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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

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