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The Lake Pend Oreille Aquatic Macrophyte Community and its Response to Higher Winter Water Levels

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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., P berchtoldii, and P. 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. spicatum 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.

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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 meso-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, Horne 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 0 m 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 corner 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 corner 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

Sample 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 Physico-Chemistry

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 1-liter Cubitainer, fixed with 2 ml H_2SO_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 l 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 Analysis

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 $g \cdot m^{-2}$) 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 Composition 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 (Kleinbaum 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:

$$\text{Percent dominance} = \left(\frac{n}{N}\right) \times 100 \tag{1}$$

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:

$$\text{Percent frequency} = \left(f/F\right) \times 100 \tag{2}$$

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 of Disimilarity (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: $\mathrm{Djk} = 1 - \left(\frac{1}{2}\left(\frac{W}{A} + \frac{W}{B}\right)\right)$ (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 0 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 0 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:

$$\mathrm{P}(substrate) = \exp^{(\hat{\beta}_o + \hat{\beta}_1 x)} \Big/ 1 + \exp^{(\hat{\beta}_o + \hat{\beta}_1 x)} \qquad (5)$$

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 $\mu g \cdot g^{-1}$) 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 RK18.5 to 7.5 % at Scenic Bay; mean percent carbon ranged from 0.7 % at RK18.5 to 8.4 % at Scenic Bay; and mean percent organic matter ranged from 1.4 % to 12.9 % at RK18.5 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 m in August, 1998 and from 3.8 m - 8.9 m in August, 1999. Mean total phosphorus and nitrate-nitrogen concentrations at selected sample stations in August, 1999 ranged less than 7 $\mu g \cdot l^{-1}$ (detection limit) - 7 $\mu g \cdot l^{-1}$ and from 21.5 $\mu g \cdot l^{-1}$ - 40.25 $\mu g \cdot l^{-1}$, 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 $g{\cdot}m^{-2}$ 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 RK16.1 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 P. 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 stations×time 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%), P. berchtoldii (25.3%), P. 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 P. crispus (8.3%). All other macrophyte species comprised small proportions of the community. Potamogeton crispus, P. 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 m in 1990. These three species were present between 1.4 m and 3.5 m in 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 Kulczynski'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 H` 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 H` Index did not significantly differ between 1990 and 1999 (*t*-test, $p = 0.64$).

Substrate Composition

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 $\mu g \cdot g^{-1}$). 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 $\mu g \cdot g^{-1}$).

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 $\mu g \cdot l^{-1}$ (detection limit) to 7 $\mu g \cdot l^{-1}$ and 21.45 $\mu g \cdot l^{-1}$ - 40.25 $\mu g \cdot l^{-1}$, respectively. Mean concentrations of total phosphorus in Lake Pend Oreille proper in 1989-90 ranged from 5 $\mu g \cdot l^{-1}$ - 10 $\mu g \cdot l^{-1}$ (Woods 1993). Summer secchi depth readings in Lake Pend Oreille proper ranged from about 5.0 - 11.0 m in 1989-90 (Woods 1993). Mean summer secchi depth ranged from 5.6 - 12.0 m in August, 1998 and from 3.8 - 8.9 m in 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 RK16.1 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 P. 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 P. crispus, P. 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, P. 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 Composition

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 (Horne 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 P. 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 (Perca 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 organisms$\cdot l^{-1}$ in late August compared to 3 organisms$\cdot l^{-1}$ 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 P. 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 (Eurasian watermilfoil)

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 of 3.7 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. spicatum occurs deeper than 5 m in 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 biota.

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 P. 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 P. foliosus dominated the aquatic macrophyte community under the 3.5 m winter drawdown, while Chara spp., P berchtoldii, P. 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 m in 1990 to areas shallower than 3.5 m in 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 $g \cdot m^{-2}$ 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 $g \cdot m^{-2}$) substrate types than on silt or sand substrates (mean macrophyte biomass of 129.0 $g \cdot m^{-2}$ and 86.6 $g \cdot m^{-2}$, 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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Figures

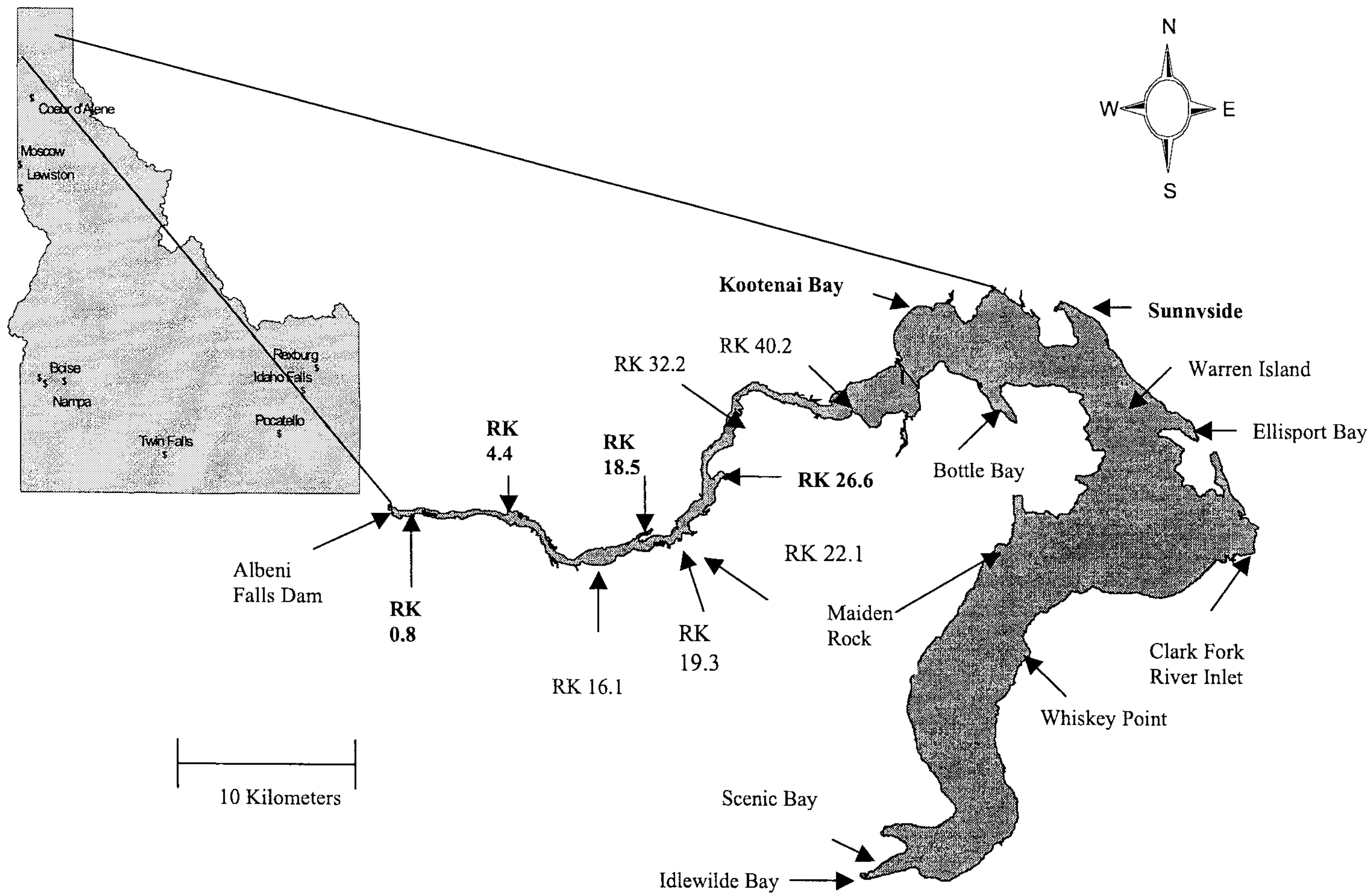

Figure 1.-Aquatic macrophyte sampling stations located on the outlet arm of Lake Pend Oreille and Lake Pend Oreille proper. Stations used in drawdown regime analysis are in bold.

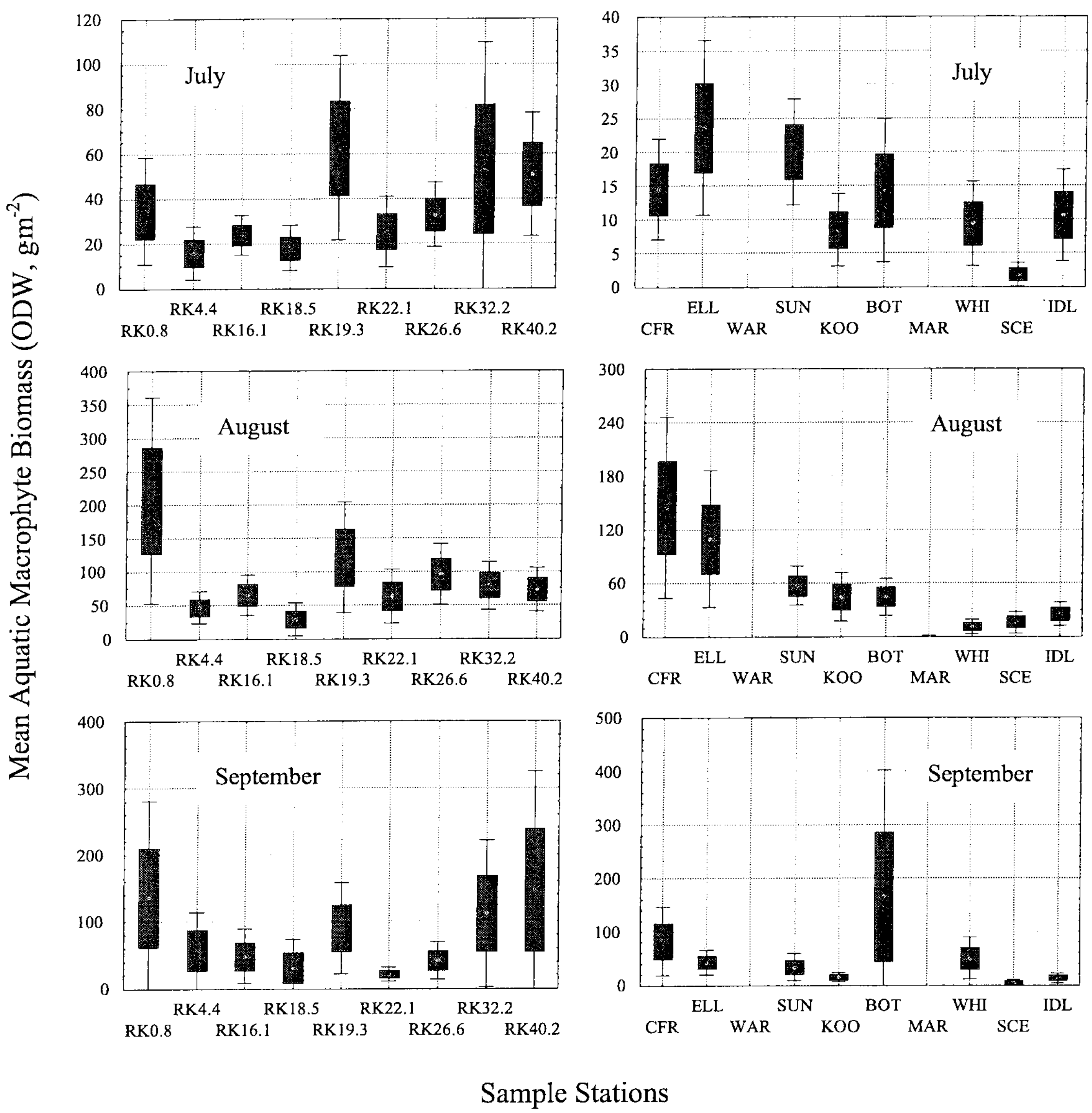

Figure 2.-Mean aquatic macrophyte biomass (oven dry weight ($g{\cdot}m^{-2}$)) at the 19 selected sample stations on Lake Pend Oreille proper and its outlet arm July, August, September, 1998. The box represents mean ± 1 standard error and the bars represent mean ± 1.96* standard error. CFR = Clark Fork River inlet, ELL = Ellisport Bay, WAR = Warren Island, SUN = Sunnyside, KOO = Kootenai Bay, BOT = Bottle Bay, MAR = Maiden Rock, WHI = Whiskey Point, SCE = Scenic Bay, and IDL = Idlewilde Bay.

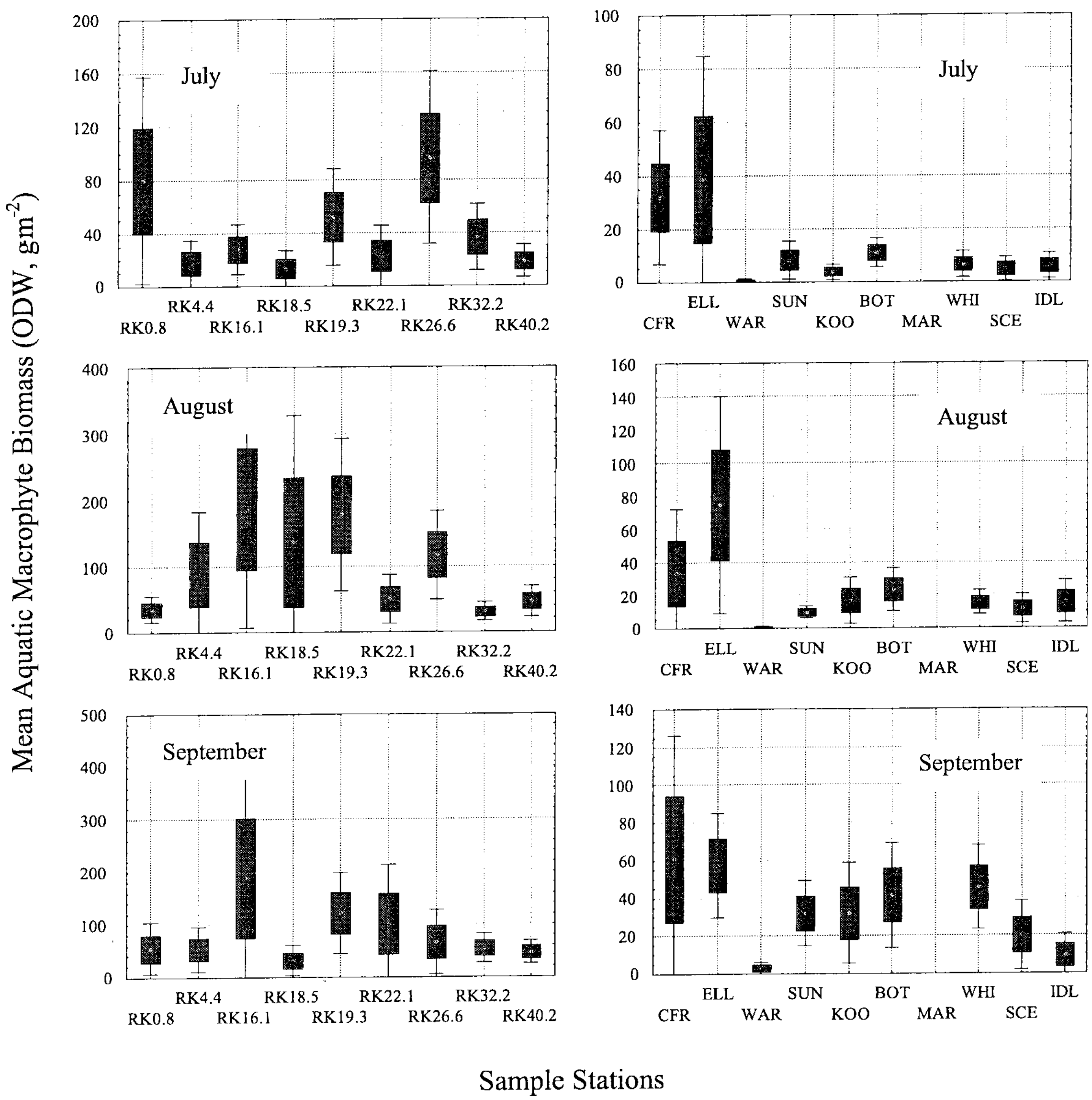

Figure 3.- Mean aquatic macrophyte biomass (oven dry weight (g·m^{-2})) at the 19 selected sample stations on Lake Pend Oreille proper and its outlet arm July, August, September, 1999. The box represents mean ± 1 standard error and the bars represent mean ± 1.96* standard error. CFR = Clark Fork River inlet, ELL = Ellisport Bay, WAR = Warren Island, SUN = Sunnyside, KOO = Kootenai Bay, BOT = Bottle Bay, MAR = Maiden Rock, WHI = Whiskey Point, SCE = Scenic Bay, and IDL = Idlewilde Bay.

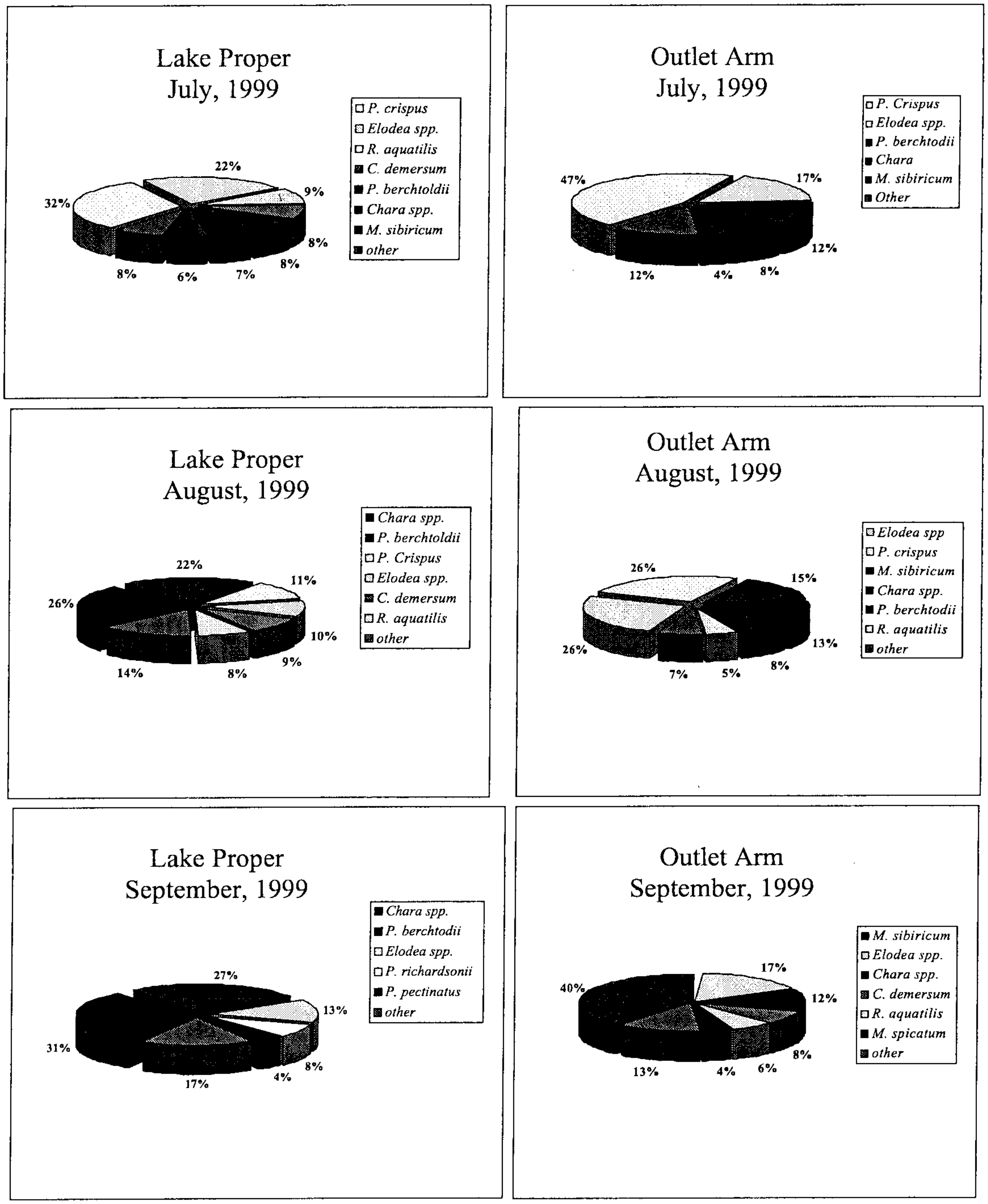

Figure 4.-Dominant aquatic macrophyte species from the 19 selected sample stations in Lake Pend Oreille proper and its outlet arm, July, August, September, 1999.

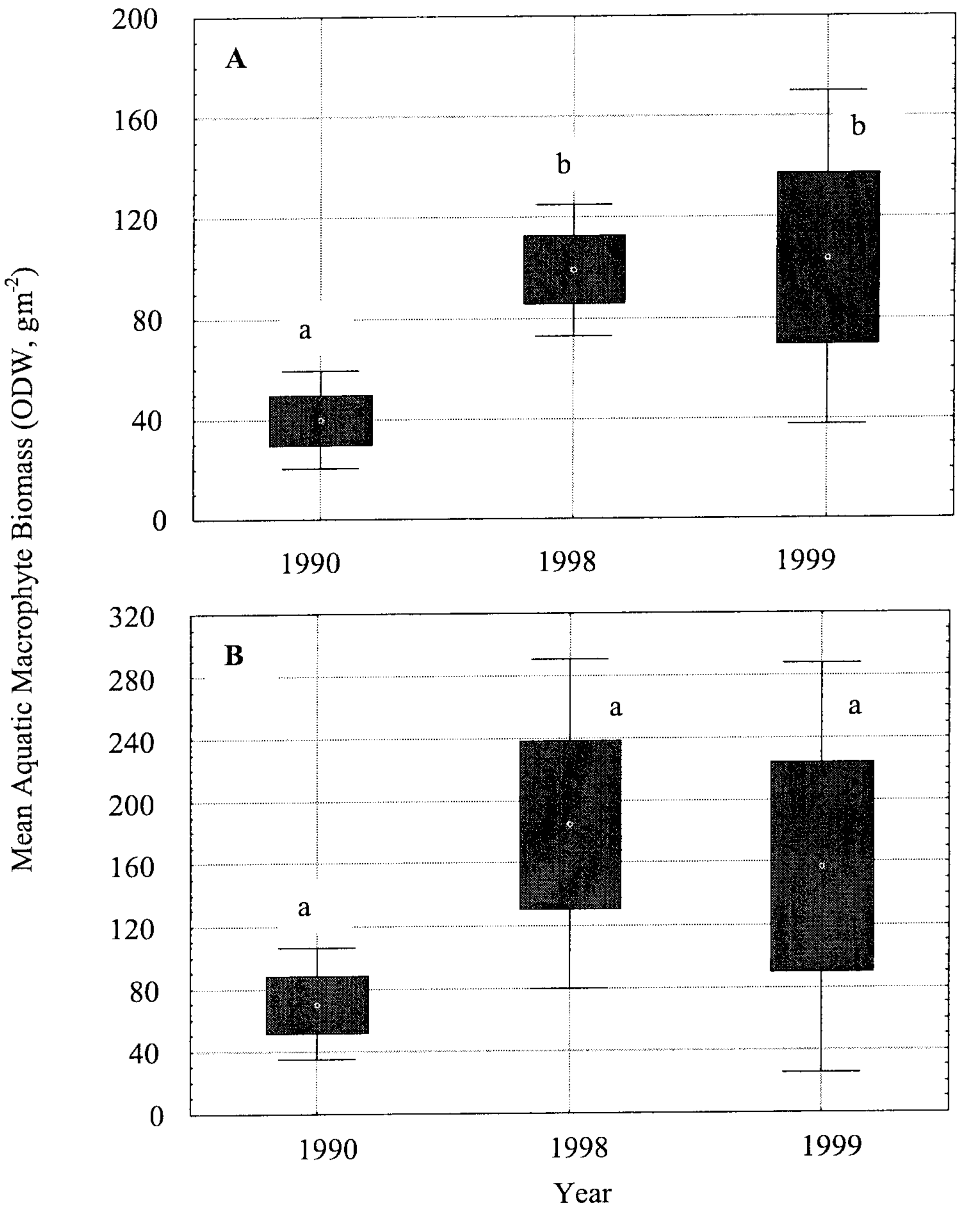

Figure 5.-Mean aquatic macrophyte biomass (oven dry weight (g·m^{-2})) in Lake Pend Oreille, Idaho, August 1990, 1998, and 1999 in (**A**) the winter drawdown zone (1.4 m - 3.5 m) and (**B**) the permanently wetted littoral (3.5 m - 7.0 m). The box represents mean ± 1 standard error and the bars represent mean ± 1.96* standard error. Different letters designate significant difference ($p < 0.05$) between mean aquatic macrophyte biomass.

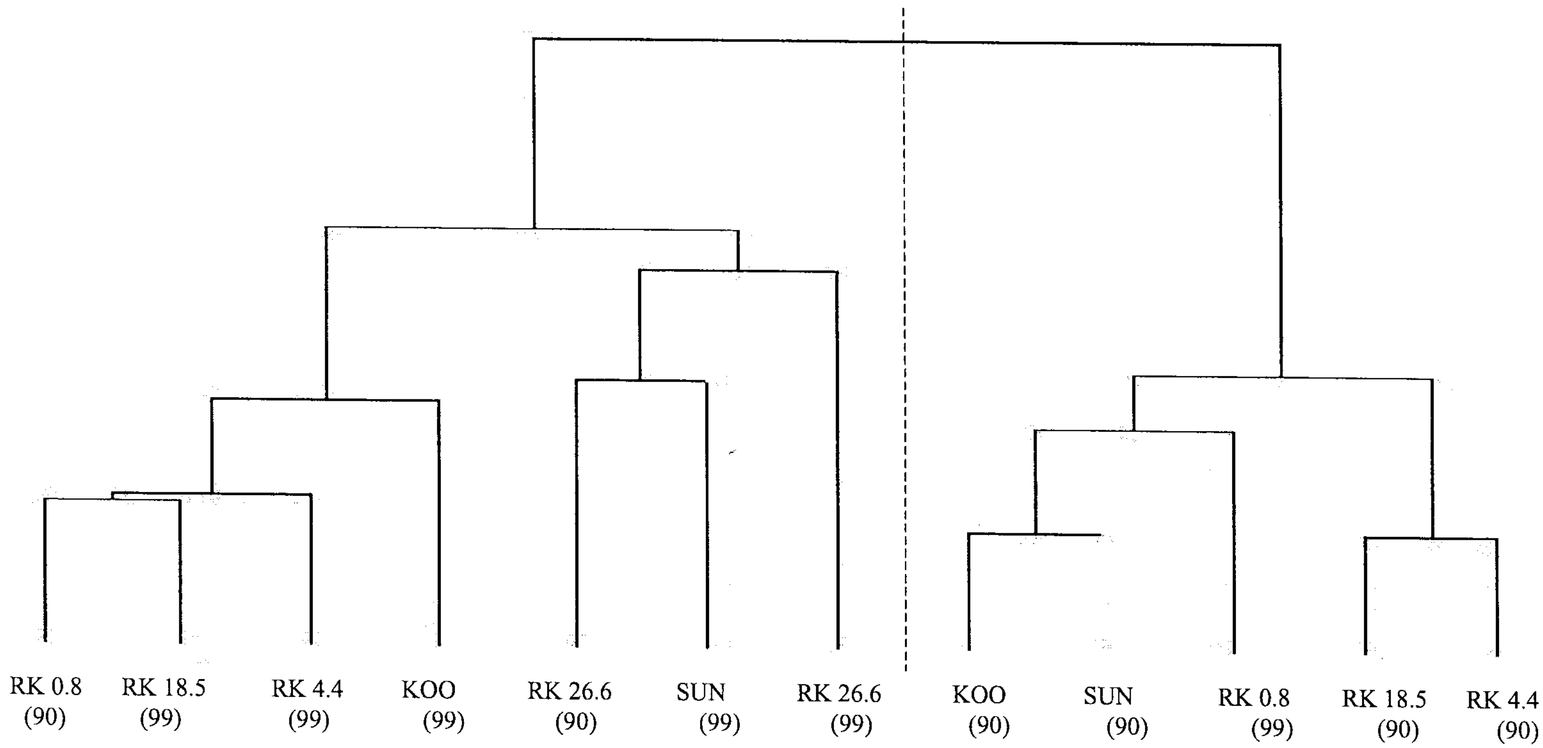

Figure 6.-Dendrogram of sample stations from Kulczynski's dissimilarity distance matrix based on aquatic macrophyte species composition and abundances in the drawdown zone (1.5 m – 3.5 m) for sample stations on the outlet arm of Lake Pend Oreille and Lake Pend Oreille proper, Idaho, August 1990 and 1999. Winter lake drawdown of 3.5 m occurred in 1990 compared to 2.1 m drawdown in 1999. Site code is followed by sample year in parenthesis (RK = River Kilometer, KOO = Kootenai Bay, SUN = Sunnyside). Dashed line represents delineation of clusters.

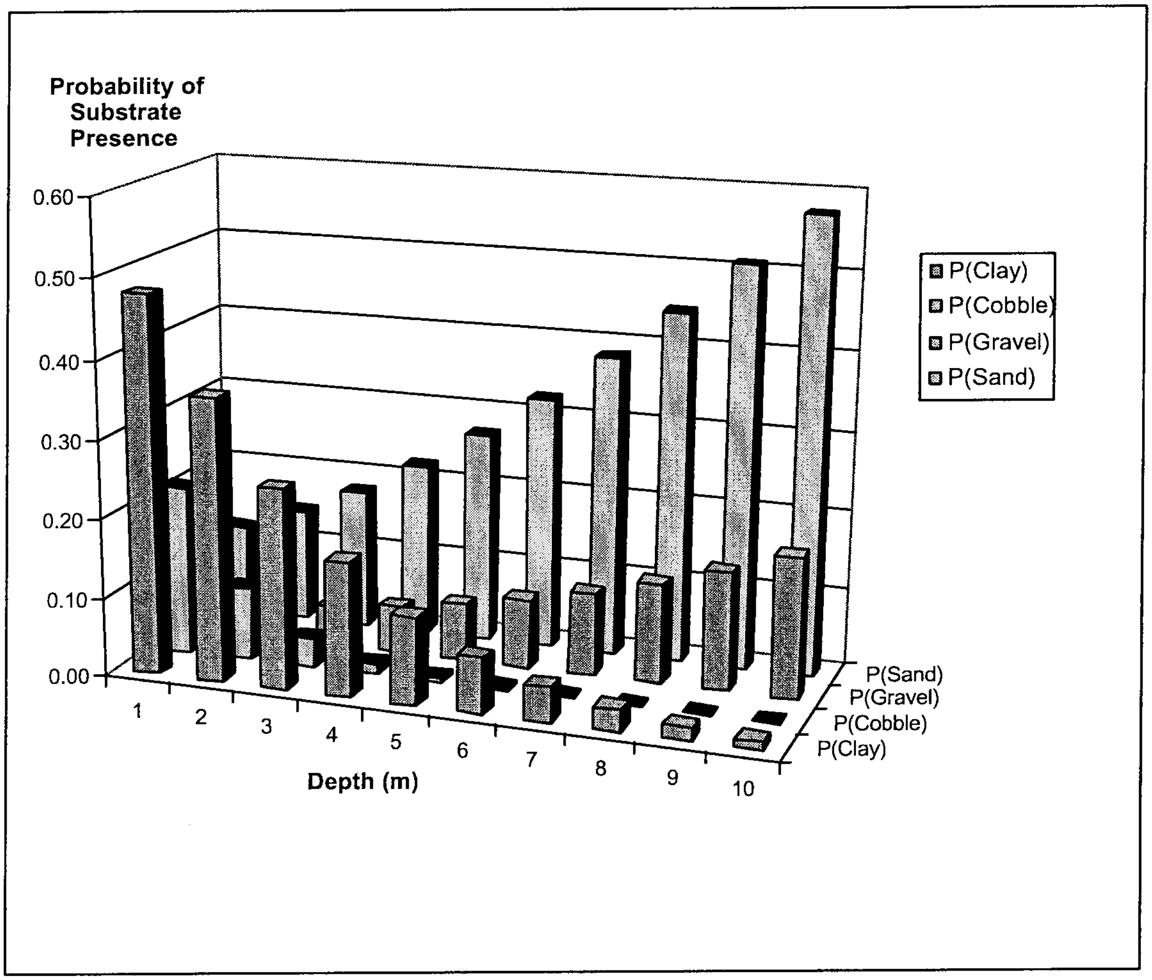

Figure 7.-Probabilities of observing four substrate classes (clay, cobble, gravel, and sand) at various increasing depths from full summer pool for selected sample station on Lake Pend Oreille, Idaho, August 1999.

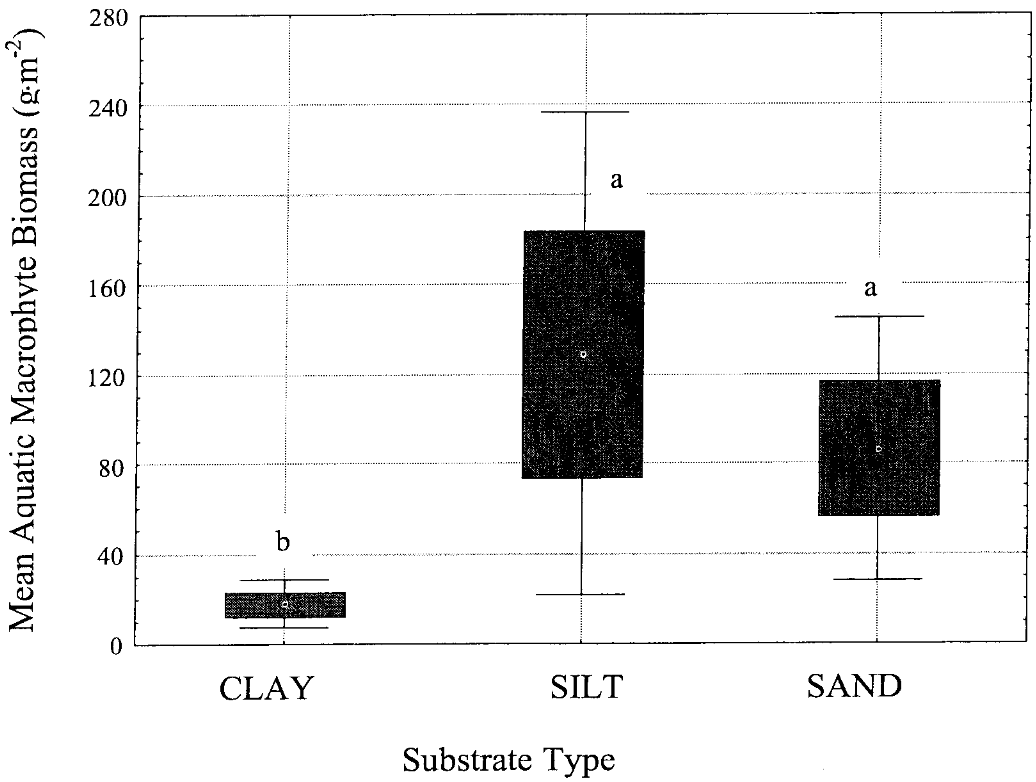

Figure 8.-Mean aquatic macrophyte biomass (oven dry weight (g·m^{-2})) on three substrate classes in Lake Pend Oreille, Idaho, August 1999. The box represents mean ± 1 standard error and the bars represent mean ± 1.96* standard error. Different letters designate significant difference ($p < 0.05$) between mean aquatic macrophyte biomass.

Tables

Table 1.- Selected physico-chemical water quality variables from Lake Pend Oreille proper and its outlet arm July – September, 1998.

Site	Date	Secchi Depth (m)	Mean Temperature (C)	Mean Conductivity (u siemens)	Alkalinity (mgl^{-1} $CaCO_3$)	Site	Date	Secchi Depth (m)	Mean Temperature (C)	Mean Conductivity (u siemens)	Alkalinity (mgl^{-1} $CaCO_3$)
Clark Fork	JUL	3.4	20.6	*	*	**RK 40.2**	JUL	2.7	20.6	*	*
	AUG	10.1	23.4	*	*		AUG	8.4	24.1	*	*
	SEP	8.5	22.0	175.0	79.0		SEP	7.9	23.1	186.0	78.0
Site Mean		**7.3**	**22.0**	*	*	**Site Mean**		**6.3**	**22.6**	*	*
Ellisport	JUL	4.1	21.1	*	*	**RK 32.2**	JUL	3.4	20.4	*	*
Bay	AUG	10.8	24.0	*	*		AUG	8.6	23.9	*	*
	SEP	7.8	22.1	175.0	79.0		SEP	7.0	22.6	186.0	76.0
Site Mean		**7.5**	**22.4**	*	*	**Site Mean**		**6.3**	**22.3**	*	*
Warren	JUL	5.6	19.8	*	*	**RK 26.6**	JUL	4.0	20.9	*	*
Island	AUG	11.3	23.8	*	*		AUG	8.5	24.5	*	*
	SEP	11.3	22.1	188.0	80.0		SEP	4.1	22.4	181.0	78.0
Site Mean		**9.4**		*	*	**Site Mean**		**5.5**	**22.6**	*	*
Sunnyside	JUL	3.8	20.0	*	*	**RK 22.1**	JUL	3.0	21.3	*	*
Bay	AUG	11.5	23.5	*	*		AUG	7.3	24.1	*	*
	SEP	9.5	21.9	181.0	79.0		SEP	4.6	22.3	179.0	78.0
Site Mean		**8.3**	**21.8**	*	*	**Site Mean**		**5.0**	**22.6**	*	*
Bottle	JUL	4.3	20.5	*	*	**RK 19.3**	JUL	3.6	21.6	*	*
Bay	AUG	8.8	23.5	*	*		AUG	8.3	23.8	*	*
	SEP	9.0	22.3	178.0	71.0		SEP	4.8	22.3	179.0	79.0
Site Mean		**7.3**	**22.1**	*	*	**Site Mean**		**5.6**	**22.6**	*	*
Kootenai	JUL	3.4	20.5	*	*	**RK 18.5**	JUL	3.9	22.3	*	*
Bay	AUG	10.6	23.2	*	*		AUG	8.5	23.7	*	*
	SEP	9.3	22.2	184.0	81.0		SEP	4.9	22.4	287.0	78.0
Site Mean		**7.8**	**22.0**	*	*	**Site Mean**		**5.8**	**22.8**	*	*
Maiden	JUL	4.9	15.1	*	*	**RK 16.1**	JUL	3.6	20.8	*	*
Rock	AUG	13.5	23.6	*	*		AUG	8.5	23.8	*	*
	SEP	11.3	21.7	191.0	79.0		SEP	4.5	22.4	183.0	77.0
Site Mean		**9.9**	**20.1**	*	*	**Site Mean**		**5.5**	**22.3**	*	*
Whiskey	JUL	6.4	19.8	*	*	**RK 4.4**	JUL	3.9	21.1	*	*
Point	AUG	12.0	22.9	*	*		AUG	5.6	23.4	*	*
	SEP	13.3	21.5	181.0	79.0		SEP	4.6	22.2	200.0	79.0
Site Mean		**10.6**	**21.4**	*	*	**Site Mean**		**4.7**	**22.2**	*	*
Scenic	JUL	6.0	13.7	*	*	**RK 0.8**	JUL	3.6	21.4	*	*
Bay	AUG	11.5	23.6	*	*		AUG	7.0	23.2	*	*
	SEP	12.4	21.6	181.0	79.0		SEP	4.6	21.9	232.0	75.0
Site Mean		**10.0**	**19.6**	*	*	**Site Mean**		5.1	22.2	*	*
Idlewilde	JUL	5.0	13.2	*	*						
Bay	AUG	7.8	22.7	*	*						
	SEP	11.8	22.1	190.0	78.0						
Site Mean		**8.2**	**19.3**	*	*						

Table 2.- Selected physico-chemical water quality variables, total phosphorus, and nitrate-nitrogen concentrations from Lake Pend Oreille proper and its outlet arm July – October, 1999. One standard deviation is shown in parenthesis for total phosphorus and nitrate-nitrogen where applicable.

Site	Date	Secchi Depth (m)	Mean Temperature (C)	Mean Dissolved Oxygen (mgl^{-1})	Mean Conductivity (u siemens)	Alkalinity (mgl^{-1}	pH	Mean Total Phosphorus (ugl^{-1})	Mean Nitrate-Nitrogen (ugl^{-1})
Clark Fork	JUL	2.5	14.6	9.8	168.9	69.0	7.9	<7	69.9 (45.0)
	AUG	6.1	18.5	9.5	168.0	80.0	7.9	<7	25.2 (3.2)
	SEP	7.1	17.4	9.3	170.0	77.5	6.6	<7	27.9 (1.1)
	OCT	6.0	11.9	9.9	170.0	83.0	*	8.31 (3.3)	26.2 (4.5)
Site Mean		**5.4**	**15.6**	**9.6**	**163.7**	**77.4**	**7.7**	**<7**	**37.3**
Ellisport Bay	JUL	3.3	15.7	10.0	167.9	72.0	8.0	<7	38.8 (47.1)
	AUG	7.0	20.1	9.8	169.4	76.0	8.0	<7	39.7 (19.5)
	SEP	8.0	18.9	9.1	211.0	77.0	7.0	<7	23.3 (3.9)
	OCT	7.9	12.2	9.8	149.0	81.0	*	<7	27.1 (2.5)
Site Mean		**6.5**	**16.7**	**9.7**	**174.3**	**76.5**	**7.8**	**<7**	**32.2**
Warren Island	JUL	3.5	14.9	10.0	171.0	68.0	7.9	<7	16.4 (1.7)
	AUG	7.7	18.6	9.3	169.8	76.0	7.9	<7	21.4 (7.7)
	SEP	9.8	19.2	9.0	176.0	79.0	6.9	<7	25.5 (3.0)
	OCT	8.1	12.3	9.9	150.5	84.0	*	<7	19.9 (4.5)
Site Mean		**7.3**	**16.2**	**9.5**	**166.8**	**76.8**	**7.7**	**<7**	**20.8**
Sunnyside Bay	JUL	3.5	15.7	9.6	222.8	43.0	7.1	<7	24.1 (6.1)
	AUG	5.6	17.9	9.9	153.4	74.0	7.2	<7	23.2 (4.0)
	SEP	8.8	18.7	8.8	171.3	73.0	6.7	<7	26.9 (1.3)
	OCT	7.9	12.2	9.8	147.0	81.0	*	<7	22.5 (4.9)
Site Mean		**6.5**	**16.1**	**9.5**	**173.6**	**61.8**	**7.0**	**<7**	**24.2**
Bottle Bay	JUL	3.9	15.3	9.9	162.2	67.0	7.5	<7	70.0 (45.2)
	AUG	6.6	18.1	9.5	198.1	77.0	7.3	<7	22.8 (2.4)
	SEP	6.0	18.8	8.9	171.5	82.0	7.0	<7	29.5 (5.3)
	OCT	7.8	11.9	9.8	147.5	81.5	*	<7	18.9 (3.2)
Site Mean		**6.1**	**16.0**	**9.5**	**169.5**	**76.9**	**7.3**	**<7**	**35.3**
Kootenai Bay	JUL	3.6	16.2	10.0	192.2	72.0	7.9	<7	25.4 (8.3)
	AUG	6.3	20.1	9.4	163.9	75.0	7.6	<7	22.4 (11.0)
	SEP	8.7	19.0	9.0	176.9	75.0	6.8	<7	24.8 (2.7)
	OCT	5.9	11.8	10.2	139.4	80.0	*	<7	28.2 (1.7)
Site Mean		**6.1**	**16.8**	**9.6**	**168.1**	**75.5**	**7.6**	**<7**	**25.2**
Maiden Rock	JUL	5.6	15.8	9.9	142.2	59.0	6.8	<7	43.0 (48.6)
	AUG	8.9	20.3	9.3	171.8	80.0	7.2	<7	25.1 (12.6)
	SEP	*	17.5	9.4	170.0	76.0	6.5	<7	24.2 (2.0)
	OCT	10.1	12.3	10.0	145.5	80.5	*	<7	26.5 (3.5)
Site Mean		**8.2**	**16.5**	**9.6**	**157.4**	**73.9**	**6.9**	**<7**	**29.7**
Whiskey Point	JUL	4.4	14.2	10.1	159.7	76.0	8.0	7.2 (1.6)	47.6 (42.4)
	AUG	8.6	18.7	10.1	165.8	79.0	7.9	<7	30.0 (6.7)
	SEP	8.1	17.6	9.3	172.5	75.0	6.7	<7	27.1 (2.2)
	OCT	10.4	12.2	9.8	148.0	80.5	*	8.2 (2.2)	22.4 (1.7)
Site Mean		**7.9**	**15.7**	**9.8**	**161.5**	**77.6**	**7.8**	**<7**	**31.8**
Scenic Bay	JUL	4.5	15.7	9.9	169.1	76.0	8.0	<7	47.3 (41.0)
	AUG	8.6	20.7	9.1	175.7	82.0	7.9	<7	20.0 (2.9)
	SEP	8.5	17.0	9.5	168.0	75.0	6.7	<7	21.0 (5.9)
	OCT	8.9	12.1	9.9	142.0	82.0	*	<7	25.0 (7.5)
Site Mean		**7.6**	**16.4**	**9.6**	**163.7**	**78.8**	**7.8**	**<7**	**29.2**
Idlewilde Bay	JUL	5.1	14.7	10.1	144.2	78.0	7.2	<7	70.9 (53.4)
	AUG	7.9	20.8	9.2	177.6	78.0	7.9	<7	40.3 (14.8)
	SEP	7.1	16.6	9.5	170.0	74.5	6.8	<7	43.5 (36.3)
	OCT	10.2	11.9	9.9	142.5	80.0	*	<7	23.8 (1.5)
Site Mean		**7.6**	**16.0**	**9.7**	**158.6**	**77.6**	**7.5**	**<7**	**44.6**

Table 2 con't.- Selected physico-chemical water quality variables, total phosphorus and, nitrate-nitrogen concentrations from Lake Pend Oreille proper and its outlet arm July – October, 1999. One standard deviation is shown in parenthesis for total phosphorus and nitrate-nitrogen where applicable.

Site	Date	Secchi Depth (m)	Mean Temperature (C)	Mean Dissolved Oxygen ($mg l^{-1}$)	Mean Conductivity (u siemens)	Alkalinity ($mg l^{-1}$ $CaCO_3$)	pH	Mean Total Phosphorus ($ug l^{-1}$)	Mean Nitrate-Nitrogen ($ug l^{-1}$)
RK 40.2	JUL	3.4	16.5	9.7	188.0	69.0	8.0	<7	14.9 (6.0)
	AUG	4.1	20.5	9.1	166.9	75.0	7.7	<7	32.3 (4.5)
	SEP	6.1	18.7	9.3	175.6	73.5	6.7	<7	26.1 (2.4)
	OCT	7.4	11.1	10.1	146.5	81.0	*	<7	24.5 (0.6)
Site Mean		**5.3**	**16.7**	**9.5**	**169.3**	**74.6**	**7.7**	**<7**	**24.5**
RK 32.2	JUL	2.8	16.2	9.6	180.0	67.0	8.0	<7	22.2 (10.4)
	AUG	4.1	20.5	9.1	166.9	74.0	7.9	<7	26.2 (1.2)
	SEP	5.8	18.7	9.1	172.9	75.5	6.7	<7	28.7 (2.3)
	OCT	7.1	11.2	10.1	143.0	82.0	*	<7	25.7 (0.9)
Site Mean		**4.9**	**16.7**	**9.5**	**165.7**	**74.6**	**7.1**	**<7**	**25.7**
RK 26.6	JUL	3.3	14.9	9.6	168.9	69.0	7.3	<7	73.5 (45.1)
	AUG	3.8	20.2	9.2	163.7	72.5	7.0	<7	30.9 (3.3)
	SEP	7.1	18.5	8.7	170.5	73.0	6.6	7.7 (2.7)	24.8 (15.4)
	OCT	6.4	11.2	10.3	148.3	81.0	*	7.1 (2.2)	23.7 (0.8)
Site Mean		**5.1**	**16.2**	**9.5**	**162.9**	**73.9**	**7.1**		**38.2**
RK 22.1	JUL	3.3	15.2	9.5	172.6	67.0	7.6	<7	43.5 (46.4)
	AUG	3.9	20.7	9.3	163.7	76.0	7.6	<7	29.2 (2.6)
	SEP	5.9	19.0	8.7	169.0	73.0	6.7	<7	26.2 (3.3)
	OCT	6.7	11.1	10.4	144.0	79.0	*	<7	21.8 (0.9)
Site Mean		**4.9**	**15.6**	**9.5**	**162.3**	**73.8**	**7.5**	**<7**	**30.2**
RK 19.3	JUL	3.1	15.8	9.4	248.9	66.0	7.8	7.5 (1.6)	20.5 (1.8)
	AUG	4.3	20.8	9.2	170.8	72.0	7.9	<7	29.7 (6.7)
	SEP	5.9	19.8	8.7	177.5	74.0	6.9	9.8 (1.1)	27.8 (2.8)
	OCT	6.4	11.1	10.3	142.0	80.0	*	9.3 (4.2)	29.9 (12.4)
Site Mean		**4.9**	**16.9**	**9.4**	**184.8**	**73.0**	**7.7**	**7.5**	**27.0**
RK 18.5	JUL	3.4	15.8	9.4	176.6	70.0	7.7	<7	66.3 (46.4)
	AUG	4.0	21.1	9.3	171.8	70.0	7.8	<7	29.4 (2.3)
	SEP	6.9	20.0	8.8	173.5	74.0	6.2	<7	34.8 (13.4)
	OCT	6.2	11.3	10.5	144.0	78.0	*	<7	17.8 (3.1)
Site Mean		**5.1**	**17.1**	**9.5**	**166.5**	**73.0**	**7.6**	**<7**	**37.1**
RK 16.1	JUL	3.0	15.7	9.5	167.4	70.0	7.6	7.1 (4.9)	45.1 (43.5)
	AUG	3.8	21.1	9.2	171.2	74.0	7.6	<7	26.9 (0.3)
	SEP	4.6	20.2	8.8	177.0	73.0	6.9	<7	26.9 (6.6)
	OCT	5.8	11.3	10.4	140.5	79.5	*	<7	23.8 (2.5)
Site Mean		**4.3**	**17.1**	**9.5**	**164.0**	**74.1**	**7.5**	**<7**	**30.7**
RK 4.4	JUL	3.4	16.7	9.5	402.5	70.0	7.5	7.3 (3.3)	44.9 (38.8)
	AUG	3.9	20.5	9.0	165.2	72.0	7.5	7.0 (4.6)	27.8 (8.4)
	SEP	4.0	20.0	8.7	176.5	73.0	7.0	<7	35.2 (1.5)
	OCT	5.6	11.5	10.4	142.3	79.0	*	11.4 (5.1)	30.4 (16.2)
Site Mean		**4.2**	**17.2**	**9.4**	**221.3**	**73.5**	**7.4**	**7.3**	**34.6**
RK 0.8	JUL	3.4	16.0	9.3	230.6	67.0	7.2	<7	42.8 (44.3)
	AUG	3.9	20.5	9.3	173.3	72.0	7.5	<7	26.8 (0.4)
	SEP	5.2	19.6	8.1	168.5	72.0	7.5	<7	33.9 (1.1)
	OCT	6.2	11.1	10.1	131.4	76.0	*	<7	18.3 (1.5)
Site Mean		**4.7**	**16.8**	**9.2**	**176.0**	**71.8**	**7.4**	**<7**	**30.5**

Table 3.-Mean selected sediment chemical values for eight sample stations on Lake Pend Oreille proper and its outlet arm, July, 2000. One standard deviation is shown in parentheses. Mean values with the same superscripted letter within a given column are not significantly different ($p > 0.05$).

Sample Station	Mean Total Phosphorus ($\mu g \cdot g^{-1}$)	Mean Percent Nitrogen (%)	Mean Percent Organic Carbon (%)	Mean Percent Carbon (%)	Mean Percent Organic Matter (%)
Bottle Bay	577.8 (56.5) ^{bc}	0.4 (0.1) ^{a}	5.6 (1.0) ^{a}	5.6 (1.5) ^{a}	9.6 (1.7) ^{a}
Ellisport Bay	546.7 (90.3) ^{bc}	0.3 (0.1) ^{abc}	3.8 (1.9) ^{ab}	3.6 (1.9) ^{ab}	6.5 (3.2) ^{ab}
Scenic Bay	1563.3 (1422.9) ^{a}	0.2 (0.2) ^{abc}	7.5 (6.0) ^{a}	8.4 (7.1) ^{a}	12.9 (10.3) ^{a}
Idlewilde Bay	395.0 (27.4) ^{c}	0.4 (0.2) ^{ab}	5.8 (1.8) ^{a}	6.1 (2.8) ^{a}	9.9 (3.2) ^{a}
RK 0.8	611.1 (113.4) ^{bc}	0.1 (0.1) ^{dc}	1.8 (1.9) ^{bc}	1.9 (2.6) ^{bc}	3.1 (3.2) ^{bc}
RK 4.4	790.0 (88.8) ^{b}	0.1 (0.1) ^{bcd}	1.9 (1.2) ^{bc}	1.7 (1.1) ^{bc}	3.3 (2.1) ^{bc}
RK 18.5	483.3 (192.4) ^{c}	0.0 (0.0) ^{d}	0.8 (0.5) ^{c}	0.7 (0.6) ^{c}	1.4 (0.9) ^{c}
RK2 6.6	545.0 (97.1) ^{bc}	0.2 (0.1) ^{abc}	2.9 (1.3) ^{ab}	2.7 (1.2) ^{ab}	5.0 (2.3) ^{ab}

Table 4.-Aquatic macrophyte species collected from the 19 selected sample stations on Lake Pend Oreille proper, Idaho and its outlet arm, 1998 and 1999. Mean percent organic content of oven dry weight biomass is included for July, August, and September, 1999. One standard deviation is shown in parentheses where applicable.

Species	Mean Percent Organics (July)	Mean Percent Organics (August)	Mean Percent Organics (September)	July-September Mean
Callitrichaceae (Water-starwort Family)				
Callitriche marginata Torr.	93.2 (--)	95.8 (--)	87.2 (5.9)	92.1
Ceratophyllaceae (Hornwort Family)				
Ceratophyllum demersum L.	84.3 (4.9)	87.1 (3.3)	83.6 (5.0)	85.0
Characeae (Stoneworts)				
Chara spp.	58.8 (14.6)	56.8 (19.9)	44.5 (11.8)	53.4
Nitella spp.	56.5 (1.3)	59.4 (16.1)	47.9 (8.8)	54.6
Crassulaceae (Stonecrop Family)				
Tillaea aquatica L.	86.1 (4.2)	87.6 (3.9)	81.2 (8.2)	85.0
Elatinaceae (Waterwort Family)				
Elatine triandra	92.9 (4.1)	Not found	Not found	--
Hippurisaceae (Mare's-tail family)				
Hippuris montana Ledeb.	78.4 (7.0)	Not found	82.7 (5.2)	80.55
Hydrocharitaceae (Frog's-bit Family)				
Elodea canadenis Rich. in Michx.	82.6 (6.1)	82.1 (2.1)	80.7 (4.8)	81.8
E. Nuttallii (Planch.) St. John	81.2 (4.9)	83.3 (2.6)	73.9 (--)	79.5
Haloragaceae (Water-milfoil Family)				
M. sibiricum (Fern.) Jeps.	83.2 (3.2)	84.2 (2.8)	87.0 (6.2)	84.8
Myriophyllum spicatum L.	80.8 (--)	85.2 (3.3)	86.4 (3.5)	84.1
Isoetaceae (Quillwort Family)				
Isoetes spp.	74.0 (9.0)	73.3 (12.4)	70.2 (8.6)	72.5
Najadaceae (Water-nymph Family)				
Najas flexilis (Willd.) Rost. & Schmidt	85.9 (7.9)	84.0 (6.6)	81.1 (4.8)	83.7
Potamogetonaceae (Pond Weed Family)				
Potamogeton berchtoldii Fieb.	85.0 (4.8)	86.0 (5.3)	84.6 (7.1)	85.2
P. crispus L.	86.7 (3.4)	86.2 (2.6)	93.7 (3.8)	88.9
P. foliosus Raf.	81.3 (--)	Not found	Not found	--
P. gramineus L.	86.0 (5.7)	83.6 (6.5)	83.9 (7.3)	84.5
P. pectinatus L.	84.7 (4.5)	86.6 (3.5)	85.3 (4.1)	85.5
P. praelongus Wulf.	89.7 (1.8)	84.6 (2.9)	77.2 (--)	83.8
P. richardsonii (Bennett) Rydb.	85.6 (4.9)	88.2 (3.6)	85.1 (3.9)	86.3
P. robbinsii Oakes	81.9 (5.6)	85.1 (2.5)	88.2 (16.7)	85.1
P. zosteriformis Fern.	86.6 (7.2)	89.6 (2.4)	92.5 (2.4)	89.6
Ranunculaceae (Buttercup Family)				
Ranunculus aquatilis L.	86.6 (3.1)	84.2 (2.6)	85.5 (4.3)	85.4
Zannichelliacaea (Horned Pondweed Family)	87.8 (5.3)	75.8 (--)	84.9 (7.2)	82.8
Zannichellia palustris L.				
Bryophytes				
Drepanocladius spp.	62.4 (13.3)	46.8 (7.9)	56.4 (9.4)	55.2

Table 5.-Percent dominance and percent frequency of aquatic macrophyte species in the drawdown zone (1.4 m – 3.5 m depth) from the six selected sample stations on the outlet arm of Lake Pend Oreille and Lake Pend Oreille proper, Idaho.

Species	**1990 Percent Dominance**	**1990 Percent Frequency**	**1999 Percent Dominance**	**1999 Percent Frequency**
Ceratophyllaceae (Hornwort Family)				
Ceratophyllum demersum L.	0.4	8.7	0.4	4.2
Characeae (Stoneworts)				
Chara spp.	29.3	60.9	27.4	54.2
Crassulaceae (Stonecrop Family)				
Tillaea aquatica L.	0.0	4.4	0.0	2.1
Hydrocharitaceae (Frog's-bit Family)				
Elodea canadenis Rich. in Michx.	1.8	17.4	12.7	47.9
E. Nuttallii (Planch.) St. John				
Haloragaceae (Water-milfoil Family)				
Myriophyllum sibiricum (Fern.) Jeps.	30.1	26.1	1.7	8.3
**M. spicatum* L.				
Isoetaceae (Quillwort Family)	2.0	8.7	0.2	14.6
Isoetes spp.				
Najadaceae (Water-nymph Family)				
Najas flexilis (Willd.) Rost. & Schmidt	0.1	13.0	0.0	4.2
Potamogetonaceae (Pond Weed Family)				
Potamogeton robbinsii Oakes	0.3	4.6	0.0	0.0
P. pectinatus L.	2.0	4.4	2.1	14.6
P. crispus L.	0.0	0.0	23.6	8.3
P. zosteriformis Fern.	0.0	0.0	0.3	4.2
P. praelongus Wulf.	0.0	0.0	0.0	2.1
P. richardsonii (Bennett) Rydb.	23.9	30.4	0.5	6.3
P. pusillus L.	0.0	8.7	0.0	0.0
P. berchtoldii Fieb.	0.5	8.7	25.3	58.3
P. gramimeus L.	1.4	8.7	0.1	8.3
P. foliosus Raf	6.3	4.4	0.0	0.0
Ranunculaceae (Buttercup Family)				
Ranunculus aquatilis L.	1.9	13.0	5.6	16.7
Bryophytes				
Drepanocladius spp.	0.0	0.0	0.0	4.2
Others	0.0	0.0	0.0	2.1

* M. spicatum did not occur frequently in the 1.0 – 3.5 m depth range and therefore was not represented in samples between 1.4 - 3.5 m depths (drawdown zone) in 1999. However this species was present at sample station RK0.8, first having appeared in Lake Pend Oreille in July, 1998.

Table 6.- Depth (m) as a predictor of substrate particle size class ($\hat{\beta}_0$ and $\hat{\beta}_1 x$ are coefficients derived from binary logistic regression; $\alpha = 0.05$).

Substrate Class	$\hat{\beta}_0$	$\hat{\beta}_1$	**p-value**
Clay	0.4225	- 0.4984	< 0.0001
Silt	-0.8984	0.0797	0.12
Sand	- 2.936	0.2594	< 0.0001
Gravel	- 3.5624	0.2045	.03
Cobble	- 0.2986	- 0.9881	0.004

Prediction of Potential Eurasian Watermilfoil Habitat in Lake Pend Oreille, Idaho

Abstract

The exotic aquatic macrophyte Eurasian watermilfoil was first observed in Albeni Cove on the outlet arm of Lake Pend Oreille, in August, 1998. We conducted a systematic random sampling of Eurasian watermilfoil throughout the cove to describe relationships between milfoil biomass and depth. These data, along with substrate composition, were used in a geographic information system (GIS) to predict the amount of potential Eurasian watermilfoil habitat in this system. This information was then used to suggest management options for future milfoil control programs. We also conducted physico-chemical measurements in the water column (light and dissolved oxygen profiles, pH, and total alkalinity) in and adjacent to the Eurasian watermilfoil bed to assess effects of this species on the surrounding physical and chemical environment. Light attenuated rapidly beneath the canopy reaching levels below 1 % incident at about 1.5 m that likely contributed to the formation of monospecific stands of milfoil in Albeni Cove. A significant relationship was found between milfoil density and depth. A model describing the relationship between milfoil biomass and depth along with a substrate grid was used in a GIS to quantify possible habitat. Approximately 39% (1438 ha) of the outlet arm area is likely Eurasian watermilfoil habitat. Management of milfoil in this system could include the use of herbicides, hand harvesting, and mechanical harvesting. Contact herbicides may be effective in backwater areas of zero current velocity, hand harvesting can be used to remove isolated, low density colonies. Systemic compounds or mechanical harvesting may be utilized in areas where current is present and densities are high.

Introduction

In 1998, Eurasian watermilfoil (Myriophyllum spicatum L.) was discovered in Lake Pend Oreille, Idaho at Albeni Cove (River Kilometer 0.8), just upstream of Albeni Falls Dam (Fig. 9). Milfoil has been present in the Pend Oreille River immediately downstream of Albeni Falls Dam since 1976, and this area was a possible source of fragments. Eurasian watermilfoil has the potential to spread rapidly in clear, lentic waters of the Pend Oreille system. For example, Eurasian watermilfoil spread at a rate of 3.7 ha·yr in the Pend Oreille River and has become a severe nuisance throughout the river (Gibbons et al. 1983a, Falter et al. 1991, WDE 1993).

Lake Pend Oreille proper is a 383 km^2 (94640 acres) meso-oligotrohic lake with mean and maximum depths of 164 m (538 ft) and 357 m (1171 ft), respectively (USGS 1996). The lake's outlet arm is the Pend Oreille River, exiting from the northwest corner of Lake Pend Oreille. Mean and maximum depths of the outlet arm are 7.4 m (24 ft) and 48 m (157 ft), respectively with a shoreline length of 152 km (94 mi.; USGS 1996). The outlet arm is impounded by Albeni Falls Dam on the Washington-Idaho border and controls water levels of the entire lake. An annual winter drawdown from mid-November through May of 2.3 m (7.5 ft) to 3.5 m (11.5 ft) is implemented primarily for spring flood control and winter power production.

The objectives of this study were to:

(1) Identify likely habitat for milfoil colonization on the outlet arm of Lake Pend Oreille using a GIS to integrate Eurasian watermilfoil biomass, water depth, and substrate composition;

(2) Describe apparent physico-chemical effects of Eurasian watermilfoil on the surrounding environment; and

(3) Develop and recommend management options to control the spread of milfoil in this system.

Ecology of Eurasian Watermilfoil

Eurasian Watermilfoil Distribution and Growth Forms

Eurasian watermilfoil is a submersed, perennial, aquatic angiosperm that was introduced into the United States near Chesapeake Bay in the late 1880's. Since its introduction, Eurasian watermilfoil has spread across the United States and become one of the most troublesome submersed aquatic plants in North America (Smith and Barko 1990). Nuisance growths of Eurasian watermilfoil (hereafter also referred to as milfoil) restrict water-based recreation through the development of dense surface canopies (Nichols 1975, Wile 1978) and create aesthetically displeasing lake littoral zones.

Biology of Eurasian Watermilfoil

Eurasian watermilfoil is a member of the Haloragaceae (watermilfoil family). This submersed perennial aquatic herb is essentially evergreen which overwinters as root-stocks forming no specialized overwinter structures such as turions (Smith and Barko 1990). Milfoil has a pillar-like growth form (vertical clumpings of 10-40 stems per clump) early in the growing season (Budd et al. 1995), but as water temperature and photoperiod increase, long stems are produced that can exceed 10 m in length. These stems are covered with finely dissected leaves arranged in whorls of 3 to 6, usually 4 per node (Hitchcock and Cronquist 1973, Aiken et al. 1979). Leaf outline is feather-like with 14 – 24 pairs of leaflets (Aiken et al. 1979). Stems branch once reaching the water surface form dense surface canopies. The formation of these dense surface canopies interferes with water-based recreation and can decrease the diversity of littoral vegetation (Madsen et al. 1991). Once canopy formation begins, leaves low on the stem senesce leaving only the surface canopy foliated.

Milfoil possesses several structural and physiological adaptations that allow it to be a superior competitor:

(1) The location of photosynthetic tissue near the water surface;

(2) C_4- fixation similarities (*i.e.*, a bicarbonate (HCO^{-3}) uptake mechanism analogous to the C_4-dicarboxylic acid pathway where CO_2 is actively transported to the site of the Calvin Cycle with a subsequent decarboxylation) (Hutchinson 1975);

(3) The ability to survive under low light (1-2% of surface light);

(4) An opportunistic use of nutrients (nutrient uptake from the most available source, whether sediments or the water column); and

(5) A life history that tolerates cool weather (the ability to overwinter as the entire plant and grow under ice; Nichols and Shaw 1986), and very rapid growth throughout the growing season out-competing native vegetation (Gibbons et al. 1983a).

Nutrient Dynamics

Milfoil communities are affected by surrounding sediment and water column nutrient concentrations (Nichols and Keeney 1976, Rattray et al. 1991). The addition of nitrogen to sediments has been shown to result in a 30-40% increase in milfoil biomass (Anderson and Kalff 1986). Eurasian watermilfoil colonies also affect surrounding nutrient dynamics *via* nutrient uptake, translocation, and release upon senescence and decomposition (Smith and Barko 1990, Nichols and Keeney 1973, Carignan 1985). DeMarte and Hartman (1974) concluded that ^{32}P was actively translocated from the roots of M. sibiricum to the shoot system and subsequently released to the surrounding water. Smith and Adams (1986) also demonstrated the importance of roots in transferring phosphorus from lake sediments into plants and concluded that roots accounted for 73% of total plant phosphorus uptake (shoot uptake accounted for 27%). During their experiment, phosphorus efflux from live milfoil shoots to the water was low. However, high efflux occurred during decay, illustrating the importance of phosphorus release upon senescence. Bristow and Whitcombe (1971) reported that most (59%) of the phosphate measured in stems of milfoil was derived from sediment, demonstrating the importance of sediment composition to growth of rooted aquatic macrophytes that derive nutrients primarily from lake sediments. Nutrient release may be an important component influencing pelagic phytoplankton community composition and abundance in fall (Brooker and Edwards 1975, Malthus et al. 1990). Landers (1982) reported that senescing mifoil beds produced about 18% of the annual total phosphorus load and a significant amount of nitrogen to an Indiana reservoir. Additionally, significant increases in phytoplankton and periphyton biomass (indicated by Chl *a*) were measured in response to the pulses of nutrient release from milfoil decay.

Effects on Benthic Macro Invertebrates and Fishes

Ecological effects of nuisance growths include the decline of native aquatic vegetation under dense milfoil canopies (Madsen et al. 1991) and lower aquatic invertebrate densities (essential food for many fishes and semi-aquatic organisms) within milfoil beds (Sloey et al. 1997). For example, Keast (1984) found five important taxa of fish prey invertebrates to be three to seven times more abundant in a Potamogeton-dominated community than in a milfoil-dominated community. In the same study, three to four times as many fish were found feeding in the benthos beneath the indigenous macrophyte bed when compared to beneath the milfoil plant community. However, Liter (1991) found higher fish densities in vegetated sloughs when compared to the main reservoir while sampling with pop nets in Box Canyon Reservoir on the Pend Oreille River, Washington. These vegetated sloughs in Box Canyon Reservoir are largely composed of milfoil (Falter et al. 1991) and contained fish densities of up to 5.2 fish $\cdot m^{-2}$ (Liter 1991). Lyons (1989) speculates that environmental degradation caused by the invasion of milfoil into Lake Mendota, Wisconsin, contributed to the extinction of eight species of small littoral fishes and consequently a reduction in prey abundance for larger fishes. Other effects include a possible decrease in foraging efficiency of littoral fishes through an increase in habitat complexity (difficulty of piscivorous fishes locating prey) and light reduction (Diehl 1988) as well as altering fish spawning site distribution (Keast 1984). Engel (1987) documented a shift in prey item occurrence in largemouth bass as the density of aquatic macrophytes (Potamogeton spp., Ceratophyllum demersum, Spirogyra, and others) increased. For example, bass and bluegill (Lepomis macrochirus) under age III utilized aquatic plant beds early in the year (low plant densities) while feeding on aquatic invertebrate larvae. As aquatic plant densities increased, bluegill in those areas shifted to feed on zooplankton and finally to aquatic plant tissue at maximum plant densities. Largemouth bass, however, began feeding on fish prey as plant densities increased, but encountered difficulties penetrating dense macrophyte beds in search for prey. Dibble and Harrel (1997) also found piscivory to be more prevalent in largemouth bass contained in milfoil enclosures than those contained in common pondweed-dominated enclosures. Diets of largemouth bass contained in the pondweed enclosures consisted primarily of macroinvertebrates. Dibble and Harrel (1997) hypothesized that differences in plant architecture were responsible for these differences in diet. For example, the frequency of vertical and horizontal interstices was higher in the pondweed communities (increased frequency of microhabitat for aquatic invertebrates) relative to milfoil communities (Dibble and Harrel 1997). This enhanced spatial complexity in the pondweed communities may increase the abundance of prey items and therefore benefit the foraging efficiency of littoral fishes.

Controlling Factors

The mechanisms of colonization and factors that affect the dispersal of milfoil have received a great deal of attention due to the profound impact milfoil invasion can have on a waterbody and surrounding ecosystems. Factors influencing the distribution of Eurasian watermilfoil on a large spatial scale include water column total phosphorus and Carlson's Index (Madsen 1998). Milfoil dominance increases as water column total phosphorus levels increase from oligotrophic (< 10 $ug \cdot l^{-1}$) to mesotrophic (< 30 $ug \cdot l^{-1}$) and then declines as total phosphorus levels exceed 50 $ug \cdot l^{-1}$. Carlson's Index (1977; TSI) is based on Secchi depth, chlorophyll *a* ($ug \cdot l^{-1}$), and total phosphorus concentrations. Lakes are then classified on a scale ranging from 0 to 100 based on these parameters. According to Carlson's Index, milfoil dominates in oligo-mesotrophic to moderately eutrophic waterbodies (TSI 35-70) (Madsen 1998).

Factors affecting milfoil within-lake distribution include water depth and substrate composition (Peltier and Welch 1969, Spence and Chrystal 1970, Anderson 1978, Spence 1982, Chambers and Kalff 1985, Duarte et al. 1986, Sheldon 1994, Middelboe and Markager 1997). The low nutrient concentrations and limited rates of nutrient diffusion found in coarse substrates provide poor habitat for macrophyte growth (Barko and Smart 1986, Aiken and

Picard 1980). Milfoil prefers substrates that range from 6 to 18% organic matter and sediment textures from 12 to 36% fine particles (< 0.5 mm diameter). However, it can be found on substrates from 0 to 32% organic matter and on sediment textures from 0 to 40% fine particles (Nichols 1994).

Higher levels of organic matter in sediments seem to retard milfoil growth (Barko 1983), largely as a result of changes in pH, redox potential, and the evolution of growth inhibiting gases (*e.g.*, hydrogen sulfide and ammonia) from eutrophic sediments (Horne and Goldman 1994). Depth also limits within-lake distribution of milfoil. Milfoil is most commonly found in depths of 1-3 m, but is commonly found in depths greater than 6 m and in depths of up to 10 m in waterbodies with high transparency (Boylen et al. 1996, Aiken et al. 1979). Poor light penetration can limit the distribution of milfoil to shallower waters (Nichols and Rogers 1997). Freezing and desiccation of milfoil plants on dewatered sediments in regulated lakes and rivers also limit the littoral distribution of milfoil colonies (Stanley 1976).

Eurasian Watermilfoil Propagation

Eurasian watermilfoil can spread rapidly within and between water bodies. Intra-lake colonization is primarily achieved through fragment production (both auto and allofragmentation) and/or clonal expansion which is mostly accomplished *via* stolon growth (Madsen and Smith 1997, Kimbel 1982). Fragment production and dispersal are likely responsible for the spread of milfoil across North America (Smith and Barko 1990). Boat movements between infested and non-infested water bodies facilitate inter-lake fragment dispersal (Williams 1993). Johnstone et al. (1985) found the plant distribution of five nonindigenous aquatic plants that spread vegetatively to be significantly associated with boating and fishing activities. Seed production does occur; however, it is less important than vegetative reproduction (Aiken et al. 1979).

Eurasian Watermilfoil Management

Management of milfoil has become a top priority for many agencies across the United States. To manage aquatic systems, several tools have been developed to study the spatial distribution of organisms and analyze relationships between environmental variables and biotic systems. Geographic information systems (GIS) are becoming increasingly popular in many biophysical sciences, including the aquatic sciences for this purpose (Lehmann and Lachavanne 1997). For example, Jensen et al. (1992) used GIS to develop a model for predicting the potential spatial distribution of cattail (Typha latifolia) and waterlilies (Nymphaea odorata) based on five biophysical criteria. Welch and Remillard (1988) used remote sensing in conjunction with GIS to monitor water quality and distribution of aquatic macrophytes in a South Carolina lake. Narumalani et al. (1997) used logistic multiple regression and GIS to determine the probability of macrophytes occurring at various water levels in a cooling reservoir in South Carolina. Many other studies (Koutnik and Padilla 1994, Janauer 1997, Williams and Lyons 1997, Gottens et al. 1998) pertaining to the management of aquatic ecosystems have also used GIS to assist in the analysis, modeling, and mapping of the spatial distributions of aquatic systems and their communities. GIS also facilitates the transfer of information between organizations and between organizations and the public and therefore represents a powerful tool in aquatic resource management.

Control techniques include the use of herbicides (both contact and systemic herbicides), rotovation, benthic barriers, benthic dredging, biological control agents (*e.g.*, the weevil Euhrychiopsis lecontei), and microbial control agents (*e.g.*, the fungus Mycoleptodiscus terrestris) (Richardson 1975, Wile 1978, Cooke and Gorman 1980, Nichols 1984, Sneh and Stack 1990, Verma and Charudattan 1993, Nelson 1996, Getsinger et al. 1997, Newman et al. 1997, Sutter and Newman 1997). Analysis of a water body with respect to potential areas of colonization and system-specific characteristics that may influence the effectiveness of control measures should be carried out prior to implementation of such control measures (Van Vierssen 1993) due to the wide variety of techniques available.

Eurasian watermilfoil was first observed in the outlet arm of Lake Pend Oreille in August, 1998. Milfoil beds in Albeni Cove were chemically treated in late August, 1998 in an attempt to reduce densities and prevent the spread of this species up the outlet arm and into Lake Pend Oreille proper. Chemical treatment consisted of applying two contact herbicides Aquathol ® (endothall (7-oxabicyclo (2,2,1) heptane-2, 3-dicarboxylic acid) and Reward ® (diquat (6,7-dihydrodipyrido[1,2-a:2',1'-c] pyrazinediium ion)) to 34 acres of water. The Bonner County (Idaho) Weed Control and Waterways Department performed the application.

Materials and Methods

Eurasian Watermilfoil Sampling and Laboratory Analysis

We used systematic random sampling design to describe milfoil densities in Albeni Cove in relation to depth. Thirty transects, 27.5 m apart, beginning at the west end of the cove and extending to the eastern-most point of the cove. The first transect sampled was randomly selected. Every third transect was sampled from that point until the entire bay was sampled. Five samples were obtained between 0 – 10 m depths on each sampled transect. Samples were labeled, stored on ice, and frozen upon returning from the field. Biomass (oven dry weight (ODW, $g{\cdot}m^{-2}$)) and species composition were determined for each sample following Standard Methods Procedure 10400 D.3 (APHA 1992).

The watermilfoil bed in Albeni Cove was also sampled in August, 1998 (pre-chemical treatment) and again in August, 1999 (post-chemical treatment) to obtain *maximum* biomass estimates. A Petite Ponar dredge (225 cm^2) was used to obtain four replicate plant grabs from the entire bed in 1998 and three in 1999. The dredge was positioned towards the center of the milfoil bed to ensure the edge of the bed was not sampled. Depth (m) and substrate type (clay, silt, sand, gravel, and cobble) were recorded for each grab. Biomass (oven dry weight (ODW, $g{\cdot}m^{-2}$)) was determined for each sample following Standard Methods Procedure 10400 D.3 (APHA 1992).

Eurasian Watermilfoil Site Limnology

Solar radiation extinction was measured with a LI-COR LI-250 (LI-COR ®,Lincoln NE) light meter in or near the center of the milfoil bed and outside of the milfoil bed from the water surface to lake bottom. A dissolved oxygen profile was obtained using a YSI model 55/25 (YSI Inc., Yellow Springs, OH) dissolved oxygen meter both within and adjacent to the milfoil bed. Electrical conductivity was taken using a YSI model 33 S-C-T. Alkalinity and pH were measured as follows: (1) water samples were taken using a 2-liter Kemmerer water sampler; (2) samples were retrieved at mid-depth near the center of the milfoil bed and; (3) three replicate water samples for the determination of pH and total alkalinity (mg $CaCO_3 \cdot l^{-1}$) were stored in full BOD bottles, and placed on ice until processing that evening (replicates were not obtained from outside the milfoil bed). Alkalinity was determined by the titration method according to Standard Methods procedure 2320.B (APHA 1992). Mean percent species composition by weight was also determined using data obtained from the *maximum* biomass samples. Together, those data were used to determine apparent effects milfoil has on the surrounding aquatic macrophyte community.

GIS Database Development

Bathymetry

A digitized bathymetric map of the outlet arm was obtained from the U. S. Geological Survey (USGS). To generate this map, the USGS measured depths at 62 bathymetric sections on the outlet arm using a calibrated video depth sounder. Depth and locations were digitized onto a base map of the shoreline that had been generated from 7.5-minute USGS topographic maps (USGS 1996).

Substrate Composition

A polygon coverage containing the dominant substrate types in the outlet arm of Lake Pend Oreille was obtained from Dupont (1994, Fig. 10). The substrate coverage was converted into a 10-m raster grid. The assumption was made that substrate particle size distribution had not changed significantly over time from that identifies in 1994.

Statistical Analysis

Eurasian Watermilfoil Biomass and Depth

Regression analysis was used to determine the relationship between water depth (m) and biomass of milfoil (ODW, $g \cdot m^{-2}$). Biomass values were log-transformed prior to analysis to accommodate homogeneity of variance (Kleinbaum et al. 1998). Substrate composition was not included in the regression analysis due to insufficient replication on the various substrate types; however, substrate composition was used in the GIS modeling process. All statistical analyses were performed using SAS GLM (SAS Institute Inc. 2000) or STATISTICA® (Statistica for the Macintosh 1994) computing software.

GIS Analysis

The bathymetric map contained discrete depth values (*i.e.*, every contour line had a measured depth value, but the area between contour lines did not have depth values). In order to generate a map consisting of continuous depth values, we converted the bathymetric coverage into a TIN (Triangulated Irregular Network) model. The TIN was then converted into a 10 m cell-sized raster grid. All coverage and grid manipulations were performed using various commands and modules in ArcInfo v. 7.2.1 and ArcView v. 3.2 (ESRI, Environmental Systems Research Institute).

The model describing the relationship between milfoil biomass and depth in Albeni Cove was applied to the depth grid to generate predicted densities of milfoil for each cell in the grid based on its depth value (Fig. 11). Substrate and biomass grids were then combined using the CON statement in ArcInfo. The CON function is a conditional statement that is evaluated on a cell-by-cell basis. For example, substrate cells were given the value from the predicted biomass grid if the substrate was "clay," "silt," or "sand" and given a value of "zero" if the substrate was "gravel" or "cobble," since milfoil was absent from all gravel and cobble substrate types sampled. This allowed a final estimation of likely available habitat taking into account substrate composition and depth. These predicted biomass values were then used as indicators of suitable milfoil habitat. We assumed that a higher predicted biomass was indicative of more suitable habitat since aquatic macrophytes can be used as bioindicators of suitable habitat (Nichols and Buchan 1997, Nichols 1994).

Results

Eurasian Watermilfoil Site Limnology

Light rapidly attenuated under the dense milfoil canopy from 17, 000 LUX at the surface to 40 LUX at 3.25 m (outlet arm bottom, Fig. 12). Only 0.59% of surface solar radiation was present at 2 m depth. Light attenuated from 16,000 LUX to 4,300 LUX at 3.25 m in open water adjacent to the milfoil canopy.

Daytime dissolved oxygen in the milfoil bed was at 115% saturation ($9.8\ mg \cdot l^{-1}$) at the surface and declined to 80% saturation ($6.8\ mg \cdot l^{-1}$) at the sediment-water interface (Fig. 13). Dissolved oxygen adjacent to the milfoil bed was at 90% saturation ($8.1\ mg \cdot l^{-1}$) at the surface and 91% saturated ($8.2\ mg \cdot l^{-1}$) at 3.25 m. Mean water-column temperature (°C) and conductivity (µsiemens) inside the milfoil bed were 19.8 and 147, respectively. Water-column temperature (°C) and conductivity (µsiemens) outside the milfoil bed were 20.5 and 173.3, respectively. Mean alkalinity inside the milfoil bed was 73.0 mg $CaCO_3 \cdot l^{-1}$ and mean pH was 7.3. Alkalinity outside the bed was 72.0 mg $CaCO_3 \cdot l^{-1}$ and pH was 7.5 (Table 10).

Milfoil was the dominant species present in the *maximum* biomass samples comprising 84% mean species composition by weight. Elodea canadensis, Ceratophyllum demersum, and Ranunculus aquatilis comprised a minor proportion of the most dense milfoil beds with 10%, 5%, and 1% mean species composition, respectively.

GIS: Predicted Available Habitat

The relationship between milfoil biomass and depth predicted that approximately 52% (2098 ha) of the outlet arm area was suitable habitat. Suitable habitat was defined as any area predicted to contain any densities of milfoil. This definition is broad, but given the coarse resolution of the analysis and the limited number of predictor variables it allows for a liberal estimation of available habitat. Using the relative predicted densities as indicators of habitat quality, approximately 33% (1346 ha) of the predicted milfoil habitat was "low" quality habitat (predicted biomass between 1 – 25 $g{\cdot}m^{-2}$, ODW), 5% (194 ha) was "moderate" quality habitat (predicted biomass between 26 – 210 $g{\cdot}m^{-2}$, ODW), and 14% (558 ha) was "high" quality habitat (predicted biomass > 210 $g{\cdot}m^{-2}$, ODW) (Fig. 11).

Eurasian Watermilfoil Biomass and Depth

Depth was a significant predictor of milfoil density ($p < 0.0001$, $r^2 = 0.57$). We found that a parabola described the relationship between milfoil biomass and depth (Fig. 14).

$$\mathrm{LOG(biomass)} = -2.257 + 2.482(\mathrm{depth}) - 0.330(\mathrm{depth})^2 \qquad (1)$$

Once the model took into account both substrate composition and depth, approximately 39% (1438 ha) of the outlet arm area was predicted as suitable habitat (*i.e.*, was in the depth range of 0 m to 7 m and was not on gravel or cobble substrates).

Approximately 24% (871 ha) was "low" quality habitat, 4% (147 ha) of "moderate" quality, and 11% (420 ha) was "high" quality habitat (Figs. 15 and 16).

Discussion

Eurasian Watermilfoil Biomass and Depth Modeling

The relationship between depth and milfoil biomass in Lake Pend Oreille was approximated by a parabolic curve with a maximum biomass attained near 4 m depth. Lehmann et al. (1994) also found this parabolic relationship between biomass and depth with three pondweed species in Lake Geneva, Switzerland, and used the relationships in modeling submerged macrophyte biomass using GIS. Low biomass in the shallow depths is partially due to the effects of winter drawdown and in many cases may be attributed to disturbance caused by wave action (Schiemer and Prosser 1976, Chambers 1987). The decrease in milfoil biomass deeper than 4 m is related to an increase in littoral slope. As depths approach 6 m, slope increases to the thalweg. Higher slope decreases physical stability of the finer sediments resulting in poor plant habitat (Duarte and Kalff 1986). Low light is often cited (Spence and Chrystal 1970, Duarte et al. 1986) as a limiting factor to the maximum depth of colonization of aquatic macrophytes. However, in this study the light compensation point for photosynthesis (1% of surface light) was deeper (8 m in Albeni cove) than the deepest milfoil communities suggesting that other factors, such as littoral slope and substrate, are controlling the maximum depth of milfoil colonization in this system. Carlson (1995) also concluded that slope and substrate were likely limiting the Eurasian watermilfoil-dominated community in the Pend Orielle River, Washington. Ballesteros et al. (1989) speculated that sediment features were responsible for the lower boundaries of aquatic macrophyte colonization in an oligotrophic lake when irradiance failed to explain the maximum depth of colonization. Irradiance was about 50% well above the compensation point (1%).

Reward ® (diquat) and Aquathol ® (endothall) application in 1998 failed to significantly reduce the *maximum* biomass of Eurasian watermilfoil in Albeni Cove from 1999 maxima (1998 mean maxima = 1119.7 $g \cdot m^{-2}$, 1999 mean maxima = 905.3 $g \cdot m^{-2}$, *t*-test, $p = 0.35$). The ineffectiveness of this application may be due to several factors. The chemical application occurred late in the growing season. Diquat is most effective early in the growing season when plants are actively photosynthesizing (Murphy and Barrett 1993). Furthermore, water velocities in the outlet arm likely limited the contact time of the chemicals in the areas of higher velocity. For example, Newroth (1979) concluded that diquat was ineffective and expensive in large spread treatments of milfoil, especially in lotic systems. Reinert et al. (1985) determined over 90% of granular endothall entered solution 24 h after application. This rapid release rate may reduce its effectiveness in lotic systems (Reinert et al. 1985).

Future management options may include different herbicides and/or mechanical control methods. For example, in the Pend Oreille River, Washington, just west of Albeni Falls Dam, mechanical rotovation was successful in reducing milfoil stem densities. Milfoil stem densities were reduced 63 - 90% immediately following rotovation and remained reduced 25 - 70% the following growing season (Gibbons and Gibbons 1988). Wile (1978) also reduced milfoil stem densities with multiple harvests by a mechanical harvester, and concluded that fish populations were unaffected by harvest activities. Population estimates of warmwater fish species (pumpkinseed Lepomis gibbosus) remained level over the duration of their study in both harvested and nonharvested control areas. However, Wile (1978) did record a direct loss of fish that were trapped in the vegetation upon removal. A loss of approximately 8.9 kg fish per ha lake area harvested. Small (12 to 190 mm) yellow perch (Perca flavescens) were the most numerous species removed accounting for 56% of the total number of fish harvested (Wile 1978). Winter drawdowns also have been successfully implemented to control milfoil populations (Goldsby et al. 1978, Tarver et al. 1978, Cooke 1980, Tarver 1980, Siver et al 1986). However, these studies occurred in enriched water bodies where milfoil is limited to shallow depths and therefore fully exposed during drawdown. Winter drawdown to 3.5 m will not be as successful in the outlet arm of Lake Pend Oreille due to high transparency and the resulting deeper milfoil colonization (depths greater than 5 m). A winter drawdown to 3.5 m would only reduce densities in the shallowest areas of the littoral zone.

Other chemicals that may be considered include systemic compounds such as triclopyr (3,5,6-trichloro-2-pyridinyl-oxyacetic acid) and 2,4-D (2,4-dichlorophenoxy acetic acid). Triclopyr is a selective herbicide that has the potential to remove the nonindigenous dicot milfoil while not affecting native monocots such as Elodea spp. (Sprecher and Stewart 1995). Getsinger et al. (1997) reduced milfoil biomass by 99% (4 weeks after treatment) using triclopyr in a portion of the Pend Oreille River, Washington, between Albeni Falls Dam and Box Canyon dams. Milfoil plants have also been shown to be highly susceptible to 2,4-D. Westerdahl and Hall (1983) determined the threshold concentration required to control milfoil was 0.10 - 0.25 $mg \cdot l^{-1}$. Diver-operated suction dredging and hand harvesting have been used for milfoil removal in the outlet arm of Lake Pend Oreille in September, 2000. Divers up-rooted the entire plant and placed it into a bag or suction dredge. This procedure effectively removed milfoil shoots and roots; however, long-term effectiveness of this procedure has not yet been determined. Suction harvesting substantially reduced the biomass and percent coverage of milfoil in Lake George, New York, while increasing species richness in the harvested areas a year later (Eichler et al. 1993). Hand harvesting has also been used effectively to reduce densities on small patches of milfoil (Titus 1994).

Eurasian Watermilfoil Site Lminology

The light attenuation under the milfoil canopy illustrates the competitive nature of this species and its ability to shade out native vegetation (Aiken et al. 1979, Madsen 1994). We found that light was reduced below the compensation point below about 1.5 m under the milfoil canopy limiting photosynthesis of indigenous plants and resulting in a monospecific milfoil stand. Milfoil becomes dominant partially as a result of its growth form and its competitive abilities. Falter et al. (1991) reported similar effects of milfoil beds on light penetration in the Pend Oreille River, Washington. Madsen et al. (1991) recorded a decline in the number of native plant species under a dense milfoil canopy. The number of plant species dropped from 20 (under low densities of milfoil) to 9 under a dense milfoil canopy cover. Falter et al. (1991) also reported that milfoil communities dominated some littoral areas in the Pend Oreille River, Washington, accounting for up to 97% of the littoral aquatic macrophyte community. All mechanisms by which milfoil out-competes native species are in need of further investigation.

The dissolved oxygen profile of the Lake Pend Oreille milfoil bed is typical of many aquatic plant communities (Carpenter and Lodge 1986). During daylight hours, photosynthesis near the surface creates supersaturated dissolved oxygen (DO) conditions, while respiration of macrophyte tissue consumes oxygen in deeper waters, especially near the sediment-water interface (Jensen 1989). Frodge et al. (1990) found elevated DO concentrations in the surface canopies of submerged species and lower DO concentrations near the sediments in Keevies Lake and Bull Lake, Washington, and concluded that canopy formation was probably more important than species composition with respect to effects on water chemistry. In our study on the outlet arm of Lake Pend Oreille, water temperature, electrical conductivity, total alkalinity, and pH in the milfoil bed were all similar to those values found in the pelagic zone of the outlet arm. However, Carter et al. (1991) observed pH to be stratified by depth in aquatic macrophyte comunities in the Potomac River with pH associated with decompositional processes in anaerobic benthos. Effects of macrophyte communities on the surrounding water chemistry, however, depends upon the type of waterbody and the size and depth of the system and can be expected to differ between and within lakes and rivers (Carter et al. 1991).

GIS: Predicted Available Habitat and Management

The GIS illustrated the potential spatial extent of milfoil in Lake Pend Oreille using two habitat variables. According to the model, a large proportion (39%) of the littoral area on the outlet arm of Lake Pend Oreille is suitable milfoil habitat (Fig 16.). The amount of potential habitat is likely overestimated due to the spatial scale of the analysis and the limited number of predictors involved in the model. At this scale, the analysis does not take into account the within-bed spatial complexity and patchiness (France 1988). Milfoil populations in oligo to meso-oligotrophic waterbodies often form patches of varying densities and sizes that may be attributed to patchy areas of habitat in these systems and/or the intrinsic growth patterns seen in nutrient-poor environments (Madsen 1994). However, the model gives an indication to the potential impacts this species can have on the outlet arm and potentially on Lake Pend Oreille proper. Future modeling efforts should include more predictor variables such as littoral slope and fetch (as a determinant of wave action). A logistic model could then be developed to determine the probability of milfoil colonization at a given location. Such a model would be valuable for management agencies when they prioritize control efforts to certain areas of a water body. This model also illustrates the need for agencies to develop an effective management plan and to inform the public of the potential effects of this species and the ease with which it is dispersed.

Based on this research, areas on Lake Pend Oreille proper that represent potential habitat for Eurasian watermilfoil (*i.e.*, have suitable depth and substrate) include Scenic and Bottle Bays, the Pack River Delta, and the Clark Fork River Inlet. Another northern lake area is the littoral zone surrounding the Sandpoint public beach. There are fine sediments and shallow depths near the public beach and the presence of public boat ramps provides a vector for its introduction. Middle and southern lake areas contain less potential milfoil habitat due to steep littoral zones and coarse substrates.

Results from literature demonstrate the profound impact Eurasian watermilfoil can have on littoral communities and human recreation. Site-specific management techniques need to be developed to maximize effectiveness and minimize costs. The use of herbicides in conjunction with mechanical harvesting in areas of high use (*e.g.*, boat ramps) may represent an effective means for reducing the rate of milfoil colonization compatible with water-based recreation. However, the elimination of this species by these methods, or any others, is unlikely if not impossible (Gibbons et al. 1983b). Eventually, the milfoil community will naturally decline in abundance (Trebitz et al. 1993). The duration of peak biomass is approximately 10 years; however, the mechanisms responsible for its decline are varied and seem to be a result of multiple interacting factors (Carpenter 1980). Trebitz et al. (1993) also noted an invasion cycle of milfoil dominance in Lake Wingra, Wisconsin. Milfoil dominated Lake Wingra in the 1960's and then declined in the 1970's. While total plant biomass remained similar between those years (between 300 – 400 $g \cdot m^{-2}$), species diversity increased with milfoil persisting at lower densities. Creed (1998) suggested that the native herbivorous weevil (Euhrychiopsis lecontei (Dietz)), whose normal host is northern milfoil (M. sibiricum), may be partly responsible for the decline of Eurasian watermilfoil in many northern states and Canada.

In summary, Eurasian watermilfoil control programs in the outlet arm of Lake Pend Oreille should be developed to take into account the physical and biological limitations present at a given point of infestation. The use of herbicides, hand harvesting, and, mechanical harvesting if necessary, represent viable control options for this system. Contact herbicides may be effective in backwater areas of zero current velocity; whereas, hand harvesting can be used to remove isolated low-density colonies. Systemic herbicides or mechanical harvesting may be utilized in areas where milfoil densities are high and current is present. Since milfoil is now a part of the littoral community in this system, fisheries managers should manage these communities to maximize the use of this new habitat. For example, in some areas channels can be cut through the vegetation to increase the forage efficiency and cover for piscivores by increasing edge effect. More diverse colonies of other aquatic macrophyte species could grow to protect emerging year classes and nursery areas of fish (Engel 1995).

Summary

- A significant relationship was found between Eurasian watermilfoil biomass and depth in the outlet arm of Lake Pend Oreille with a maximum biomass attained near 4 m.
- Approximately 52% (2098 ha) of the outlet arm area was likely Eurasian watermilfoil habitat based on depth alone. Once the GIS accounted for areas consisting of gravel and cobble substrate, approximately 39% (1438 ha) of the outlet arm area was predicted as likely habitat (*i.e.*, was in the depth range of 0 m to 7 m and was not on gravel or cobble substrates).
- Reward ® (diquat) and Aquathol ® (endothall) application failed to significantly reduce the mean *maximum* biomass in 1999 (905.3 $g \cdot m^{-2}$) from1998 maxima (1119.7 $g \cdot m^{-2}$). The ineffectiveness of this treatment may be associated with a single application late in the growing season.
- Eurasian watermilfoil management should be site-specific, allow for the degree of infestation, and take into account the surrounding physical environment.
- Future modeling efforts could include more predictor variables such as littoral slope and fetch (as a determinant of wave action). A logistic model could then be developed to determine the probability of milfoil colonization at a given location.

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Figures

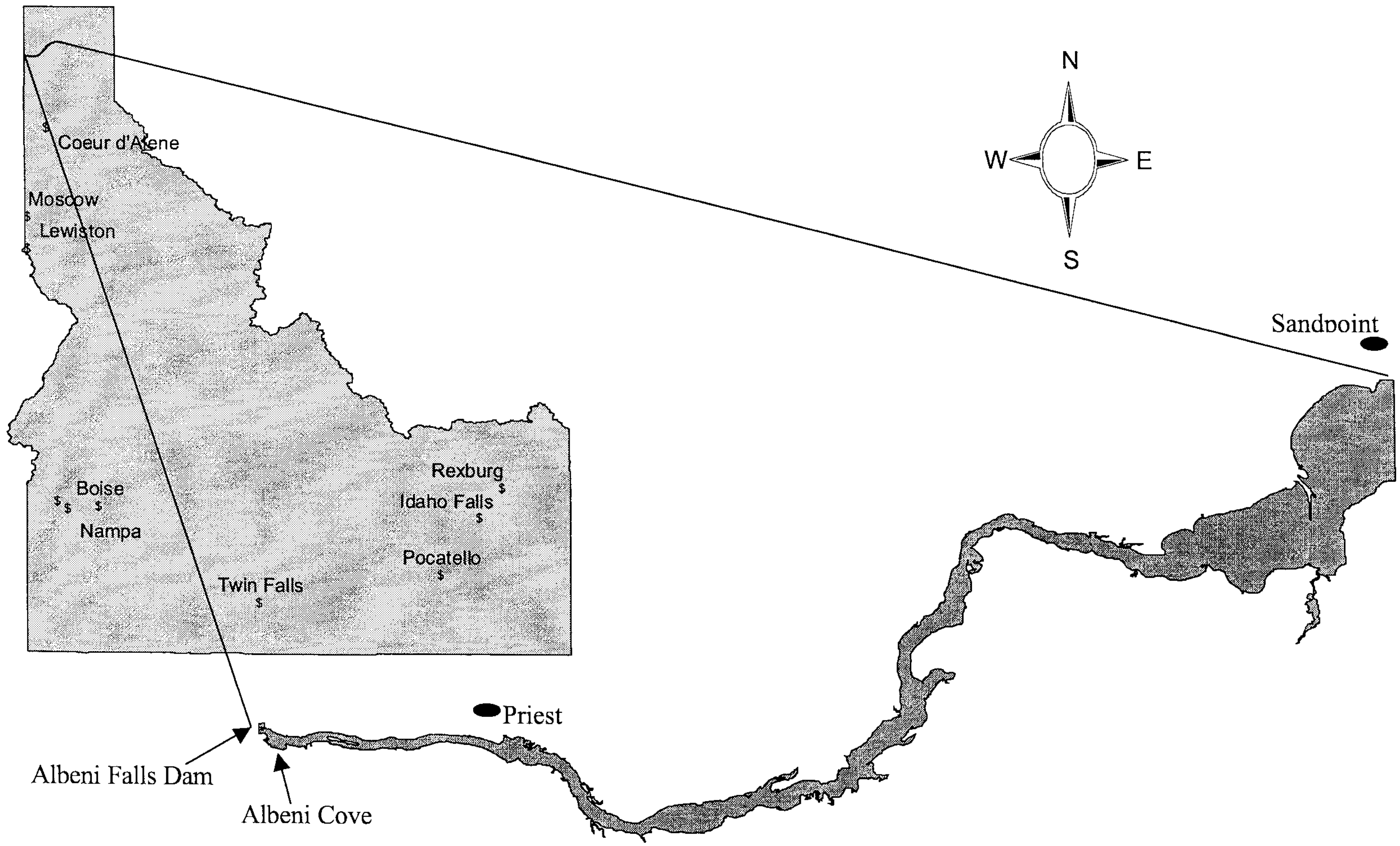


Figure 9.-The outlet arm of Lake Pend Oreille, Idaho. Albeni Falls Dam impounds the outlet arm at the Idaho-Washington border. Eurasian water was discovered in Albeni Cove in August, 1998.

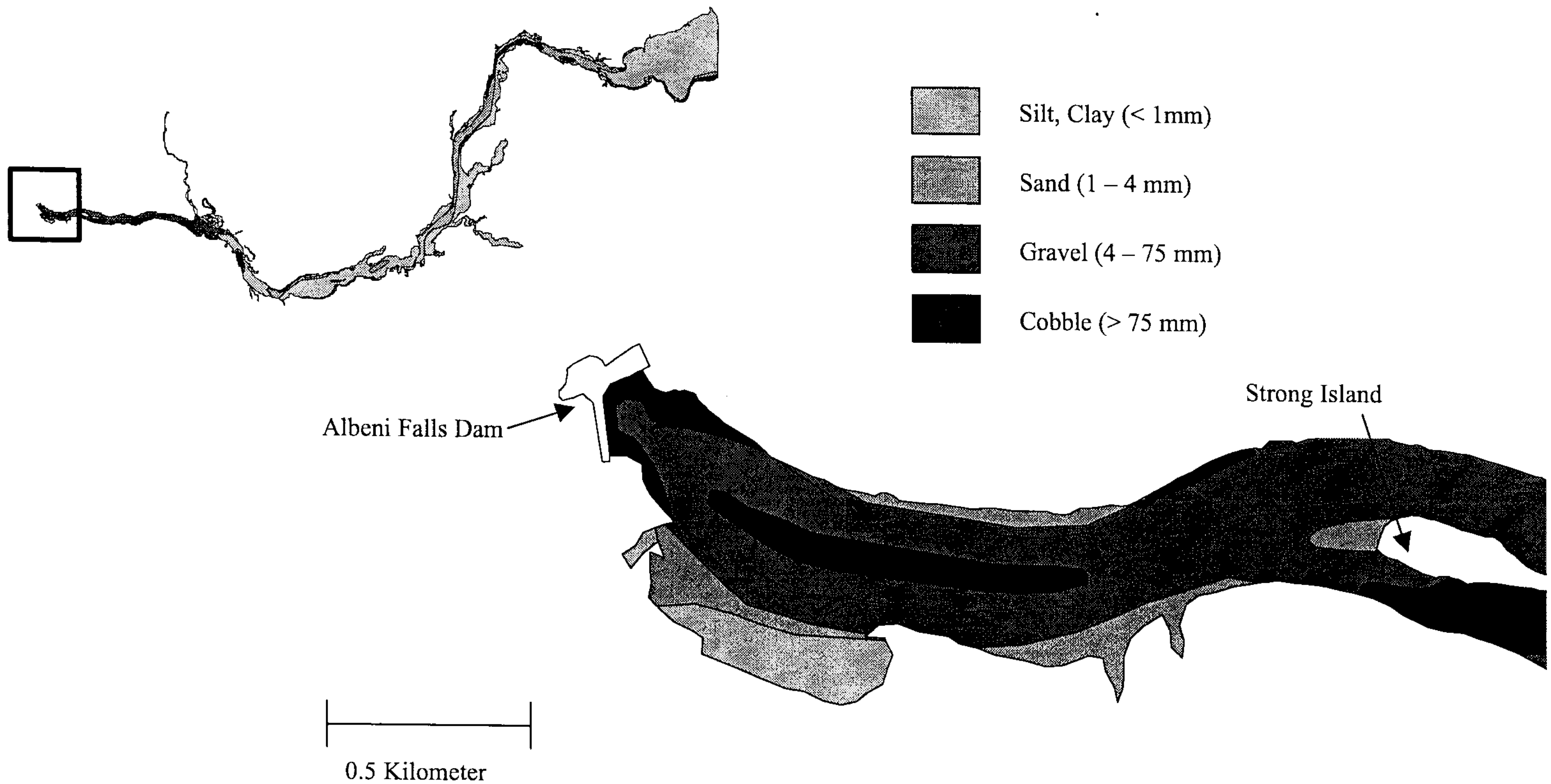


Figure 10.-Substrate composition grid of the outlet arm of Lake Pend Oreille, Idaho. Substrate size classes ranged from clay to boulder-sized substrates (Dupont 1994).

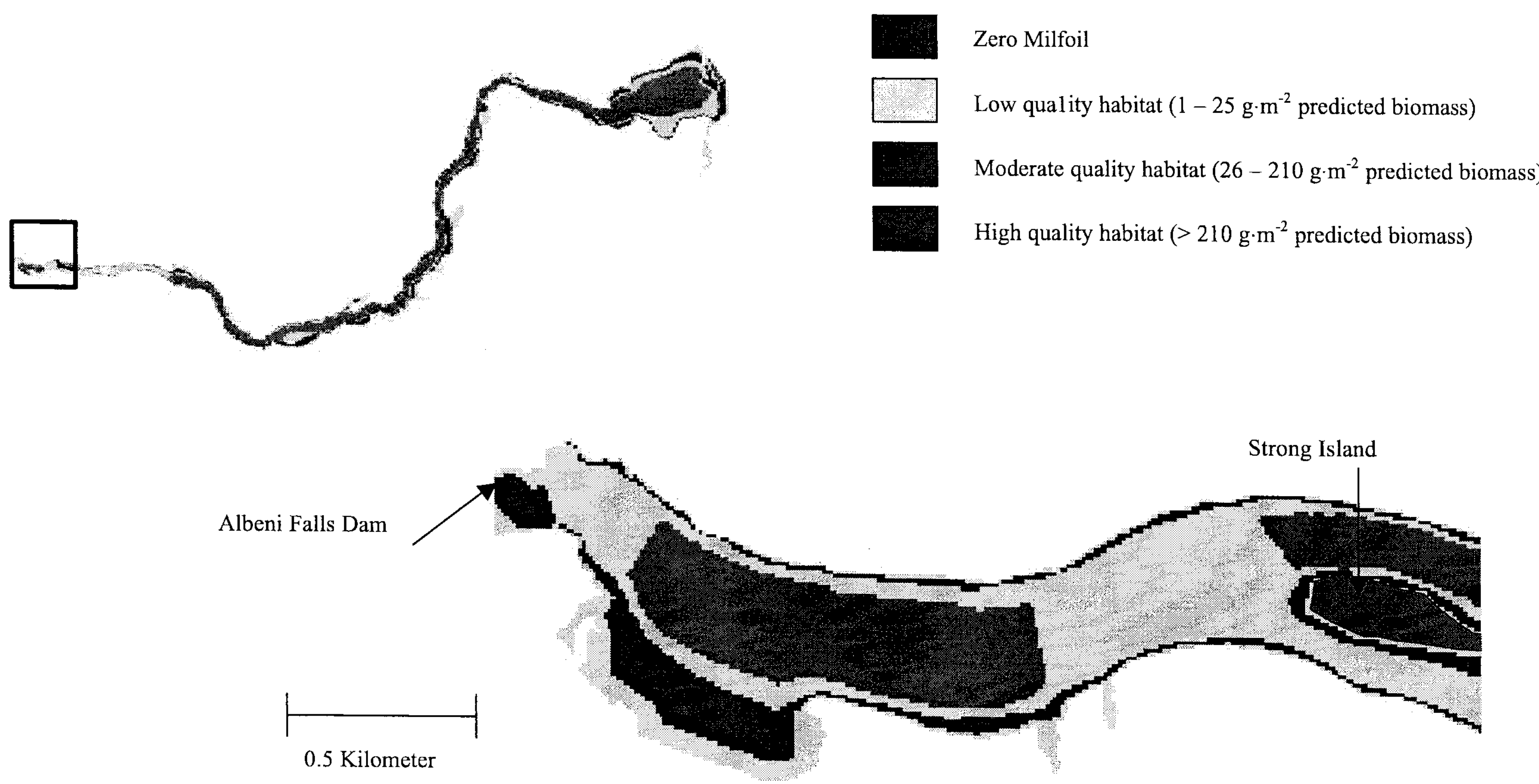


Figure 11.-Predicted milfoil densities based on the depth-density relationship in the outlet arm of Lake Pend Oreille, Idaho, 1999.

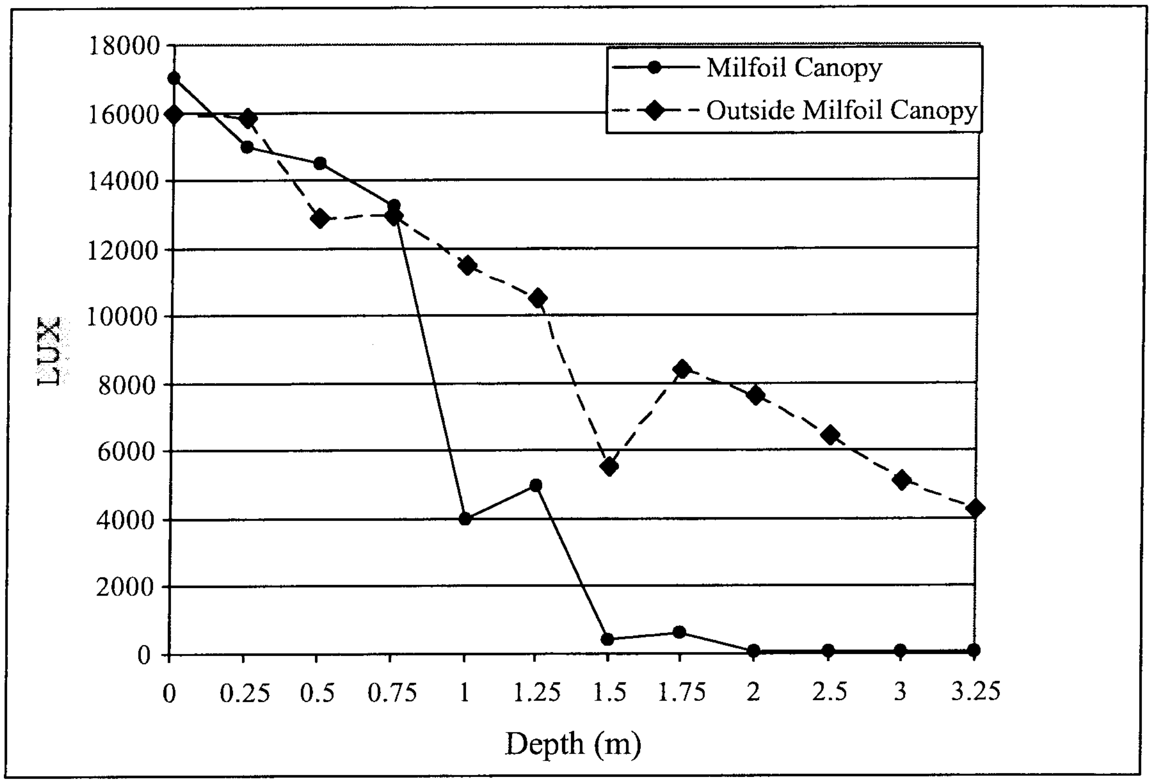


Figure 12.-Light profiles of Eurasian watermilfoil bed (maximum densty of 905.3 g·m^{-2}) compared to open water adjacent to the milfoil bed in Albeni Cove, outlet arm of Lake Pend Oreille, Idaho, 1999.

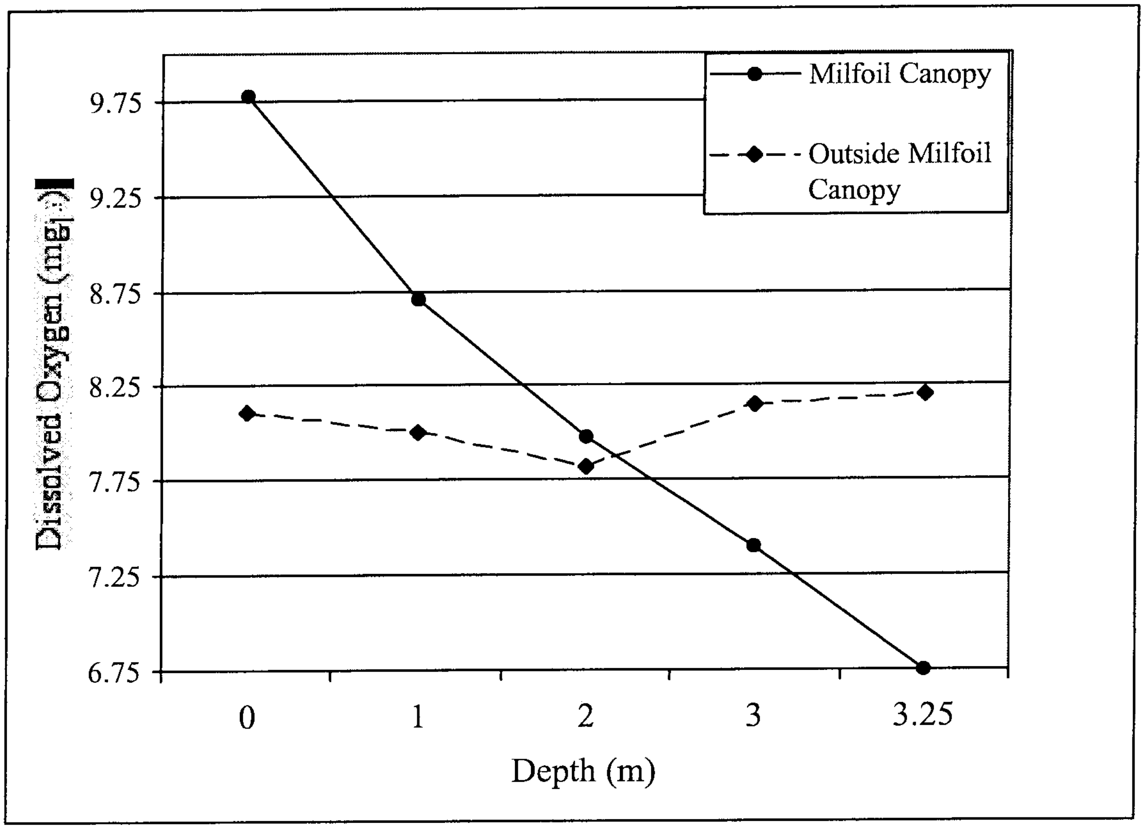


Figure 13.-Dissolved oxygen profiles of of Eurasian watermilfoil bed (maximum densty of 905.3 g·m^{-2}) compared to open water adjacent to the milfoil bed in Albeni Cove, outlet arm of Lake Pend Oreille, Idaho, 1999.

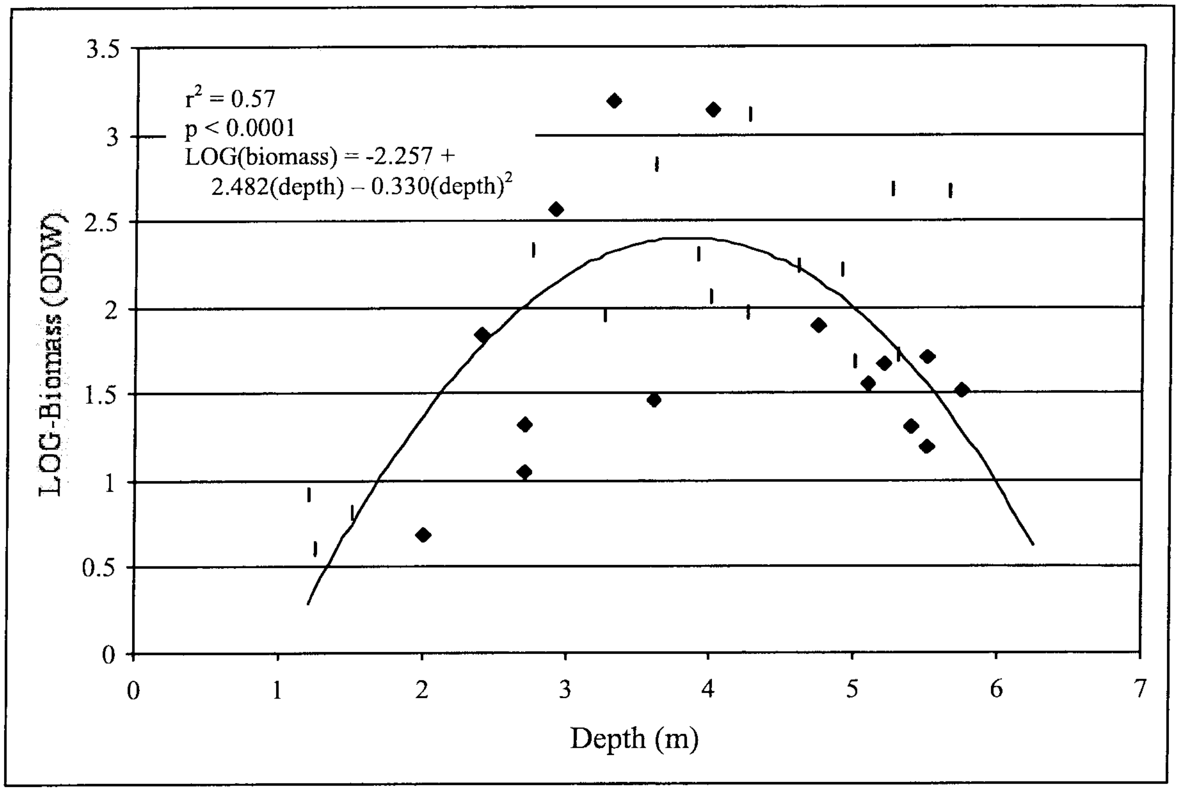


Figure.-14. Log Eurasian watermilfoil biomass (oven dry weight, g·m^{-2}) in relation to depth (m) in Albeni Cove, outlet arm of Lake Pend Oreille, Idaho.

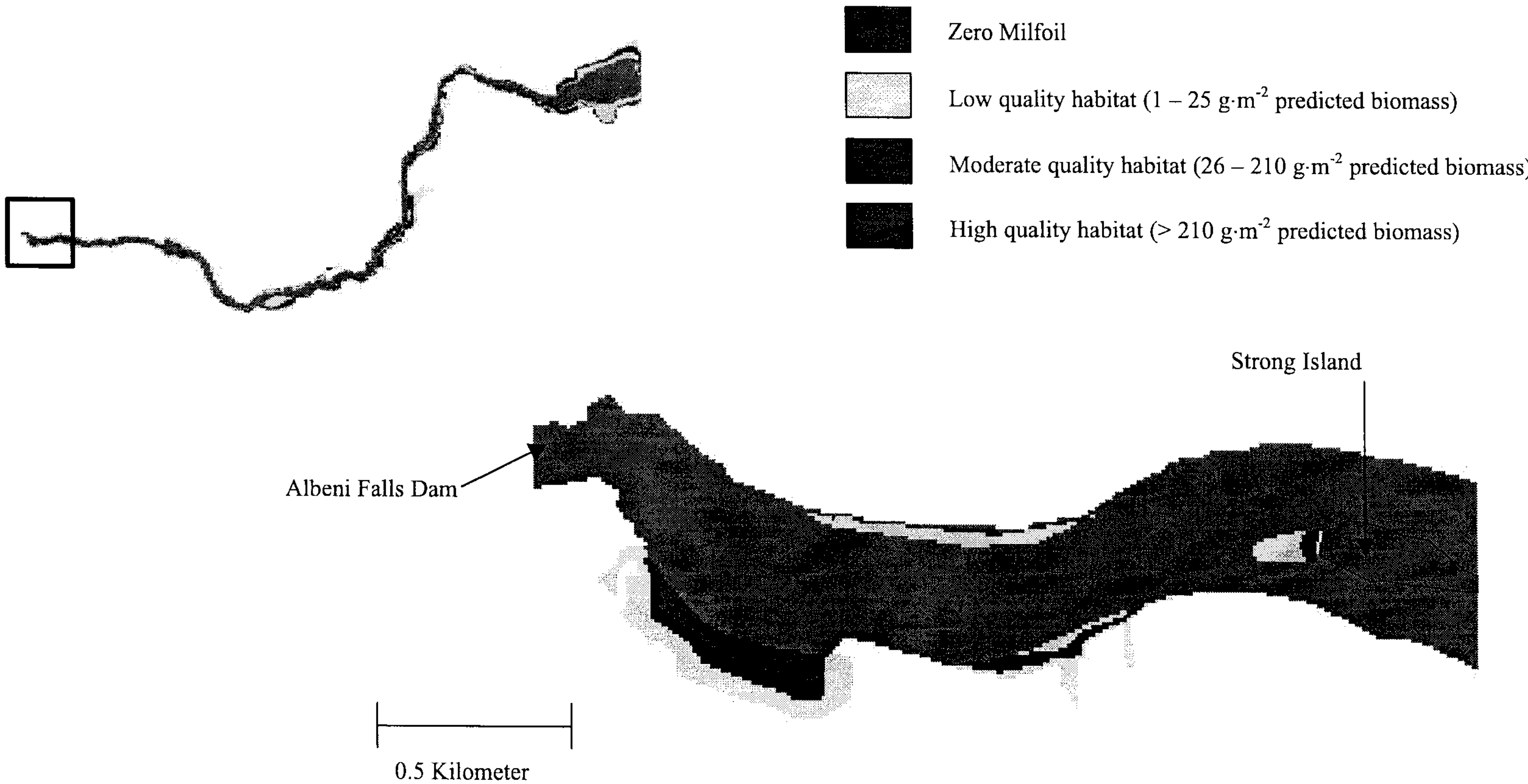
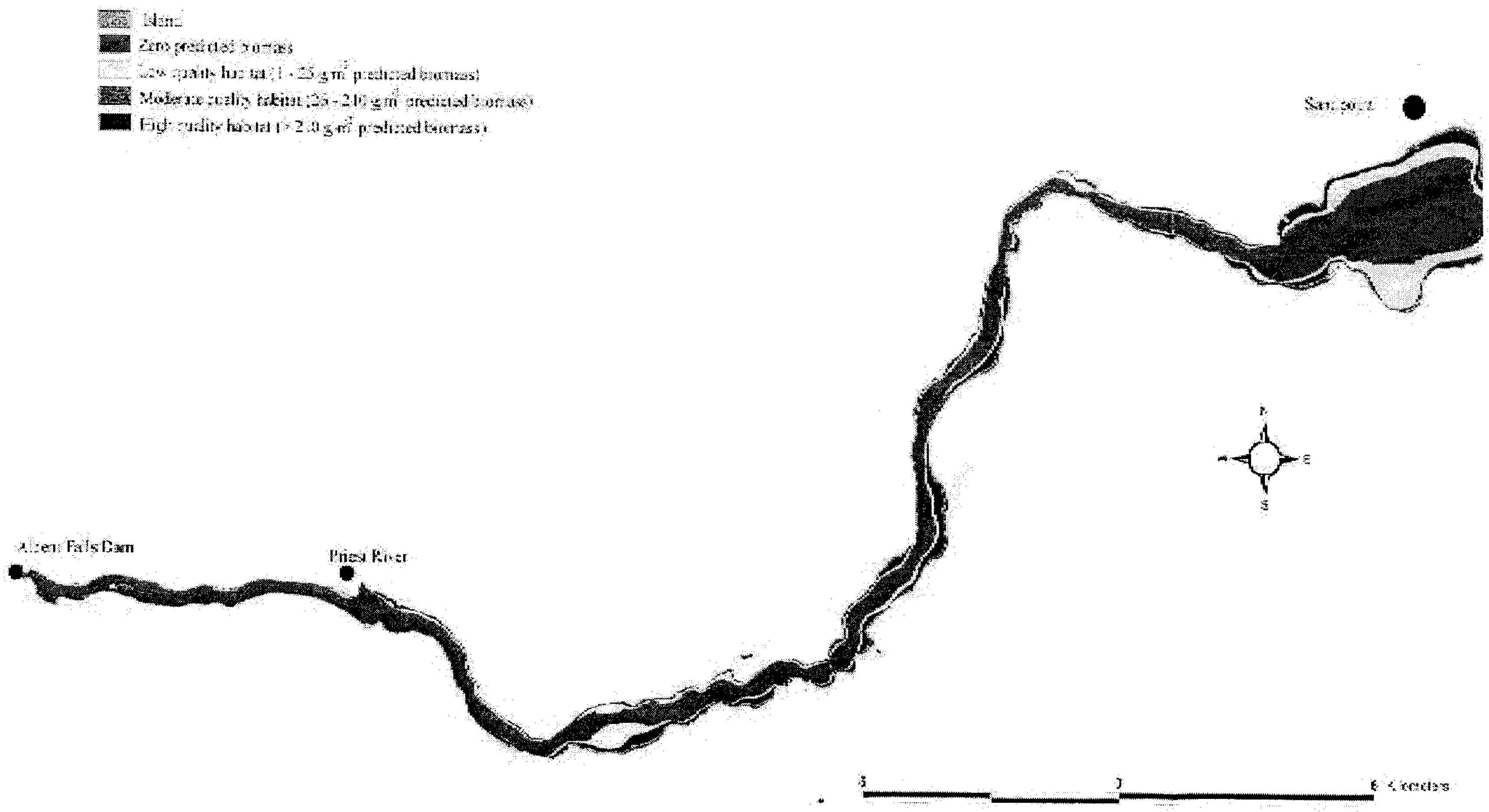


Figure 15.-Predicted densities of Eurasian watermilfoil based on depth and substrate type in the outlet arm of Lake Pend Oreille, Idaho, 1999.


Island
Zero predicted biomass
Albeni Falls Dam
Priest River
Sandpoint

Tables

Table 7.- Water chemistry parameters measured from in a Eurasian watermilfoil bed and in open water adjacent to the milfoil bed in Albeni Cove on the outlet arm of Lake Pend Oreille, Idaho, 1999.

	Temperature (°C)	Electrical Conductivity (μmhos)	Total Alkalinity (mg $CaCO3 \cdot l^{-1}$)	pH
Within milfoil bed	19.8	147.0	73.0	7.3
Open water	20.5	173.3	72.0	7.5