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From land to lake: Contrasting microbial processes across a Great Lakes gradient of organic carbon and inorganic nutrient inventories

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ABSTRACT

Freshwater aquatic biota receive carbon and nutrients from within the system as well as from the terrestrial environment in varying proportions. During 2010–2011, we examined seasonal changes in carbon and nutrient inventories, plankton community composition and metabolism along a land-to-lake gradient in a major western Michigan watershed at four interconnected habitats ranging from a small creek to offshore Lake Michigan. In all seasons Lake Michigan had significantly lower concentrations of CDOM and DOC than any of the other sites. Lake levels of nitrate were not significantly lower than tributaries other than Cedar Creek, and SRP was not measurable in any of the sites other than Cedar Creek. Bacterial production as % of GPP revealed a distinct land-to-lake gradient from an average of 448% in Cedar creek to 5% in Lake Michigan. Microbial activity in Cedar Creek (bacterial production 3–93 μg C/L/d, and plankton respiration 9–193 μg C/L/d) was generally higher than other sites. Muskegon Lake dominated GPP among the sites reaching a peak of >1000 μg C/L/d during a fall *Microcystis* bloom. Offshore Lake Michigan had less variation in GPP and R than other sites, with GPP:R ratio close to 1 in all seasons but spring. Aquatic metabolism appears to be substantially subsidized by terrigenous inputs in the creek/river ecosystem with heterotrophy dominant over autotrophy. Autotrophy was maximized in the coastal/estuary "Goldilocks Zone" with longer residence times, whereas both autotrophy and heterotrophy were minimal but in near-balance in offshore waters receiving little subsidy from the land.

Introduction

Primary production and respiration fuel the cycle of life in the biosphere linked to movement of many elements through Earth's geochemical cycles. On a global basis, phytoplankton, including photosynthetic bacterioplankton, carry out close to half of net photosynthesis (Field et al., 1998) and aquatic heterotrophic bacterioplankton respire about half of this carbon (Cole et al., 1988; Karl, 2007). Planktonic metabolism thus tightly links the planet's atmosphere as well as the hydrosphere to the aquatic microbial community. There is also a strong terrestrial link to aquatic productivity. Approximately 20% of marine net primary production occurs in coastal zones even though coastal zones represent only 10% of total ocean area (Schlesinger and Bernhardt, 2013). Aquatic production and respiration are both higher closer to land due to terrestrial inputs of organics and nutrients and where larger eukaryotic organisms often play a bigger role in community metabolism (Cotner and Biddanda, 2002). However, in waters farther from land margins, such as the vast pelagic waters that cover some 70% of Earth's surface, production and respiration by autotrophic and heterotrophic prokaryotic bacterioplankton dominate carbon flux (del Giorgio et al., 1997; Karl, 1999). Here bacterioplankton substrate, dissolved organic carbon (DOC), makes up one of the largest reservoirs of carbon in the biosphere, comparable to carbon in the atmosphere and on land (Hedges and Oades, 1997). Photosynthetic microbes contribute most of the aquatic organic matter and heterotrophic microbes degrade and recycle it (del Giorgio and Williams, 2005). Collectively, microbial activity regulates environmental redox states, nutrient cycling, and gases relevant to global climate, making microorganisms the major movers of energy and materials in the aquatic world and beyond (Falkowski et al., 2008).

The Laurentian Great Lakes contain about 20% of Earth's fresh surface water (Beeton, 1984), and the Lake Michigan basin is the second largest, by volume (~4900 km^3), of these five Great Lakes. The Straits of Mackinac provide a major waterway between Lake Michigan and Lake Huron, a hydrological connection that equilibrates lake levels and combines the two basins to form the largest freshwater lake, by surface area, in the world. Much remains to be revealed about the composition of the microbial community in these important freshwater systems (Keough et al., 2003; Wilhelm et al., 2006) and about how ongoing ecosystem changes (Scavia et al., 2014), especially those caused by dreissenid mussels in the Lake Michigan basin, affect lake planktonic microbial communities and food web structure (Allan et al., 2013; Cuhel and Aguilar, 2013; Evans et al., 2011; Fahnenstiel et al., 2010;

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Hecky et al., 2004; Turschak et al., 2014). In low-productivity lakes, such as Lake Michigan, autotrophic and heterotrophic bacteria play key roles in ecosystem metabolism (Fahnenstiel and Scavia, 1987; Scavia and Laird, 1987). It's commonly accepted that strong coupling between autotrophic and heterotrophic processes is required to regenerate scarce nutrients when bacterioplankton respiration is equal to or greater than primary production, resulting in little organic matter left over for support of higher trophic levels and export to sediments (del Giorgio et al., 1997). On the other hand, in high-productivity lakes and rivers, where larger eukaryotic autotrophs and phagotrophic metazoans utilize a rich supply of inorganic and particulate organic nutrients, autotrophic-heterotrophic coupling is weak (leading to increased export by sedimentation or riverine discharge). The heterotrophic microbial community shifts along the gradient from domination by osmotrophs to domination by phagotrophs, and moves from dissolved organic matter (DOM) in the oligotrophic system to particulate organic matter (POM) in the eutrophic system as the primary carbon source (Cotner and Biddanda, 2002; Wetzel, 2001).

Freshwater aquatic ecosystems receive organic carbon from primary production occurring within the system (autochthonous) as well as from the terrestrial environment (allochthonous). It is estimated that allochthonous contributions of organic carbon provide for approximately 10% of the metabolism of heterotrophic bacteria in Lake Michigan and about 20% of the lake's primary production relies on riverine loading of phosphorus (Biddanda and Cotner, 2002). These and other recent findings support the idea of terrestrial materials substantially subsidizing the aquatic ecosystem (Dagg and Breed, 2003; Gergel et al., 1999; Karlsson et al., 2002; Lennon and Pfaff, 2005; Pace and Cole, 1996; Prairie and Kalff, 1986; Smith et al., 2003) and are conceptually analogous to "outwelling", where highly productive estuaries or mixing zones subsidize coastal ecosystems by discharging surplus nutrients and organic matter (Larson et al., 2013; Odum and Barrett, 2005). However, prior to discharge to receiving waters, rivers and estuaries actively process terrigenous nutrients and carbon during transport (Marko et al., 2013). Productivity peaks in many estuaries and nearshore coastal zones around the world, as exemplified by the Mississippi River estuary, have a dramatic increase in phytoplankton growth and primary production measured from point of discharge to near- and mid-field plume (Dagg and Breed, 2003). In fact, land margin coastal ecosystems are recognized as key hotspots with hot moments in the global carbon cycle (Cole et al., 2007; McClain et al., 2003; Weinke et al., 2014). Cole and others argue that freshwater ecosystems are not merely "passive pipes", but are highly "reactive sites" of global carbon cycling. Lakes and rivers, which cover about 1% of the planet's surface, receive an estimated ~2.4 Pg/year of carbon exported from terrestrial sources. Of that carbon, resident heterotrophs respire ~1.1 Pg and ~0.4 Pg is buried in freshwater sediments (an amount comparable with carbon buried annually in all of Earth's oceans); thus, only half of this terrestrially derived carbon ever reaches the oceans (Cole et al., 2007; Tranvik et al., 2009). These findings emphasize the reactive role of inland waters in the global carbon cycle in terms of globally significant respiration as well as carbon sequestration.

Lake Michigan is a critical ecological and economic resource in the region, but a variety of environmental stressors are degrading it on many fronts. Increased understanding of tributary influence on Lake Michigan's seasonal cycles is crucial to the lake's future health. Riverine discharge and other energy subsidies from the nearshore zone affect production, respiration and energy pathways in Lake Michigan (Johengen et al., 2008; Turschak et al., 2014); and it follows that there may be important links between environmental gradients, ecosystem metabolism and microbial community composition. In this study we examined seasonal changes in biogeochemical inventories, microbial community metabolism and the general composition of the phytoplankton and bacterioplankton communities along a land-to-lake gradient in a major western Michigan watershed. Our objective was to describe concurrent seasonal changes in environmental gradients, ecosystem production–respiration processes and broad categories of associated microbes (such as autotrophs and heterotrophs) along the sub-ecosystems of a Lake Michigan watershed. We tested the hypotheses that: 1) nutrient and carbon inventories decrease systematically from highly productive riverine waters to oligotrophic pelagic offshore lake waters, and 2) seasonal variations in community metabolism reflect changes in phytoplankton and bacterioplankton abundance in this Great Lake watershed.

Methods

Study sites

The Muskegon River watershed drains approximately 7000 km^2 of west-central Michigan. Drainage basin boundaries include portions of 12 counties and around 90 tributaries that flow into the main stem of the Muskegon River. The river ends in a 17 km^2 drowned river mouth lake (43.2331°N, 086.2903°W), which discharges into central Lake Michigan through a single, 1.6 km-long navigational channel. Over an 11-month period, four sites located along the lower southwest portion of the watershed (Fig. 1) were sampled once in each season to evaluate temporal variations in community metabolism and microbial abundance, within and between sites. The four sites are distinct yet interconnected habitats along a land-to-lake gradient: 1) Cedar Creek (43.3057°N, 086.1150°W), 2) Muskegon River (43.2631°N, 086.2453°W), 3) Muskegon Lake (43.2261°N, 086.2935°W) and 4) Lake Michigan (43.2062°N, 086.4497°W). These landward sites are traditional sampling sites chosen by Annis Water Resources Institute for their representativeness in the watershed. The Lake Michigan site was part of the ongoing National Oceanic and Atmospheric Administration-Great Lakes Environmental Research Laboratory (NOAA-GLERL) long-term transect study. Cedar Creek is a cold-water tributary of the Muskegon River, and the shallow forest-canopied sampling site was located approximately 9.5 km from its mouth at the Muskegon River. Muskegon River is approximately 350 km long with a 175 m drop in elevation between its source at Houghton Lake (44.3147°N, 084.7647°W) and the river mouth. We collected from a causeway bridge near the river mouth in an urbanized high-traffic area amid wetland. At this location, river width is about 76 m and depth is ~3 m. Muskegon Lake is a drowned river mouth lake with a surface area of 17 km^2, a mean depth of 7 m and maximum depth of 23 m. Surface water was sampled at the deepest point of the lake. The Lake Michigan site is at the NOAA M-45 buoy about 8 km offshore located over the 45 m isobath. All of the sites except for Cedar Creek were in open sunlight most of the day.

Sample collection

During the period from May 2010 to April 2011, at a depth of approximately 0.5 m, surface water samples were collected in each season. Four discrete 10 L water samples were collected at each site, placed in acid-cleaned carboys, transported on ice in coolers to the Annis Water Resources Institute and analyzed.

Physical and biogeochemical inventories

In the field, basic water quality observations (temperature, pH, conductivity and dissolved oxygen) were measured using a calibrated YSI 6600 Datasonde. In the laboratory we measured dissolved organic carbon (DOC), colored dissolved organic matter (CDOM), chlorophyll a (Chl a) and dissolved inorganic nitrogen and phosphorus concentrations in each sample. DOC samples were filtered through 0.7 μm pre-combusted GF/F filters (4 h at 450 °C) and stored frozen in pre-combusted glass vials (4 h at 550 °C) with Teflon-lined caps until a convenient time to analyze. After thawing, sample acidification with 4–5 drops of 2 N HCl and inorganic C removal by purging with