EFFECTS OF SHORELINE DEVELOPMENT ON THE NEARSHORE ENVIRONMENT OF A LARGE DEEP NUTRIENT-POOR LAKE (LAKE CRESCENT, USA)

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ABSTRACT:

Human development around lakes has a variety of impacts on the nearshore habitat. A common impact is increased nutrient addition via septic tanks leaching nutrients through the soil into the groundwater. While nutrient additions frequently increase primary productivity due to a fertilization effect, this increase may or may not translate into greater productivity at higher trophic levels, depending in part on complex trophic dynamics. In large deep oligotrophic lakes, the shallow water region nearshore may provide the most important habitat for feeding and breeding as well as a large proportion of primary production in the form of periphyton. I used multivariate techniques to examine the spatially explicit effects of residential development on nearshore periphyton communities in three large deep nutrient-poor lakes in the Pacific Northwest that have all experienced modest residential development. For my primary study site (Lake Crescent, WA), I found that productivity and accumulation of detritus was higher at developed sites. In addition, both macroinvertebrate and periphyton communities exhibited a shift in composition with more detritivores and filamentous green algae at developed sites. These differences were more pronounced during the spring than at other times of year. When looking for general patterns between Lake Crescent and two other similar lakes (Priest Lake and Lake Pend Oreille, ID) I found that periphyton community composition was significantly affected by development status despite other lake-specific trends. These localized changes in community composition of primary producers in the nearshore due to nutrient loading could potentially have strong bottom-up effects throughout the food web, while the open water conditions remain unchanged.

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This thesis is dedicated to my father, Robert Reneau, and my grandfather, George Reneau, who both fostered my interest in the natural world and science in general. It’s also dedicated to my mother, Micheline Seminet, who has supported me throughout all of my academic endeavors.

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INTRODUCTION:

Humans are drawn to live on lakes for recreational and aesthetic reasons, but their lakeside activities can degrade the quality of the lake environment. As populations increase, an increasing number of people live on lakes. In one Wisconsin county (Vilas), 61% of residential buildings were located less than 100 meters from a lake (Schnaiberg et al. 2002). Preferential development near lakes has been evident in aerial photographs as far back as 1938 in Southeast Michigan, and has substantially increased in the intervening years (Walsh et al. 2003). Not only are there high proportions of residences in the riparian zone of a lake (within 100m), but the presence of a lake influences residential development as far away as 800 m from the lakeshore (Walsh et al. 2003). Ironically, the activities of humans on lakes can degrade the lake qualities that initially attracted them. Developing lakeside land decreases the riparian density of trees around the shoreline, which in turn decreases the recruitment of coarse woody debris into the littoral zone (Christensen et al. 1996). Coarse woody debris provides physical structure in the nearshore, serving as complex habitat for fish foraging and refuge (Christensen et al. 1996; Schindler et al. 2000). Schindler et al. (2000) found that fish growth decreased with intensity of lakeshore development, a phenomenon those authors attributed to littoral zone degradation. Changes in riparian vegetation due to development can also impact water quality because of alterations in terrestrial run-off patterns (Groffman et al. 2004) and increased water temperatures due to loss of shade (Brown and Krygier 1970, Johnson and Jones 2000). Human shoreline activities can also alter nutrient inputs into the littoral zone and nearshore waters.

Human activities alter nutrient dynamics in aquatic food webs through both addition and removal of nutrients. For example, human harvest of anadromous salmon from a productive system can alter nutrient cycles in streams and lakes (Gresh et al. 2000). However, humans more commonly impact aquatic nutrient cycles by adding nutrients to streams and lakes, through overland runoff of fertilized or disturbed land and the direct introduction of effluents such as sewage (Vitousek et al. 1997). Such nutrient additions can have complex effects.

Harmful algal blooms resulting from increased anthropogenic nutrients (nitrogen and phosphorus) have been extensively documented, from freshwater to marine systems (Jacoby et al. 2000; Keto 1982; Nolen et al. 1989, Paerl 1997), throughout the world. Lake Washington (Seattle, WA) is a classic case study that demonstrated the linkage of secondary sewage disposal over time on primary productivity and nuisance cyanobacteria blooms (Edmondson et al. 1956, Edmondson and Lehman. 1981, Edmondson 1991). Algae stimulated by nutrient inputs in eutrophied systems typically have a rapid life cycle, and accumulate dead material quickly, a process that consumes oxygen. The Gulf of Mexico “dead zone” is an example of a nearshore coastal system that, due to increased anthropogenic nutrient loading from the Mississippi River and subsequent increase in bacterial degradation of dead material, has experienced massive fish kills due to hypoxia (Rabalais et al. 2002).

Even with such evidence of undesirable outcomes from nutrient pollution, some have argued that modest increases in nutrients may not harm water quality and in fact may encourage fish growth by providing more food at lower trophic levels. Such arguments have typically been made for systems in systems that are purposefully manipulated for fisheries management purposes or in cases where humans have nearly eliminated fish migrations, thereby disrupting nutrient cycles (Stockner and Shortreed. 1988, Stockner and MacIsaac. 1996, Budy et al. 1998). However, if the organisms that respond to higher nutrients are well-defended against consumption, such transfers may not be efficient and effects on higher trophic levels are difficult to predict. For example in Packers Lake, AK, Mazumder and Edmundson (Mazumder and Edmundson 2002) found that juvenile salmon only responded to experimental nutrient additions when fry densities were low and large-bodied *Daphnia* were abundant as potential forage.

While nutrient additions frequently increase primary productivity due to a fertilization effect, this increase may or may not translate into greater productivity at higher trophic levels, depending in part on complex trophic dynamics. Algal growth may exceed consumers' capacity to consume it, or nutrient enrichment may decrease edibility of primary producers. For example, increased CO_2 emissions from fossil fuel combustion are integrated by terrestrial plants via increased photosynthesis. However, this abundance of CO_2 allows plants to allocate more carbon to defense structures such as lignins and tannins that make them more difficult for grazers to digest (Rier et al. 2002, Tuchman et al. 2002). Thus nutrient addition can non-intuitively decrease the bottom-up transfer of nutrients. Nutrient additions are, with few exceptions such as fisheries enrichment management programs, treated as pollution in aquatic systems.

Most residential lakeshore development uses septic treatment instead of sewer systems to treat human waste (Census 1990). Septic tanks diffuse waste into drain fields that filter waste before it enters surface waters through shoreline sediments. This treatment method, while superior to introducing raw sewage, is still imperfect because as septic tanks age and their drain fields become saturated, more nutrients can pass through the soil. Algal growth, nutrient levels, and proportion of inedible blue-green algae in lakes ringed by septic tanks are higher than those in undeveloped lakes or urban lakes with sewer systems (Moore et al. 2003).

Effects of sewage pollution have been well studied in relatively shallow lakes (Edmondson and Lehman 1981, Keto 1982, Nolen et al. 1989 and Jacoby et al. 2000). The effects of sewage on large, deep lakes may be pronounced as well. Large, deep lakes are less numerous than shallow lakes, but their beauty and water clarity attracts residential development and recreation. Schnaiberg et al. (2002) found a positive correlation between lakeside residential development and lake surface area, indicating a preference for large lakes. It might be expected that these large, deep lakes are less endangered by pollution simply due to dilution effects. However, because sewage enters lakes from the shoreline, it may be retained in critical habitat for aquatic organisms, especially when the shallow nearshore region has disproportionate importance in the food web (Figure 1).

In large deep oligotrophic lakes, the shallow water region nearshore may provide the most important habitat for both feeding and breeding. In these lakes, a large proportion of primary productivity occurs in the nearshore. This high proportion of productivity in the nearshore is due the lack of pelagic productivity occurring, which results in high water clarity and allows for significant accumulation of periphyton in the nearshore (Vadeboncoeur et al. 2003). Since the food web may rely disproportionately on this relatively small area that provides edible carbon, these large lakes thus may actually be more affected by pollution than smaller eutrophic lakes where productivity primarily occurs in the open water. Thus, any localized changes in community composition of primary producers in the nearshore due to nutrient loading could potentially have strong bottom-up effects throughout the food web, whether this signal is seen among algae offshore or not (Figure 1). For example, a change in periphyton composition could change the macroinvertebrate community composition, thus changing the food availability to fish that move inshore to feed. Additionally, many fishes and other organisms require shallow water for breeding. If changes in algal composition or the associated chemical environment, such as oxygen levels, are significantly degraded by residential development, impacts on breeding or rearing habitats could affect lake-wide population and community dynamics.

Despite the importance of primary producers to entire food webs, researchers often only quantify increases or decreases in overall productivity in a system (for example, Lohman et al. 1991, Wipfli et al. 1998, Forrester et al. 1999, Taylor et al. 2004, Nyogi et al. 2007), but the compositional changes among nearshore taxa may be important if the algal taxa favored by eutrophication promote more or less growth among their consumers. Additionally, the amount of decaying material is likely to increase where productivity increases, which will influence consumers through alterations in the type of food available and the nearshore chemical environment.

Here I have examined the spatially explicit effects of residential development on nearshore periphyton communities in three large deep lakes in the Pacific Northwest that have all experienced modest residential development. The study of nearshore change in response to pollution serves two purposes. First, algal compositional changes nearshore may have inherent importance for lakewide management when lake organisms rely on nearshore breeding and feeding resources. Second, periphyton responses to residential development can serve as an early warning to managers of changes in water quality. Periphyton is a useful indicator of eutrophication because it is attached to rocks and thus reliant on nutrients entering the nearshore via ground water for productivity as opposed to nutrients in the sediments (Goldman 1988, Jacoby et al. 1991). Due to its proximity to the nutrients entering water at the shoreline and its rapid nutrient assimilation, periphyton is likely to respond to nutrient loading before biota or chemical parameters measured in the pelagic water, thus acting as an early warning of eutrophication (Hadwen and Bunn 2005). None of the lakes under study is thought to be experiencing offshore effects of pollution, but nearshore effects of development have been indicated by lake managers. I focused this work on Lake Crescent (Figure 2) in Washington’s Olympic National Park, to understand spatial and temporal trends in pollution effects. I compared these results to data collected at a coarser scale from two other similar lakes (Lake Pend Oreille and Priest Lake in Idaho, Figure 2) to determine whether trends in nearshore effects of residential development are generalizable to large deep oligotrophic lakes can be detected.

I had three main hypotheses associated with my lake sampling and one hypothesis that was addressed through laboratory experimentation. First, due to periphyton's ability to rapidly assimilate nutrients, I hypothesized that measures of primary productivity would be different at developed sites compared to developed sites. Second, with this change in primary productivity, I expected to see a shift in macroinvertebrate community composition at developed sites. And third, in addition to a change in productivity, I hypothesized that the community composition of periphyton would be changed at developed sites. To test the bottom-up implications of this third hypothesis, I hypothesized that macroinvertebrates would display preferential ingestion of algae types in a lab experiment.

METHODS:

Study Sites:

Lake Crescent is a large deep oligotrophic lake in Olympic National Park on Washington State's Olympic Peninsula. Lake Crescent is a tourist destination for recreation, and there are over 100 private residences and two resorts on the lake that were 'grandfathered' into the area when the Park was formed in 1938 (Myer and Fradkin 2002). All of the houses and resorts rely on septic tanks for their sewage treatment, and recent nearshore observations of periphyton blooms by Park managers (Myer and Fradkin 2002) suggest that these aging septic systems are supplying an increased nutrient load to the nearshore habitat. Human impacts in the shallow water warrant special attention because two species of particular interest depend on the nearshore environment in Lake Crescent. The Beardslee trout (*Oncorhynchus mykiss*), is a genetically distinct trout population endemic to Lake Crescent (Myer and Fradkin 2002). These trout only spawn in one location- the Lyre outlet, which is the area of the lake that has experienced the most shoreline development. Park scientists have observed that Beardslee trout seem to avoid areas of high periphyton growth (personal communication, Dr. Steven C. Fradkin, Olympic National Park). A sensitive and unique plant species that resides in Lake Crescent is Water Lobelia (*Lobelia dortmanna*) (Olson and Cereghino 2002). This plant, specially adapted to nutrient-poor water, is listed as "threatened" in Washington State, mainly due to loss of habit (WADNR 2003). *Lobelia's* presence has been used as an indicator of oligotrophic conditions and its decline has been associated elsewhere with added nutrients or eutrophication (Szmeja 1987). Although Lake Crescent has areas of development, there are still vast areas of shoreline that are undeveloped, and the offshore waters do not show signs of eutrophication (Hampton et al. unpublished manuscript*)*.

In order to determine localized development impacts, paired nearshore sites were chosen in developed and undeveloped areas around the lake (Figure 3). These sites were sampled every 3 months for one year from August 2005 through August 2006 to capture all seasons. Twelve sites included 4 undeveloped and 4 developed sites that were distributed throughout the basin, and 4 sites within the shallow Lyre outlet basin. The Lyre outlet is of particular interest because it is the only known spawning site for Beardslee trout and is one of the most heavily developed areas of the lake.

The two northern Idaho lakes against which Lake Crescent results were compared, Lake Pend Oreille and Priest Lake (Figure 4, Table 1), are under patchy development pressure like Lake Crescent and are exhibiting nearshore responses to nutrient loading. Located in the panhandle of Idaho (Figure 2), Lake Pend Oreille is the largest and deepest lake in the state. Glacially fed and low in nutrients, its clear waters are a popular recreation destination for fishing, swimming, and boating (Falter 2004). Lake Pend Oreille, though unchanged in the pelagic zone since studies began in 1911, has exhibited uncharacteristically high periphyton productivity in the littoral zone relative to its low nutrient status (Falter 2004), with higher productivity near developed sites (Kann and Falter. 1989). Similarly, Priest Lake is oligotrophic and exhibits no changes in pelagic water quality, but has shown unusually high productivity in the littoral zone (Rothrock and Mosier 1997). No detectable difference in productivity biomass between developed and undeveloped sites in Priest Lake were found by Rothrock & Mosier

(1997). Approximately 75 miles north of Lake Pend Oreille, Priest Lake is also a popular recreation destination. Land ownership around Priest Lake and Lake Pend Oreille is a mix of private residences and U.S. Forest Service land, creating a patchy distribution of development similar to that of Lake Crescent. Here, the Idaho lakes were subject to parallel study, with a comparable sampling regime to that of Lake Crescent, at a coarser temporal and spatial resolution. On each Idaho lake, I sampled 6 sites, collecting 9 replicates within site, during the spring and fall of 2006.

Data Collection & Analyses:

Analytical design

In order to take advantage of the more extensive information gathered on Lake Crescent, results from this lake were first examined independently and then a reduced Lake Crescent data set was compared to data from the other two lakes. To determine whether similar patterns in nearshore response to development could be discerned across all three lakes, data from comparable sampling periods (spring and fall 2006) were analyzed for all three lakes together. Data loss from Lake Pend Oreille and Priest Lake samples prevented comparisons of primary productivity measures in the spring.

Environmental and community differences among sampling sites were investigated with multivariate analyses using PRIMER v6 (Clarke and Gorely 2006). All data were log (x +1) transformed to moderately deemphasize the most abundant organisms (*sensu* Clarke and Warrick 2001) unless otherwise noted. All subsequent analyses were performed on the Bray-Curtis similarity matrix. The Bray-Curtis similarity matrix was chosen for several reasons. First, the Bray-Curtis similarity matrix determines differences between samples by species that are present in both samples, but joint absences are not considered. This quality is frequently desirable in ecological studies such as this, because samples that share the same species absences are not necessarily similar (*sensu* Clarke and Warrick 2001). Second, the Bray-Curtis comparison between two sampling units is independent of the addition or removal of a third sample, since it does not standardize for each variable like many other similarity coefficients. This lack of standardization is also useful for determining differences in total abundance between two samples when relative abundances may be the same (Bray and Curtis. 1957, Anderson 2001, Clarke and Warwick 2001).

I used permutational analysis of variance (PERMANOVA; Anderson 2001), with 9999 permutations, to examine differences in univariate and multivariate biological variables between developed and undeveloped sites within each lake as well as among lakes (Table 2). PERMANOVA was chosen because of its ability to partition variance like other analysis of variance (ANOVA) methods, while also providing the flexibility and robustness of non-parametric methods. This framework can accommodate complex designs, and multivariate analyses are executed on similarity matrices that are chosen by the user, depending on the question at hand. PERMANOVA's flexibility is important because community assemblage data frequently include many potential responses, and they often do not meet formal assumptions of normality needed to use traditional general linear models that rely on tabled statistics. Instead, the PERMANOVA test statistic is based on permutation, and represents the true probability of observing the differences present among groups that were sampled. P-values are obtained by comparing the F-statistic calculated from the observed data to F-statistics obtained by randomly shuffling the treatment labels into other units. If there is a significant treatment effect, the F-statistic calculated from the observed data should be large relative to F-statistics derived from the permutations; as with other frequentist methods, the user determines the level at which an effect is considered “significant” (e.g., $\alpha = 0.05$ or $\alpha = 0.10$). Since tabled test statistics are not used, PERMANOVA does not rely on assumptions of homoscedasticity and normality, which famously plague the use of MANOVA (Olson 1974). Multi-factorial PERMANOVA allows rigorous examination of the complex interactions potentially affecting multivariate responses, creating a flexible and robust hybrid between the traditional univariate and multivariate statistical approaches currently available to ecologists.

For data visualization, I used non-metric multidimensional scaling (MDS) in PRIMER. MDS was chosen because, unlike Principal Components Analysis, it is more flexible in choice of dissimilarity matrix and it is better at preserving distances between samples (Clarke and Warwick 2001). In choosing MDS, the user recognizes the arbitrariness of similarity coefficients, which can change drastically under transformation and instead, MDS uses relative values of similarity to ordinate samples (Clarke 1993, Clarke and Warwick 2001). This means that samples with the highest similarity coefficient will receive the lowest rank (i.e. “1”) whereas samples that are dissimilar will receive higher ranks. The MDS method preserves Euclidean distances of samples because the ranked distances between points will correspond to the ranked similarities between samples. MDS attempts to choose a configuration of points that minimize stress between the similarity rankings and the corresponding distance rankings in the plot. A Kruskal's stress value of less than 0.1 corresponds to a good representation without a large chance of misinterpretation whereas a stress value greater than 0.1 indicates an ordination that is not entirely reliable, suggesting another method should be used to compare results.

To determine which variables were most strongly associated with community assemblage differences between developed and undeveloped sites, I used the SIMPER routine in PRIMER (Clarke and Warwick 2001). The SIMPER routine calculates the percent contribution of each variable to the Bray-Curtis dissimilarity between treatments, resulting in the value "similarity percentage" for each variable. Those taxa (or other variables) that contribute the most to the differences among groups are those with the highest similarity percentages.

Below, I outline the applications of these techniques to each of the data sets collected from developed and undeveloped sites at each of the three lakes. PERMANOVA designs are shown in Table 2.

Water nutrients

I collected water column samples from Lake Crescent from each nearshore site during the November 2005 sampling period to ascertain levels of total nitrogen (TN) and total phosphorus (TP). Two 125 mL acid washed plastic bottles were filled with water collected from mid-column at a depth of 0.50 meters, preserved (0.25 mLs of sulfuric acid and 0.25 mLs of hydrochloric acid respectively) and stored at 4.0° C until analysis was conducted by the University of Idaho Analytical Sciences laboratory. This laboratory uses EPA method 365.4 for TP and high temperature combustion for TN. All 12 Lake Crescent sites contained nutrient concentrations that were below the minimum detectable level for phosphorus and nitrogen (less than 0.01 and 0.05 mg/L respectively), and further nutrient sampling on Lake Crescent was not pursued. At Lake Pend Oreille and Priest Lake, water nutrient samples were taken from 4 of the 6 sites for each lake during the spring 2006 sampling period (2 from developed sites, 2 from undeveloped sites).

Productivity measures

Algal pigments and organic matter biomass were used to characterize the productivity of developed and undeveloped sites. These results were analyzed together as multivariate measures of productivity in a multifactorial PERMANOVA. For SIMPER analysis, I removed productivity measures that were correlated (keeping one AFDM as a proxy for the ones removed) in order to determine which forms of productivity were driving the differences between groupings.

Algal pigments -- To use chlorophyll a concentration as a proxy for primary productivity, I collected algal samples of known area from the surfaces of rocks at three different depths (0.25, 0.50, 0.75 m from waterline) in the nearshore of each site in the spring and fall sampling periods. Each algal sample was filtered through a 2.5 cm glass fiber filter (VWR, 0.7 μm particle retention) using a 25 mm filter holder (Hach, standard syringe with Luer-type fitting). Samples were frozen, in the dark, until analysis. Chlorophyll a analysis was performed using a Turner Designs Trilogy (model 7200-000) fluorometer using EPA method 445.0 (Arar and Collins 1997). Calibration was performed using two standards (18.70 ug/L and 187.00 ug/L). The frozen filters used for samples were placed in vials containing 10 mL of 90% aqueous acetone and left to sit in the dark for 12-24 hours. After extraction, chlorophyll a absorbance of the 2.2 mL solution was determined by fluorometry.

As cells age and die, they lose magnesium ions from the chlorophyll molecule, forming a degradation product called pheophytin a. Pheophytin interferes with analysis of chlorophyll from cells that were living during collection, so an acidification step was added to the chlorophyll determination procedure (60 microliters of hydrochloric acid 0.1 normal molar) to calculate pheophytin relative to chlorophyll a in each sample. In addition to improving chlorophyll a determination, this analysis has the benefit of providing a measure of the detritus present in a sample of known area in order to quantify biovolume per surface area for each sample.

Ash-Free Dry Mass & Autotrophic Index -- Ash-free dry mass (AFDM) is a measure of the total amount of organic material which includes, for example, autotrophs, heterotrophs, and detritus. For AFDM analysis, three samples of a known surface area were collected from three different depths (0.25, 0.50, and 0.75 m from waterline) and pooled into one sample jar. These samples were frozen until further analysis. Glass fiber filters (VWR 4.7 cm, pore size 1.5 µm) were ashed for 2 hours in a muffle furnace at 400° C in crucibles and weighed prior to analysis. Each algal sample was thawed, brought to a known volume with distilled water, and homogenized in a blender for 20 seconds. Three 5 mL aliquots were then concentrated on a glass fiber filter, using a vacuum filtration. Each filter with sample was dried in a crucible at 105° C for 24 hours, allowed to cool, and weighed. The filters and crucibles were then ashed at 400° C for 4 hours and allowed to cool before taking a final weight. Ash-free dry mass was calculated as the difference between dried weight and ashed weight, which yielded the total amount of organic material in the sample including autrophs, heterotrophs, and dead material (Table 3, Biggs and and Kilroy 2000).

Using the ratio of AFDM to chlorophyll a, I calculated the autotrophic index (AI) to determine the proportion of autotrophic to heterotrophic organisms in the periphyton samples (Table 3). This value has been used most commonly in stream systems to gauge effects of eutrophication on periphyton dynamics. A high AI value indicates that a high proportion of the AFDM is comprised of heterotrophic organisms and dead organic matter. Generally, a value of 50-200 is characteristic of pristine conditions where photosynthesis dominates, and values greater than 400 typically indicate organic enrichment (Biggs 1989).

Macroinvertebrates

In order to coarsely characterize the macroinvertebrate communities at each site where periphyton was collected, I captured macroinvertebrates with a kicknet for approximately 5 minutes at each site. Macroinvertebrate samples were collected at Lake Crescent over 4 sampling periods (November 2005, March 2006, May 2006, and August 2006). At Lake Pend Oreille and Priest Lake, macroinvertebrates were sampled twice, in April 2006 and September 2006. These invertebrates were identified and enumerated on site and were later classified to functional feeding group (Merritt and Cummins 1996). I standardized the samples by dividing each entry by total abundance in each sample (*sensu* Clarke and Warrick 2001), in order to determine whether the composition of macroinvertebrates differed among sites of different development status. A Bray-Curtis similarity matrix was created from these transformed data. To determine differences in macroinvertebrate community composition at developed and undeveloped sites Lake Crescent, I used a 2-way PERMANOVA testing the effects of “development” and “date” on multivariate macroinvertebrate composition (Table 2). Examining macroinvertebrate communities across all three lakes, I considered only May and August dates from Lake Crescent to correspond with the spring and fall sampling periods of Lake Pend Oreille and Priest Lake. Comparing all three lakes I executed a 2-way PERMANOVA on “lake” (as a fixed factor) and “development” (as a random factor).

Shoreline tree community composition

Recognizing that an important effect of development is the alteration of shoreside vegetation and associated terrestrial inputs, I surveyed tree composition on the Lake Crescent sites. A 20 m long, 10 m wide transect was established at each of the sampling sites on Lake Crescent in August 2006. At each transect every tree was enumerated, identified to species, and diameter at breast height (DBH) was measured. To determine whether there was a difference in total number of tree at developed and undeveloped sites, I used a one-way PERMANOVA to examine effects of "development," as a random factor, on these multivariate tree responses (Table 2).

Community composition and abundance of periphyton

At each of the twelve sites on Lake Crescent, 9 periphyton samples were collected for community abundance and composition analysis during 5 sampling periods (August 2005, November 2005, March 2006, May 2006, and August 2006), for a total of 300 samples between first date and last date. In Lake Pend Oreille and Priest Lake, samples were collected in April 2006 and September 2006 for a total of 60 samples from each lake. Three replicates from three depths (0.25 m, 0.5 m, and 0.75 m) were collected using a double syringe periphyton sampler (Loeb 1981). Where the growth of algae prevented the efficient use of the double syringe sampler (surface area sampled = 573 mm^2), I used a razor blade (surface area = 1521 mm^2) to cut through and scrape the algae of a known surface area instead of brushing it off. The samples were immediately preserved with Lugol's fixative (100g KI, 50g I_2, 100 ml acetic acid, and 900 mL double-distilled water) and kept cool and dark until processed. Samples were homogenized with a blender and brought to a known volume with distilled water. Subsamples taken from the thoroughly mixed samples were counted using a 1.0 mL Sedgwick-Rafter counting chamber under a compound microscope at 20x magnification. Subsamples were scanned and all cells counted in a series of randomly located transects until 300 cells had been enumerated (*sensu* Biggs and Kilroy 2000). Each cell of a filament or colony was counted individually. Soft-bodied algae were identified to genus and diatoms to basic type (centric, pinnate, naviculoid, cymbelloid, gomphonemoid) and size. Only cells with chloroplasts were counted, to restrict counts to living cells. Based on these counts in the known volume of the Sedgwick-Rafter chamber, the field of view of the eyepiece, the number of transects counted, and the sample volumes, I calculated total densities of cells: # cells/ mm^2 = ((count * # possible transects / # transects counted) * total sample volume) / (surface area sampled)

In addition to density (cells/mm^2), I calculated biovolume (μm^3 / mm^2) by estimating the average volume for cells within the major taxonomic groupings (Table 4). For any taxon that comprised at least 5% of the sample, I measured up to 5 cells in dimensions that allowed volumetric calculations for its basic geometric shape (*sensu* Hillebrand et al. 1999, Table 4) and photographed representative cells for archiving of its identification. For Lake Crescent, I used a 3-way PERMANOVA (Table 2) to test effects of “development” (fixed factor), “date” (fixed factor), and “site” (fixed factor nested within development) on algal community composition. I present results from this design instead of the blocked design (Table 2) because the blocked model did not yield significant effects of blocking ("pairing" P = 0.3419 and "date x pairing" P = 0.2506), and using the nested model allowed simultaneous consideration of the four developed sites in Lake Crescent (located in the Lyre River outlet basin, figure 3) that could not be paired with undeveloped sites.

To compare algal community assemblages among all three lakes, the Lake Crescent Lyre basin data were removed, because pairing was not used for sites within this basin and no reasonable corollaries for this basin are found in the other two lakes. The Lake Crescent samples were also reduced to spring and fall for equivalence to Lake Pend Oreille and Priest lake sample periods. A 4-way PERMANOVA was run on "development" (nested in "pairing"), "season", "lake", and "pairing" (nested in "lake") to determine differences in periphyton community composition between lakes.

Stable Isotope Analysis of Field-Collected Samples

Periphyton samples and macroinvertebrates were collected for stable isotope analysis from each site at the same sampling dates and using the same methods as for periphyton community composition collections. These samples were analyzed for stable isotope ratios of nitrogen, in order to infer the source of nutrients (e.g., sewage vs. natural), since human sewage carries a higher δN^{15} that may be differentiated from natural or other common sources such as artificial fertilizers (Steffy and Kilham 2004). Filamentous and diatomaceous algae were cultured in the laboratory and analyzed for stable isotope ratios to determine whether there is any inherent difference in their fractionation of carbon and nitrogen that would prevent one from confidently inferring the sources of nutrients from stable isotope analysis. Samples were analyzed by personnel in the Idaho Stable Isotopes Laboratory (University of Idaho) using continuous-flow stable isotopic analyses (CE Instrument's NC 2500 elemental analyzer). An exploratory one-way ANOVA was run testing δN^{15} values at developed and undeveloped sites in total and separated by sample date.

Laboratory Grazing Experiment

In the laboratory, we assessed the proportional uptake of filamentous vs. diatomaceous algae by two common macroinvertebrates, the amphipod *Gammarus* and a gastropod *Physa*. Diatoms (*Navicula pelliculosa*) and filamentous green algae (*Mougeotia* spp.) were cultured in a standard medium (modified MBL, (Stemberger 1981) in the laboratory and background δN^{15} values (i.e. prior to isotope labeling) were measured.

Macroinvertebrates were collected from local ponds in Idaho and kept in a common tank with locally collected periphyton for several weeks to standardize food exposure and equilibrate background δN^{15} of macroinvertebrates prior to isotope labeling. Amphipods and snails were starved for 24 hours to determine background δN^{15} values in the absence of gut content isotope values. I added a ^{15}N tracer (Ammonium –^{15}N Chloride, 98 atom % ^{15}N made by Sigma Aldrich Isotech), to a stock of filamentous algae (*Mougeotia* spp.). This label imparts an elevated δN^{15} signature to organisms that assimilate it and allows us to quantify the relative importance of filamentous (with label) and diatomaceous (without label) ingestion. After 48 hours in the labeled medium, the filamentous algae were rinsed with unlabeled culture medium and added to two flasks that contained diatomaceous algae stock at background ^{15}N levels. To begin the experiment each one of the two experimental flasks were stocked with either 16 amphipods or 6 snails. At 3, 6, and 9 days, two snails and 5 amphipods were lethally sampled for isotope analysis. At these times, I also sampled filamentous and diatomaceous algae from each flask for isotope analysis. Macroinvertebrate and algal samples were dried at 60°C for 24 h, without macroinvertebrate stomach evacuation, and sent to University of California-Davis Stable Isotope facility for nitrogen and carbon isotope analysis. Samples were analyzed using continuous flow Isotope Ratio Mass Spectrometer (IRMS) on a Seven Isotope Ratio Mass Spectrometer (Europa Integra).

A mixing model was used to estimate the proportion of each food source that was assimilated by the macroinvertebrates. The form of the two-source mixing model used to quantify the proportional representation of diatomaceous algae assimilation is:

Diatom assimilation (proportion) $= (\delta_S - \delta_2) / (\delta_1 - \delta_2)$

where δs is the δN^{15} value of macroinvertebrates corrected for a 3.0 ‰ trophic enrichment (Peterson and Fry 1987), δ2 is the δN^{15} value of the spiked filamentous algae, and δ1 represents the δN^{15} of the unspiked diatoms.

RESULTS:

Water nutrients

Total nitrogen and total phosphorus were both below the University of Idaho Analytical Sciences laboratory's minimum detectable limits (<0.05 and 0.01 mg / L respectively) at all developed and undeveloped Lake Crescent sites. For Lake Pend Oreille, total nitrogen and total phosphorus values were similarly low at developed (TN = 0.10 +/- 0.02 mg/ L, TP = 0.01 +/- 0.01) and undeveloped (TN = 0.16 +/- 0.04 mg/ L, TP = 0.01 +/- 0.01 mg/ L) sites. Priest Lake also exhibited low values of total nitrogen and total phosphorus at developed (TN = 0.06 +/- 0.01, TP = 0.011 +/- 0.01) and undeveloped (TN = 0.07 +/- 0.02 TP = 0.01 +/- 0.01) sites.

Productivity

For Lake Crescent, the productivity variables chlorophyll *a*, pheophytin a, and AFDM, % OM, and AI were treated as multivariate responses related to general levels of productivity. Date (P = 0.04) and development status (P = 0.01) significantly affected the characteristics of living and dead materials nearshore in a 2-way multivariate PERMANOVA, but there was no significant interaction between the two main effects (P = 0.30). Chlorophyll *a* and pheophytin in Lake Crescent were higher at developed sites than undeveloped sites in the spring (figure 5a) while fall values were low for both types of sites (figure 5b). Ash-free dry mass, % organic matter, and autotrophic indices were highly variable from site to site but were, on average, higher at developed sites (Table 5). Post-hoc pairwise comparisons revealed that developed and undeveloped productivity variables were significantly different during May ($P = 0.04$) while August showed a weaker, non-significant difference ($P = 0.08$). SIMPER analysis of three of the productivity variables (chlorophyll *a*, pheophytin and AFDM) revealed that AFDM contributed the most (56.42 %) to the difference between developed and undeveloped sites in Lake Crescent (Table 5) followed by chlorophyll *a* (23.67 %), implying that increased organic material (AFDM) and productivity are driving the differences between developed and undeveloped sites.

Productivity variables from the Idaho lakes from September samples were analyzed together with the August data from Lake Crescent in order to determine whether general responses could be detected in the multivariate productivity responses. Lakes differed significantly in their productivity characteristics in general ($P = 0.05$), but no general trend in response to development status was detected ($P = 0.12$). Like Lake Crescent, Lake Pend Oreille productivity was slightly higher at developed sites (figure 6a), but productivity values for Priest Lake were indistinguishably low at both developed and undeveloped sites (figure 6b). As within the full Lake Crescent data set, SIMPER analysis of productivity (Table 6) values for all three lakes highlighted the role of AFDM in driving the difference between sites (56.08 %) followed by chlorophyll *a* (23.05 %).

Macroinvertebrates

Within Lake Crescent the macroinvertebrate community composition varied significantly with both date ($P < 0.01$) and development status ($P = 0.05$), and there was no significant interaction between these main effects. Post-hoc pairwise comparisons of developed and undeveloped sites revealed that these sites differed significantly in May 2006 ($P < 0.01$) but this effect was not evident in the other months ($P > 0.11$).

Results from SIMPER analysis by date and functional feeding group suggested that detritivores (amphipods), grazers (mayflies, snails, caddis flies) and piercer-grazers (corixids) were primarily responsible for observed differences between developed and undeveloped sites in Lake Crescent (Table 7). Average proportion of detritivores, relative to grazers, was higher at developed than undeveloped sites during the spring (March 2006) but these differences weakened later into the season (August 2006) when detritivores were more abundant everywhere (Figure 7).

The three lakes differed significantly in macroinvertebrate community composition ($P = 0.01$) but general patterns were not evident for development status ($P = 0.08$), or interactions of the main effects ($P = 0.68$). Post-hoc pairwise comparisons of developed and undeveloped sites indicated Lake Crescent was the only lake showing a trend toward difference between developed and undeveloped sites in this grouped analysis, although the trend was non-significant ($P = 0.10$). In post-hoc pairwise comparison, undeveloped sites at all three lakes resembled each other ($P > 0.11$), and it was apparent that it was high variability in developed sites that drove the differences apparent among lakes at the larger scale. Within developed sites, Lake Crescent and Priest Lake were significantly different from each other ($P = 0.04$). Developed sites on Lake Crescent and Pend Oreille trended toward differentiation, although non-significant ($P = 0.08$), and Lake Pend Oreille and Priest Lake showed characteristic similarity to each other ($P = 0.32$).

Like the macroinvertebrate community in Lake Crescent, grazers and detritivores were the primary contributors to the differences between developed and undeveloped sites at both Lake Pend Oreille and Priest Lake, but without consistent trends (Table 7). In Lake Pend Oreille, both the spring and fall samples had more detritivores at developed sites and more grazers at undeveloped sites (figure 8). Priest Lake followed this pattern in the spring; however, fall samples resulted in a higher proportion of grazers and detritivores at developed sites (figure 9).

Shoreline tree community composition

In the univariate PERMANOVA, total tree density did not differ between developed and undeveloped sites on Lake Crescent (P = 0.397), tree diameters however, were significantly different at developed sites (P < 0.01). On average, trees were larger at developed (22.04 cm +/- 20.02) sites than undeveloped (14.90 cm +/- 20.22) sites. In the multivariate PERMANOVA, tree species assemblage differed significantly with development status (P = 0.03). In the SIMPER results, alder (*Alnus rubra*) and western red cedar (*Thuja plicata*) were the top two discriminating species (Table 8). Alder were generally more common at developed sites while cedar were more common at undeveloped sites.

Community composition and abundance of periphyton

Algae community composition changed spatially and temporally at all three lakes. Exploratory analysis using non-metric multidimensional scaling (MDS) suggested that analysis at a relatively coarse taxonomic resolution (i.e., divided into groups: filamentous greens, non-filamentous greens, diatoms, and cyanobacteria) provided the best characterization by MDS, as indicated by the lowest Kruskal's stress value (stress = 0.08). Using these data in a multivariate PERMANOVA, algal community composition was significantly affected by date, development status and their interaction (Table 9). A PERMANOVA model with data at finer taxonomic resolution data yielded the same results. MDS plots suggest that samples from developed and undeveloped sites in the spring were more different from each other than samples from the late summer and fall (Figure 10). SIMPER analysis of each sample date revealed that diatoms and filamentous green algae were the algal taxa most descriptive of differences between developed and undeveloped sites at Lake Crescent (Table 10). Spring samples (March 2006) showed a large proportion of filamentous algae in developed sites and a high proportion of diatoms in undeveloped sites (Figure 10). Fall samples (August 2005) showed an increase in cyanobacteria in undeveloped and developed sites (Figure 11).

Although lakes differed in algal composition overall, development status significantly affected algal communities across lakes and dates (Table 11). A MDS plot for Lake Pend Oreille showed a strong separation between spring and fall sample assemblages, as well as separation between developed and undeveloped sites within the fall (Figure 12a). Priest Lake exhibited similar seasonal separation but less difference between developed and undeveloped sites (Figure 12b). SIMPER analysis of each sample date indicates that diatoms and filamentous green algae are the main contributors to the observed algal composition differences between developed and undeveloped sites (Table

10). In Lake Pend Oreille, filamentous green algae were more abundant at developed sites in the spring, but dominated the samples at both undeveloped and developed sites in the fall sampling period (Figure 13). Priest Lake had more filamentous algae at developed sites than did undeveloped sites in the spring, but in the fall samples, filaments were only slightly more abundant at developed sites while cyanobacteria increased at undeveloped sites (Figure 14). Thus, while development affected algal communities across lakes and tended to favor filamentous green algae and diatoms, the patterns were idiosyncratic among lakes.

Stable Isotope Analysis of Field Samples

Stable isotope analysis of δN^{15} of periphyton and macroinvertebrates from each site on Lake Crescent revealed highly variable nitrogen signatures (figure 15), suggesting that δN^{15} was not a reliable indicator of residential development effects. Developed and undeveloped sites did not differ significantly in δN^{15} values of macroinvertebrates ($P = 0.56$) nor periphyton ($P = 0.65$). Analysis of $\delta 15N$ ‰ by sample date revealed no significant difference between developed and undeveloped samples either ($P > 0.54$).

Isotope analysis of laboratory-cultured filamentous green algae and diatoms showed that filamentous algae have a slightly higher δN^{15} (5.559‰) than diatoms (2.997‰) when cultured under the same conditions.

Laboratory Grazing experiment:

To determine whether macroinvertebrates showed a preference among periphyton types, I spiked the filamentous green algae to extremely high $\delta^{15}N$ levels (7,600‰). The filamentous green algae's nitrogen signature became depleted over time, but still stayed high (2,400‰) as the experiment progressed (figure 16). Diatoms remained at roughly their original values (2.997‰) and the snails and amphipods both exhibited increased $\delta^{15}N$ values (figure 16), indicating that the grazers did ingest filamentous algae and that diatoms did not incorporate the artificially spiked nitrogen from the green algae innoculum. Proportion of nitrogen from diatomaceous vs. filamentous green algae incorporated into macroinvertebrate tissue at each sampling time during the experiment was calculated using the mixing model (figure 17). Amphipods started the experiment at a very high diatom:green ratio (1.74) and stayed high throughout the experiment (0.98 by day 16). Snails also started at a high diatom:green ratio (1.11) but dropped to lower ratios than the amphipods (0.88) , indicating a small degree of filamentous green algae assimilation. Values over 1.00 probably indicate the consumption of detritus prior to start of experiment.

DISCUSSION:

Lakes are valued by the general public for their aesthetic appeal and recreational opportunities (David 1971, Wilson and Carpenter 1999, Schnaiberg et al. 2002). Unfortunately, this appeal increases lakeshore development which has been shown to impact nutrient cycles (Carpenter et al. 1998, Vadeboncoeur et al. 2001, Chandra et al. 2005), productivity of higher organisms like fish (Schindler et al. 2000), and aesthetic properties that humans value (Edmondson 1991, Rothrock and Mosier 1997, Jacoby et al. 2000). In large deep oligotrophic lakes, where most of the primary productivity is in the littoral zone (Vadeboncoeur et al. 2003), such nearshore changes may impact the lakewide food web, that is dependent on this productivity, before offshore changes are noticeable.

Monitoring primary production variables in the nearshore may be a helpful tool for managers. Many agencies monitor pelagic water quality, which is effective in tracking major open water changes in mesotrophic and eutrophic lakes (Gannon and Stemberger 1978, Stemberger et al. 2001). The ability to monitor changes in nutrient inputs becomes more difficult in large oligotrophic lakes because nearshore changes may occur without any sign of eutrophication in the open water (Jacoby et al. 1991, Rothrock and Mosier 1997, Falter 2004). The ability of periphyton to rapidly assimilate nutrients makes it difficult to use basic water quality parameters such as total nitrogen and phosphorus to determine possible increases in nutrients from human activities, particularly in an oligotrophic system where these parameters are below detection limits for standard laboratory tests. In addition to quantifying basic increases or decreases in productivity via chlorophyll *a* analysis, managers may choose to monitor dynamics of particular taxa that respond to nutrient loading. For my research, I found strong variation in temporal and lake to lake patterns, such that a general prescription for nearshore monitoring is not easily written.

Algal growth and detritus at developed sites

The low concentrations of nearshore water nutrients in all the study lakes, even where productivity is clearly higher, suggests that periphyton in the littoral zone of these oligotrophic lakes quickly incorporates nutrients that are leached into the water from shoreline developments. Using ^{15}N tracers, periphyton uptake of nitrogen in lotic systems has been shown to be rapid, ranging from 5 minutes (Mulholland et al. 2000) to 20 minutes (Hall et al. 1998) in streams and up to an hour in a large river (Peterson et al. 1997). Though slower in lentic systems due to low water velocity and subsequently thicker diffusive boundary layers (Jumars et al. 2001, Larned et al. 2004), even periphyton in an oligotrophic lake has been shown to incorporate ^{15}N tracers within 5 hours of addition (Hadwen and Bunn 2005). Such rapid nutrient incorporation reduces the usefulness of water column nutrient data as an early warning of local nutrient enrichment.

While stable isotope signatures in plant and animal tissues are promising as indicators of human sewage in aquatic systems due to the enrichment of ^{15}N that occurs during nitrogen transformations in sewage (Heaton 1986, Axler and Reuter 1996, Lindau et al. 1997, Steffy and Kilham 2004), here stable isotope results were too variable to be useful as an indicator. The absence of a directional isotope indicator in this study could be due to the conflicting nitrogen signatures of lawn fertilizer (-2 to +4 per mil) and human sewage (+10 to +22 per mil), which have lower and higher $\delta^{15}N$ values than naturally found in freshwater (+3 to +9 per mil) (Cole et al. 2004). Confounding effects of a fertilizer signature may have been particularly problematic during this study year, when unusually high spring precipitation may have increased the contribution of nutrients from run-off. It should also be noted that we estimated green filamentous algae to be enriched in ^{15}N relative to diatoms grown on the same medium, indicating that interpretation of higher ^{15}N values as carrying a human sewage signal should be cautious in future studies.

Whether nutrients are derived from sewage or runoff, increased overall productivity at developed sites strongly suggests that developed sites receive increased nutrients. The productivity data showed increases in living and dead material at developed sites, as indicated by higher chlorophyll *a*, pheophytin, ash-free dry mass and autotrophic index. These results are consistent with other studies that quantified the impact of nutrient additions on nearshore periphyton productivity in a diversity of lakes. In Lake Chelan, WA, Jacoby et al. (1991) found that nearshore sites close to agriculture enriched tributaries exhibited elevated periphyton chlorophyll *a*. In a nutrient addition experiment on Lake Okeechobee (Florida), increases in nitrogen and phosphorus stimulated periphyton growth resulting in increased chlorophyll *a* (Havens et al. 1999). Hadwen et al. (2005) found that increasing nitrogen and phosphorus to an oligotrophic dune lake (Fraser Island, Australia) increased periphyton productivity compared to control sites. Nutrient inputs associated with human activity near oligotrophic lakes can rapidly elevate algal growth nearshore.

As expected, productivity trends changed throughout the year in all three lakes. In Lake Crescent productivity was highest in the spring compared to the fall. In a previous study, Rothrock and Mosier (1997) found that a few Priest Lake sites were dominated by filamentous green algae, which peaked in the spring and were sloughed off by mid-summer. This spring peak in periphyton has been observed in other studies. Castenholtz (1960) observed highest productivity in lakes occurring in the spring and the fall and the lowest productivity occurring in the late summer. Jacoby et al. (1991) found this bimodal peak in Lake Chelan with chlorophyll *a* peaking in May and September while being low in mid-summer (July). Similarly, Rosemond et al. (2000) found spring and fall to be the seasons when periphyton in a stream system was most responsive to nutrient additions. The fall peaks noted in the aforementioned studies were not observed in Lake Crescent. In Lake Crescent, where differences between developed and undeveloped sites were the strongest, monitoring algal trends in the spring is likely to provide the greatest contrast between developed and undeveloped sites.

The increased productivity associated with development that was observed in Lake Crescent was not as evident in Lake Pend Oreille and Priest Lake, although there were non-significant trends toward higher productivity at developed sites across all three lakes. This trend is consistent with previous studies on Lake Pend Oreille that found higher chlorophyll *a* and AFDM at developed sites (Falter 2004). That the differences among sites in this study were primarily related to ash-free dry mass and autotrophic index suggests that as productivity increases at developed sites, detritus accumulates. Falter (2004) hypothesized that the high levels of detritus were attributed to the thick mats of diatoms that were observed on nearshore rocks.

Results from the shoreline assessment suggest that a higher number of deciduous trees (*Alnus rubra*) compared to conifers at developed sites could also contribute more detritus to the nearshore. Tree density at Lake Crescent does not differ between sites although the diameter and species composition does. There tended to be bigger trees at developed sites, which is consistent with other studies. Christensen et al. (1996) found that the mean size of riparian trees on developed lakes was significantly larger than those on undeveloped lakes while density of snags was much lower. This may be due to homeowners' tendencies to keep big decorative trees while clearing away understory vegetation and snags for lawns. Nitrogen fixing species (red alder) were also much more abundant at developed sites, perhaps a potential influence on the amount of nutrients reaching the water (Compton et al. 2003).

A change in the amount of detritus may have driven the shift from grazing macroinvertebrates to detritivorous macroinvertebrates at developed sites, especially at Lake Crescent where the productivity and macroinvertebrate shifts were highly significant. Increases in detritivorous macroinvertebrates when detritus is increased have been shown in other studies. Richardson (1991) found that artificially increased leaf litter in experimental channels (British Columbia) resulted in higher densities and mass of detritivores. Similarly, Pretty and Dobson (2004) found an increase in detritivore abundance when logs were added to streams (Northumberland, UK) to increase retention of leaf detritus. As periphyton productivity increased in my study lakes, the proportion of detritus associated with the periphyton increased, possibly increasing the food source for detritivorous macroinvertebrates.

Algal community characteristics at developed sites

Algae composition at Lake Crescent exhibited a shift from predominately diatoms at undeveloped sites to greater filamentous green algae at developed sites, a result that is consistent with previous studies of periphyton response to nutrients. Increased filamentous green algae at sites near inflows of nutrient rich tributaries associated with agriculture were also reported in nearby Lake Chelan (Jacoby et al. 1991). Chetelat et al. (1999) found increased productivity associated with nutrient rich rivers due primarily to increases in filamentous green algae. In shallow Danish lakes, Liboriussen and Jeppesen (2006) found a shift in periphyton community composition from diatoms in low nutrient lake conditions to dominance by filamentous green algae in high nutrient lake conditions. Welch et al. (1988), in a study of 22 streams, found that relative proportion of filamentous algae increased with higher chlorophyll *a* biomass values. The increase in filamentous algae at sites receiving nutrient inputs may be attributed to the ability of taxa with elongate forms (such as filamentous green algae) to maximize access to nutrients in the water column compared to prostrate taxa (such as crust forming diatoms) (Biggs and Hickey 1994, Larned et al. 2004). Undeveloped sites were characterized by slightly higher abundance of filamentous cyanobacteria. Cyanobacteria, though commonly associated with openwater eutrophication, have been shown to thrive in oligotrophic conditions due to their ability to fix nitrogen (Reuter et al. 1986).

In addition to these spatial differences in algal community assemblages at developed and undeveloped sites, temporal trends were evident. Algal community composition changed over time across all three lakes, and springtime generally showed the greatest differentiation between developed and undeveloped sites, but in every other respect the characteristics of seasonality varied strongly among the lakes. While other studies report temporal change in periphyton assemblages, these seasonal trends are not stereotyped across lakes in general. For example, Casterlin and Reynolds (1977) found a seasonal periphyton pattern in Harveys Lake (Pennsylvania) with diatoms dominant from winter through spring, green algae dominant in the spring and summer, and cyanobacteria dominating in the late summer. In shallow Danish lakes, Liboriussen and Jeppesen (2005) found that under low nutrient conditions, cyanobacteria dominated the periphyton community composition in the fall. In our study lakes, compositional differences between developed and undeveloped sites were strongest in the spring and minimal during late summer and fall, primarily due to lush growth of filamentous green algae only at developed sites during the early spring and different trajectories of growth across lakes through the rest of the year. Temporal trends in periphyton growth may be lake-specific depending upon the delivery pathways and timing for nutrients in different systems, which will be influenced by such large-scale variables as precipitation (Humphrey and Stevenson 1992, Correll et al. 1999) and run-off patterns (McMahon and Harned 1998, Groffman et al. 2004), wind dynamics that influence mixing and upwelling (O'Reilly 2006), and the seasonality of human activities in the watershed.

On Lake Pend Oreille and Priest Lake, a very strong temporal pattern emerged that was not seen in Lake Crescent and we speculate that this difference was caused by water level changes related to hydroelectric dams on both lakes. Filamentous algae dominated both developed and undeveloped sites in Lake Pend Oreille in the fall, but not the spring. Water level changes of up to 3 meters between spring and fall may occur as a result of the management of hydroelectric dams. During the spring sampling, the water level was low so samples were collected from "deep" rocks (i.e. they were submerged much more deeply at other times) whereas in the fall, the water had risen so samples were collected from rocks that had been newly colonized. Filamentous algae may be superior at new growth on newly revealed substrate compared to diatoms, which usually accumulate slowly in thick mats (Biggs and Kilroy 2000, Rothrock and Mosier 1997). In another study, periphyton community composition in Volta Lake was also found to be strongly impacted by changes in water level (Obeng-Asamoa et al. 1980). However, in Volta Lake, diatoms dominated newly covered substrate while filamentous algae were most abundant during and after the flood period, which was during the lowest lake level. In Volta Lake however, the primary substrate available for colonization is tree trunks, which cover much more vertical space in the water column, perhaps reducing the height advantage conveyed to filamentous algae on rock substrate.

Priest Lake water level is manipulated for dam operations as well, and in the spring developed sites showed higher proportions of filamentous algae, like both other lakes. However, the fall samples, which were also newly submerged under high water like Lake Pend Oreille, did not exhibit domination by filamentous green algae. Instead, filamentous green algae were slightly more common at developed sites and cyanobacteria appeared to increase at undeveloped sites.

In spite of lake-specific trends, particularly with regard to timing of productivity changes, significant general differences between developed and undeveloped sites across all three lakes emerged. This general consistency suggests that nutrient inputs from development have had significant effects on nearshore periphyton community composition as well as overall productivity.

Implications of algal changes for grazers

In addition to increased productivity creating more food for detritivores, changes in nearshore periphyton community composition due to nutrient loading could impact the composition of grazing macroinvertebrates depending upon taxon-specific electivity and ability to assimilate specific algal groups. Field collections demonstrated greater prevalence of detritivores at developed sites where detritus was more abundant, but did not reveal finer-scale changes among grazers. However, the laboratory experiment suggested that such shifts among grazers are possible due to changes in food source, and a literature review suggests these shifts are likely as algal composition changes.

My preliminary results from the laboratory experiment indicate that amphipods and snails both assimilated a higher proportion of diatoms than filamentous algae, and previous studies are consistent with the hypothesis that nearshore grazers prefer diatoms.

Moore (1975) found that isopods (*Asellus aquaticus*) and amphipods (*Gammarus pulex*) - both of which have highly omnivorous diets including resources as diverse as detritus and other insects - consumed periphyton with a pronounced selectivity. Both species avoided filamentous cyanobacteria while selecting for diatoms that were both filamentous and non-filamentous. Bowker et al. (1983) found that an oligochaete species (*Nais elinguis*) in a Welsh river preferred unicellular chlorophytes and pinnate diatoms while avoiding colonial and filamentous algae. Gray and Ward (1979) studied food habits of herbivore-detritivores, whose diets typically were comprised of 73% detritus, and found that 22 % of their diet was composed of diatoms and only 5% was from filamentous green algae. They attributed this low proportion of filamentous green algae in the diet to difficulty of ingestion due to particle size. Mihuc and Toetz (1994) determined that macroinvertebrate diets in an alpine wetland were a mix of detritus and periphyton with a complete absence of filamentous algae.

Not all studies have found that filamentous green algae are avoided by macroinvertebrates however. Kornijow et al. 1990 found that some macroinvertebrates in Lake Zwemlust (Utrecht, Netherlands) actively consumed filamentous green algae. For Chironomidae and Dipterans (Tipulidae and Ephydridae), 50 to 100 % of the diet was composed of filamentous green algae (*Mougeotia and Oedogonium*). Lowe and Hunter (1988) found that snails (*Physa integra*) tended to prefer “upper story” algae such as large diatoms and filamentous green algae without thick cell walls (such as *Mougeotia*) while avoiding small prostrate linked diatoms that occupied the understory. Snails however, avoided filamentous green algae that had grazer resistant qualities like a basal holdfast cell and thick cell walls with a tough inner cellulose layer (such as *Oedogonium*).

Regardless of whether filamentous green algae are an inferior food source, research has shown that macroinvertebrates do display preferences for certain types of algae, and this finding has major implications for lake food webs when periphyton community composition changes due to human activities. Increased nutrient availability has been shown to increase productivity and detritus while also changing the composition of periphyton on a small scale. Macroinvertebrates and the fish that move inshore to consume them may be affected by these changes in the nearshore environment. This phenomenon is especially important to acknowledge in large deep oligotrophic lakes where pelagic water quality can remain unchanged despite nearshore impacts.

Further research on the linkages between trophic levels in the littoral habitat of large deep oligotrophic lakes would improve our understanding of how anthropogenic changes in algal community composition may have lake-wide impacts. Use of a wider range of macroinvertebrate and algal taxa in a more comprehensive set of grazing experiments would refine our understanding of how changes in the basal food web translate into productivity at higher levels. Similar feeding preference experiments with fish as consumers on macroinvertebrates, foraging in the new nearshore environments created by development (e.g., strands of filamentous algae trailing off rocks vs. diatom covered rocks) may provide novel insights into the complex bottom-up effects that may occur in response to nutrient additions. Finally, longer term study is necessary to understand whether the strong temporal patterns reported here are consistent across years;

the spring of 2007 had unusually high precipitation which may have altered hydrologic and nutrient dynamics in ways that are important to understand.

CONCLUSIONS:

In Lake Crescent, a reliance on the nearshore environment that is disproportionate to its availability has been demonstrated *(Hampton et al., unpublished manuscript*)and may be common to other large steep-sided oligotrophic lakes where productivity occurs primarily in shallow water (Vadeboncoeur et al. 2003). Activities that alter the nearshore environment where top predators must breed and feed may have strong effects on the lakewide food web in spite of continuing high water quality offshore. Here I found that developed sites across all lakes differed from undeveloped sites in a manner consistent with nutrient enrichment, although water column nutrients were not useful indicators of development in these oligotrophic lakes where periphyton rapidly scavenges nutrients. Filamentous green algae were typically more common at developed sites during the spring. Detritus was higher at developed sites during all sampling periods and detritivorous macroinvertebrates were more common at developed sites during the spring. These basal changes in the food web may have lakewide implications as detritivorous macroinvertebrates and grazers that favor green algae become more common. Additionally these nearshore environmental changes may impact the habitat required by certain species, such as oligotrophic adapted plant species (*Lobelia dortmanna*) and fish that spawn in the nearshore, through changes in both the biological and physical environment. It is noteworthy that the significant changes reported here were associated with relatively modest levels of shoreline development, indicating that important nearshore impacts may manifest well before high levels of development occur on a lake. Monitoring algae nearshore can not only indicate to managers that nearshore resources may be changing in a manner that impacts the broader food web but also provide early warning of pollution well before eutrophication spreads to the pelagic environment.

Figure 1: Simplified food web of a large deep nutrient-poor lake. Nutrient additions can cause an increase in the nearshore algal growth (periphyton) as well as a change in community composition. This may positively or negatively impact the invertebrates and vertebrates linked through trophic interactions in the food web.

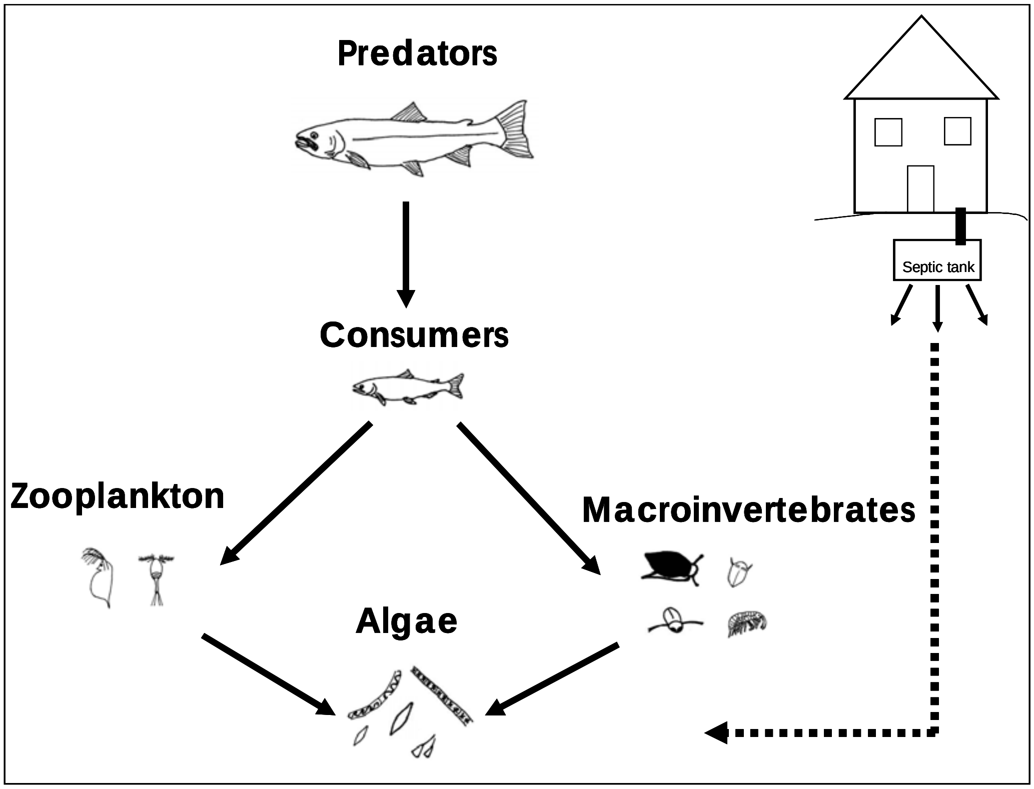

Figure 2: Map of the three study lake locations in the Pacific Northwest. Lake Crescent is on the Olympic Peninsula of Washington State. Lake Pend Oreille and Priest Lake are both located in the panhandle of Idaho State.

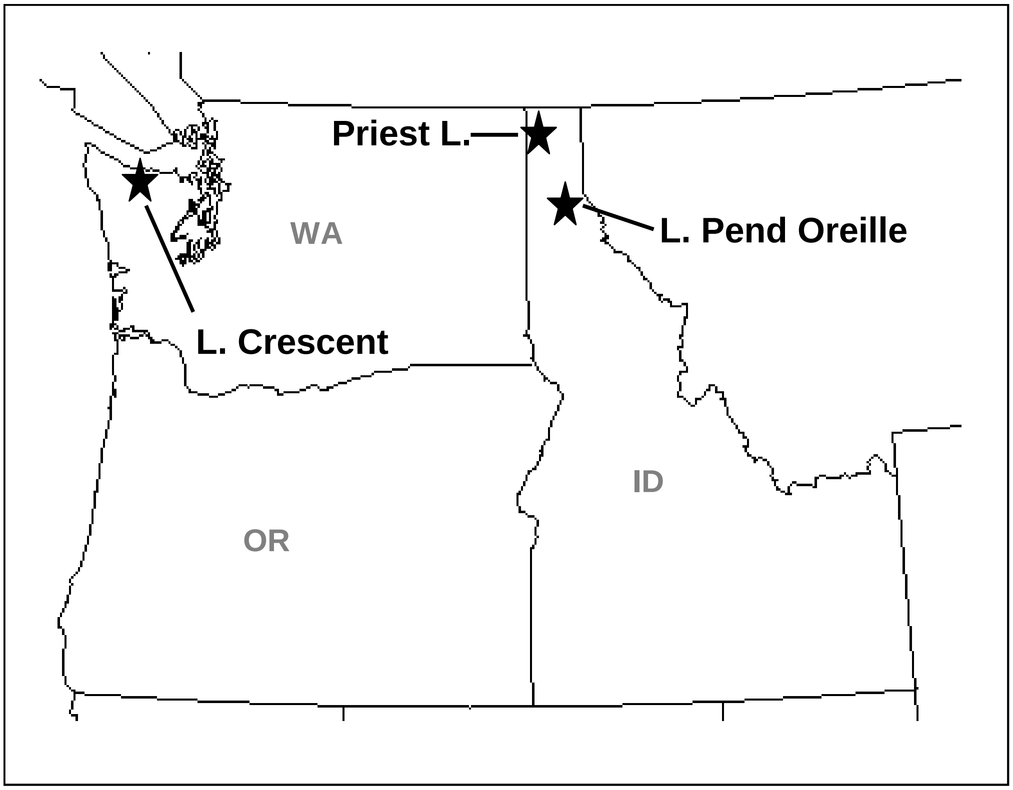

Figure 3: Detailed map of Lake Crescent and its sample sites. Open triangles depict undeveloped sites, black squares are the paired developed sites, and grey squares are the unpaired developed sites in the Lyre basin outlet.

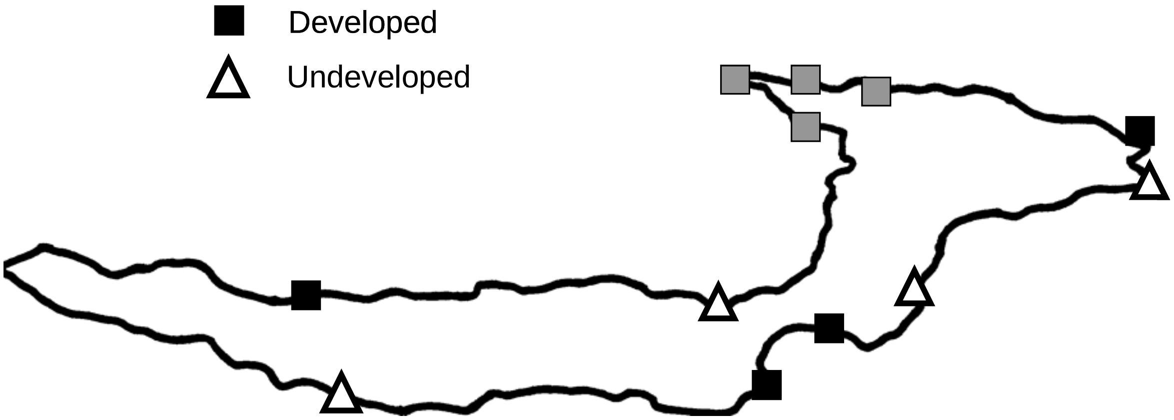

Figure 4: Detailed map of Lake Pend Oreille and Priest Lake. Open triangles depict undeveloped sites and black squares are the paired developed sites. In Priest Lake, the open triangle located in the openwater at the south end of the lake is on an island.

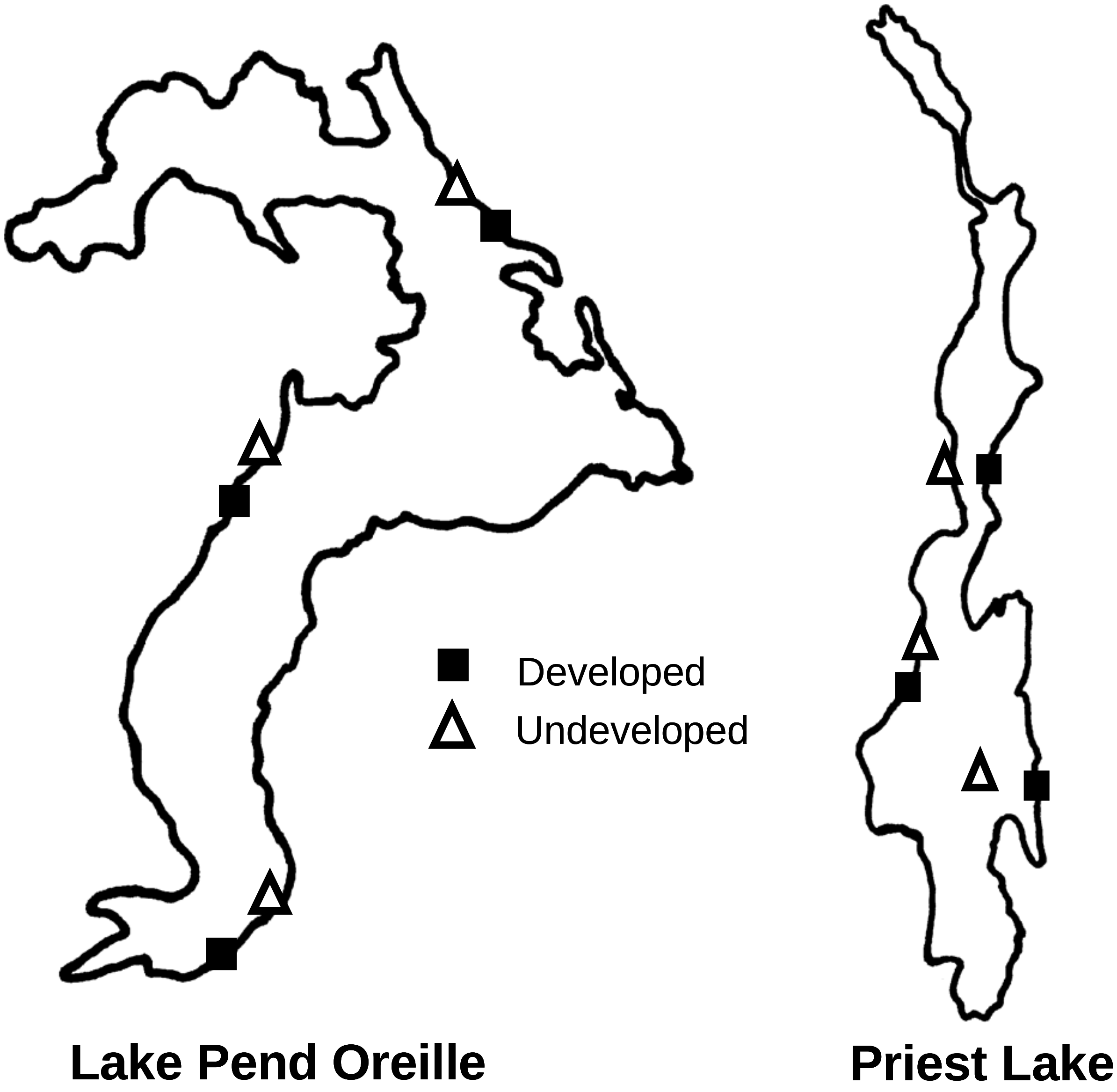

Figure 5: Productivity measures, chlorophyll *a* and pheophytin (mg/m^2), from nearshore sites with and without residential development on Lake Crescent in May 2006 (a) and August 2006 (b). Chlorophyll *a* is an indicator of living primary producers and pheophytin is a pigment associated with dead plant material.

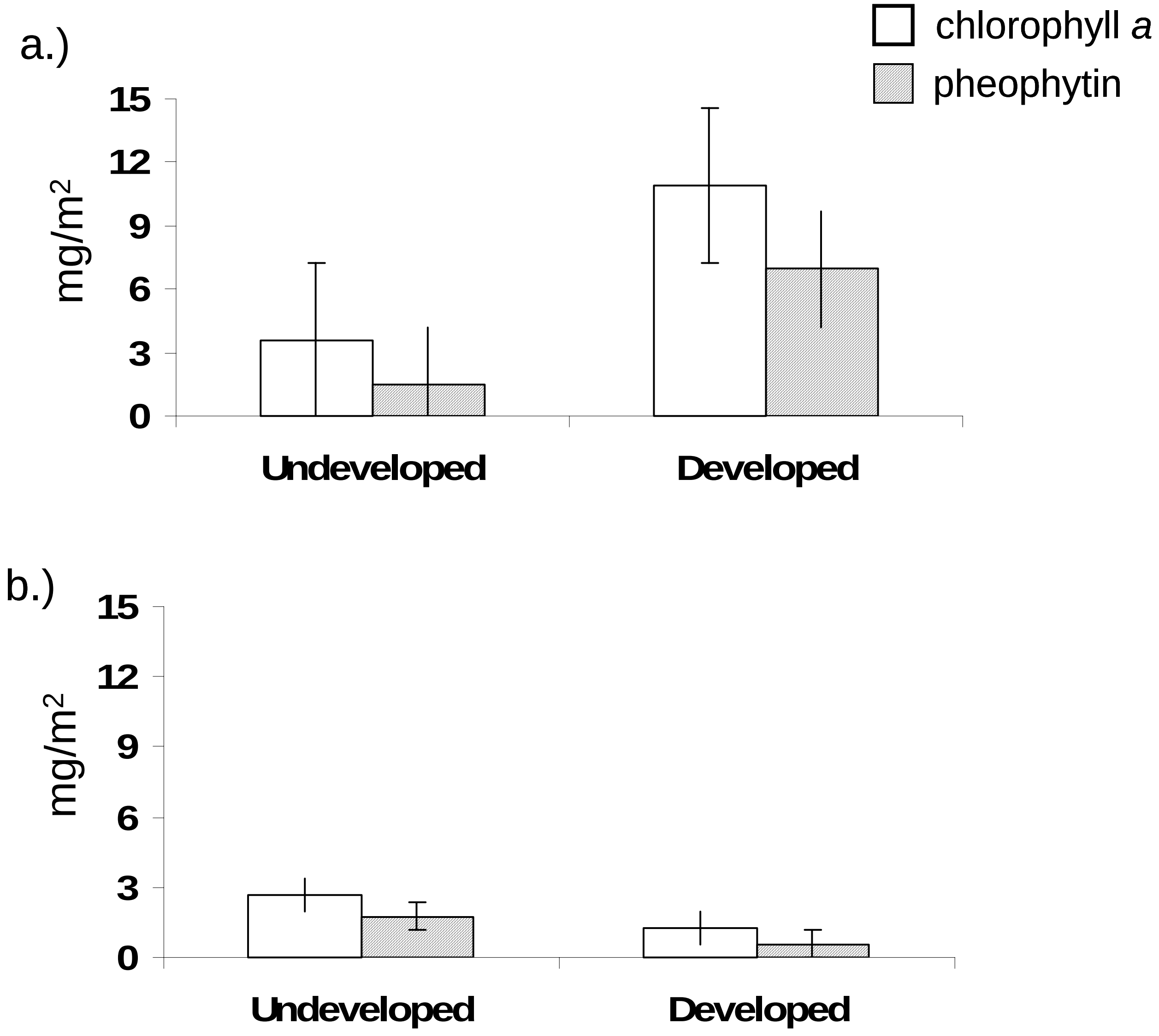

Figure 6: Productivity measures, chlorophyll *a* and pheophytin (mg/m^2), from nearshore sites with and without residential development September 2006 on Lake Pend Oreille (a) and Priest Lake (b). Chlorophyll *a* is an indicator of living primary producers and pheophytin is a pigment associated with dead plant material.

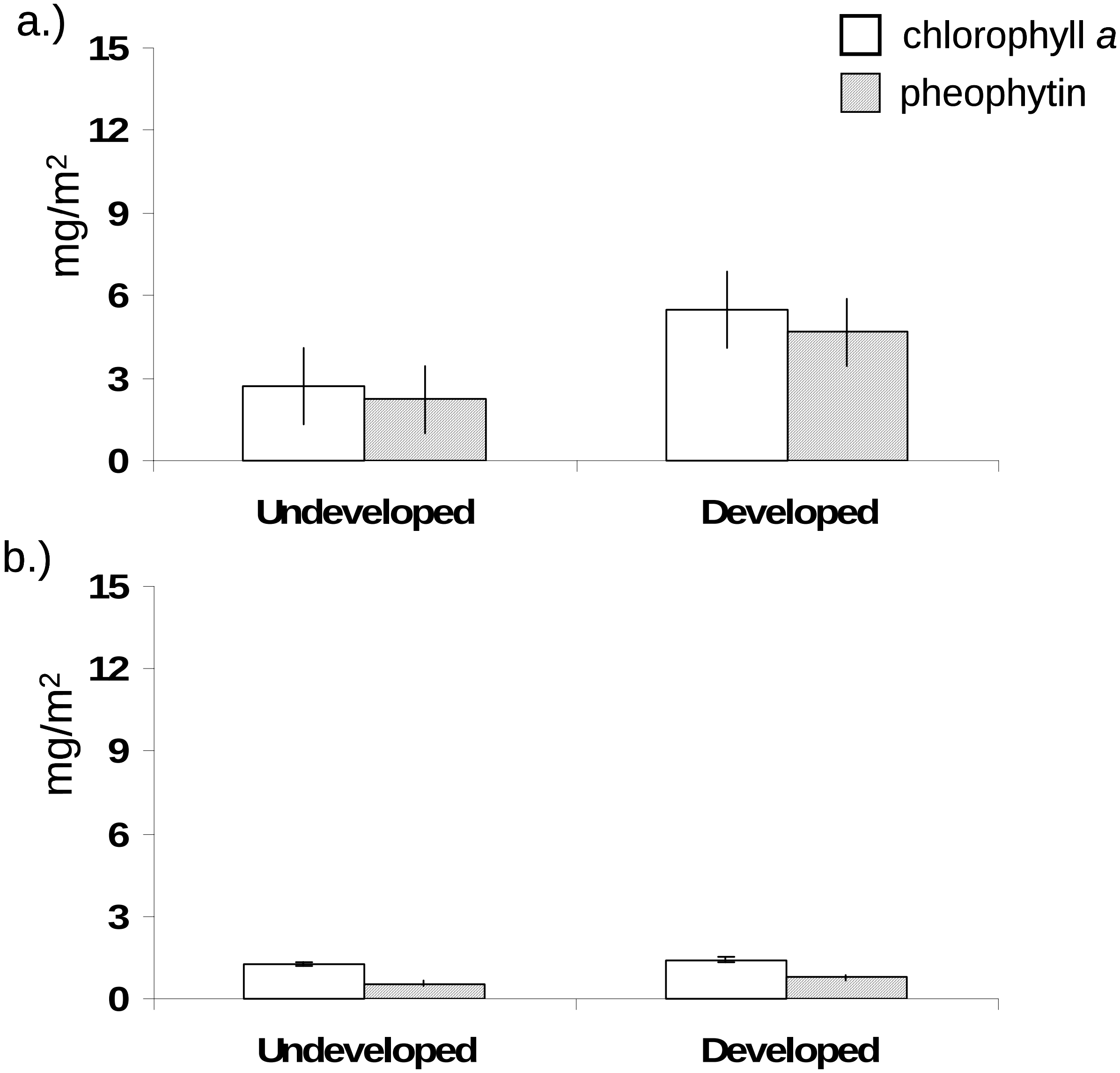

Figure 7: Proportions of macroinvertebrate functional feeding groups that contributed the most to differences as determined by SIMPER analysis between communities at developed and undeveloped sites at Lake Crescent in a) March 2006 and b) August 2006.

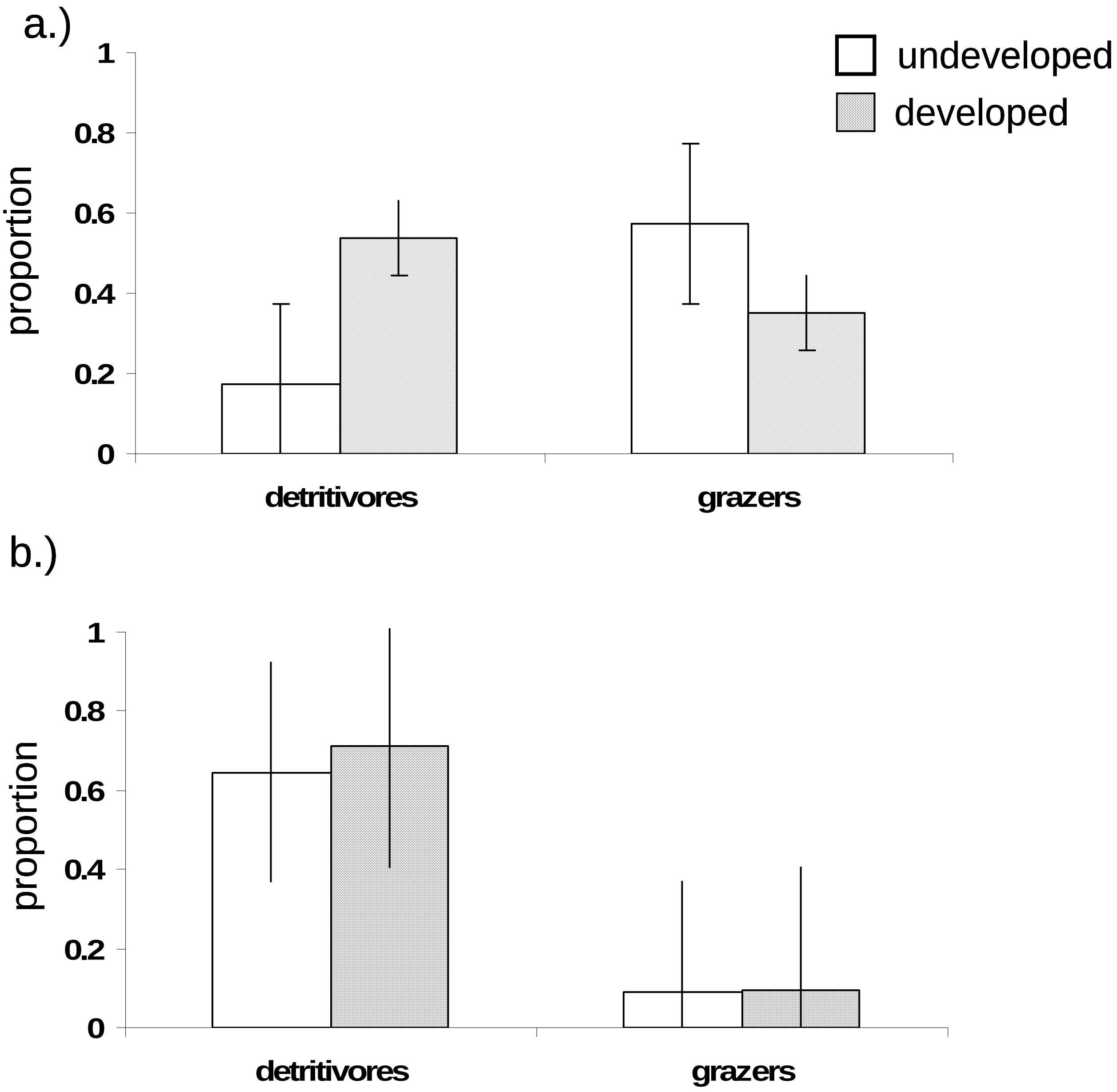

Figure 8: Proportions of macroinvertebrate functional feeding groups that contributed the most in SIMPER analysis to differences between communities at developed and undeveloped sites at Lake Pend Oreille in a) April 2006 and b) September 2006.

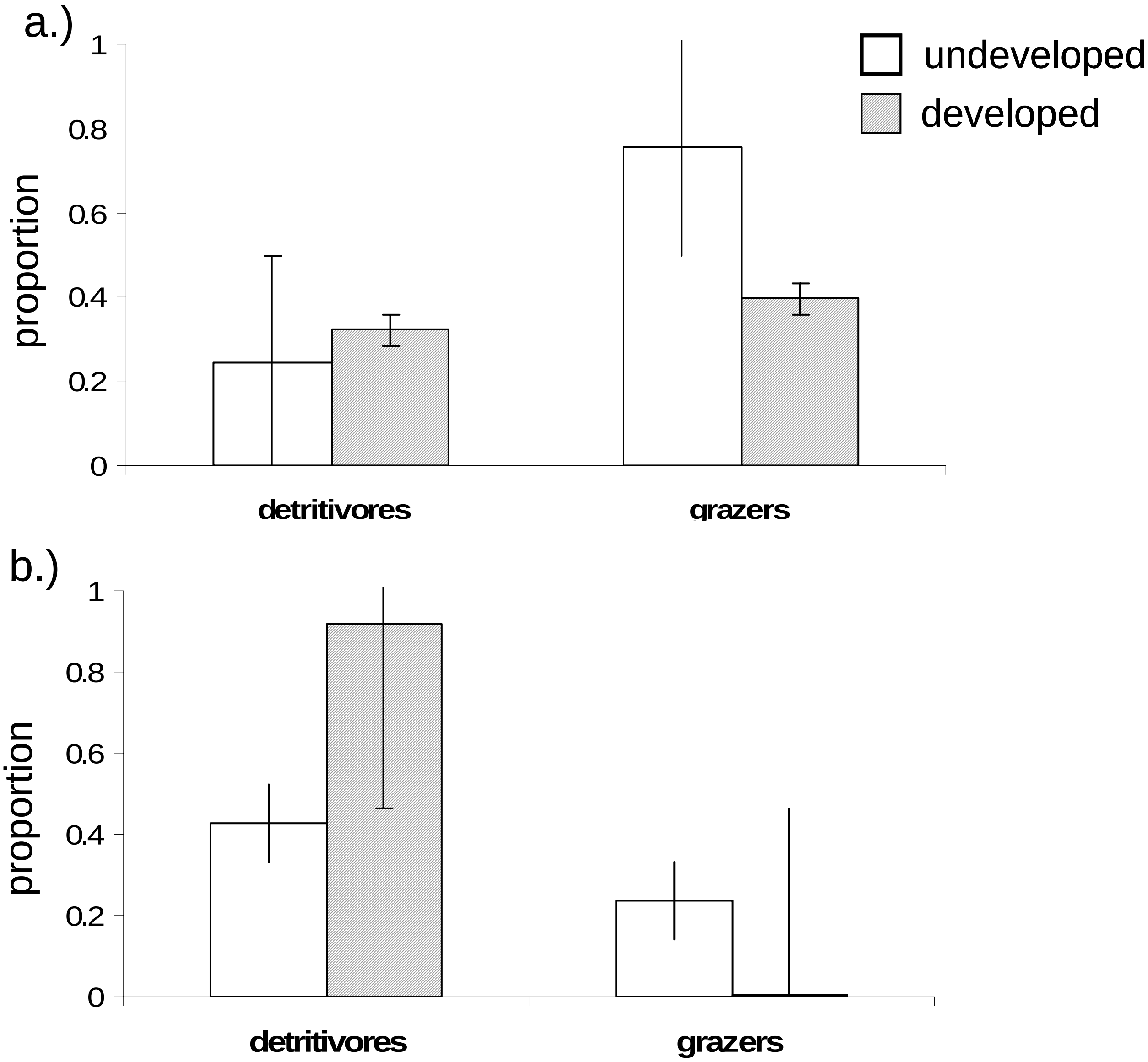

Figure 9: Proportions of macroinvertebrate functional feeding groups that contributed the most to differences, in SIMPER analysis, between communities at developed and undeveloped sites at Priest Lake in a) April 2006 and b) September 2006.

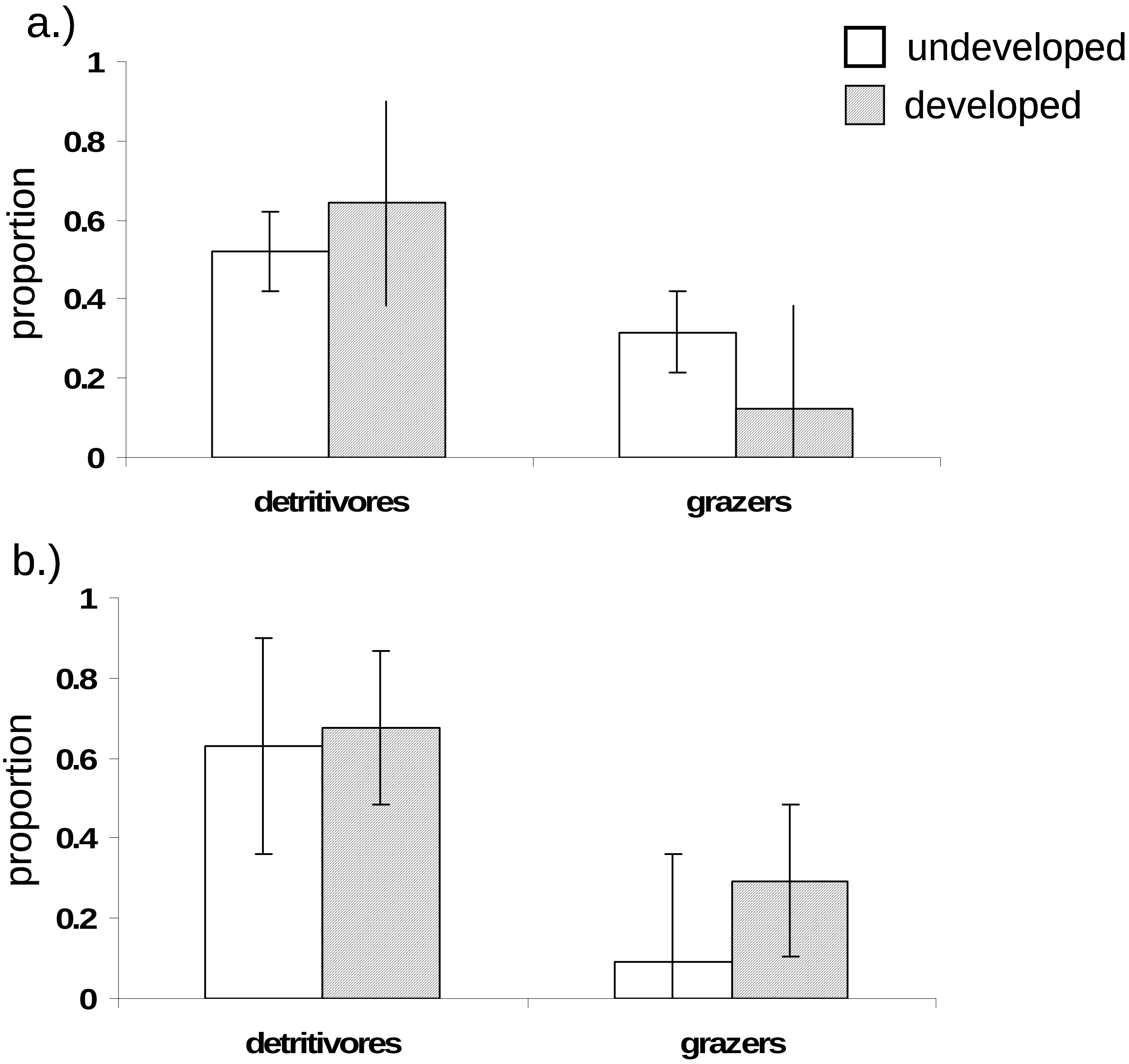

Figure 10: MDS plot for groups of algae genera from Lake Crescent developed and undeveloped sites in a) May 2006 and b) August 2006. Kruskal's stress value = 0.08 for both dates.

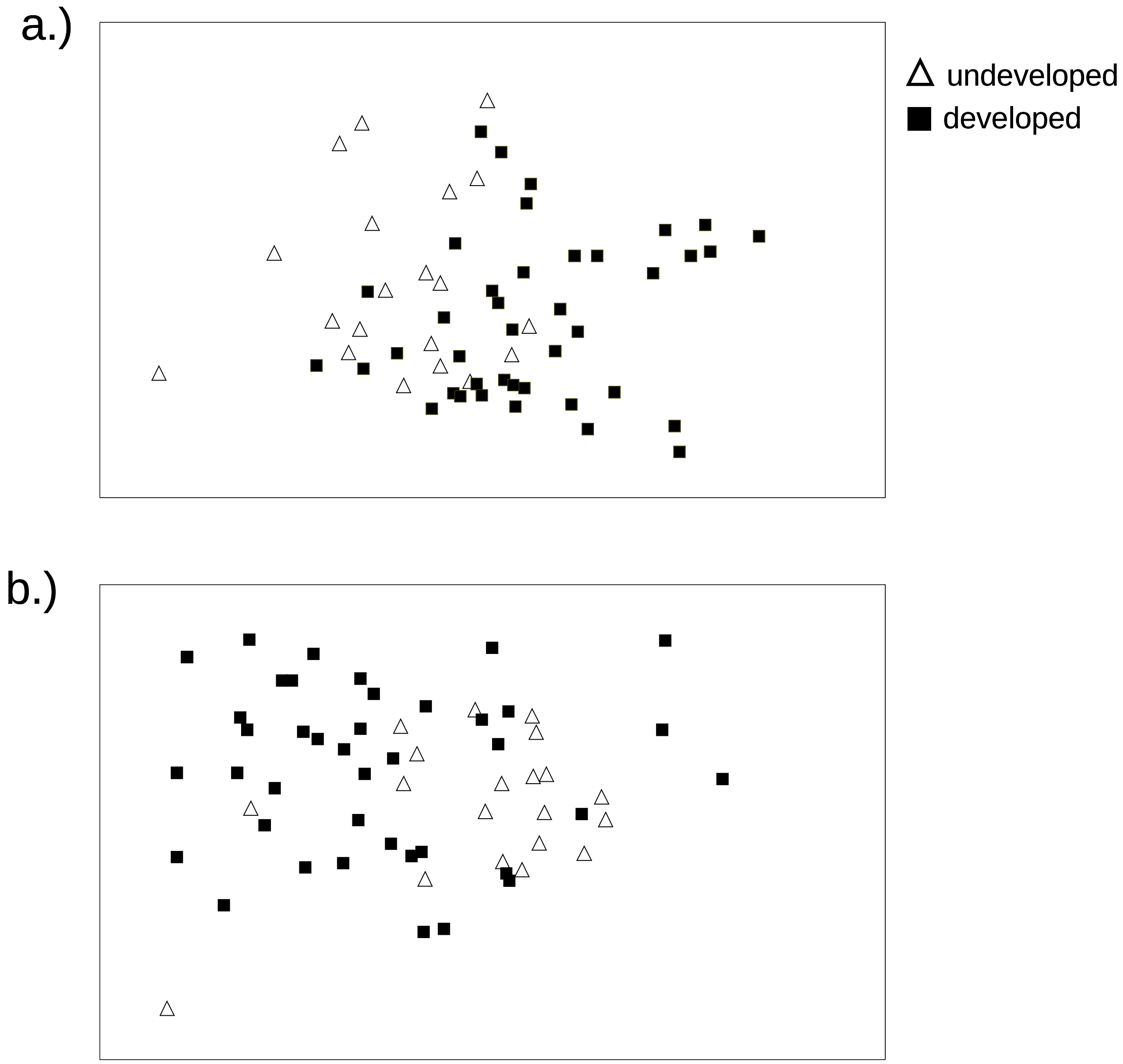

Figure 11: Relative proportions of the algal taxa found to best discriminate between developed and undeveloped groupings in SIMPER analyses for Lake Crescent.

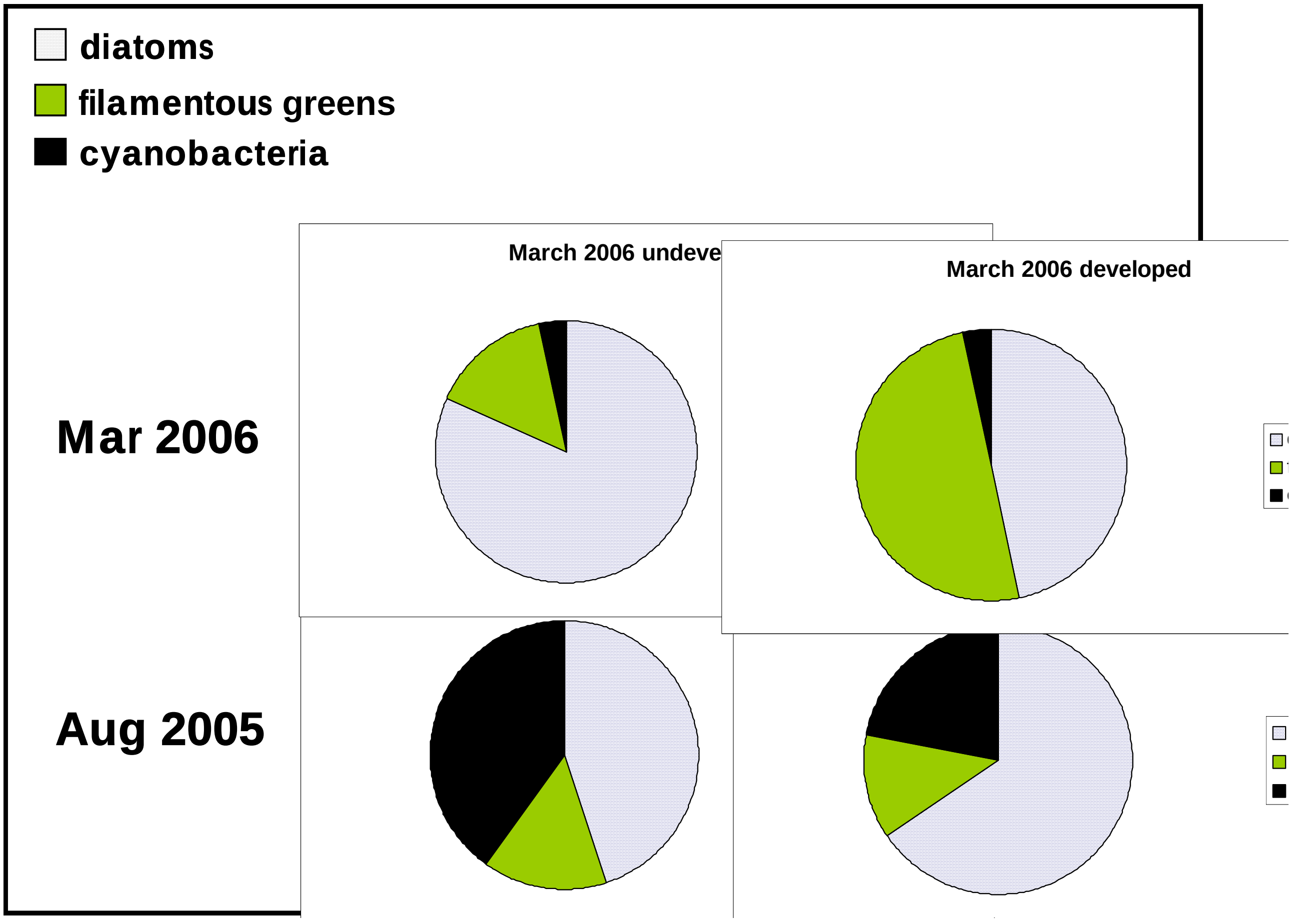

Figure 12: MDS plot for groups of algae genera from developed and undeveloped sites during April and September 2006 sampling dates at a) Lake Pend Oreille and b) Priest Lake. Kruskal’s stress = 0.08 and 0.10 respectively.

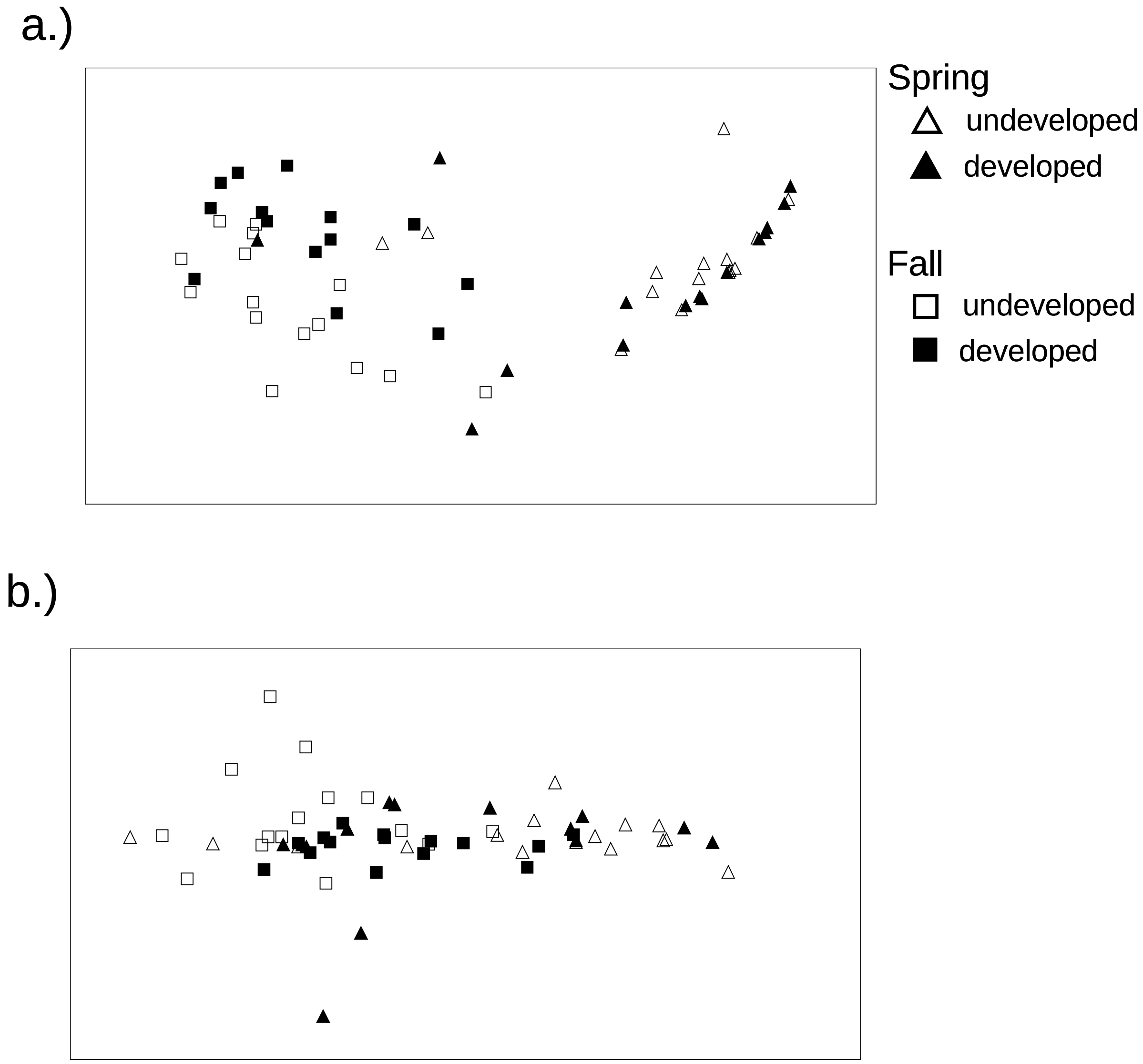

Figure 13: Relative proportion of discriminating groups of algae found at developed and undeveloped sites in Lake Pend Oreille.

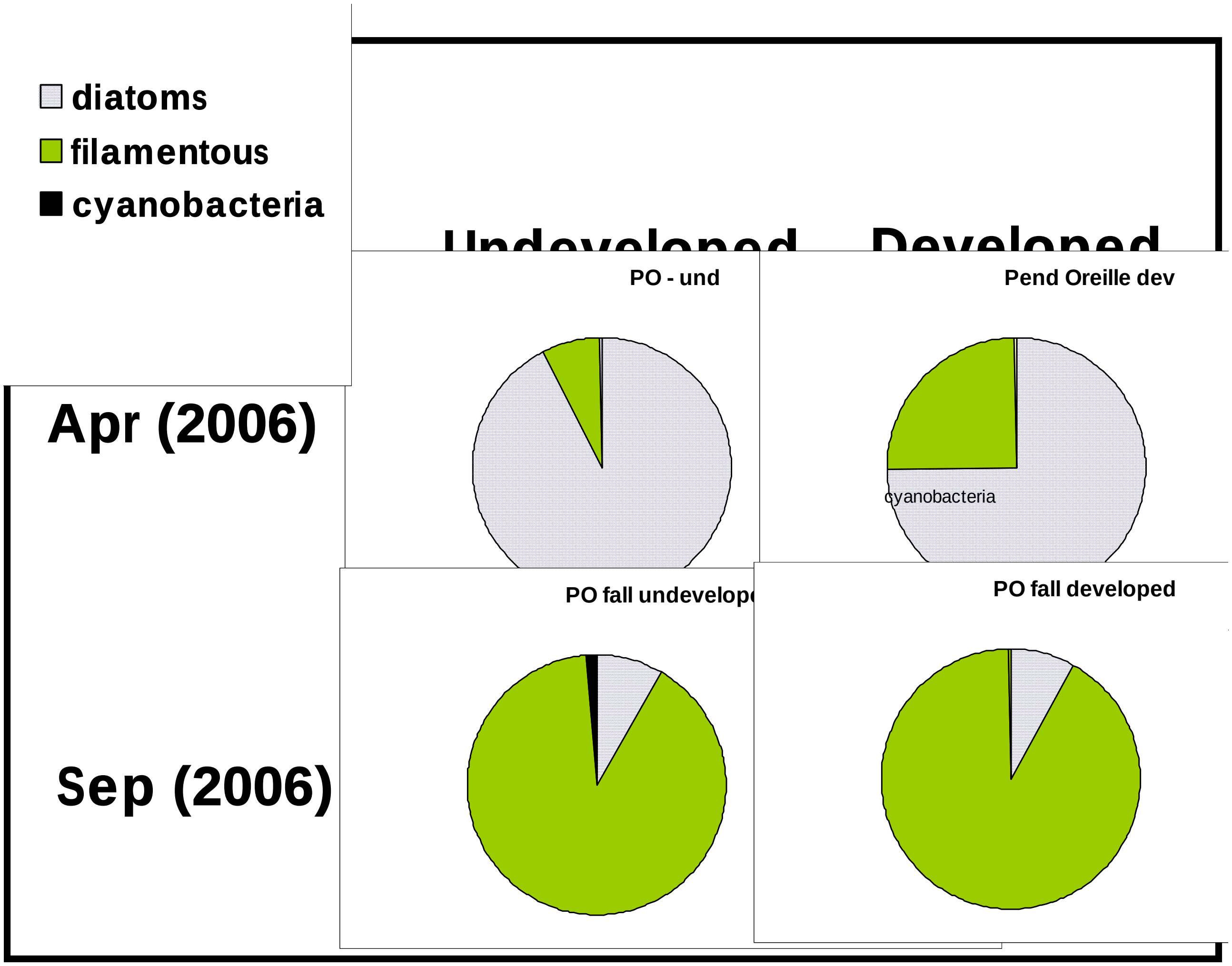

Figure 14: Relative proportion of discriminating groups of algae found at developed and undeveloped sites in Priest Lake.

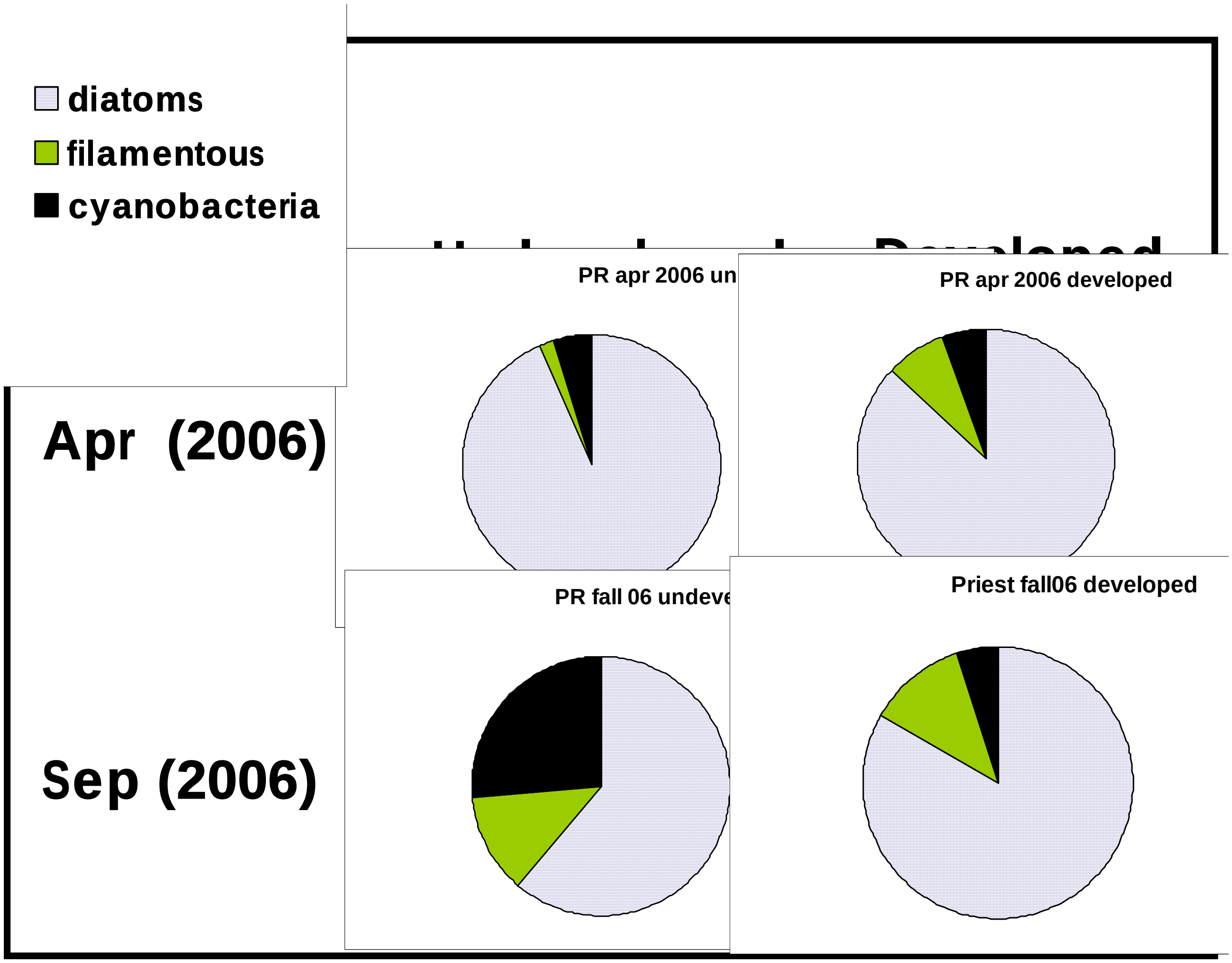

Figure 15: Stable isotope analysis of δ15N ‰ in macroinvertebrates and periphyton tissue samples from Lake Crescent. A one-way ANOVA indicates that neither macroinvertebrates (P = 0.56) or periphyton (P = 0.65) differed significantly between developed and undeveloped sites. Analysis of δ15N ‰ by sample date revealed no significant difference between developed and undeveloped samples (P > 0.54).

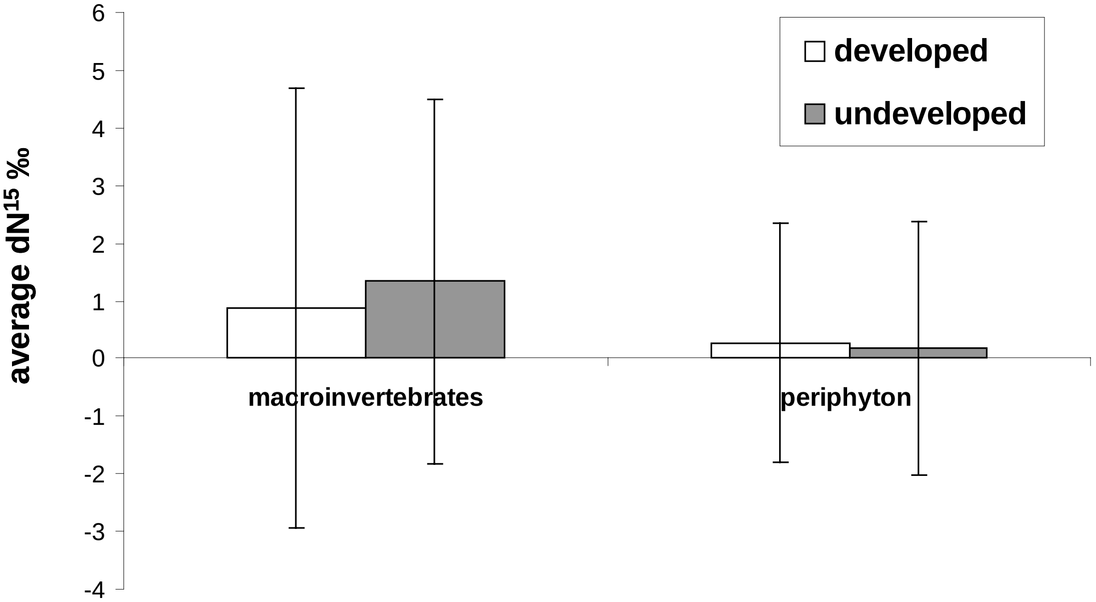

Figure 16: N^{15} per mil (log scale) of macroinvertebrates and algae used in the tracer experiment. Filamentous green algae were spiked with an elevated N^{15} tracer, rinsed, and added to a flask containing unspiked diatoms. Amphipods and snails were added to individual flasks and sampled over 9 days to determine the proportion of diatoms vs. filamentous algae in their diet.

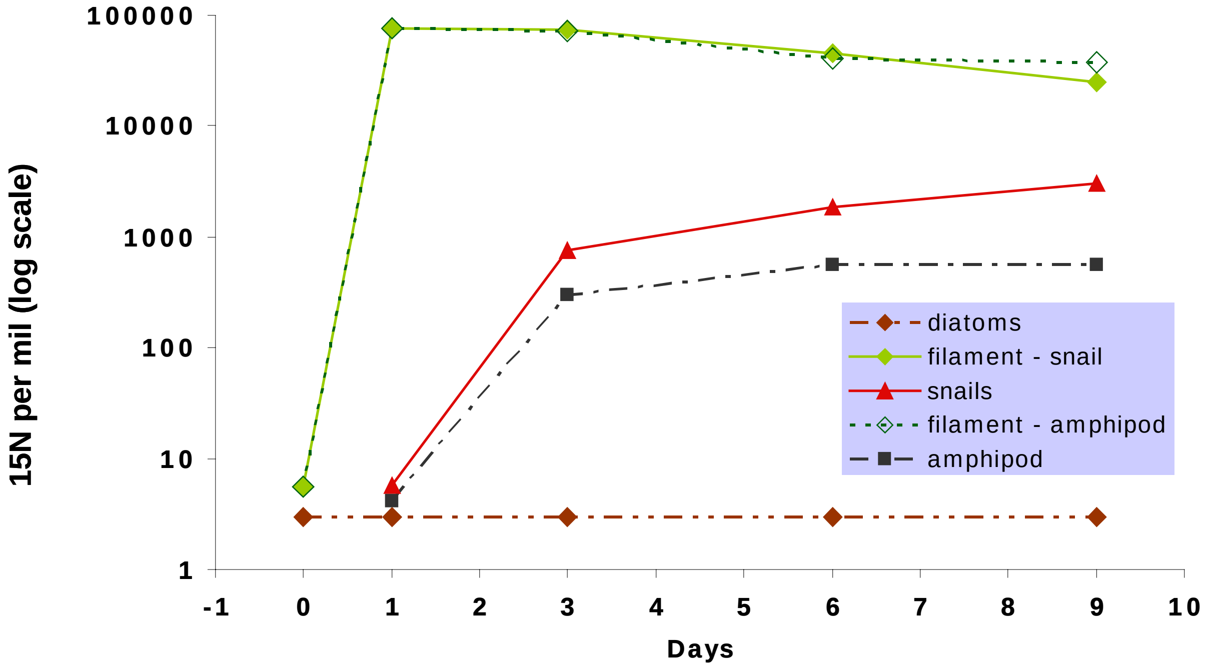

Figure 17: Proportion of N^{15} (per mil) from diatomaceous vs. filamentous algae incorporated into macroinvertebrate tissues at the beginning of the experiment (prior to tracer addition) and final proportion of filamentous green vs. diatomaceous algae assimilation by macroinvertebrates. Values over 1.00 are indicative of consumption of detritus prior to start of experiment.

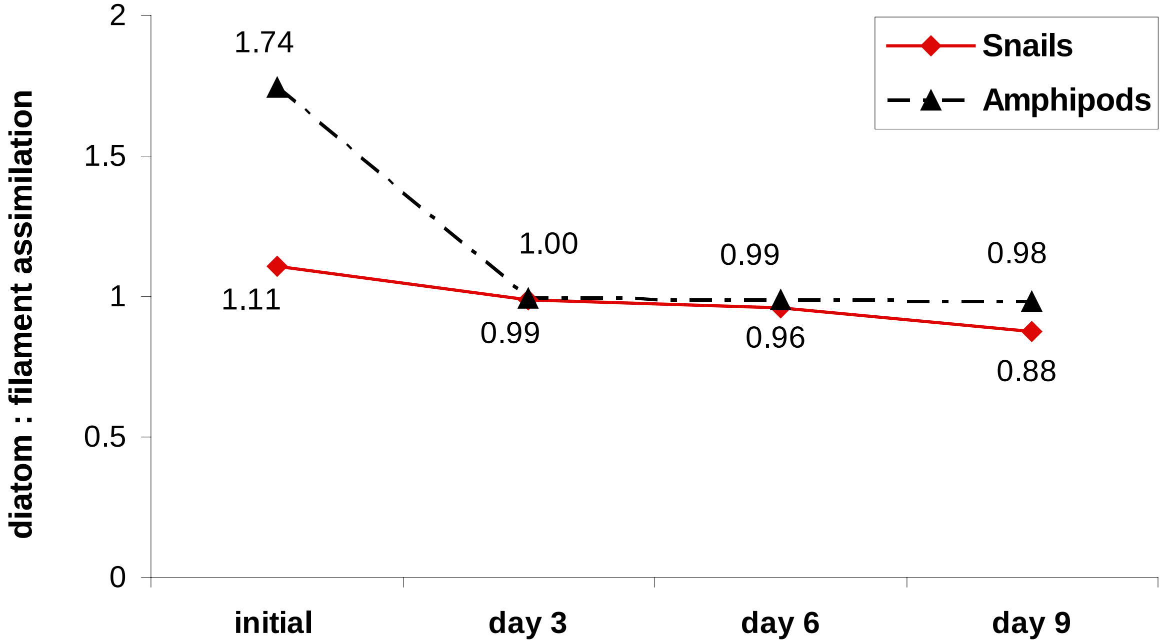

Table 1: Characteristics of Lake Crescent compared to Lake Pend Oreille and Priest Lake (Rothrock & Mosier 1997, Meyer & Fradkin 2002, Falter 2004).

	Lake Crescent	**L. Pend Oreille**	**Priest Lake**
Limnology			
Surface area	29,158 acres, 118 sq.km	94,641 acres, 383 sq km	24,710 acres, 100 sq km
Depth (mean, max)	101 m, 190 m	164 m, 357m	39 m, 112 m
Trophic status	ultra-oligotrophic	meso-oligotrophic	oligotrophic
Secchi depth (mean, max)	15 m, 25 m	10 m , 21 m	9.8 m, 14 m
Development			
Family residences	121 (16% year round)	> 1,000 (unknown seasonality)	1,707 (15% year round)
Peak visitors	12,000	> 10,000	5,000
Waste disposal	Sewage treatment plants, septic tanks	Sewage lagoons, septic tanks	Sewage lagoons, septic tanks, vaulted outhouses.

Table 2: Analyses and models used for PERMANOVA analysis in PRIMER. Factors followed by a factor in parentheses indicates the former variable is nested in the latter.

Analysis	**Lake**	**Model**	**Factors tested with interactions**	**Fixed or random**
Productivity				
	Crescent	2-way PERMANOVA	date development	fixed random
	All 3 lakes	2-way PERMANOVA	lake development	fixed random
Macroinvertebrates				
	Crescent	2-way PERMANOVA	date development	fixed random
	All 3 lakes	2-way PERMANOVA	lake development	fixed random
Tree community				
	Crescent	1-way PERMANOVA	development	fixed
Periphyton community				
	Crescent	Nested 3-way PERMANOVA	site (development) date development	random fixed fixed
	Crescent	Blocked 3-way PERMANOVA	development (pairing) date pairing	random fixed random
	All 3 lakes	4-way PERMANOVA	development (pairing) season pairing (lake) lake	random fixed random fixed

Table 3: Productivity measures calculated with corresponding equations, where c = crucible weight and f = filter weight. Ash-free dry mass (AFDM) is a measure of the total amount of organic material such as autotrophs, heterotrophs, dead material, and leaf debris**.** Percent organic matter describes the amount of sample lost during high temperature combustion, after which only inorganic matter remains. Autotrophic index (AI) is an index of the proportion of autotrophic to heterotrophic organisms in the periphyton samples. A high AI value indicates that a high proportion of the AFDM is comprised of heterotrophic organisms and dead organic matter.

Parameter	**Equation used**
Dry mass (g/sample)	((c + f + dried) - (c + f) * total mL sampled) / subsample mL
AFDM (g/sample)	((c + f + dried) - (c + f + ashed) * total mL sampled) / subsample mL
AFDM (g/ m^2)	AFDM (g) / area of sample (m^2)
% organic matter	(AFDM * 100) / dry mass
Autotrophic Index	AFDM (mg/m^2) / chla (mg/m^2)

Table 4: Geometric shapes used to calculate biovolume where V = volume, π = 3.14159, r = radius, h = height, L = length, and a, b, c, = length, width, height when a square or rectangle (adapted from Hillebrand et al. 1999).

Shape	**Equation**	**Algae types assigned shape**
Cylinder	$V= (\pi/4) *d^2 * h$	Filamentous green algae, cyanobacteria, filamentous diatoms
Rectangular box	$V= a * b * c$	Naviculoid diatoms, *Fragilaria* and *Tabellaria*
Half elliptic prism	$V= (\pi /4) * a * b *c)$	Cymbelloid diatoms
Pyramid	$V= 1/3 * L^2 * h$	Gomphonemoid diatoms
Sphere	$4/3 * \pi * r^3$	Non-filamentous green algae and centric diatoms

Table 5: Ash-free dry mass g/m^2 (AFDM), percent organic matter (%OM), and autotrophic index (AI) for Lake Crescent, Lake Pend Oreille, and Priest Lake.

Lake	**Development**	**AFDM**	**stdev**	**% OM**	**stdev**	**AI**	**stdev**
Crescent							
May-06	Undeveloped	65.43	103.94	39.51	36.50	16.20	24.26
	Developed	1361.32	2247.22	43.40	30.76	151.86	260.43
Aug-06	Undeveloped	3.36	3.48	17.93	11.62	5.00	2.80
	Developed	18.53	24.95	21.24	12.57	7.20	5.96
Pend Oreille							
Sep-06	Undeveloped	5.48	2.91	26.27	14.99	2.30	0.99
	Developed	12.34	3.84	24.48	22.94	2.31	0.26
Priest							
Sep-06	Undeveloped	23.52	5.86	25.98	24.17	21.34	10.88
	Developed	15.12	5.17	10.61	6.41	10.83	2.86

Table 6: Results of SIMPER analysis of productivity variables. Variables with a relatively high percent contribution are “discriminating” variables which means they were most strongly associated with community assemblage differences between developed and undeveloped sites. AFDM and Chlorophyll *a* contributed the most to the difference between developed and undeveloped), implying that developed sites have more organic material (AFDM) and higher productivity (chlorophyll *a)* than undeveloped sites. Percent organic material (%OM) and autotrophic index (AI) were excluded from this analysis because they are both calculated from AFDM.

Productivity Variable	**Lake Crescent only**		**Crescent, Pend Oreille, Priest**	
	% Contribution	Cumulative %	% Contribution	Cumulative %
AFDM	56.42	56.42	56.08	56.08
Chlorophyll *a*	23.67	80.08	23.05	79.13
Pheophytin	19.92	100.00	20.87	100.00

Table 7: SIMPER results from macroinvertebrate analysis for Lake Crescent by date. Variables with a high percent contribution are “discriminating” variable which means they were most strongly associated with community assemblage differences between developed and undeveloped sites. Detritivores and grazers contributed the most to the difference between developed and undeveloped sites.

Lake	**Sample Date group**	**Feeding**	**% Contribution**	**Cumulative %**
CRESCENT				
	Nov 2005	detritivores	49.33	49.33
		piercer grazers	31.60	80.93
		grazers	19.07	100.00
	Mar 2006	detritivores	48.84	48.84
		grazers	45.07	93.92
	May 2006	detritivores	49.09	49.09
		grazers	35.76	84.85
		piercer grazers	8.36	93.22
	Aug 2006	detritivores	59.22	59.22
		grazers	16.44	75.66
		piercer grazers	15.95	91.61
PEND OREILLE				
	Spring 06	grazers	45.52	45.52
		detritivores	27.87	73.39
		collectors	26.61	100.00
	Fall 06	detritivores	77.32	77.32
		grazers	22.68	100.00
PRIEST				
	Spring 06	grazers	54.03	54.03
		detritivores	28.39	82.43
		predators	17.57	100.00
	Fall 06	detritivores	43.20	43.20
		grazers	28.96	72.16
		piercer grazers	27.84	100.00

Table 8: SIMPER analysis results for tree species driving tree community assemblage differences at developed and undeveloped sites in Lake Crescent. Variables with a high percent contribution are "discriminating" variables which means they were most strongly associated with community assemblage differences between developed and undeveloped sites. Red-alder and cedar contributed the most to differences between developed and undeveloped sites.

Tree species	**% contribution**	**Cumulative %**
Alnus rubra	28.12	28.12
Thuja plicata	23.54	51.66
Pseudotsuga menziesii	20.05	71.71
Acer macrophyllum	19.88	91.59

Table 9: PERMANOVA results for Lake Crescent algae community composition.

Source	**d.f.**	**MS**	**Pseudo-F**	**P-value**
Date	4	24807.00	6.00	0.0001
Development	1	22202.00	3.08	0.0152
Site (Development)	10	7216.40	4.69	0.0001
Date x Development	4	7457.60	1.80	0.0162
Site (Dev) x Date	40	4143.10	2.69	0.0001

Table 10: SIMPER results of all three lakes algae community composition. Variables with a high percent contribution are "discriminating" variables which means they were most strongly associated with community assemblage differences between developed and undeveloped sites. Diatoms and filamentous green alga tended to contribute the most to differences between developed and undeveloped sites.

Lake	Sample Date	Algae group	% Contribution	Cumulative %
CRESCENT				
	Aug 2005	diatoms	52.37	52.37
		cyanobacteria	28.35	80.71
		filamentous greens	19.27	99.98
	Nov 2005	diatoms	46.50	46.50
		filamentous greens	38.95	85.45
		cyanobacteria	14.44	99.89
	Mar 2006	diatoms	55.67	55.67
		filamentous greens	37.57	93.24
	May 2006	diatoms	56.22	56.22
		filamentous greens	34.99	91.21
	Aug 2006	diatoms	43.08	43.08
		filamentous greens	36.32	79.41
		cyanobacteria	20.53	99.94
PEND OREILLE				
	Spring 06	diatoms	76.74	76.74
		filamentous greens	22.76	99.49
	Fall 06	filamentous greens	87.14	87.14
		diatoms	11.52	98.66
PRIEST				
	Spring 06	diatoms	81.91	81.91
		filamentous greens	9.62	91.53
	Fall 06	diatoms	69.10	69.10
		cyanobacteria	17.65	86.75
		filamentous greens	13.23	99.97

Table 11: PERMANOVA results of all three lakes algal community composition.

Source	**d.f.**	**MS**	**Pseudo-F**	**P-value**
season	1	54745.00	13.60	0.0001
lake	2	41248.00	11.88	0.0001
pairing (lake)	7	3473.40	0.93	0.5897
season x lake	2	32493.00	8.07	0.0001
development (pairing(lake))	10	3739.70	2.76	0.0001
season x pairing (lake)	7	4027.6	0.95	0.5662
development (pairing(lake)) x season	10	4256.40	3.14	0.0001

REFERENCES CITED:

Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32-46.

Arar, E.J., and G.B. Collins. 1997. Method 445.0: In vitro determination of chlorophyll *a* and pheophytin in marine and freshwater algae by fluorescence. National Exposure Research Laboratory, U.S. Environmental Protection Agency, Cincinnati, Ohio.

Axler, A.P., and J.E. Reuter. 1996. Nitrate uptake by phytoplankton and periphyton: whole-lake enrichment and mecosm-15N experiments in an oligotrophic lake. Limnology and Oceanography 41:659-671.

Biggs, B.J.F. 1989. Biomonitoring of organic pollution using periphyton. South Branch, Canterbury, New Zealand. New Zealand Journal of Marine and Freshwater Research. 23:263-274.

Biggs, B.J.F., and C. Kilroy. 2000. Stream periphyton monitoring manual. NIWA, Christchurch, New Zealand.

Biggs, B.J.F., and C.W. Hickey. 1994. Periphyton responses to a hydraulic gradient in a regulated river in New Zealand. Freshwater Biology 32:49-59.

Bowker, D.W., M.T. Wareham, and M.A. Learner. 1983. The selection and ingestion of epilithic algae by *Nais elinguis* (Oligochaeta: Naididae). Hydrobiologia 98:171-178.

Bray, J.R., and J.T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27.

Brown, G.W., and J.T. Krygier. 1970. Effects of clear-cutting on stream temperature. Water Resources Research 6:1133-1139.

Budy, P.C. Luecke, and W.A. Wurtsbaugh. 1998. Adding nutrients to enhance the growth of endangered sockeye salmon: Trophic transfer in an oligotrophic lake. Transactions of the American Fisheries Society 127:19-34.

Carpenter, S.R., N.F. Caraco, D.L. Correll, R.W. Howarth, A.N. Sharpley, and V. H. Smith. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. Ecological Applications 8:559-568.

Castenholz, R.W. 1960. Seasonal changes in the attached algae of freshwater and saline lakes in the Lower Grand Coulee, Washington. Limnology and Oceanography 5:1-28.

Casterlin, M.E. and W.W. Reynolds. 1977. Seasonal algal succession and cultural eutrophication in a north temperate lake. Hydrobiologia 54:99-108.

Census, US. 1990. Decennial Census of Population and Housing.

Chandra, S., M.J. Vander Zanden, A.C. Heyvaert, B.C. Richards, B.C. Allen, and C.R. Goldman. 2005. The effects of cultural eutrophication on the coupling between pelagic primary producers and benthic consumers. Limnology and Oceanography 50:1368-1376.

Chetelat, J., F.R. Pick, A. Morin, and P.B. Hamilton. 1999. Periphyton biomass and community composition in rivers of different nutrient status. Canadian Journal of Fisheries and Aquatic Science 56:560-569.

Christensen, D.L., B.R. Herwig, D.E. Schindler, and S.R. Carpenter. 1996. Impacts of lakeshore residential development on coarse woody debris in north temperate lakes. Ecological Applications 6:1143-1149.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18:117-143.

Clarke, K.R. and R.N. Gorely. 2006. Primer v6: User manual/ Tutorial. Pages 190 *in*. PRIMER-E: Plymouth.

Clarke, K. R., and a. R. M. Warwick. 2001. Change in marine communities: An approach to statistical analysis and interpretation, 2nd edition. *in*, PRIMER-E: Plymouth.

Cole, M. L., I. Valiela, K.D. Kroeger, G.L. Tomasky, J. Cebrian, C. Wigand, R.A. McKinney, S.P. Grady, and M.H.C. da Silva. 2004. Assessment of a $\delta^{15}N$ isotopic method to indicate anthropogenic eutrophication in aquatic ecosystems. Journal of Environmental Quality 33:124-132.

Compton, J.E., M.R. Church, S.T. Larned, and W.E. Hogsett. 2003. Nitrogen export from forested watersheds in the Oregon Coast Range: The Role of N_2-fixing Red Alder. Ecosystems 6:773-785.

Correll, D.L., T.E. Jordan, and D.E. Weller. 1999. Transport of nitrogen and phosphorus from Rhode River watersheds during storm events. Water Resources Research 35:2513-2521.

David, E.L. 1971. Public perceptions of water quality. Water Resources Research 7:453-457.

Edmondson, W.T. 1991. The uses of ecology: Lake Washington and beyond. University of Washington Press, Seattle, Washington.

Edmondson, W.T., G.C. Anderson, and D.R. Peterson. 1956. Artificial eutrophication of Lake Washington. Limnology and Oceanography 1:47-53.

Edmondson, W.T., and J.T. Lehman. 1981. The effect of changes in the nutrient income on the condition of Lake Washington. Limnology and Oceanography 26:1-29.

Falter, M.C. 2004. Lake Pend Oreille Littoral Periphyton Community: An updated trophic status assessment 2003. Final Report submitted to Tri-state Water Quality Council. Moscow, Idaho.

Forrester, G.E., T.L. Dudley, and N.B. Grimm. 1999. Trophic interactions in open systems: Effects of predators and nutrients on stream food chains. Limnology and Oceanography 44:1187-1197.

Gannon, J.E., and R.S. Stemberger. 1978. Zooplankton (especially Crustaceans and Rotifers) as indicators of water quality. Transactions of the American Microscopical Society 97:16-35.

Goldman, C.R. 1988. Primary productivity, nutrients, and transparency during the early onset of eutrophication in ultra-oligotrophic Lake Tahoe, California-Nevada. Limnology and Oceanography 33:1321-1333.

Gray, L.J., and J.V. Ward. 1979. Food habits of stream benthos at sites of differing food availability. American Midland Naturalist 102:157-167.

Gresh, T., J. Lichatowich, and P.Schoonmaker. 2000. An estimation of historic and current levels of salmon production in the Northeast Pacific ecosystem: evidence of a nutrient deficient in the freshwater systems of the Pacific Northwest. Fisheries 25:15-21.

Groffman, P.M., N.L. Law, K.T. Belt, L.E. Band, and G.T. Fisher. 2004. Nitrogen fluxes and retentions in urban watershed ecosystems. Ecosystems 7:393-403.

Hadwen, W.L., and S.E. Bunn. 2005. Food web response to low-level nutrient and 15N-tracer additions in the littoral zone of an oligotrophic dune lake. Limnology and Oceanography 504:1096-1105.

Hadwen, W.L., S.E. Bunn, A.H. Arthington, and T.D. Mosisch. 2005. Within-lake detection of the effects of tourist activities in the littoral zone of oligotrophic dune lakes. Aquatic Ecosystem Health & Management 8:159-173.

Hall Jr, R.O., B.J. Peterson, and J.L. Meyer. 1998. Testing a nitrogen-cycling model of a forest stream by using a nitrogen-15 tracer addition. Ecosystems 1:283-298.

Hampton, S.E., S.C. Fradkin, P.R. Leavitt, E.E. Seminet-Reneau, D.E. Schindler, and P. Romare. Disproportionate importance of nearshore habitat in a deep oligotrophic lake. *In prep.*

Havens, K.E., T.L. East, S.J. Hwang, A.J. Rodusky, B. Sharpsteing, and A.D. Steinman. 1999. Algal responses to experimental nutrient addition in the littoral community of a subtropical lake. Freshwater Biology 42:329-344.

Heaton, T.H.E. 1986. Isotopic studies of nitrogen pollution in the hydrosphere and atmosphere: A review. Chemical Geology 59:87-102.

Humphrey, K.P., and a. R.J. Stevenson. 1992. Responses of benthic algae to pulses in current and nutrients during simulations of subscouring spates. Journal of the North American Benthological Society 11:37-48.

Jacoby, J.M., D.C. Collier, E.B. Welch, F.J. Hardy, and M. Crayton. 2000. Environmental factors associated with a toxic bloom of *Microcystis aeruginosa.* Canadian Journal of Fisheries and Aquatic Science 57:231-240.

Jacoby, J.M., D.D. Bouchard, and C.R. Patmont. 1991. Response of periphyton to nutrient enrichment in Lake Chelan, WA. Lake and Reservoir Management 7:33-43.

Johnson, S.L., and J.A. Jones. 2000. Stream temperature responses to forest harvest and debris flows in western Cascades, Oregon. Canadian Journal of Fisheries and Aquatic Science 57:30-39.

Jumars, P.A., J.E. Eckman, and E. Koch. 2001. Macroscopic animals and plants in benthic flows, p 320-347. *in* B. P. B. a. B. B. Jorgensen, editor. The Benthic Boundary Layer. Oxford University Press.

Kann, J., and C. M. Falter. 1989. Periphyton as indicators of enrichment in Lake Pend Oreille, Idaho. Lake and Reservoir Mangagement 5:39-48.

Kornijów, R., R.D. Gulati, and E. van Donk. 1990. Hydrophyte-macroinvertebrate interactions in Zwemlust, a lake undergoing biomanipulation. Hydrobiologia 200/201:467-474.

Larned, S.T., V.I. Nikora, and a. B.J.F. Biggs. 2004. Mass-transfer-limited nitrogen and phosphorus uptake by stream periphyton: A conceptual model and experimental evidence. Limnology and Oceanography 49:1992-2000.

Liboriussen, L., and E. Jeppesen. 2006. Structure, biomass, production and depth distribution of periphyton on artificial substratum in shallow lakes with contrasting nutrient concentrations. Freshwater Biology 51:95-100.

Lindau, C.W., R.D. Delaune, and D.P. Alford. 1997. Monitoring nitrogen pollution from sugarcane runoff using ^{15}N analysis. Water, Air, and Soil Pollution 89:389-399.

Loeb, S.L. 1981. An in situ method for measuring the primary productivity and standing crop of the epilithic periphyton community in lentic systems. Limnology and Oceanography 26:394-399.

Lohman, K., J.R. Jones, and C. Baysinger-Daniel. 1991. Experimental evidence for nitrogen limitation in a northern Ozark stream. Journal of the North American Benthological Society 10:14-23.

Lowe, R.L., and R.D. Hunter. 1988. Effect of grazing by *Physa integra* on periphyton commnunity structure. Journal of the North American Benthological Society 7:29-36.

Mazumder, A., and J.A. Edmundson. 2002. Impact of fertilization and stocking on trophic interactions and growth of juvenile sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Science 59:1361-1373.

McMahon, G., and D.A. Harned. 1998. Effect of environmental setting on sediment, nitrogen, and phosphorus concentrations in Albemarle-Pamlico drainage basin, North Carolina and Virginia, USA. Environmental Management 22:887-903.

Merritt, R.W., and K.W. Cummins. 1996. An introduction to the aquatic insects of North America. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Mihuc, T., and D. Toetz. 1994. Determination of diets of alpine aquatic insects using stable isotopes and gut analysis. American Midland Naturalist 131:146-155.

Moore, J.W. 1975. The role algae in the diet of *Asellus aquaticus L.* and *Gammarus pulex L.* The Journal of Animal Ecology 44:719.

Moore, J.W., D.E. Schindler, M.D. Scheuerell, D. Smith, and J. Frodge. 2003. Lake eutrophication at the urban fringe, Seattle region, USA. Ambio 32:13-18.

Mulholland, P.J., J.L. Tank, D.M. Sanzone, W.M. Wollheim, B.J. Peterson, J.R. Webster, and J.L. Meyer. 2000. Nitrogen cycling in a forest stream determine by a 15 N tracer addition. Ecological Monographs 70:471-493.

Myer, J., and S. Fradkin. 2002. Summary of fisheries and limnological data for Lake Crescent, Washington. Olympic National Park.

Nyogi, D.K., M. Koren, and C.J. Arbuckle. 2007. Stream communities along a catchment land-use gradient: Subsidy-stress responses to pastoral development. Environmental Management 39:213-225.

Obeng-Asamoa, E.K., D.M. John, and H.N. Appler. 1980. Periphyton in the Volta L. seasonal changes on the trunks of flooded trees. Hydrobiologia 76:191-200.

Olson, C.L. 1974. Comparative robustness of six tests in multivariate analysis of variance. Journal of the American Statistical Association 69:894-908.

Olson, R.W., and P.R. Cereghino. 2002. Baseline survey of *Lobelia dortmanna* (Campanulaceae) in Lake Crescent, Olympic National Park. Natural Resources Division, Olympic National Park, Port Angeles.

O'Reilly, C.M. 2006. Seasonal dynamics of periphyton in a large tropical lake. Hydrobiologia 553:293-301.

Paerl, H.W. 1997. Coastal eutrophication and harmful algal blooms: Importance of atmospheric deposition and groundwater as "new" nitrogen and other nutrient sources. Limnology and Oceanography 42:1154-1165.

Peterson, B.J., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18:293-320.

Peterson, B.J., M. Bahr, and G. W. Kling. 1997. A tracer investigation of nitrogen cycling in a pristine tundra river. Canadian Journal of Fisheries and Aquatic Science 54:2361-2367.

Pretty, J.L., and M. Dobson. 2004. The response of macroinvertebrates to artificially enhanced detritus levels in plantation streams. Hydrology and Earth System Sciences 8:550-559.

Rabalais, N.N., R.E. Turner, and W.J. Wiseman Jr. 2002. Gulf of Mexico hypoxia, a.k.a "The Dead Zone". Annual Review of Ecology and Systematics 33:235-263.

Reuter, J.E., S.L. Loeb, and C. R. Goldman. 1986. Inorganic nitrogen uptake by epilithic periphyton in a N-deficient lake. Limnology and Oceanography 31:149-160.

Richardson, J.S. 1991. Seasonal food limitation of detritivores in a montane stream: An experimental test. Ecology 72:873-887.

Rier, S.T., N.C. Tuchman, R.G. Wetzel, and J. A. Teeri. 2002. Elevated CO_2-induced changes in the chemistry of quaking aspen (*Populus tremuloides Michaux*) leaf litter: subsequent mass loss and microbial response in a stream system. Journal of the North American Benthological Society 21:16-27.

Rosemond, A.D., P.J. Mulholland, and S. H. Brawley. 2000. Seasonally shifting limitation of stream periphyton: response of algal populations and assemblage biomass and productivity to variation in light, nutrients, and herbivores. Canadian Journal of Fisheries and Aquatic Science 57:66-75.

Rothrock, G.C., and D.T. Mosier. 1997. Phase 1 Diagnostic Analysis: Priest Lake, Bonner County, Idaho 1993-1995., Boise, Idaho.

Schindler, D.E., S.I. Geib, and M.R. Williams. 2000. Patterns of fish growth along a residential development gradient in North temperate lakes. Ecosystems 3:229-237.

Schnaiberg, J., J. Riera, M.G. Turner, and P.R. Voss. 2002. Explaining human settlement patterns in a recreational lake district: Vilas County, Wisconsin, USA. Environmental Management 30:24-34.

Steffy, L.Y., and S.S. Kilham. 2004. Elevated $\delta^{15}N$ in stream biota in areas with septic tank systems in an urban watershed. Ecological Applications 14:637-641.

Stemberger, R.S. 1981. A general approach to the culture of planktonic rotifers. Canadian Journal of Fisheries and Aquatic Science 38:721-724.

Stemberger, R.S., D.P. Larsen, and T.M. Kincaid. 2001. Sensitivity of zooplankton for regional lake monitoring. Canadian Journal of Fisheries and Aquatic Science 58:2222-2232.

Stockner, J. G., and E. A. MacIsaac. 1996. British Columbia lake enrichment programme: Two decades of habitat enrichment for sockeye salmon. Regulated rivers: Research & Management 12:547-561.

Stockner, J.G., and K. S. Shortreed. 1988. Responses of *Anabaena* and *Synechococcus* to manipulation of nitrogen:phosphorus rations in a lake fertilization experiment. Limnology and Oceanography 33:1348-1361.

Szmeja, J. 1987. The seasonal development of *Lobelia dortmanna L.* and annual balance of its population size in an oligotrophic lake. Aquatic Botany 28:15-24.

Taylor, S.L., S.C. Roberts, C.J. Walsh, and B.E. Hatt. 2004. Catchment urbanisation and increased benthic algal biomass in streams: linking mechanisms to management. Freshwater Biology 49:835-851.

Tuchman, N.C., R.G. Wetzel, S.T. Rier, K.A. Wahtera, and J.A. Teeri. 2002. Elevated atmospheric CO_2 lowers leaf litter nutritional quality for stream ecosystem food webs. Global Change Biology 8:163-170.

Vadeboncoeur, Y., D.M. Lodge, and S.R. Carpenter. 2001. Whole-lake fertilization effects on distribution of primary production between benthic and pelagic habitats. Ecology 82:1065-1077.

Vadeboncoeur, Y., E. Jeppesen, M.J. Vander Zanden, H.H. Schierup, K. Christoffersen, and D.M. Lodge. 2003. From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in lakes. Limnology and Oceanography 48:1408-1418.

Vitousek, P.M., J.D. Aber, R.W. Howarth, G.E. Likens, P.A. Matson, D.W. Schindler, W.H. Schlesinger, and D.G. Tilman. 1997. Technical report: Human alteration of the global nitrogen cycle: Sources and consequences. Ecological Applications 7:737-750.

[WADNR] 2003.Washington Department of Natural Resources, Washington Natural Heritage Program, and U.S.D.I. Bureau of Land Management.

Walsh, S.E., P.A. Soranno, and D.T. Rutledge. 2003. Lakes, wetlands, and streams as predictors of land use/cover distribution. Environmental Management 31:198-214.

Wilson, M.A., and S.R. Carpenter. 1999. Economic valuation of freshwater ecosystem services in the United States: 1971-1997. Ecological Applications 9:772-783.

Wipfli, M.S., J. Hudson, and J. Caouette. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic Science 55:1503-1511.