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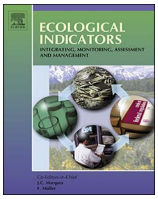

Original Articles

Scale-dependent effects of natural environmental gradients, industrial emissions and dispersal processes on zooplankton metacommunity structure: Implications for the bioassessment of boreal lakes

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ABSTRACT

Environmental controls were traditionally considered as sole determinants of community assembly for freshwater bioassessment studies, whereas potential importance of dispersal processes and spatial scale have received limited attention. We conducted a bioassessment of lakes across northeast Alberta, Canada using crustacean zooplankton to develop a framework for evaluating if and how atmospheric emissions from the nearby Athabasca Oil Sands Region could impact their community assemblages. We quantified the effects of environmental gradients and spatially contingent dispersal processes for determining zooplankton community composition of 97 lakes at two spatial scales (regional and sub-regional) using constrained ordination, spatial modeling and variance partitioning techniques. Our findings indicated that effects of both environmental gradients and dispersal processes on species composition were scale-dependent. Zooplankton community composition was significantly correlated to environmental parameters that are directly and indirectly sensitive to industrial deposition including nitrate, sulphate, dissolved organic carbon, base cation, chloride, trace metal concentrations and predation regime, indicating their potential to track future environmental impacts. The relative importance of these environmental predictors varied with spatial scale, yet unraveling the effects of natural environmental heterogeneity vs. industrial deposition on this scale-dependency was not possible due to lack of regional baseline information. Dispersal processes were not important in shaping zooplankton communities at the sub-regional scale, but had limited, yet significant influence on species composition at the regional scale, emphasizing the need for cautious interpretation of broad-scale community patterns. Beyond establishing crucial regional baselines, our study highlights the necessity for explicit incorporation of dispersal effects and spatial scale in bioassessment of lakes across landscapes.

1. Introduction

A robust bioassessment system requires thorough understanding of the ecological processes structuring biotic communities, whereas the metacommunity concept provides a sound mechanistic framework for explaining the relative importance of such processes (Heino, 2013; Leibold et al., 2004; Logue et al., 2011). A metacommunity represents a set of local communities connected via species dispersal, such that local communities are structured by interactions between local processes (abiotic environmental conditions and biotic interactions) and regional (dispersal) processes (Leibold et al., 2004; Logue et al., 2011). Dispersal limitation can be particularly important in freshwater habitats which are isolated in a matrix of inhospitable terrestrial landscapes (Alahuhta and Aroviita, 2016). Traditionally, mainly local environmental conditions were considered to shape community structure in freshwater bioassessments (Heino, 2013), while the simultaneous role of dispersal processes has only recently been established (Alahuhta and Aroviita, 2016; Anas et al., 2014a; Gray and Arnott, 2011).

Evaluating effects of local and regional processes on community assembly is confounded by their scale-dependency, whose importance in structuring biotic communities has increasingly been recognized (Menge and Olson, 1990). For example, heterogeneity of environmental factors that shape communities may vary among spatial scales (Borcard et al., 2004). Furthermore, relative importance of dispersal limitation in structuring freshwater biotic communities may also vary with spatial scale (Alahuhta and Heino, 2013; Cottenie, 2005; Declerck et al., 2011;

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Havel and Shurin, 2004). Hence, 'scale' can confound our understanding of underlying ecological processes (Wiley et al., 1997) and should be a critical consideration in bioassessments (Alahuhta and Heino, 2013).

Lentic crustacean zooplankton communities possess several attributes that make them effective biological indicators of environmental conditions. First, substantial differences in zooplankton community composition can be expected in response to environmental variation because of their high taxonomic diversity (Gyllström et al., 2005; Havens and Hanazato, 1993). Moreover, zooplankton composition is responsive to variations in abiotic factors such as pH, temperature, salinity, dissolved oxygen, turbidity and heavy metals due to differential physiological tolerances of species (Havens and Hanazato, 1993; Steiner, 2004; Wissel et al., 2011, 2003). Given the intermediate trophic position of zooplankton in lake food webs, they are also indirectly impacted by modifications in bottom-up (algal resources) and top-town (predation) processes caused by environmental perturbations (Anas et al., 2014b; Brett, 1989; McQueen et al., 1986; Stenson and Eriksson, 1989). Furthermore, most zooplankton taxa have relatively short generation times that allow changes in recruitment success resulted from altered environmental conditions to be rapidly reflected as changes in community structure. Finally, zooplankton are cost-effective indicators because they are easy to collect and more representative than fish or benthos due to higher densities and more homogenous distributions in lakes (Marmorek and Korman, 1993). Consequently, zooplankton assemblages are common indicators to assess the impacts of anthropogenic perturbations of lakes, including acidification (Brett, 1989; Havens and Hanazato, 1993; Marmorek and Korman, 1993), metal contamination (Valois et al., 2010; Yan and Strus, 1980; Zhou et al., 2008) and eutrophication (Gannon and Stemberger, 1978; Haberman and Haldna, 2014).

However, divergent evidences persist on dispersal ability of lentic zooplankton (Bohonak and Jenkins, 2003), which is a prerequisite for species to track environmental changes across landscapes (Anas et al., 2014a; Heino, 2013). Zooplankton disperse passively among lakes in both live and dormant forms, either via overland (e.g., wind and animal vectors) or watercourse routes (Gray and Arnott, 2011; Havel and Shurin, 2004). Several studies provided empirical evidence for the importance of dispersal as a determinant of compositional variation of zooplankton communities in lakes (Beisner et al., 2006; Gray and Arnott, 2011; Strecker et al., 2008), whereas others did not find a significant effect (Anas et al., 2014a; Kurek et al., 2011; Pinel-Alloul et al., 1995; Shurin et al., 2009). This discrepancy may be related to varying spatial extents used in different studies (ranging from tens to thousands of kilometers), which emphasizes the importance of a scale-dependent framework to evaluate the effect of dispersal on zooplankton compositional variability across a geographic area (Declerck et al., 2011).

Rapid expansion in oil sand operations in northern Alberta, Canada (from 0.1 to 1.5 million barrels per day from 1980 to 2010) (Canadian Association for Petroleum Producers, 2011) has led to concerns on potential ecological consequences (Schindler, 2010). One such concern is potential impacts of elevated emissions of atmospheric pollutants from oil sands mining and processing (Percy, 2013) on surrounding boreal lake ecosystems. Among them, deposition of acid precursors i.e. sulfur (S) and nitrogen (N) oxides in both wet and dry forms can lead to acidification of lakes (Hazewinkel et al., 2008), while N deposition in nutrient-limited lake systems can increase primary productivity (Baron et al., 2011; Curtis et al., 2010). Moreover, atmospheric deposition of toxic pollutants associated with oil sands activities, such as trace metals and polycyclic aromatic compounds can also have detrimental effects on lake ecosystems (Kurek et al., 2013; Laird et al., 2013). The vulnerability of lakes to acidification varies across northeast Alberta, as determined by the geographic coincidence of elevated S and N deposition and geologically sensitive terrain (Environment Canada, 2011; Saffran and Trew, 1996; Watmough et al., 2014). On the other hand, potential nutrient enrichment of lakes due to N deposition can be much more localized across the region, mostly depending on local characteristics such as catchment area, proportion of forested area in the catchment, lake morphometry, etc., in addition to deposition levels (Baron et al., 2011; Caraco et al., 2003). To this point however, findings from current monitoring activities (principally the Regional Aquatic Monitoring Program, RAMP) and other studies of lakes in northeast Alberta (Curtis et al., 2010; Hazewinkel et al., 2008; Kurek et al., 2013; Parsons et al., 2010; Summers et al., 2016) have not led to any consensus with respect to the spatial scale and degree of impact caused by industrial deposition. Several recent studies indicated that atmospheric fallout of industrial pollutants declines exponentially with the distance from industrial center, with varying deposition patterns for different pollutants (Bari et al., 2014; Fenn et al., 2015; Watmough et al., 2014). Notwithstanding this attenuation, likely ecological responses to industrial deposition have been detected in remote systems (Anas et al., 2014a; Laird et al., 2013; Wolfe, 2016).

A comprehensive bioassessment program using zooplankton was recently implemented in lakes encompassing a broad geographic radius around oil sands operations in northeast Alberta as part of the Clean Air Regulatory Agenda (CARA) lakes monitoring program of the Canadian government, of which thorough baseline characterization is a primary objective (Environment Canada, 2011). The goal of this study was to evaluate the effects of natural environmental gradients, industrial emissions and dispersal processes for structuring crustacean zooplankton communities of the region. Specifically, we first identified environmental correlates of zooplankton species composition at two spatial scales: within the entire study region and within five physiographic sub-regions (located within the study region) and secondly, assessed their relationships to natural environmental heterogeneity and industrial deposition. Thirdly, we quantified the relative roles of dispersal processes vs. environmental control on zooplankton compositional variation at different spatial scales. We expected, based on evidence from previous studies of zooplankton communities (Declerck et al., 2011; Havel and Shurin, 2004), a greater importance of dispersal processes at the regional scale compared to the sub-regional scale. Finally, we discussed the implications of dispersal effects for bioassessment of lakes subject to industrial impacts.

2. Methods

2.1. Study area

The study domain consisted of five physiographic sub-regions in northeast Alberta (55°–60° latitude; −113°– −108° longitude), namely Athabasca Plain (AP), Tazin River Plain (TRP), Birch Mountains (BM), Muskeg River Uplands (MRU) and Stony Mountains (SM) (Fig. 1). Of these, AP is part of the Boreal Shield ecozone and TRP is part of the Taiga Shield ecozone, while all other regions were located in the Boreal Plain ecozone. AP and TRP are characterized by Archaean crystalline bedrock of the Precambrian Shield and Brunisolic soils in outwash deposits, with jack pine forest and lowland peatlands. BM, MRU and SM are underlain by Cretaceous shales and sandstones draped predominantly by Luvisolic soils. Mixed coniferous forest interspersed with peatlands is typical to these regions. The landscape changes from undulating to hummocky across the study area. Altitude across the regions is between 200 and 825 m a.s.l (Turchenek and Lindsay 1982). The hydrological variability across the area is influenced by bog cover, thaw features in bogs, permafrost thawing, elevation and watershed morphometry, while most lakes in the area are located in headwater catchments (Gibson et al., 2015). We refer to Turchenek and Lindsay (1982) and Gibson et al. (2015) for more detailed descriptions of geological characteristics and hydrological conditions of the survey domain, respectively. Meanwhile, the Athabasca Oil Sands Region is located primarily in MRU.

The study area is characterized by a low subarctic climate with long, cold winters and short, cool summers. The average January (coldest