winter drawdown of 2.1 m).
- Mean aquatic macrophyte biomass (oven dry weight) in the permanently wetted littoral did not significantly increase from 70.3 $g \cdot m^{-2}$ in 1990 when compared to 1998 and 1999 (mean aquatic macrophyte biomass of 185.0 $g \cdot m^{-2}$ and 157.1 $g \cdot m^{-2}$, respectively). This suggests the observed increased biomass in the drawdown zone can at least partially be attributed to decreased winter mortality from freezing and desiccation under higher winter water levels.
- Two distinct aquatic macrophyte communities existed in the drawdown zone under the two drawdown regimes. Myriophyllum sibiricum, Chara spp., Potamogeton richardsonii, and .e_. foliosus dominated the aquatic macrophyte community under the 3.5 m winter drawdown, while Chara spp., £ berchtoldii, .e_. crispus, and Elodea spp. dominated under higher winter water levels (winter drawdown of 2.1 m). The spatial expansion of species previously restricted to depths below 3.5 min 1990 to areas shallower than 3.5 min 1998 and 1999 contributed to the observed differences in community structure.

- The patchy distribution of M. spicatum in the 1.0 - 3.5 m depth range and subsequent exclusion from the drawdown regime analysis should not minimize the potential effects this species can have on surrounding littoral habitats. Illustrated by the production of large monospecific beds, which attained mean *maximum* densities in excess of 900 $g\text{-}m^{-2}$ one year after it was first observed in 1998.
- A higher probability of observing clay and cobble substrate types existed in the drawdown zone than in the permanently wetted littoral. These two substrate types provided relatively poor habitat for aquatic macrophytes. For example, significantly lower densities of aquatic vegetation was observed on clay (17.9 $g\text{-}m^{-2}$) substrate types than on silt or sand substrates (mean macrophyte biomass of 129.0 $g\text{-}m^{-2}$ and 86.6 $g\text{-}m^{-2}$, respectively), and few plants were observed on cobble substrates.
- A 40 % increase in macrophyte biomass in the drawdown zone increased littoral habitat heterogeneity and therefore available overwintering habitat for littoral fishes that utilize these areas.
- Possible management of this system could include utilizing a winter drawdown of 3.5 m every few years to control nuisance aquatic vegetation and maximize the available wetted littoral zone for aquatic biota.

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