

Disproportionate importance of nearshore habitat for the food web of a deep oligotrophic lake

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Abstract. In large deep oligotrophic lakes, multiple lines of evidence suggest that the shallow nearshore water provides disproportionately important feeding and breeding habitat for the whole-lake food web. We examined the trophic importance of the nearshore environment, human impacts nearshore, and several approaches to disturbance detection in a deep (190 m) oligotrophic lake with relatively modest residential development. In Lake Crescent, on the Olympic Peninsula of Washington (USA), stable isotope analysis demonstrated that apex salmonid predators derived more than 50% of their carbon from nearshore waters, even though this nearshore water accounted for only 2.5% of total lake volume. Unfortunately, it is this land–water interface that is initially degraded as shorelines are developed. We hypothesised that under these conditions of relatively modest disturbance, the effects of residential development would be strongly localised near to shore. Indeed, we found striking differences between developed and undeveloped sites in periphyton and associated organic matter, though there were no offshore signals of human impact in water nutrient analysis or paleolimnological investigations. Together, these results suggest that nearshore biological monitoring should be integrated in lake management plans to provide ‘early warning’ of potential food-web repercussions before pollution problems are evident in open water and comparatively intractable.

Additional keywords: habitat coupling, littoral zone, *Oncorhynchus clarkii*, *Oncorhynchus mykiss*, recreational fisheries, septic systems.

Introduction

Knowledge of the processes that couple pelagic, benthic, littoral, and terrestrial environments has increased dramatically over the past several decades. Although historically, limnological studies have treated these environments as functionally isolated (Threlkeld 1994; Reynolds 2008), the abiotic and biotic pathways among these habitats are now widely acknowledged and provide fertile ground for more integrative research (Schindler and Scheuerell 2002; Reynolds 2008; Vadeboncoeur *et al.* 2008). Our understanding of the pelagic food web, in particular, has been rapidly refined by integrating not only the vertical fluxes that connect it to the benthos, but also its relationship with the shallow-water nearshore area where lakes meet the land (Reynolds 2008).

Nearshore waters can be ‘hotspots’ for both autotrophic and heterotrophic production. Periphyton and macrophytes growing in these shallow areas can contribute substantially to the overall productivity of lakes (Vadeboncoeur *et al.* 2002), particularly in large oligotrophic lakes (Vadeboncoeur *et al.* 2008). This

nearshore primary production may be fuelled by autochthonous and allochthonous dynamics, to varying degrees, as carbon and other nutrients from land enter the lake at the littoral edges (Carpenter *et al.* 2005; Ask *et al.* 2009). Associated with these littoral resources are rich aquatic macroinvertebrate communities that provide important forage for larger predators. Predators may also benefit substantially from foraging nearshore on terrestrial invertebrates that fall from overhanging vegetation (Francis and Schindler 2009).

These nearshore dynamics are connected with the offshore environment and its inhabitants through both physical and biological processes. Hydrodynamics may variously move littoral inputs (e.g. nutrients) horizontally along the shoreline, towards deeper benthic zones, and into pelagic waters (MacIntyre and Melack 1995). However, the distribution of elements entering at the shoreline is not entirely dependent on hydrodynamic processes. For example, highly mobile organisms may move between the nearshore and offshore environments – for feeding, breeding, and refuge from predators – and accordingly they may

move littoral matter offshore. Fish exploit nearshore hotspots of productivity, distributing nearshore carbon and nutrients throughout the lake (Schindler and Scheuerell 2002; Vander Zanden and Vadeboncoeur 2002; Dolson *et al.* 2009). In addition to feeding in the nearshore areas, many fish that are normally found offshore mate and lay their eggs in shallow water, and are active near shore during breeding seasons (Cott *et al.* 2008; Probst *et al.* 2009). Finally, these shallow waters and associated structural complexity also provide refuge from predators for juvenile fish and other vulnerable organisms; these prey organisms may hide in nearshore vegetation and submerged debris, but also move offshore at times (Lewin *et al.* 2004; Sass *et al.* 2006). Thus nearshore waters serve a wide range of functions for the lake ecosystem.

Importantly, the nearshore environment is the area of the lake with which humans directly interface (Strayer and Findlay 2010). Humans build homes at the lakeshore, disturbing sediment (Francis *et al.* 2007; Donohue and Molinos 2009) and altering inputs of coarse woody debris and other terrestrial litter that harbours insects important in fish diets (Francis and Schindler 2006, 2009). At the lake perimeter, humans also frequently contribute sewage even when treatment systems are in place (Moore *et al.* 2003), and directly physically perturb the nearshore area with boating and wading activity (Lewin *et al.* 2006; O'Toole *et al.* 2009). Given the variety of services provided to the lake ecosystem by the nearshore environment, human impacts in the nearshore environment may have disproportionate effects on the food web, resonating all the way up to the apex fish predators.

If a goal of lake monitoring is early detection of human impacts, then it should be alarming that so many monitoring plans focus almost exclusively on open-water measures, with relatively few programs incorporating nearshore measures (e.g. Jeppesen *et al.* 2005). Nutrients entering the nearshore environment can be quickly scavenged and retained by nearshore biota, so that nutrients may not detectably increase in samples taken in the water column or offshore during early stages of pollution (Hadwen and Bunn 2005). Paleolimnological analyses can help to discern pollution signals that are integrated over long time periods and large areas, but sedimentary records may not carry strong signals in early stages of shoreline development (Garrison and Wakeman 2000). By the time pollution effects are evident in offshore water samples or offshore sediments, the problem may be comparatively difficult to address with management actions (Jeppesen *et al.* 2005). Of course, monitoring programs are established for many different reasons, but if a goal is environmental protection, incorporating nearshore measures appears to be important.

Here we test the hypotheses that, in a naturally nutrient-poor lake with relatively strong management controls on human disturbance: (1) food resources for apex predators are concentrated at the shoreline, (2) even modest residential development can result in dramatic, localised nearshore pollution effects, and (3) these pollution effects may not be observable in standard measures offshore. Taken together, the multi-proxy approach we employ ultimately illustrates that nearshore disturbance has strong potential to affect the whole-lake food web, highlighting the need for nearshore biological monitoring. Such monitoring can help managers to detect pollution problems in relatively early stages, before pollution is evident offshore.

Materials and methods

Study area

Lake Crescent is a deep, nutrient-poor lake within the federally protected Olympic National Park (established in 1938), in the state of Washington (USA). In a basin that is 17.7 km long, the maximum depth of the lake is 190 m, and more than 50% of the surface overlies water that is at least 90 m deep (Fig. 1). Most of the shallow water occurs in the northern basin, near the Lyre river outlet, the area that has the highest density of residential development. Over half of the 121 houses in the National Park lie along East Beach Road, which traverses the northern end of the lake (Meyer and Fradkin 2002). The lake's nearshore waters do visibly differ near residences in general (Rosenberger *et al.* 2008), possibly owing to aging septic systems (*sensu* Moore *et al.* 2003); however, this level of residential development is considered very low for a lake of this size relative to other lakes in the North American Pacific Northwest (Francis and Schindler 2006), and its offshore waters are very clear. The annual average Secchi depth is 18 m, and the maximum seasonal Secchi depth is 28 m. The lake is ultra-oligotrophic and water-column nutrients are typically below standard detectable limits (Seminet-Reneau 2007; Fradkin 2010). Given the lake's large size and current protection from further watershed development, Lake Crescent could be viewed as relatively well-buffered against potential effects of the comparatively modest residential development that has occurred at its shoreline.

The lake's fisheries and environmental integrity are viewed by the National Park Service (NPS) as resources to be protected for future generations (Meyer and Fradkin 2002). Two salmonid species are apex predators of conservation interest because they are native, unique, and important recreational fisheries. The Beardslee trout (*Oncorhynchus mykiss*) is an endemic coastal rainbow trout (Baker 2000). Similarly, the Crescenti trout (*Oncorhynchus clarkii*) is a morphologically, but not genetically, distinct coastal cutthroat trout (Baker 1998). Historically, Beardslee trout provided a popular fishery that resulted in a steep population decline. This population has rebounded with the introduction of catch-and-release regulations in 2000 (Meyer and Fradkin 2002). Native kokanee (*Oncorhynchus nerka*) are prominent in the diets of the Beardslee and Crescenti trout. Less is known of the ecology of the prickly sculpin (*Cottus asper*) and pygmy whitefish (*Prosopium snyderi*) in the lake. Although residential development and corresponding nearshore impacts may be thought to be modest compared with other lakes, salmonids use both open water and littoral areas (O'Connell *et al.* 2005; Jonsson *et al.* 2008), raising the question: in a large deep lake, how much does the nearshore environment ultimately matter to these apex predators? We used several analytical approaches to examine the extent to which human impact is evident in the offshore and nearshore environments under such conditions of modest shoreline development, and the importance that human impacts at the shoreline may have for a lake-wide food web.

Nearshore water volume and area

Nearshore and offshore water volumes were calculated using lake area and bathymetric data (NPS, unpubl. data). Nearshore waters were characterised as the volume of water above bottom

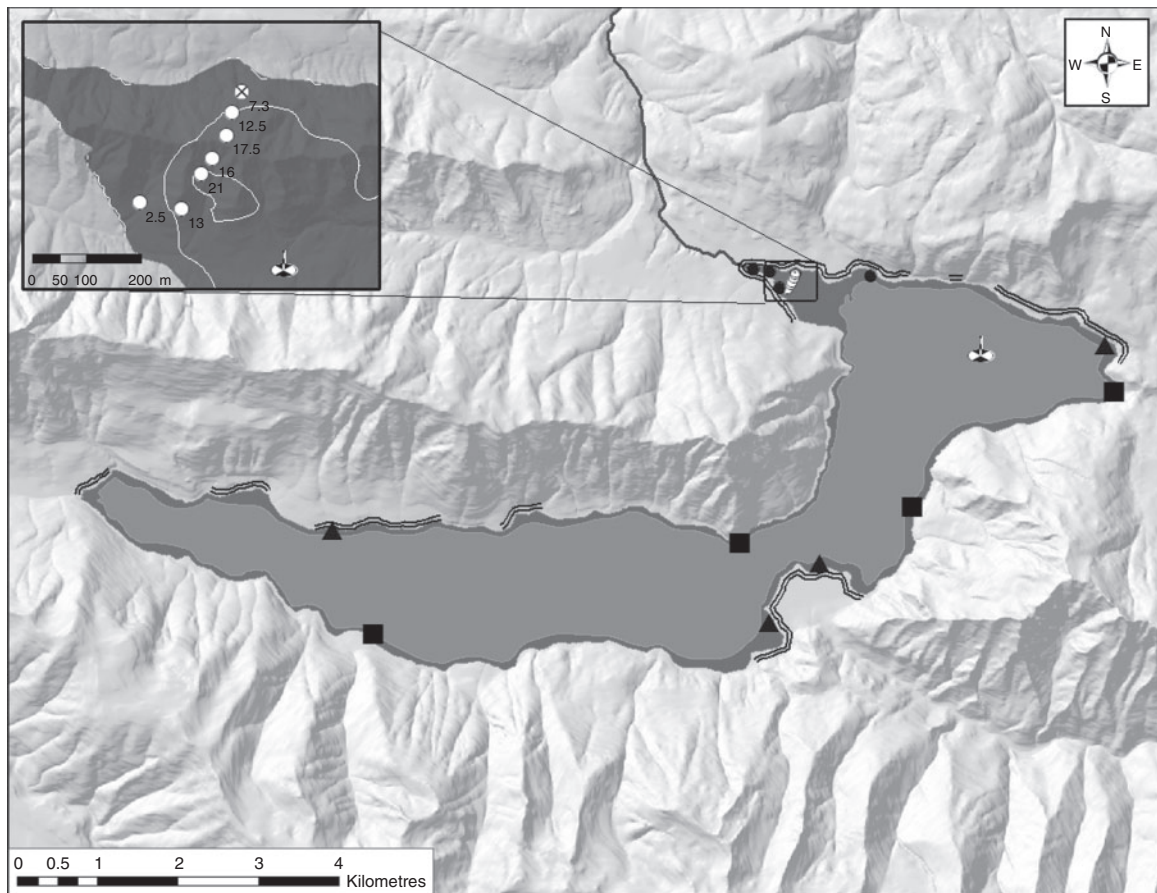


Fig. 1. Lake Crescent with nearshore zone delimited in dark grey by 30-m depth line. Double lines on the lakeshore denote areas of residential development. Triangles and squares denote paired developed and undeveloped sample sites, respectively, for periphyton and water nutrients. Black circles in the Lyre river outlet area denote Lyre outlet developed sites for periphyton and water nutrient sampling. The inset shows the location of the series of nearshore sediment cores and the corresponding water depths (m). The latitude of these cores ranged from 48.092 to 48.094, and longitude ranged from -123.797 to -123.780 . The symbol marked with 'x' (7.3 m water depth, lat 48.094, long -123.798) denotes the location of the 26-cm core selected for temporal characterisation. The black and white Secchi disk symbol indicates the locations of the NPS pelagic plankton monitoring stations.

depths of 30 m or less. This depth is approximately twice the annual average Secchi depth and represents a liberal characterisation of well-illuminated shallow waters near the shoreline of this deep oligotrophic lake. In the literature, the littoral zone has been variously delineated by the presence of macrophytes or light penetration; both definitions have limited usefulness to address our questions about nearshore effects in Lake Crescent, where macrophytes are uncommon and the compensation depth may be >60 m and distant from the shoreline.

Food-web analysis

We used stable isotopes to construct a model of the Lake Crescent food web and to compare the dependence of biota on nearshore versus offshore resources. The resulting model was considered in tandem with the gut content data from a previous study (Pierce 1984).

Fish

We obtained dorsal muscle samples from individual Lake Crescent fish. Conservation concerns constrain contemporary

sampling of Crescenti and Beardslee trout, so samples previously collected for a study designed to assess population status of Crescenti and Beardslee trout were used. The National Park Service collected these fish during breeding surveys on 47 different dates between November and March when Crescenti and Beardslee trout were aggregated in known breeding areas (Meyer and Fradkin 2002). All Beardslee trout were collected from their only known breeding area, the Lyre River outlet within the lake, and Crescenti trout were collected from the Lyre River and Barnes Creek, two of the three known Crescenti trout breeding areas. Ripe females were avoided and effort was spread out over 1996–1999 to minimise impact on populations. Fish were frozen for later scientific use, such as in the present study. In July 2005, we collected tissue from 32 individuals of each species. We attempted to sample similarly sized fish from the Park collection (total length of Beardslee trout: mean = $504 \text{ mm} \pm 24 \text{ mm s.e.}$; total length of Crescenti trout: mean = $451 \text{ mm} \pm 14 \text{ mm s.e.}$); we sampled tissues from equal numbers of Crescenti trout collected at each of the two breeding areas and the average total length of the fish we sampled did not differ

significantly between collection sites ($P = 0.12$). Kokanee collections were attempted on five dates in 2005, using a modified surface trawl, and were successful on two dates ($n = 6$). Breeding sites and timing are not well known for Lake Crescent kokanee, so collection of this highly dispersed and very small-bodied population is difficult (Meyer and Fradkin 2002). Dorsal muscle tissue samples were immediately collected from kokanee and frozen for later processing.

Invertebrates

Macroinvertebrates were collected with D-nets on seven dates between 2004 and 2005 at the developed and undeveloped locations (Fig. 1). Samples were sorted and frozen for later processing. Amphipods and corixids were the most abundant groups, but we also collected trichopterans, zygopterans, ephemeropterans, neuropterans, dytiscids, plecopterans, anisopterans, and chironomids. Because our primary interest in this work was to differentiate nearshore from offshore signals, we have grouped the stable isotope data from all nearshore macroinvertebrates, acknowledging that the inclusion of so many trophic levels would lead to higher variability in the isotope signals ($n = 62$) for this analysis. Crayfish ($n = 2$) were occasionally encountered and tail tissue sampled.

Zooplankton were collected with a 120- μm -mesh net from a standard open water sampling station (Fig. 1) on five dates between June 2004 and August 2005. Individual crustacean zooplankton were isolated from associated algae via pipette. Zooplankton samples contained dozens of individuals (primarily species within the genera *Daphnia*, *Bosmina*, *Holopedium*, *Leptodiatomus*) to achieve a dried sample weight of 1–2 mg ($n = 7$), which was frozen after sorting for later processing. Twenty mussels were collected by SCUBA divers near Barnes Point at $\sim 6\text{ m}$ depth in June 2004, and muscle tissue was extracted and frozen for later processing.

Terrestrial arthropods were collected with a sweep net from vegetation overhanging the water at developed and undeveloped sites in August 2006. Taxa included hemipterans, dipterans, lepidopterans, and arachnids. Individuals were frozen for later processing, with each individual comprising a single sample ($n = 12$).

Analysis of stable isotope data

Contributions of nearshore and offshore carbon to fish tissue were estimated and statistically compared using the IsoError model (Phillips *et al.* 2005), a linear mixing model that is enhanced by the estimation of 95% confidence intervals for the resultant source contributions. Because our primary goal in this work was to examine the importance of habitat rather than particular prey taxa, we grouped organisms that were found in the nearshore environment to create a single nearshore carbon signature (i.e. macroinvertebrates, crayfish, and terrestrial insects from overhanging vegetation). An offshore signature was obtained from zooplankton samples alone, as zooplankton comprise the primary available prey in the offshore environment. However, we also verified that grouping zooplankton and mussels to create an offshore signature yielded nearly identical patterns. We compared the resulting food web with gut content data from a previous study on Lake Crescent fish (Pierce 1984).

Nearshore environmental heterogeneity

Water nutrient status and periphyton characteristics were assessed in nearshore environments at developed and undeveloped sites. Twelve sites were selected at Lake Crescent (Fig. 1) to represent developed ($n = 8$) and undeveloped ($n = 4$) shorelines (Rosenberger *et al.* 2008). Four developed sites were paired with four undeveloped sites that had similar physical characteristics, and four further developed sites were located within the Lyre basin where Beardslee trout spawn.

Water nutrients

In November 2005, two water samples were collected from a depth of 0.5 m at the twelve nearshore sampling sites for analysis of total nitrogen and total phosphorus in the water column, using EPA method 365.4 (APHA 1998). Analysis of the 24 samples revealed nutrient levels below standard detectable limits for both phosphorus ($<0.01\text{ mg L}^{-1}$) and nitrogen (0.05 mg L^{-1}), a result consistent with long-term NPS water quality monitoring data (Fradkin 2010). Although it is possible to attain measurements below these limits, it is impractical for many monitoring programs, and we did not pursue further analysis.

Periphyton measures

Periphyton scavenge nutrients efficiently in nearshore environments (Hadwen and Bunn 2005), and samples were collected and analysed for differences that would suggest human influences at sites with residential development. Periphyton samples were collected from rock surfaces, using the modified syringe developed by Loeb (1981), at three depths from the waterline (0.25 m, 0.50 m, and 0.75 m) and pooled into a single sample at each of the 12 sampling sites during May and August 2006. Samples were filtered through a 2.5-cm glass fibre filter (VWR, 0.7- μm particle retention) and frozen until analysis. Standard fluorometry was used to evaluate chlorophyll-*a* as an indication of primary production, and pheophytin-*a* as an indication of dead material (Arar and Collins 1997). Ash-free dry mass measurements were obtained from similarly pooled samples of known area that were filtered and ashed at 400°C (Arar and Collins 1997). From separate syringe samples, collected at all 12 sites over 5 sampling periods (August 2005, November 2005, March 2006, May 2006, and August 2006), periphyton cells were enumerated and biovolume was calculated (Rosenberger *et al.* 2008). We used Welch's ANOVA (allowing for unequal variance between groups) to determine whether there was an effect of development status on periphyton characteristics.

Paleolimnological reconstruction of nutrient history

Analyses of sedimentary stable isotopes and fossil pigments were used to determine whether nearshore development over the past century has altered the nutrient content (as reflected in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) and primary production (pigments) of offshore biotic assemblages. Specifically, eight sediment cores were collected along a transect across the north arm of Lake Crescent (Fig. 1) using a Glew gravity corer fitted with a 10-cm-diameter core barrel (Leavitt *et al.* 2006). Each 30–50-cm core was sectioned in 0.3-cm intervals, and samples frozen in the dark until analysis of stable isotopes of N and C, and fossil pigments (chlorophylls,

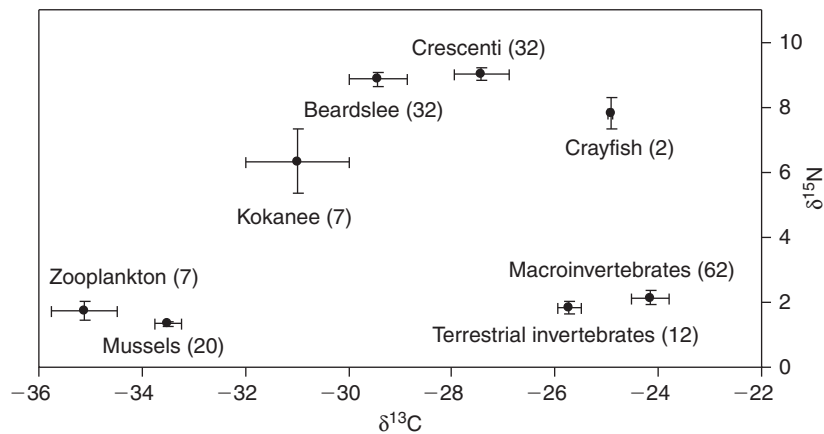


Fig. 2. Lake Crescent food web constructed from stable carbon and nitrogen isotopes, with number of replicates shown in parentheses. Error bars represent 95% confidence limits.

carotenoids, derivatives) at University of Regina. From the eight cores collected along the transect we chose a single core 26 cm long (Fig. 1) for detailed analysis of historical changes in algal production and stable isotope content. We anticipated that the location at which this core was taken would be most sensitive to human effects on nearshore habitats because it is close to the shoreline (30-m distance) and within a relatively shallow basin that has the highest density of shoreline development.

Historical changes in N and C inputs and sources were inferred from analysis of sedimentary stable isotope ratios, and pigments were used to characterise algal productivity trends. Stable isotope ratios and elemental composition were determined from freeze-dried whole sediments using a ThermoQuest (F-MAT) Delta^{PLUS}XL isotope ratio mass spectrometer equipped with continuous flow (Con Flo II) unit and an automated Carlo Erba elemental analyser as an inlet device (Savage *et al.* 2004). Pigments were extracted from freeze-dried sediments, filtered (0.2-µm pore), and dried under pure N₂ gas (Leavitt and Hodgson 2001), and analysis was restricted to taxonomically-diagnostic carotenoids, including β-carotene (all algae), alloxanthin (cryptophytes), diatoxanthin (diatoms), canthoxanthin (colonial cyanobacteria), and lutein-zeaxanthin (chlorophytes and cyanobacteria), and chlorophyll-*a* and pheophytin derivatives. All pigment concentrations were expressed as nmol pigment g⁻¹ dry sediment, a metric that is linearly related to algal biomass in whole-lake calibrations.

We attempted to determine the age of sediments deposited in the north arm of Lake Crescent using the concentrations (activities) of naturally-occurring radioisotopes of Pb (²¹⁰Pb) and Cs (¹³⁷Cs) measured by gamma spectrometry using an Ortec High-Purity Germanium (HPGe) Coaxial Well Photon Detector System on 15 evenly-spaced samples from within the 26-cm core (Bunting *et al.* 2010). Unfortunately, activities of unsupported (excess) ²¹⁰Pb and ¹³⁷Cs were below detection limits in most samples, and reliable sediment chronologies could not be established. Instead, we used similar analysis of cores from adjacent, and historically contiguous, Lake Sutherland (<1.0 km from Lake Crescent's north arm) to determine that the 26-cm core encompassed ~100 years. Lake Sutherland was separated from Lake Crescent by a landslide ~7000 years ago (Tabor 1975).

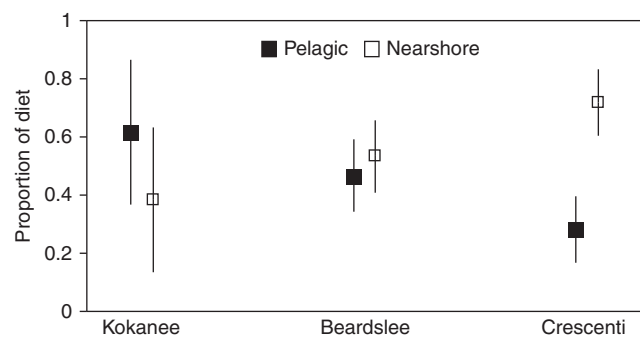


Fig. 3. Results from the mixing model IsoError showing estimated mean contribution of pelagic and nearshore carbon to the major fishes of Lake Crescent, with 95% confidence intervals obtained through bootstrapping.

Results

Nearshore water volume and area

As anticipated, the 'nearshore' waters in this steep-sided basin (Fig. 1) constitute a relatively small fraction of the total lake area and volume. The nearshore area (bottom ≤ 30 m) of the lake is 16.3% of the total area, with a mean depth of 13.5 m, whereas the mean depth of the basin interior is 104.1 m. The total volume of the nearshore water is only 2.5% of the total lake volume.

Stable-isotope food-web analysis

Although the nearshore water represents a relatively small area of habitat, the diets of apex predators depend heavily on nearshore resources. Analysis of stable isotope ratios in the Lake Crescent food web (Fig. 2) revealed distinct signatures for each of the three fish, and for offshore and nearshore resources. Both Crescenti and Beardslee trout derive more than 50% of their carbon near to shore compared with offshore, a significant difference for Crescenti trout (Figs 2, 3). This stable isotope analysis corroborates gut content analysis of Beardslee and Crescenti trout from the 1970s and 1980s (Pierce 1984). Pierce (1984) found only kokanee in the gut contents of large (>508 mm) Beardslee and Crescenti trout (*n* = 32). Pelagic prey were virtually absent from the guts of small (<356 mm; *n* = 80) and medium-sized (356–508 mm; *n* = 25) Beardslee and

Table 1. Characteristics of periphyton samples at developed and undeveloped sites on Lake Crescent

Mean concentrations (± 1 s.e.) of chlorophyll-*a* (mg m^{-2}), pheophytin-*a* (mg m^{-2}), ash-free dry mass (AFDM, g m^{-2}), and total biovolume (BV, $\mu\text{m}^3 \text{mm}^{-2}$) of periphyton are from samples at developed ($n = 8$) and undeveloped ($n = 4$) sites. Chlorophyll-*a*, pheophytin-*a*, and ash-free dry mass values were available from May and August 2006. Periphyton biovolume was calculated from samples taken at five sampling periods between November 2005 and August 2006. Differences between developed and undeveloped sites were significant for all variables ($P < 0.05$)

Site	Chl- <i>a</i>	Pheophytin	AFDM	Total BV
Undeveloped	2.1463 (0.6774)	0.9913 (0.2580)	34.3945 (26.7766)	0.0043 (0.0005)
Developed	6.4639 (1.3283)	4.1496 (0.8845)	689.9288 (421.14)	0.0165 (0.0027)

Crescenti trout; gut content in these size classes was dominated by nearshore invertebrates. Aquatic macroinvertebrates comprised 82% (± 18 s.e.) of this gut content for small fish and 96% (no s.e. reported) for medium fish, with the remainder consisting of terrestrial prey presumably trapped at the water surface. In 1997 collections of Beardslee and Crescenti trout (Olympic National Park, unpubl. data), some large- and medium-sized trout had both fish eggs and nearshore macroinvertebrates in their guts.

In contrast to the Beardslee and Crescenti trout in our stable isotope analysis, kokanee had a greater pelagic signal (Fig. 2), although high variability in this signal and, probably, lower sample size for kokanee prevent distinction from the other fishes (Fig. 3). Taken together, our isotope data and Pierce's (1984) data suggest that feeding on kokanee is thus the primary link to pelagic carbon for the Beardslee and Crescenti trout, once they mature to sizes large enough to take kokanee prey.

Localised nearshore effects of residential development

Residential development effects were evident nearshore (Table 1) with conditions differing greatly from undeveloped sites. Developed sites had significantly higher biomass ($P < 0.05$ for all variables), composed of both living (chl-*a*) and dead (pheophytin) material.

Offshore sediment analysis to reconstruct history of human impacts

In spite of strong nearshore influences of residential development, offshore signals of pollution impacts were not evident in the paleolimnological samples. For example, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in surface (top 1 cm) samples showed no consistent trend along the horizontal transect of coring sites (Fig. 4a), beyond a slight (0.5‰) statistically non-significant decline in N isotope signatures towards the north-east shoreline. Similarly, in the single longer core, $\delta^{15}\text{N}$ values were depleted $\sim 0.5\%$ in the top half of the core (Fig. 4b), but the extent of change was similar to the intersample variability. Further, neither $\delta^{13}\text{C}$, β -carotene (all algae), nor the predominant algal pigment diatoxanthin (diatoms) revealed pronounced changes (Fig. 4c), suggesting that algal production has been relatively constant at this site during the past century, at least in comparison to the 5‰ variation in N and C isotope values seen at other lakes experiencing eutrophication (Leavitt *et al.* 2006).

Discussion

A relatively small area and volume of Lake Crescent is responsible for supporting apex predators that integrate lake resources, and this shoreline area is where humans interface most strongly with the lake. The vast volume and low nutrient concentrations of

Lake Crescent, and other similarly deep oligotrophic lakes, may contribute to an impression that the lake is resistant to modest human disturbance – an echo of the axiom 'dilution is the solution to pollution.' However, development-related impacts on most lakes occur at the shoreline interface between land and water. The present study demonstrates that the Lake Crescent food web has a strong reliance on nearshore resources, and also that residential development produces highly localised impacts on the nearshore environment. Thus the sampling approach most common in limnological monitoring – offshore water column sampling – may not be sufficient to detect nearshore anthropogenic impacts that have the potential to alter lake food-web structure. Accordingly, early detection of human impacts through nearshore monitoring is receiving increasing attention in lake management (Hadwen *et al.* 2005; Lambert *et al.* 2008).

Critical nearshore contributions to whole-lake food webs

The disproportionate importance of nearshore resources to the whole-lake food web, evident in our food web reconstruction, is not unique to Lake Crescent. The stable isotope data here suggest that apex trout predators gather more than half of their carbon from food in the nearshore environment, with Crescenti trout showing the strongest reliance on these resources, consistent with previous gut content analyses of these fishes (Pierce 1984). Studies of benthic productivity (Loeb *et al.* 1983; Vadeboncoeur *et al.* 2002, 2008) have demonstrated the important contribution of benthic productivity, relative to pelagic productivity, in oligotrophic lakes. In a deep lake, such benthic productivity is constrained to a very small volume of water near the shore. In lakes with low nutrients, pelagic zooplankton occur at low densities (McCauley and Kalff 1981), and the nearshore environment may provide the greatest productivity (Vadeboncoeur *et al.* 2002, 2008) and fish forage in the form of macroinvertebrates and terrestrial prey trapped at the water surface (Francis and Schindler 2009). Benthic macroinvertebrates such as dipteran larvae and amphipods, and terrestrial prey such as spiders and termites, may be not only more readily available than pelagic prey in oligotrophic lakes, but also generally more energy-rich (Francis and Schindler 2009).

The loss of terrestrial prey as lakeshore residents clear away vegetation at the waterline is increasingly recognised as an important problem in urbanising watersheds. Francis and Schindler (2009) demonstrated through field and literature surveys that terrestrial insects associated with nearshore vegetation comprised as much as 100% of trout diets in undeveloped lakes, dropping to 2% in the most-developed lakes. Terrestrial prey items provide a significantly higher-quality diet than do aquatic prey, such that the loss of lakeshore vegetation may

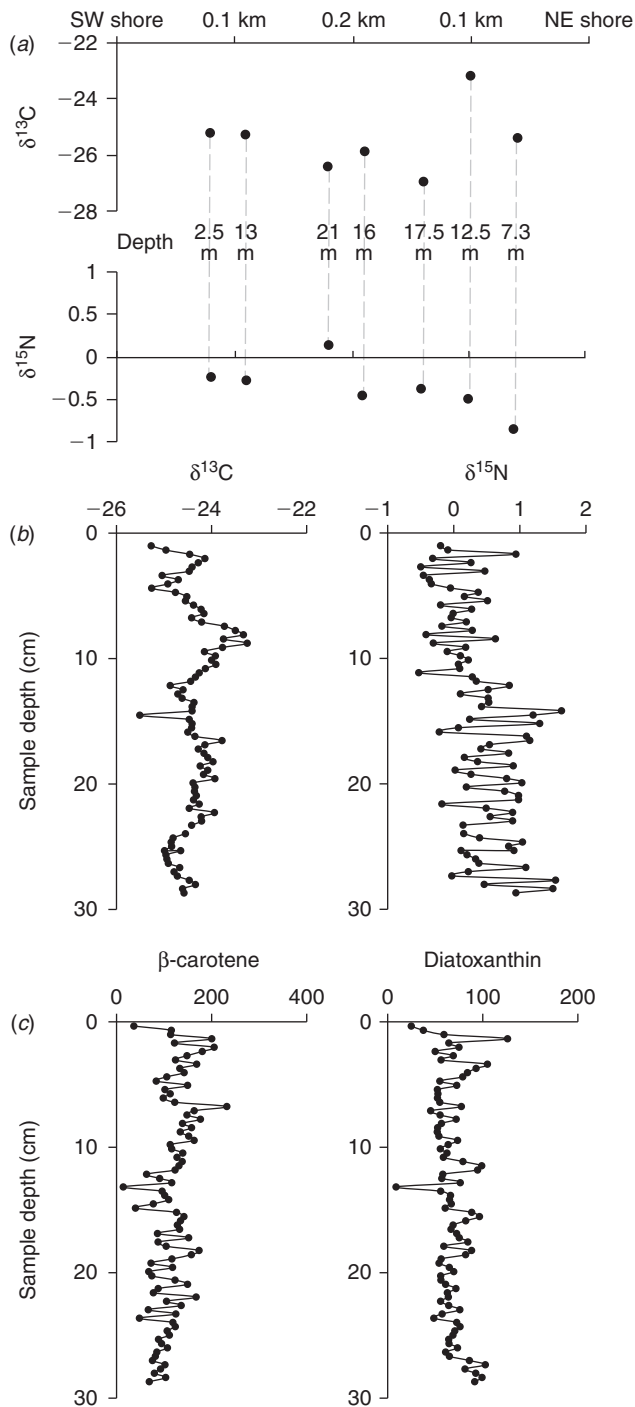


Fig. 4. Stable carbon and nitrogen isotope signatures from (a) cores taken on a transect from the south-west to north-eastern shores, with water depths at each of the sampling locations that are shown in Fig. 1. Distance did not significantly affect carbon ($P = 0.71$) or nitrogen ($P = 0.10$) values. Isotopes were profiled in a 26-cm-long core at a single station (b) in the northern basin where human impacts are most likely to be seen offshore due to comparatively high housing density and shallow basin, the symbol marked 'x' in the Fig. 1 inset. (c) Fossil pigments β -carotene (a proxy for total algae), and the dominant algal pigment diatoxanthin (a proxy for diatoms), from the same 26-cm core, are expressed as nmol pigment g^{-1} organic matter.

impact fish growth by reducing terrestrial prey availability (Francis and Schindler 2009). Pierce (1984) found that use of terrestrial prey by both Beardslee and Crescenti trout occurred almost exclusively in the early autumn in 1982, when terrestrial prey constituted $\sim 25\%$ of the diet for each, a seasonality that likely reflects pulses of these 'terrestrial subsidies' (Nakano and Murakami 2001; Francis and Schindler 2009). Potential also exists for terrestrial vegetation modifications to exacerbate shoreline development effects on benthic productivity by altering light availability, further contributing to a change in balance between aquatic and terrestrial prey availability nearshore.

Heterogeneous nearshore human impacts

Rapid periphyton response to nutrient pollution

As it becomes increasingly clear that nearshore waters are disproportionately important in lake food webs, it also becomes more apparent that human impacts nearshore can be substantial and sometimes highly localised. In our study, periphyton and detritus accumulation was much higher at the developed sites compared with the undeveloped sites, suggesting fertilisation effects, without discernible nutrient differences in the water column. At the land–water boundary around developed lakes, nutrients seep out of septic fields, run off lawns, and are bound to sediments disturbed by development activity (Aloi *et al.* 1988; Jacoby *et al.* 1991; Donohue and Molinos 2009). Nutrients can be assimilated into nearshore organisms that respond quickly to fertilisation, resulting in localised effects (Jacoby *et al.* 1991; Hadwen and Bunn 2005; Andersson and Brunberg 2006). Rates of uptake of nutrients by periphyton may range from 5 min (Mulholland *et al.* 2000) in streams to 5 h in lakes (Hadwen and Bunn 2005). When nutrients enter the lake through subsurface flow, as is the case with groundwater delivery, periphyton can significantly increase without any corresponding increase in local phytoplankton (Hadwen *et al.* 2005; Andersson and Brunberg 2006; Lambert *et al.* 2008). Rapid periphyton nutrient uptake in the nearshore is consistent with both our observed periphyton biomass differences between developed and undeveloped sites and our determinations that water-column nutrients remained at levels below standard limits of detection across sites.

Periphyton community shifts and grazers

Although nutrient inputs at developed sites can fuel algal growth, this productivity does not necessarily translate directly into increased forage for fish. Rosenberger *et al.* (2008) noted that developed sites at three large oligotrophic lakes, including our sites at Lake Crescent, were dominated by filamentous green algae (*Mougeotia* spp.), whereas undeveloped sites were dominated by diatoms. Such compositional changes may alter trophic pathways in aquatic food webs. Not only are diatoms nutritionally superior to filamentous green algae (Brett and Muller-Navarra 1997), but Rosenberger *et al.* (2008) also found that filamentous green algae were not readily assimilated by common macroinvertebrate grazers when offered both algal resources in laboratory experiments. Avoidance of filamentous algae has been reported in other studies (Moore 1975; Bowker *et al.* 1983). In Lake Crescent, the macroinvertebrate communities at developed sites have higher abundances of detritivores (Rosenberger *et al.* 2008), corresponding with dead periphyton mats accumulating at the sites. Together, these studies suggest that eutrophication has

complex trophic effects on nearshore macroinvertebrate communities, rather than simply providing more of the same resources to sequentially higher trophic levels.

Reduced coarse woody debris

Further physical change occurs as human activities at the lakeshore increase, such as reduced inputs of coarse woody debris (Francis and Schindler 2006; Marburg *et al.* 2006), which correspondingly reduces the availability of spatially complex habitat for biota and also alters sediment composition (Sass *et al.* 2006; Francis *et al.* 2007; Glaz *et al.* 2009). Coarse woody debris provides refuge for prey from visually hunting predators and such spatial complexity can help to maintain stable populations of predators and prey (Diehl 1992). Spatial complexity is frequently associated with greater availability of benthic invertebrates that provide forage for fish (Diehl 1992). Coarse woody debris can entrain organic matter that significantly alters sediment composition (Francis *et al.* 2007), further altering resources for nearshore organisms. Nearshore complex environments formed by vegetation and coarse woody debris provide habitat for many juvenile fish (Lewin *et al.* 2004) and throughout the life history of some species.

Nearshore breeding

Although the focus of the present study has been the disproportionate reliance on nearshore habitats for trophic interactions and energy flow, lake biota also use nearshore habitats for reproduction. Anthropogenic habitat changes, such as increased periphyton biomass associated with reduced shade and eutrophication, can alter these habitat uses by organisms. In Lake Crescent, Beardslee trout breed only in the shallow water of the Lyre River outlet, which also has the highest density of residential development (Meyer and Fradkin 2002). Over the past decade, dense mats of filamentous algae in the Beardslee trout spawning grounds have led to avoidance of areas with algae and superimposition of redds in the limited clear spawning gravels (NPS, unpubl. data).

The role of nearshore monitoring

In conclusion, our study strongly suggests that where shoreline human activity is a concern, limnological monitoring should include nearshore environments for at least three reasons. First, these environments are impacted by even the modest shoreline development examined here. Second, these habitats are important for the whole-lake food web, not just the organisms that are most frequently observed nearshore. Third, the nearshore environment responds rapidly to disturbance and may provide 'early warning' before deteriorations in water quality or other effects are seen offshore, at which time they may be extremely difficult to reverse. Anthropogenic nutrient loading is one of the most intractable human disturbances in lakes, and recovery from eutrophication is slow and highly idiosyncratic (Jeppesen *et al.* 2005). Nearshore monitoring can provide signals of lake response while nutrient pollution is still relatively localised and management options include those that are primarily preventative rather than restorative.

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