

APPLIED ISSUES

Effects of shoreline development on the nearshore environment in large deep oligotrophic lakes

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SUMMARY

1. In large deep oligotrophic lakes, the shallow nearshore waters may provide the most important habitat for animals to feed and breed, and it is this area of the lake where humans are most likely to have initial impacts as the shoreline is developed. Nutrients in fertilizers, sediments and sewage effluents are likely to be rapidly intercepted by nearshore algae at the lake edge, having heterogeneous effects nearshore before offshore effects are noted.
2. Here we examined the spatially explicit effects of residential development on nearshore periphyton communities in three large deep oligotrophic lakes that have all experienced modest residential development in the Pacific Northwest of the United States. We demonstrate that substantial nearshore changes in the basal food web are detectable even with low levels of shoreline development. These changes can potentially affect whole-lake food web dynamics.
3. For our primary study site (Lake Crescent, Washington, USA), we found that algal biomass and accumulation of detritus were 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.
4. A complementary investigation of field patterns in Priest Lake and Lake Pend Oreille (Idaho, USA) suggested that, although spatial and temporal patterns were idiosyncratic, indicators of productivity and the presence of filamentous green algae were generally higher at developed sites across lakes.
5. Stable isotope signatures and water column nutrients were not useful in distinguishing developed and undeveloped sites, increasing the potential usefulness of periphyton monitoring during early stages of lake development.
6. A laboratory investigation suggested that common macroinvertebrate grazers assimilated a much greater proportion of diatoms than the filamentous green algae that are associated with fertilization at developed sites.
7. These findings have at least two clear implications: (i) periphyton may be used to detect human impacts before disturbance is evident in offshore monitoring programmes and (ii) nearshore impacts in response to modest residential development have the potential to disrupt lake food web dynamics.

Keywords: eutrophication, littoral, *Mougeotia*, septic systems, sewage

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Introduction

Humans are drawn to live on lakes for recreational and aesthetic reasons; however the pressures that residential developments place on lake systems can degrade the very qualities that initially attracted residents. Developing lakeside land decreases the riparian density of trees around the shoreline, which subsequently decreases the recruitment of coarse woody debris into the littoral zone (Christensen *et al.*, 1996; Francis & Schindler, 2006) reducing potential terrestrial subsidies and complex habitat for fish (Christensen *et al.*, 1996; Schindler, Geib & Williams, 2000). Schindler *et al.* (2000) found that fish growth decreased with intensity of lakeshore development as a result of littoral zone degradation. Such riparian changes can also affect water quality by altering terrestrial run-off patterns (Groffman *et al.*, 2004) and increasing water temperatures because of loss of shade (Brown & Krygier, 1970; Johnson & Jones, 2000). Lastly, lakeshore development commonly disrupts nutrient cycles by introducing fertilizers, sediments and sewage effluents.

Nutrient pollution is viewed as a serious threat to water quality for both its documented direct effects and hypothesized subtle, or indirect, impacts on lake communities (Carpenter *et al.*, 1995). While nutrient additions tend to increase primary productivity via a fertilization effect, complex trophic dynamics affect the extent to which anthropogenic fertilization translates into increased productivity at higher trophic levels (Carpenter *et al.*, 1995). For example, algal growth may exceed consumers' capacity to consume it, or nutrient enrichment may decrease the edibility of primary producers (Rier *et al.*, 2002; Tuchman *et al.*, 2002). 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).

Collectively, the shoreline changes associated with development can have complex and varied impacts on the biological communities and integrity of lentic systems (Edmondson, 1994; Leavitt *et al.*, 2006) and our understanding of such effects is primarily derived from studies on heavily impacted systems. Consequently, our knowledge of the *process* of lake system degradation is less mature than our ability to identify human impacts; at what point in the catchment development process are impacts evident in lakes

and at what point can these effects be considered important? The American West is home to a suite of large nutrient-poor lakes in relatively 'early' stages of catchment development, providing opportunities to evaluate localized nearshore effects of development before lake-wide degradation is evident.

In large deep oligotrophic lakes, the shallow water nearshore may provide the most important feeding and breeding habitat for organisms, particularly fish and amphibians. In these lakes, a large proportion of primary productivity occurs as periphyton in nearshore waters (Vadeboncoeur *et al.*, 2003). If such food webs rely disproportionately on this relatively small area for edible carbon, large lakes may be much more affected by pollution than smaller eutrophic lakes where productivity primarily occurs in the open water. In addition to altering food availability, pollution may affect reproductive habitat for the many fishes and other organisms that require shallow water for breeding.

Here, we 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 but do not yet exhibit offshore water quality changes. The study of nearshore change of periphyton communities in response to pollution in these modestly impacted systems serves two purposes. First, algal compositional changes nearshore may have inherent importance for lake-wide management when organisms rely on nearshore breeding and feeding resources. Secondly, periphyton responses to residential development in moderately impacted environments can serve as an early warning for managers concerned with water quality. Periphyton is a useful indicator of eutrophication because it rapidly assimilates nutrients, and can intercept nutrients from shoreline development as they enter the lake, either through ground water or surface flow (Goldman, 1988; Jacoby, Bouchard & Patmont, 1991; Hadwen & Bunn, 2005). The role of such a biological sentinel is important in oligotrophic systems, in which water column nutrients are frequently below standard detectable limits (Seminet-Reneau, 2007). We focused this work on Lake Crescent (Fig. 1) in Washington's Olympic National Park (U.S.A.), to understand spatial and temporal trends in nutrient enrichment effects, and compared these results to data collected at a coarser scale from two

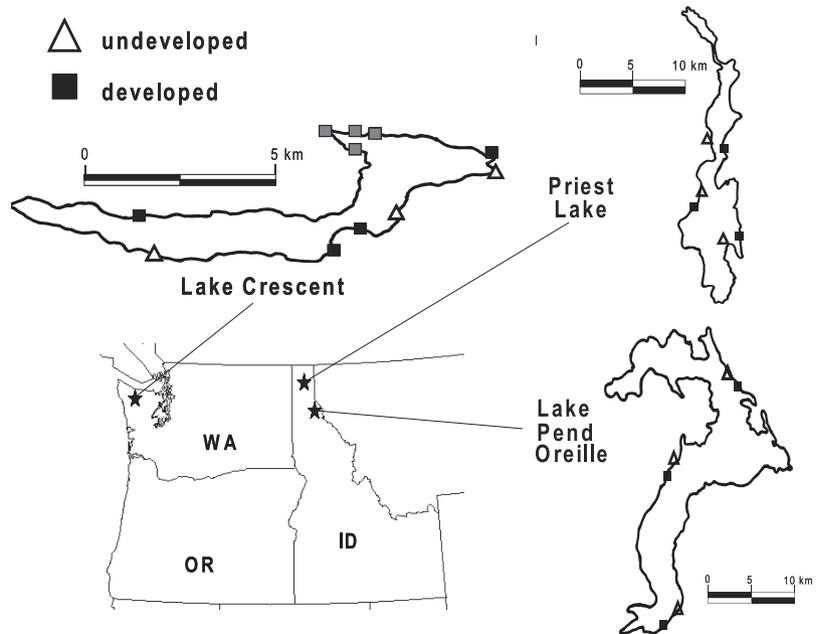


Fig. 1 Map of the three Falter, 2004 study lake locations in the Pacific Northwest. Lake Crescent is on the Olympic Peninsula of Washington, while Lake Pend Oreille and Priest Lake are both located in the panhandle of Idaho. Detailed maps show locations of paired developed and undeveloped sample sites in each lake along with the four unpaired developed sites in Lake Crescent. The four unpaired sites (depicted by grey squares) on Lake Crescent are in the Lyre Basin at the far northwest end.

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

| | Lake Crescent | Lake Pend Oreille | Priest Lake |
|--------------------------|---------------------------------------|------------------------------|---|
| Surface area | 118 km ² | 383 km ² | 100 km ² |
| Depth (mean–max.) | 101–190 m | 164–357 m | 39–112 m |
| Trophic status | Ultra-oligotrophic | Meso-oligotrophic | Oligotrophic |
| Secchi depth (mean–max.) | 15–25 m | 10–21 m | 9.8–14 m |
| Family residences | 121 (16% year round) | >1000 (unknown seasonality) | 1707 (15% year round) |
| Peak visitors | 12 000 | >10 000 | 5000 |
| Waste disposal | Sewage treatment plants, septic tanks | Sewage lagoons, septic tanks | Sewage lagoons, septic tanks, vaulted outhouses |

other similar lakes (Lake Pend Oreille and Priest Lake in Idaho, USA; Fig. 1; Table 1) to determine whether generalizable trends in nearshore responses to residential development could be detected.

We addressed three hypotheses through field sampling and multivariate statistical analyses, and one related hypothesis through laboratory experimentation. First, because of periphyton's ability to rapidly assimilate nutrients, we hypothesized that indicators of benthic productivity would differ between developed and undeveloped sites. Secondly, with this change in productivity characteristics we expected to see a resource-related shift in macroinvertebrate community composition at developed sites. In addition to a change in algal biomass, we hypothesized that taxonomic composition of periphyton would shift

with development. To explore the food web implications of this third hypothesis in a laboratory setting, we examined differential assimilation of algae by common macroinvertebrates offered the algal taxa that were characteristic of developed and undeveloped sites.

Methods

Study sites

Lake Crescent is a large deep oligotrophic lake in Olympic National Park on Washington State's Olympic Peninsula (Fig. 1; Table 1). Development in the nearshore of Lake Crescent includes about 100 private residences and two resorts that rely primarily on

septic systems. Evidence that the septic systems are aging and becoming less effective includes the recent occurrence of periphyton blooms (Meyer & Fradkin, 2002). Although Lake Crescent has areas of development and exhibits incipient stages of developmental impact, the vast majority of the shoreline is undeveloped, and the offshore waters do not show signs of eutrophication (S.E. Hampton, unpubl. data; National Park Service OLYM long-term monitoring programme, unpubl. data). Water column nutrients are below standard detectable limits, even at the shoreline near development (Seminet-Reneau, 2007). As is probably common in relatively unimpacted habitats, Lake Crescent supports small endemic populations that have high vulnerability to the impacts of development. The Beardslee trout (*Oncorhynchus mykiss* Walbaum), is a genetically distinct rainbow trout endemic to Lake Crescent (Meyer & Fradkin, 2002). Despite avoiding areas of high periphyton growth (S.J. Brenkman, pers. comm.), these trout spawn in only one location – the Lyre outlet, which is the area of the lake that has experienced the most shoreline development (Fig. 1). Additionally, water lobelia (*Lobelia dortmanna* Linnaeus) is a sensitive plant in Lake Crescent that is adapted for nutrient-poor water and is listed as 'threatened' in Washington State, mainly because of loss of habit (Olson & Cereghino, 2002; WADNR, 2003). *Lobelia* has been used as an indicator of oligotrophic conditions and its decline has been associated elsewhere with eutrophication (Szmeja, 1987).

In order to quantify localized development impacts in Lake Crescent, we chose paired nearshore sites in developed and undeveloped areas around the lake (Fig. 1). The sites were sampled every 3 months for 1 year from August 2005 through August 2006. Twelve sites included four undeveloped and four developed sites that were distributed throughout the main basin, and four sites within the shallow Lyre outlet basin. Developed sites average 0.012–0.016 houses m⁻¹, and undeveloped sites are 0.75–4.5 km away from any residential development (S.C. Fradkin, unpubl. data). The Lyre outlet has no undeveloped sites and was targeted for more detailed sampling because of its importance for fish spawning habitat.

The two northern Idaho lakes against which Lake Crescent results were compared, Lake Pend Oreille and Priest Lake (Fig. 1; Table 1), have patchy development like Lake Crescent and are exhibiting

nearshore responses consistent with nutrient loading. This large, clear lake is 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 biomass in the littoral zone relative to its low nutrient status (Falter, 2004) with higher biomass near developed sites (Kann & Falter, 1989). Similarly, Priest Lake is oligotrophic and exhibits no changes in pelagic water quality, but has shown unusually high algal biomass in the littoral zone (Rothrock & Mosier, 1997). No difference in algal biomass was detected between developed and undeveloped sites in Priest Lake by Rothrock & Mosier (1997). 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. Nearshore water column nutrients in 2006 (Seminet-Reneau, 2007) were similarly low and indistinguishable between developed and undeveloped sites at both lakes, and just reached the standard minimum detectable limit (EPA method 365.4) for total phosphorus at each lake (0.01 mg L⁻¹). Here, the Idaho lakes were subject to parallel study with Lake Crescent, using the same collection methods, but at a coarser temporal and spatial resolution. On each Idaho lake we sampled six sites (Fig. 1), collecting five replicates within each site during the spring and autumn of 2006.

Data collection and 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 autumn 2006) were analysed for all three lakes together. Sample loss from Lake Pend Oreille and Priest Lake prevented comparisons of chlorophyll *a* measures in the spring.

Environmental and community differences among sampling sites and dates were investigated with

multivariate analyses using Plymouth Routines in Multivariate Ecological Research (PRIMER version 6; Plymouth Marine Laboratory, Plymouth, U.K.; Clarke & Gorely, 2006). All data were $\log(x + 1)$ transformed to moderately deemphasize the most abundant organisms (*sensu* Clarke & Warwick, 2001) unless otherwise noted. All subsequent analyses were performed on the Bray-Curtis similarity matrix. We used permutational analysis of variance (PERMANOVA; Anderson, 2001a,b), with 9999 permutations, to examine differences in univariate and multivariate biological variables between developed and undeveloped sites within and among lakes (Table 2). PERMANOVA has the advantage of accommodating complex experimental designs for multivariate data, without the assumptions of normality and homoscedasticity that limit the use of traditional MANOVA (Olson, 1974). The PERMANOVA technique is based on permutations that iteratively re-label data, calculating the true probability of observing the differences present among groups that were sampled rather than relying on tabled statistics. Patterns in the data were visually represented with non-metric multidimensional scaling (MDS) in PRIMER, and we used the SIMPER routine to determine which variables were most strongly associated with community assemblage differences among groupings (Clarke & Warwick, 2001).

Below, we 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.

Productivity measures

Algal pigments and organic matter (OM) biomass were used to characterize the productivity of developed and undeveloped sites. These results were analysed together as multivariate measures of productivity in a multifactorial PERMANOVA.

Algal pigments. To use chlorophyll *a* concentration as a proxy for primary productivity, we collected algal samples of known area from the surfaces of rocks at three different depths (0.25, 0.50 and 0.75 m from waterline) in the nearshore of each site in the spring and autumn sampling periods. Chlorophyll *a* analysis was performed using a fluorometer (Turner Designs Trilogy, model 7200-000, Sunnyvale, CA, U.S.A.) using EPA method 445.0 (Arar & Collins, 1997).

Table 2 Analyses and models used for PERMANOVA analysis

| Analysis | Lake | Model | Factors tested with interactions | Fixed or random |
|----------------------|----------------------|---|-------------------------------------|---------------------------|
| Productivity | Crescent | Two-way PERMANOVA | Date development | Fixed random |
| | All three lakes | Two-way PERMANOVA | Lake development | Fixed random |
| Macroinvertebrates | Crescent | Two-way PERMANOVA | Date development | Fixed random |
| | All three lakes | Two-way PERMANOVA | Lake development | Fixed random |
| Tree community | Crescent | Three separate one-way PERMANOVA s | Development | Fixed |
| | Periphyton community | density, diameter and species composition | Site (development) Date development | Random fixed fixed |
| Periphyton community | Crescent | Nested three-way PERMANOVA | Development (pairing) date pairing | Random fixed random |
| | All three lakes | Blocked three-way PERMANOVA | Development (pairing) season | Random fixed random |
| | | Four-way PERMANOVA | pairing (lake) lake | Random fixed random fixed |

A factor followed by a second factor in parentheses indicates the former variable is nested in the latter.

As cells age and die, they lose magnesium ions from the chlorophyll molecule, forming a degradation product called pheophytin *a*. An acidification step was added to the chlorophyll determination procedure to calculate pheophytin *a* 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.

Ash-free dry mass and 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. AFDM was calculated as the difference between dried weight and ashed weight (Biggs & Kilroy, 2000).

Using the ratio of AFDM to chlorophyll *a*, we calculated the autotrophic index (AI) to determine the proportion of autotrophic to heterotrophic organisms in the periphyton samples. This value has been used most commonly in stream systems to gauge effects of eutrophication on periphyton dynamics (Biggs, 1989).

For SIMPER analysis, AI and %OM were not included because of their high correlations with AFDM, which complicate interpretation.

Macroinvertebrates

In order to coarsely characterize the macroinvertebrate communities at each site where periphyton was collected, we collected macroinvertebrates with a kicknet for 5 min at each site. Macroinvertebrate samples were taken from Lake Crescent over four 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 later classified to functional feeding group (Merritt & Cummins, 1996). We standardized the samples by dividing each entry by total abundance in each sample (*sensu* Clarke & Warwick, 2001) 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 test for differences in macroinvertebrate community composition at developed and

undeveloped sites in Lake Crescent, we used a two-way PERMANOVA testing the effects of ‘development’ and ‘date’ on multivariate macroinvertebrate composition (Table 2). Examining macroinvertebrate communities across all three lakes, we considered only May and August dates from Lake Crescent, to correspond with the spring and autumn sampling periods of Lake Pend Oreille and Priest Lake. Comparing all three lakes we executed a two-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 shoreline vegetation and associated terrestrial inputs, we 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 was measured. To determine whether tree composition differed between the developed and undeveloped sites, we used a one-way PERMANOVA to examine effects of ‘development,’ as a random factor, on the multivariate tree responses (Table 2). We also examined univariate differences in tree density and diameter using one-way PERMANOVA.

Community composition and abundance of periphyton

At each of the 12 sites on Lake Crescent, five periphyton samples were collected for community abundance and composition analysis during five sampling periods (August 2005, November 2005, March 2006, May 2006 and August 2006), for a total of 300 samples. 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, 0.5 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 mm²), we used a razor blade (surface area = 1521 mm²) to cut through and scrape the algae of a known surface area. The samples were preserved with Lugol’s fixative (Edmondson, 1959) and kept cool and dark until

processed. Samples were homogenized with a blender and brought to a known volume with distilled water. Subsamples were scanned and all cells counted in a series of randomly located transects until 300 cells had been enumerated (*sensu* Biggs & 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.

In addition to density (cells mm⁻²), we calculated biovolume (µm³ mm⁻²) by estimating the average volume for cells within the major taxonomic groupings. For any taxon that comprised at least 5% of the sample, we measured up to five cells in dimensions that allowed volumetric calculations for its basic geometric shape (*sensu* Hillebrand *et al.*, 1999) and photographed representative cells for archiving of its identification. For Lake Crescent, we used a three-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. We present results from this design instead of the blocked design, which explicitly used the *a priori* pairing (Table 2), because the blocked model did not yield significant effects of blocking ('pairing' $P = 0.3419$ and 'date × pairing' $P = 0.2506$). In addition, using the nested model allowed simultaneous consideration of the four developed sites in Lake Crescent (located in the Lyre River outlet basin; Fig. 1) 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 data were also reduced to spring and autumn for equivalence to Lake Pend Oreille and Priest lake sample periods. A four-way PERMANOVA was executed with 'development' (nested in 'pairing'), 'season', 'lake' and 'pairing' (nested in 'lake') as effects on periphyton community composition among lakes.

Stable isotope analysis of field-collected samples

Periphyton samples and macroinvertebrates were collected for stable isotope analysis from each site on the same sampling dates and using the same methods

as for periphyton community composition collections. These samples were analysed for stable isotope ratios of nitrogen, to infer the source of nutrients (e.g. sewage versus natural), since human sewage may contain an enriched ¹⁵N signature that can be differentiated from natural or other common sources such as artificial fertilizers (Steffy & Kilham, 2004). Filamentous and diatomaceous algae were cultured in the laboratory and analysed for stable isotope ratios to determine whether there was any inherent difference in their fractionation of nitrogen that would prevent confidently inferring the sources of nutrients from stable isotope analysis. Samples were analysed at the Idaho Stable Isotopes Laboratory (University of Idaho) using a continuous-flow stable isotopic elemental analyser (model NC-2500; CE Instruments, Milan, Italy). A one-way ANOVA was used to examine δ¹⁵N values at developed and undeveloped sites in total, and separated by sample date.

Laboratory grazing experiment

In the laboratory, we explored the hypothesis that increased algal biomass may shift in its vulnerability to herbivory when filamentous green algae become dominant over diatoms, as a result of differential assimilation by grazers. We estimated proportional uptake of filamentous versus diatomaceous algae by two common macroinvertebrates, the amphipod *Gammarus* and a gastropod *Physa*. Diatoms (*Navicula pelliculosa* Bréb) and filamentous green algae (*Mougeotia* spp.) were cultured in a standard medium (Stemberger, 1981) in the laboratory and background δ¹⁵N values (i.e. prior to isotope labelling) 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 δ¹⁵N of macroinvertebrates prior to isotope labelling. Amphipods and snails were starved for 24 h to determine background δ¹⁵N values in the absence of gut content isotope values. We added a ¹⁵N tracer (Ammonium – ¹⁵N Chloride, 98 atom % ¹⁵N made by Sigma Aldrich Isotech), to a stock of filamentous algae (*Mougeotia* spp.). This label imparts an elevated δ¹⁵N signature to organisms that assimilate it and allowed us to quantify the relative importance of filamentous (with label) and diatomaceous (without label) ingestion. After

48 h in the labelled medium, the filamentous algae were rinsed with unlabelled 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 six snails. At 3, 6 and 9 days, two snails and five amphipods were sampled for isotope analysis. At these times, we 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. Ultimately, samples from each taxon on each sampling day had to be pooled to create enough material for analysis. Samples were analysed using continuous flow isotope ratio mass spectrometer (IRMS; Europa Integra, Cheshire, U.K.).

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 was:

$$\text{Diatom assimilation (proportion)} = (\delta_s - \delta_2) / (\delta_1 - \delta_2)$$

where δ_s is the $\delta^{15}\text{N}$ value of macroinvertebrates corrected for a 3.0‰ trophic enrichment (Peterson &

Fry, 1987), δ_2 is the $\delta^{15}\text{N}$ value of the spiked filamentous algae and δ_1 represents the $\delta^{15}\text{N}$ of the unspiked diatoms.

Results

Productivity

For Lake Crescent, the productivity variables chlorophyll *a*, pheophytin *a*, 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 two-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 (Fig. 2a) while autumn values were low for both types of sites (Fig. 2b). AFDM, %OM and autotrophic indices were highly variable from site to site but were, on average, higher at developed sites (Table 3). *Post hoc* pairwise comparisons revealed that developed and undeveloped productivity indicators 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 *a* and AFDM) revealed that

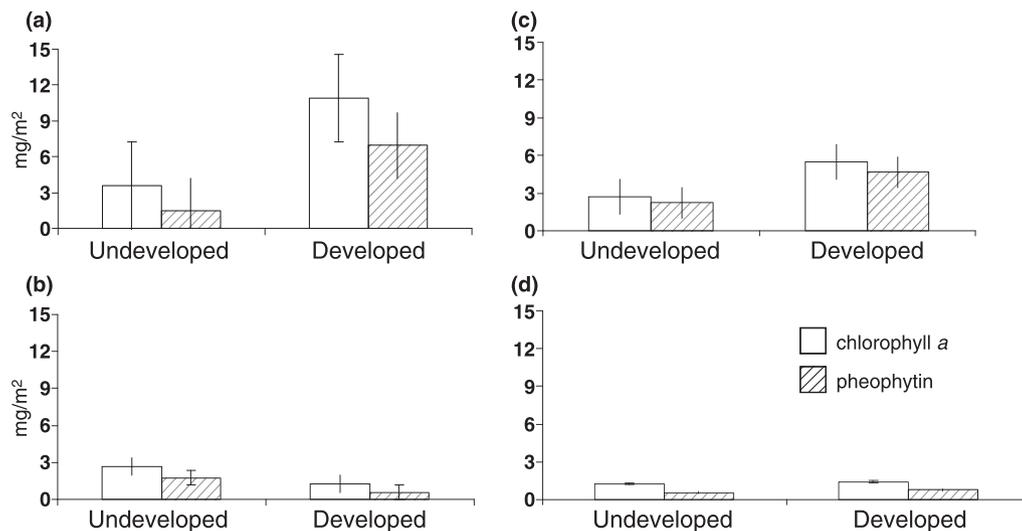


Fig. 2 Productivity measures, chlorophyll *a* and pheophytin *a* (mg m^{-2}), from nearshore sites with and without residential development on Lake Crescent in (a) May 2006 and (b) August 2006 and September 2006 samples for (c) Lake Pend Oreille and (d) Priest Lake. The April 2006 samples from these Idaho lakes were lost. Chlorophyll *a* is an indicator of living primary producers and pheophytin is a pigment associated with dead plant material.

Table 3 Average AFDM (g m^{-2}), %OM and AI for Lake Crescent, Lake Pend Oreille and Priest Lake

| Lake | Development | No. samples | AFDM | SD | % OM | SD | AI | SD |
|----------------|-------------|-------------|------|------|------|----|-----|-----|
| Crescent | | | | | | | | |
| May 2006 | Undeveloped | 4 | 65 | 104 | 40 | 37 | 16 | 24 |
| | Developed | 8 | 1361 | 2247 | 43 | 31 | 151 | 260 |
| August 2006 | Undeveloped | 4 | 3 | 3 | 18 | 12 | 5 | 3 |
| | Developed | 8 | 19 | 25 | 21 | 13 | 7 | 6 |
| Pend Oreille | | | | | | | | |
| September 2006 | Undeveloped | 3 | 6 | 3 | 26 | 15 | 2 | 1 |
| | Developed | 3 | 12 | 4 | 25 | 23 | 2 | 0 |
| Priest | | | | | | | | |
| September 2006 | Undeveloped | 3 | 24 | 6 | 26 | 24 | 21 | 11 |
| | Developed | 3 | 15 | 5 | 11 | 6 | 11 | 3 |

AFDM, ash-free dry mass; %OM, per cent organic matter; AI, autotrophic index, SD, standard deviation.

AFDM contributed the most (56.42%) to the difference between developed and undeveloped sites in Lake Crescent followed by chlorophyll *a* (23.67%), implying that a general increase in organic material was more descriptive of development effects than algal biomass alone.

Productivity variables from September samples of the Idaho lakes were analysed 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 from each other in their productivity characteristics in general ($P = 0.05$), and no overall trend in response to development status was detected ($P = 0.12$). Like Lake Crescent, Lake Pend Oreille productivity was slightly higher at developed sites, but productivity values for Priest Lake were low and indistinguishable between developed and undeveloped sites. As within the full Lake Crescent data set, SIMPER analysis of productivity values for all three lakes highlighted the role of AFDM in describing 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 development status affected macroinvertebrate communities 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, grazers and piercer-grazers were primarily responsible for observed differences between macroinvertebrate assemblages at developed and undeveloped sites in Lake Crescent. Average proportion of detritivores, relative to grazers, was higher at developed than undeveloped sites during the spring (March 2006) but these differences weakened later (August 2006) when detritivores were more abundant everywhere (Fig. 3a).

The three lakes differed significantly in macroinvertebrate community composition ($P = 0.01$) but general patterns were not evident for development status ($P = 0.08$), nor in 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 of macroinvertebrate composition, although the trend for this analysis was non-significant ($P = 0.10$). In *post hoc* pairwise comparison, undeveloped sites at all three lakes resembled each other ($P > 0.11$), but the macroinvertebrate community composition of developed sites differed from lake to lake. 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 ($P = 0.32$). Thus, the macroinvertebrate communities among lakes differed only at developed sites.

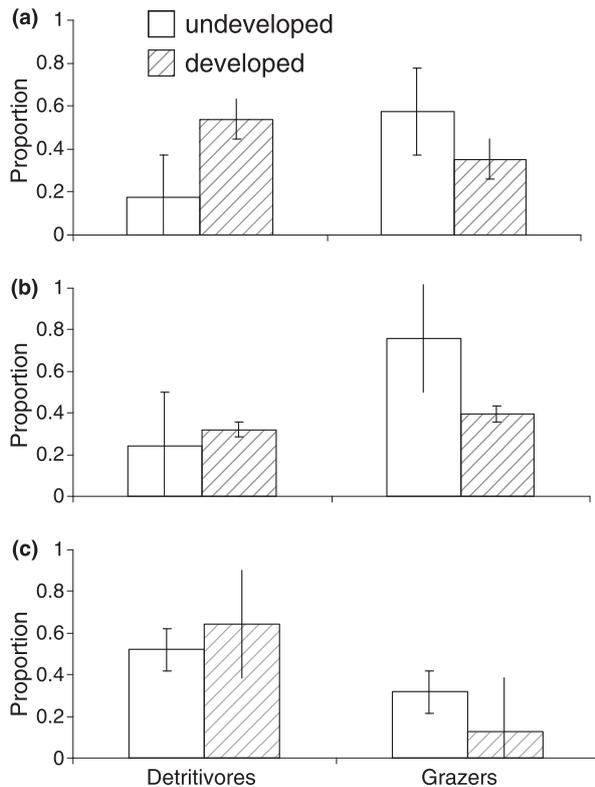


Fig. 3 Proportions of macroinvertebrate functional feeding groups that contributed the most to differences as determined by SIMPER analysis between communities at developed and undeveloped sites in the spring 2006 samples for (a) Lake Crescent, (b) Lake Pend Oreille and (c) Priest Lake.

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. In Lake Pend Oreille, both the spring and autumn samples had more detritivores at developed sites and more grazers at undeveloped sites (Fig. 3b). Priest Lake followed this pattern in the spring; however, autumn samples showed higher proportions of both grazers and detritivores at developed sites (Fig. 3c).

Trees

In univariate PERMANOVA analyses, total tree density did not differ between developed and undeveloped sites on Lake Crescent ($P = 0.397$), but tree diameters were significantly different ($P < 0.01$). On average, trees were larger at developed (22.04 ± 20.02 cm) sites than undeveloped (14.90 ± 20.22 cm) sites. Results

Table 4 SIMPER analysis results for tree species driving tree community assemblage differences between developed and undeveloped sites in Lake Crescent

| Tree species | % contribution | Cumulative % |
|------------------------------|----------------|--------------|
| <i>Alnus rubra</i> | 28.12 | 28.12 |
| <i>Thuja plicata</i> | 23.54 | 51.66 |
| <i>Pseudotsuga menziesii</i> | 20.05 | 71.71 |
| <i>Acer macrophyllum</i> | 19.88 | 91.59 |

Variables with a high per cent contribution are 'discriminating' variables, which means they were most strongly associated with community assemblage differences between developed and undeveloped sites. *A. rubra* and *T. plicata* contributed the most to differences between developed and undeveloped sites.

from multivariate PERMANOVA indicated that tree species assemblage differed significantly with development status ($P = 0.03$). In the SIMPER results, alder (*Alnus rubra* Bong) and western red cedar (*Thuja plicata* Lamb) were the top two discriminating species (Table 4). Alder were generally more common at developed sites (Alder: mean = 10.75 ± 10.83 , Cedar: mean = 0.36 ± 1.06) while cedar were more common at undeveloped sites (Alder: mean = 2.50 ± 3.11 , Cedar: mean = 4.50 ± 6.45).

Algal composition

Algae community composition changed spatially and temporally at all three lakes. Exploratory analysis using 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. A PERMANOVA model with data at finer taxonomic resolution 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 autumn (Fig. 4a). 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. Spring samples (March 2006) showed a large proportion of filamentous algae in developed sites and a high proportion of diatoms in

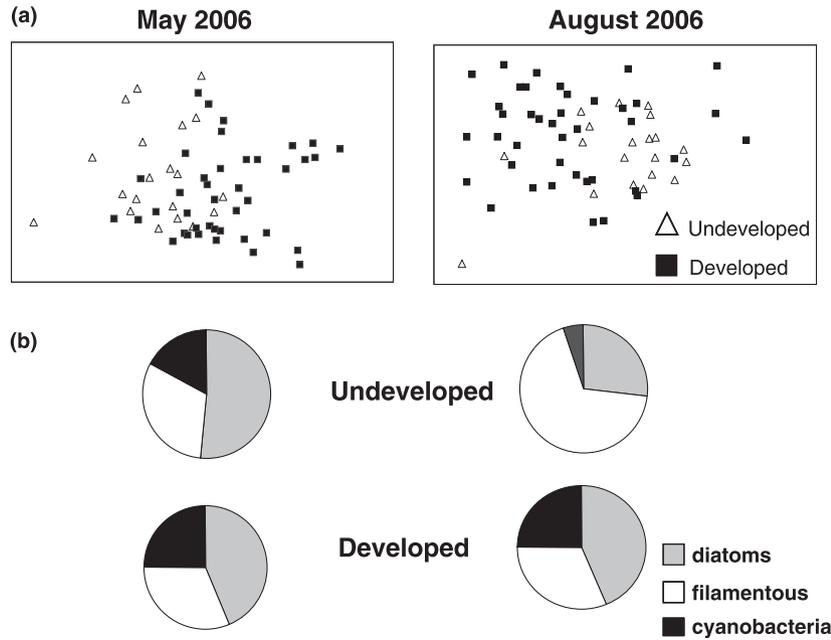


Fig. 4 Lake Crescent algae samples from (a) May 2006 and August 2006 mapped using MDS to differentiate composition of groups of algae genera from developed and undeveloped sites and (b) relative proportions of diatoms, filamentous green algae and cyanobacteria found at developed and undeveloped sites in May 2006 and August 2006 that were determined to best discriminate between developed and undeveloped groupings in SIMPER analyses.

undeveloped sites (Fig. 4b). In the late summer (August 2006), cyanobacteria increased at developed sites but decreased at undeveloped sites (Fig. 4b).

Although lakes differed in algal composition overall, development status significantly affected algal communities across lakes and dates. A MDS plot for Lake Pend Oreille showed a strong separation between spring and autumn sample assemblages, as well as separation between developed and undeveloped sites within the autumn (Fig. 5). Priest Lake exhibited similar seasonal separation but less difference between developed and undeveloped sites (Fig. 5). SIMPER analysis of each sample date indicated that diatoms and filamentous green algae were the main contributors to observed algal composition differences between developed and undeveloped sites. 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 autumn sampling period. Priest Lake had more green filamentous algae at developed sites than at undeveloped sites in the spring, but in the autumn samples, green filaments were only slightly more abundant at developed sites and cyanobacteria increased at undeveloped sites. In

all three lakes, *Spirogyra* and *Zygnema* were the most common genera of filamentous green algae, with *Mougeotia* similarly abundant at Lake Crescent, and *Bulbochaete* similarly abundant in the Idaho lakes. Thus, while development affected algal communities across lakes and tended to favour filamentous green algae and diatoms, the patterns were idiosyncratic among lakes.

Stable isotope analysis

Stable isotope analysis of periphyton and macroinvertebrates from each site on Lake Crescent revealed highly variable nitrogen signatures, suggesting that $\delta^{15}\text{N}$ was not a reliable indicator of residential development effects. Developed and undeveloped sites did not differ significantly in $\delta^{15}\text{N}$ values of macroinvertebrates ($P = 0.56$) nor periphyton ($P = 0.65$). Analysis of $\delta^{15}\text{N}$ values 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 the filamentous green algae (*Mougeotia* spp.) have a slightly higher $\delta^{15}\text{N}$ (5.559‰ , $n = 1$) than diatoms ($2.997\text{‰} \pm 0.179$,

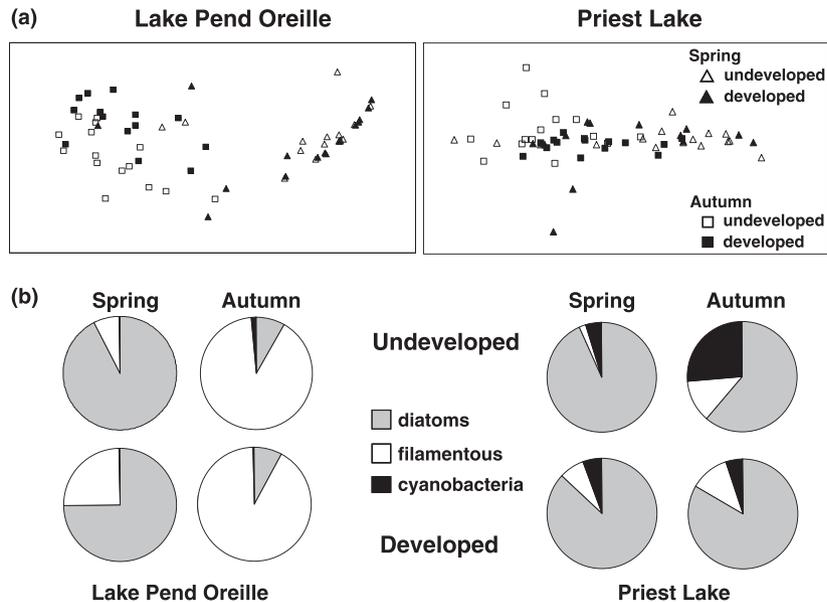


Fig. 5 Spring and autumn algal community composition (a) mapped using MDS to differentiate composition of groups of algae genera from developed and undeveloped sites for Lake Pend Oreille and Priest Lake, and (b) relative proportions of the algal taxa found to best discriminate between developed and undeveloped groupings in SIMPER analyses for Lake Pend Oreille and Priest Lake in the spring and autumn.

$n = 3$, for *N. pelliculosa*) when cultured under the same conditions.

Grazing experiment

To determine whether macroinvertebrates displayed differential assimilation of periphyton taxa that were characteristic of developed and undeveloped sites, we spiked the filamentous green algae to extremely high $\delta^{15}\text{N}$ levels (7600‰) and tracked its retention in grazer tissues. The filamentous green algae's nitrogen signature became depleted over time, but still stayed high (2400‰) as the experiment progressed (Fig. 6a). Diatoms remained at roughly their original values (2.997‰) and the snails and amphipods both exhibited increased $\delta^{15}\text{N}$ values (Fig. 6a), indicating that the grazers did ingest filamentous algae and that diatoms did not incorporate the artificially spiked nitrogen from the green algae inoculum. Proportions of nitrogen from diatomaceous compared to filamentous green algae that was incorporated into macroinvertebrate tissue were calculated using the mixing model (Nadelhoffer & Fry, 1994). 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), suggesting a small degree of filamentous green algae assimilation. Values over 1.00 probably indicate the consumption of detritus prior to start of experiment.

Discussion

Human settlement along lakeshores can substantially impact aquatic nutrient cycles (Carpenter *et al.*, 1998; Vadeboncoeur, Lodge & Carpenter, 2001; Chandra *et al.*, 2005), productivity of higher organisms like fish (Schindler *et al.*, 2000) and aesthetic properties that humans value (Edmondson, 1991; Rothrock & Mosier, 1997; Jacoby *et al.*, 2000). In large deep oligotrophic lakes, where a substantial proportion of primary productivity can occur in the littoral zone (Vadeboncoeur *et al.*, 2003), such nearshore changes may impact the lake-wide food web dependent on this productivity before offshore changes are noticeable.

Our results suggest that monitoring indicators of productivity in the nearshore may be a helpful tool for managers. Many agencies monitor pelagic water quality, which is effective in tracking major open

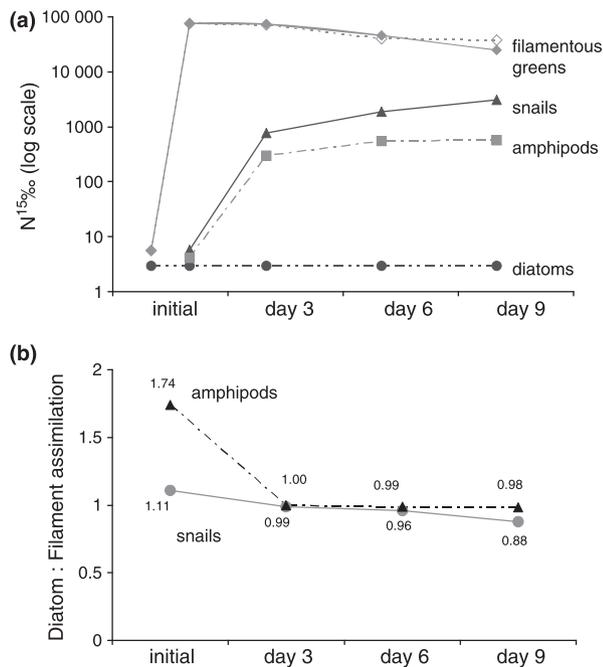


Fig. 6 Laboratory experiment results showing: (a) $N^{15}\text{‰}$ (log scale) of macroinvertebrates and algae used in the tracer experiment. Filamentous green algae were spiked with an elevated N^{15} tracer, rinsed and added to a flask containing unspiked diatoms. Amphipods and snails were added to individual flasks and sampled over nine days to determine the proportion of diatoms versus filamentous algae in their diet. (b) Proportion of N^{15} (‰) from diatomaceous versus filamentous algae incorporated into macroinvertebrate tissues at the beginning of the experiment (prior to tracer addition) and final proportion of filamentous green versus diatomaceous algae assimilation by macroinvertebrates. Values over 1.00 are indicative of consumption of detritus prior to start of experiment.

water changes in mesotrophic and eutrophic lakes (Gannon & Stemberger, 1978; Stemberger, Larsen & Kincaid, 2001). However, nearshore changes may occur without any sign of eutrophication in the open water (Jacoby *et al.*, 1991; Rothrock & Mosier, 1997; Falter, 2004), and the ability of periphyton to rapidly assimilate nutrients complicates the use of water nutrient levels to expose the presence of nutrient pollution. In oligotrophic lakes such as Lake Crescent, pelagic nutrient concentrations are frequently below standard analytical detection limits (Seminet-Reneau, 2007, National Park Service unpublished data), further complicating their usefulness as monitoring indicators. Here, in spite of strong lake-specific temporal and spatial patterns, some general littoral indicators of development impacts did emerge that may prove to be useful for managers.

Algal growth and detritus at developed sites

Periphyton biomass was higher at developed sites in this study, even though water column nutrient levels at these sites were extremely low and in many cases below standard detection limits (Seminet-Reneau, 2007), suggesting that periphyton in the littoral zone of these oligotrophic lakes quickly incorporates nutrients near shoreline development. Using ^{15}N tracers, significant uptake of nitrogen by periphyton in lotic systems has been shown to be rapid, ranging from 5 (Mulholland *et al.*, 2000) to 20 min (Hall, Peterson & Meyer, 1998) in streams and up to an hour in a large river (Peterson, Bahr & Kling, 1997). Uptake is slower in lentic systems because of low water velocity and subsequently thicker diffusive boundary layers (Jumars, Eckman & Koch, 2001; Larned, Nikora & Biggs, 2004), but significantly enriched nitrogen levels still occur within 5 h of addition in oligotrophic lakes (Hadwen & Bunn, 2005). Nutrients from shoreline septic systems probably enter lakes as groundwater flow and are susceptible to interception by periphyton. Thus, for nutrient enrichment of littoral origin, littoral variables may be particularly valuable indicators relative to pelagic ones. Here these significant differences occurred within a range of periphyton chlorophyll *a* values (1–16 mg m^{-2}) that is much lower than many values reported for similarly large oligotrophic lakes, such as Lake Tahoe (10–150 mg m^{-2} ; Loeb, 1986) and Lake Chelan (1–140 mg m^{-2} ; Jacoby *et al.*, 1991).

Stable isotope signatures have been used to distinguish among aquatic systems that have been impacted by human sewage, fertilization or urbanization (Heaton, 1986; Axler & Reuter, 1996; Lindau, Delaune & Alford, 1997; Steffy & Kilham, 2004). In the present study, our stable isotope measurement did not distinguish between developed and undeveloped sites. Our inability to discriminate among sites could be because of a number of factors, but suggests that either processes that fractionate nitrogen isotopes do not govern the nitrogen cycle in developed sites or that changes in the $\delta^{15}\text{N}$ signature over relatively small spatial scales become diluted in the littoral environment. A combination of multiple N sources in developed sites could provide an explanation for the dilution of a $\delta^{15}\text{N}$ signature in developed sites. Nitrogen isotope signatures of lawn fertilizer (-2‰ to $+4\text{‰}$) and human sewage ($+10$ to $+22\text{‰}$),

could mix in these sites resulting in $\delta^{15}\text{N}$ values that are not significantly different from undeveloped sites (+3 to +9‰; Cole *et al.*, 2004). Mixed isotopic signatures may have been particularly problematic during this study, when very high spring precipitation may have increased the contribution of nutrients from overland sources in 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 under controlled laboratory conditions, suggesting that future studies should be cautious when interpreting enriched $\delta^{15}\text{N}$ values of autotrophs as indicative of an altered nitrogen cycle (e.g. agricultural or sewage enhancement).

Whether nutrients are derived from sewage or runoff, increased algal biomass at developed sites strongly suggests that these sites receive increased nutrients. The indicators of productivity showed increases in living and dead material at developed sites in the form of higher chlorophyll *a*, pheophytin *a*, AFDM and AI. These results are consistent with other studies that have documented increased periphyton growth in response to nutrient additions in a diversity of lake types (Jacoby *et al.*, 1991; Havens *et al.*, 1999; Hadwen *et al.*, 2005).

The observed increased algal biomass associated with development in Lake Crescent was not as evident in Lake Pend Oreille and Priest Lake, although there were non-significant trends toward higher levels of 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 multivariate differences among sites in this study were primarily related to AFDM, with chlorophyll *a* of secondary importance, suggests that as algal biomass increases at developed sites, the accumulation of detritus is important. Falter (2004) hypothesized that the high levels of detritus could be attributed to the thick mats of diatoms that were observed on nearshore rocks.

Accumulation of detritus may also be related to terrestrial inputs at developed sites, in the form of deciduous leaves (Francis *et al.*, 2007). Homeowners appeared to favour deciduous trees (*A. rubra*) over the conifers present at undeveloped sites, and while they did not have significantly more or fewer trees, cultivated trees were typically larger than those at undeveloped sites. This result is consistent with

other work showing increased size of riparian trees at developed sites, but a decrease in the density of woody debris in the water (Christensen *et al.*, 1996). These results may reflect homeowners' tendencies to keep big decorative trees while clearing away understory vegetation and snags for lawns. Nitrogen fixing species (*A. rubra*) were also much more abundant at developed sites, potentially because they are an early pioneering species that responds well to disturbance, which may ultimately influence nutrient inputs to the lake (Compton *et al.*, 2003).

Higher detritus at developed sites was accompanied by a shift from grazing macroinvertebrates to detritivorous macroinvertebrates, especially at Lake Crescent where the algal biomass and macroinvertebrate shifts were highly significant. Such shifts toward detritivores have been experimentally induced in other studies by controlled additions of dead material (Richardson, 1991; Pretty & Dobson, 2004).

Algal community characteristics at developed sites

In Lake Crescent, filamentous green algae were clearly more common at developed sites than at undeveloped sites, where diatoms dominated, and this trend was distinguishable across the three lakes. Thus, periphyton monitoring may be a useful tool for assessing nutrient pollution by detecting shifts in algal community composition towards species associated with eutrophication. For example, increased filamentous green algae associated with elevated nutrients have been reported in nearby Lake Chelan (Jacoby *et al.*, 1991), for nutrient-rich rivers (Chetelat *et al.*, 1999) and across a gradient of shallow Danish lakes (Liboriussen & Jeppesen, 2006). Undeveloped sites were characterized by slightly higher abundance of cyanobacteria. Cyanobacteria, though commonly associated with openwater eutrophication (Edmondson, 1994), can also thrive in oligotrophic conditions because of the ability of some species to fix nitrogen (Reuter, Loeb & Goldman, 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. 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 & Stevenson, 1992; Correll, Jordan & Weller, 1999) and run-off patterns (McMahon & Harned, 1998; Groffman *et al.*, 2004), wind dynamics that influence mixing and upwelling (O'Reilly, 2006) and the seasonality of human activities in the catchment. In Lake Crescent, where differences between developed and undeveloped sites were the strongest, monitoring algal trends in the spring is probably to provide the greatest contrast between developed and undeveloped sites.

On Lake Pend Oreille and Priest Lake, temporal patterns were lake-specific, and we speculate that these differences among lakes were affected by water level changes related to hydroelectric dams on both lakes. Water level may drop as much as three metres between autumn and spring as a result of hydroelectric dam management on these lakes. During the spring sampling, the water level at each Idaho lake was at a low stage so samples were collected from 'deep' rocks (i.e. they were submerged much more deeply at other times) whereas in the autumn, the water had risen so samples were collected from rocks that had been newly immersed. While the hydrologic conditions thus appeared roughly the same at these lakes, the algal responses were not – filamentous green algae came to dominate the autumn samples at Lake Pend Oreille without such a strong temporal change at Priest Lake. Of course differences may also relate to scouring of periphyton during storm events, although we are unable to evaluate in this study how such differences may emerge among these lakes.

In spite of lake-specific trends, significant general differences between developed and undeveloped sites across all three lakes emerged. As multivariate productivity measures differed between developed and undeveloped sites overall, with AFDM being most indicative of development, developed sites were also associated with a greater proportion of filamentous green algae. 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

Field collections revealed 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 algal food source. Amphipods and snails both assimilated a much higher proportion of diatoms (0.88–0.98) than filamentous algae. Avoidance of filamentous algae has been noted among other nearshore grazers, with these herbivores frequently showing a pronounced selectivity for diatoms (Moore, 1975; Gray & Ward, 1979; Bowker, Wareham & Learner, 1983; Mihuc & Toetz, 1994). Conversely, some macroinvertebrates consume a substantial amount of filamentous green algae, including the *Mougeotia* that dominated many of our samples (Lowe & Hunter, 1988; Kornijow, Gulati & Donk, 1990). Together this evidence from the literature and our experimental results illustrates that macroinvertebrates differentially assimilate the algal taxa available to them, such that higher productivity at developed sites is not simply producing 'more of the same' food resources that are found at undeveloped sites – for either the macroinvertebrates or the fish that move inshore to feed. This complexity in food web response to nutrient pollution is especially important to acknowledge in large deep oligotrophic lakes where nearshore productivity characteristics can strongly influence a food web dependent on nearshore resources.

In summary, activities that alter the nearshore environment where top predators breed and feed may have strong effects on the lake-wide food web in spite of continuing high water quality offshore. Here we found that developed sites across all lakes differed from undeveloped sites in a manner consistent with nutrient enrichment. 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 lake-wide implications as detritivorous macroinvertebrates and grazers that favour green algae become more common. Additionally, these nearshore environmental changes may impact the habitat required by certain species, such as plant species

adapted to oligotrophic conditions (i.e. *L. 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 shoreline development reaches high levels. Monitoring nearshore periphyton can indicate to managers nearshore resources changes that may impact the broader food web, in addition to providing an early warning of eutrophication before profound effects are evident in the pelagic environment.

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References

Anderson M.J. (2001a) A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, **26**, 32–46.

Anderson M.J. (2001b) Permutation tests for univariate or multivariate analysis of variance and regression. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 626–639.

Arar E.J. & Collins G.B. (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, OH.

Axler A.P. & Reuter J.E. (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. & Kilroy C. (2000) *Stream Periphyton Monitoring Manual*. NIWA, Christchurch.

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

Brown G.W. & Krygier J.T. (1970) Effects of clear-cutting on stream temperature. *Water Resources Research*, **6**, 1133–1139.

Carpenter S.R., Christensen D.L., Cole J.J. et al. (1995) Biological-control of eutrophication in Lakes. *Environmental Science & Technology*, **29**, 784–786.

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

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

Chetelat J., Pick F.R., Morin A. & Hamilton P.B. (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., Herwig B.R., Schindler D.E. & Carpenter S.R. (1996) Impacts of lakeshore residential development on coarse woody debris in north temperate lakes. *Ecological Applications*, **6**, 1143–1149.

Clarke K.R. & Gorely R.N. (2006) *Primer v6: User Manual/Tutorial*. PRIMER-E Ltd, Plymouth.

Clarke K.R. & Warwick R.M. (2001) *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. PRIMER-E Ltd, Plymouth.

Cole M.L., Valiela I., Kroeger K.D., Tomasky G.L., Cebrian J., Wigand C., Mckinney R.A., Grady S.P. & Carvalho Da Silva M.H. (2004) Assessment of a $\delta^{15}\text{N}$ isotopic method to indicate anthropogenic eutrophication in aquatic ecosystems. *Journal of Environmental Quality*, **33**, 124–132.

- Compton J.E., Church M.R., Larned S.T. & Hogsett W.E. (2003) Nitrogen export from forested watersheds in the Oregon Coast Range: the role of N₂-fixing red alder. *Ecosystems*, **6**, 773–785.
- Correll D.L., Jordan T.E. & Weller D.E. (1999) Transport of nitrogen and phosphorus from Rhode River watersheds during storm events. *Water Resources Research*, **35**, 2513–2521.
- Edmondson W.T. (1959) *Freshwater Biology*, Wiley, New York.
- Edmondson W.T. (1991) *The Uses of Ecology: Lake Washington and Beyond*. University of Washington Press, Seattle, WA.
- Edmondson W.T. (1994) Sixty years of Lake Washington: a curriculum vitae. *Lake and Reservoir Management*, **10**, 75–84.
- Falter M.C. (2004) *Lake Pend Oreille Littoral Periphyton Community: An Updated Trophic Status Assessment 2003*. Final Report submitted to the Tri-state water quality council, Moscow, ID.
- Francis T.B. & Schindler D.E. (2006) Degradation of littoral habitats by residential development: woody debris in lakes of the Pacific Northwest and Midwest, United States. *Ambio*, **35**, 274–280.
- Francis T.B., Schindler D.E., Fox J.M. & Seminet-Reneau E. (2007) Effects of urbanization on the dynamics of organic sediments in temperate lakes. *Ecosystems*, **10**, 1057–1068.
- Gannon J.E. & Stemberger R.S. (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. & Ward J.V. (1979) Food habits of stream benthos at sites of differing food availability. *American Midland Naturalist*, **102**, 157–167.
- Groffman P.M., Law N.L., Belt K.T., Band L.E. & Fisher G.T. (2004) Nitrogen fluxes and retentions in urban watershed ecosystems. *Ecosystems*, **7**, 393–403.
- Hadwen W.L. & Bunn S.E. (2005) Food web response to low-level nutrient and 15N-tracer additions in the littoral zone of an oligotrophic dune lake. *Limnology and Oceanography*, **50**, 1096–1105.
- Hadwen W.L., Bunn S.E., Arthington A.H. & Mosisch T.D. (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 R.O., Peterson B.J. & Meyer J.L. (1998) Testing a nitrogen-cycling model of a forest stream by using a nitrogen-15 tracer addition. *Ecosystems*, **1**, 283–298.
- Havens K.E., East T.L., Hwang S.J., Rodusky A.J., Sharpsteing B. & Steinman A.D. (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.
- Hillebrand H., Durselen C.D., Kirschtel D., Pollinger U. & Zohary A.T. (1999) Biovolume calculations for pelagic and benthic microalgae. *Journal of Phycology*, **35**, 408–424.
- Humphrey K.P. & Stevenson R.J. (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., Bouchard D.D. & Patmont C.R. (1991) Response of periphyton to nutrient enrichment in Lake Chelan, WA. *Lake and Reservoir Management*, **7**, 33–43.
- Jacoby J.M., Collier D.C., Welch E.B., Hardy F.J. & Crayton M. (2000) Environmental factors associated with a toxic bloom of *Microcystis aeruginosa*. *Canadian Journal of Fisheries and Aquatic Science*, **57**, 231–240.
- Johnson S.L. & Jones J.A. (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., Eckman J.E. & Koch E. (2001) Macroscopic animals and plants in benthic flows. In: *The Benthic Boundary Layer* (Eds B.P. Boudreau & B.B. Jorgensen), pp. 320–347. Oxford University Press, Oxford.
- Kann J. & Falter C.M. (1989) Periphyton as indicators of enrichment in Lake Pend Oreille, Idaho. *Lake and Reservoir Management*, **5**, 39–48.
- Kornijow R., Gulati R.D. & Donk E.V. (1990) Hydrophyte-macroinvertebrate interactions in Zwemlust, a lake undergoing biomanipulation. *Hydrobiologia*, **200/201**, 467–474.
- Larned S.T., Nikora V.I. & Biggs B.J.F. (2004) Mass-transfer-limited nitrogen and phosphorus uptake by stream periphyton: a conceptual model and experimental evidence. *Limnology and Oceanography*, **49**, 1992–2000.
- Leavitt P.R., Brock C.S., Ebel C. & Patoine A. (2006) Landscape-scale effects of urban nitrogen on a chain of freshwater lakes in central North America. *Limnology and Oceanography*, **51**, 2262–2277.
- Liboriussen L. & Jeppesen A.E. (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., Delaune R.D. & Alford D.P. (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.
- Loeb S.L. (1986) Algal biofouling of oligotrophic Lake Tahoe: causal factors affecting production. In: *Algal Biofouling* (Eds L.V. Evans & K.D. Hoagland), pp. 159–173. Elsevier Science Publishers, Amsterdam.
- Lowe R.L. & Hunter R.D. (1988) Effect of grazing by *Physa integra* on periphyton community structure. *Journal of the North American Benthological Society*, **7**, 29–36.
- McMahon G. & Harned D.A. (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. & Cummins K.W. (1996) *An Introduction to the Aquatic Insects of North America*. Kendall/Hunt Publishing Company, Dubuque, IA.
- Mihuc T. & Toetz D. (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., Schindler D.E., Scheuerell M.D., Smith D. & Frodge J. (2003) Lake eutrophication at the urban fringe, Seattle region, USA. *Ambio*, **32**, 13–18.
- Mulholland P.J., Tank J.L., Sanzone D.M., Wollheim W.M., Peterson B.J., Webster J.R. & Meyer J.L. (2000) Nitrogen cycling in a forest stream determined by a ^{15}N tracer addition. *Ecological Monographs*, **70**, 471–493.
- Meyer J. & Fradkin S. (2002) *Summary of Fisheries and Limnological Data for Lake Crescent, Washington*. Olympic National Park report, Port Angeles, WA.
- Nadelhoffer K.J. & Fry B. (1994) Nitrogen isotope studies in forest ecosystems. In: *Stable Isotopes in Ecology and Environmental Science* (Eds K. Lajtha & R.H. Michener), pp. 22–44. Blackwell Scientific, Cambridge, MA.
- O'Reilly C.M. (2006) Seasonal dynamics of periphyton in a large tropical lake. *Hydrobiologia*, **553**, 293–301.
- 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. & Cereghino P.R. (2002) *Baseline Survey of Lobelia Dortmanna (Campanulaceae) in Lake Crescent, Olympic National Park*. Olympic National Park report, Port Angeles, WA.
- Peterson B.J. & Fry B. (1987) Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics*, **18**, 293–320.
- Peterson B.J., Bahr M. & Kling G.W. (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. & Dobson A.M. (2004) The response of macroinvertebrates to artificially enhanced detritus levels in plantation streams. *Hydrology and Earth System Sciences*, **8**, 550–559.
- Reuter J.E., Loeb S.E. & Goldman C.R. (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., Tuchman N.C., Wetzel R.G. & Teeri J.A. (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.
- Rothrock G.C. & Mosier D.T. (1997) *Phase 1 Diagnostic Analysis: Priest Lake, Bonner County, Idaho 1993–1995*. Idaho Department of Health and Welfare, Division of Environmental Quality Report, Boise, ID.
- Schindler D.E., Geib S.I. & Williams M.R. (2000) Patterns of fish growth along a residential development gradient in North temperate lakes. *Ecosystems*, **3**, 229–237.
- Seminet-Reneau E.E. (2007) *Effects of Shoreline Development on the Nearshore Environment of a Large Deep Nutrient-Poor Lake (Lake Crescent, USA)*. Master's Thesis, University of Idaho, Moscow, ID.
- Steffy L.Y. & Kilham S.S. (2004) Elevated $\delta^{15}\text{N}$ 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., Larsen D.P. & Kincaid T.M. (2001) Sensitivity of zooplankton for regional lake monitoring. *Canadian Journal of Fisheries and Aquatic Science*, **58**, 2222–2232.
- 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.
- Tuchman N.C., Wetzel R.G., Rier S.T., Wahtera K.A. & Teeri J.A. (2002) Elevated atmospheric CO_2 lowers leaf litter nutritional quality for stream ecosystem food webs. *Global Change Biology*, **8**, 163–170.
- Vadeboncoeur Y., Lodge D.M. & Carpenter S.R. (2001) Whole-lake fertilization effects on distribution of

- primary production between benthic and pelagic habitats. *Ecology*, **82**, 1065–1077.
- Vadeboncoeur Y., Jeppesen E., Zanden M.J.V., Schierup H.H., Christoffersen K. & Lodge D.M. (2003) From Greenland to green lakes: cultural eutrophication and the loss of benthic pathways in lakes. *Limnology and Oceanography*, **48**, 1408–1418.
- WADNR (2003) *Lobelia Dortmanna* L. Washington Department of Natural Resources Report. Olympia, WA.
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